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A GENERIC MONOGRAPH OF THE MELIACEAE [1]

T. D. PENNINGTON[2] and B. T. STYLES[3]

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INTRODUCTION

by F. White[4]

Of all plant families the *Meliaceae* is among the more useful to man, chiefly for its high quality timbers and for the ease with which some species can be grown in plantations. Almost confined to the tropics, its species nevertheless pervade them, and occur, often conspicuously, in a variety of habitats from rain forest to mangrove swamp and semi-desert.

For its size, the family probably contains a wider range of floral and fruit structures than any comparable group. In what other family is there such a diversity of primitive 'arillate'[5] seeds, side-by-side with such an array of derived fruits and seeds, and still connected by intermediates? Or, to take the flower, where else can be found such a diversity of forms, from the minute, but structurally complex, flowers of *Aglaia*, often no larger than a pin-head, to the moth-pollinated flowers of some *Turraea*, with their slender staminal tubes reaching a length of 12 cm or more?

This diversity is a source of rich material for the student of evolution and of plant and animal inter-relationships, and provides an interest so often lacking in taxonomic studies. But it is also a source of taxonomic difficulty, as the taxonomic history of the group so clearly shows.

With a few exceptions mentioned below, most of the genera currently recognized as

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[1] Materials for a Monograph of the Meliaceae III. This series is being prepared at the Commonwealth Forestry Institute, Oxford, U.K.

[2] Present address: Clarke's Farmhouse, Northmoor, Oxon, U.K.

[3] Department of Forestry, Commonwealth Forestry Institute, Oxford, U.K.

[4] Curator of the Herbaria, Botany School, Oxford University, U.K.

[5] Used in the wide sense of Corner. In my opinion careful comparative and developmental studies are needed before the term can be applied more precisely.

Meliaceous have been regarded as such since the time of their discovery. But there has been persistent disagreement as to the number of genera and their circumscription, and as to the best way to accommodate them in tribes and subfamilies. Even the number of families has been uncertain from the time of de Jussieu (1789) to that of Harms (1940).

More than in other families, this uncertainty has been due to the diffuse and often reticulate nature of the variation, frequently aggravated by a lack of complete material. There is a quasi-absolute dearth of information on the functions of the structures concerned. Parallel evolutionary trends are numerous and have affected the flower and fruit independently. Complete material necessary for generic diagnosis has often been, and in some cases still is, lacking. Much of the material on which this work is based was specially collected in South-East Asia and tropical America by Dr. Pennington himself, and, to a lesser extent, by Dr. Styles and myself in Africa.

Previous workers have often attached undue weight to single diagnostic characters, e.g. position of anther insertion on the staminal tube or presence or absence of endosperm. These can now be shown to have arisen or been lost, as the case may be, more than once, and to be poorly correlated with other characters. Some genera and most tribes can only be diagnosed by using a combination of several 'differential' characters (as defined by White, 1962), each one of which, taken separately, may occasionally break down, although the combination itself reveals a pronounced discontinuity. Thus, members of the *Turraeeae* cannot be distinguished from all other *Meliaceae* on the basis of a single diagnostic character. Most character-states typical of *Turraeeae* have at least a few exceptions in the tribe, and also occur, at least occasionally, in other tribes, but always in markedly different combinations. The overall pattern, however, is such that all members of the *Turraeeae* possess many more of the tribal character-states than any excluded species. Thus, the *Turraeeae* is objectively circumscribed, being based on a real and definable gap in the variation pattern. Similarly for other subfamilies and genera.

Only a selection of available characters has been used in the diagnoses of the tribes and in the keys to and descriptions of the genera. Further study, especially in the field, is expected to reveal complex syndromes of confirmatory characters, for the most part individually small, but well correlated among themselves, and functionally related to the methods of pollination or means of dispersal.

Many *Meliaceae* have unisexual flowers, but always with well-developed rudiments of the opposite sex. In contrast to most rudimentary structures, the shapes and positions of these, relative to other parts of the flower, are remarkably constant within species and genera and even tribes, and vary greatly between them. Compare, for instance, the flowers of *Aglaieae* (figs. 9—10) and *Guareeae* (figs. 11—14). Their function is to restrict access to nectar, so that it is only available to the 'right kind' of insect, which must adopt postures that make possible the transfer of pollen from fertile anther to receptive stigma.

There are few observations on this, but I myself have seen how the small *Hymenoptera* which visit the flowers of *Trichilia havanensis* Jacq. are forced to insert their proboscides into very narrow slots between the anthers or antherodes, and, in so doing, pick up pollen from the male flowers and transfer it to the stigmatic surfaces of the female flowers. A glance at the illustrations in this generic monograph is sufficient to show that the *precise* configuration of antherodes and pistillodes in relation to other floral parts is likely to prove of considerable taxonomic value and evolutionary interest, when the floral biology of the family has been adequately investigated.

The claims of certain genera to inclusion in the family have been frequently disputed up to the present time. Of the two most-controversial genera, *Nymania* and *Ptaeroxylon*, the present study convincingly shows that the former is Meliaceous and that the latter, as had been previously suggested (Leroy, 1959, 1960 a; White & Styles, 1966), must be excluded.

Shortly after its discovery, the un-Meliaceous-looking *Nymania* was placed by de Jussieu (1789) in his *Melieae* (as *Aitonia*). Some subsequent authors have sought a place for it elsewhere. As recently as 1966, Airy-Shaw kept it in the monotypic family *Aitoniaceae* of Harvey & Sonder. In the present work it is shown that, both in its pollen grain and secondary xylem, it clearly belongs, not merely to *Meliaceae*, but to the *Turraeeae*, and that in its floral structure it is connected to *Turraea* by other genera, particularly by the recently discovered Malagasy genus, *Calodecaryia*.

Another monotypic South African genus, *Ptaeroxylon*, which was formerly prized for its valuable timber, together with its Malagasy relative, *Cedrelopsis*, have sometimes been placed in *Meliaceae*, sometimes elsewhere. At the onset of this study, it was known that *Ptaeroxylon* differed markedly from all other *Meliaceae*, at that time investigated, in certain features of its pollen grain. Since a few other undisputed *Meliaceae*, notably certain species of *Turraea*, were also known to be anomalous in other pollen grain features, it was decided to regard the matter as *sub judice* until the pollen and wood-structure of the whole family had been adequately studied and the gross morphology re-assessed. It was then confirmed that *Ptaeroxylon* is distinct from all *Meliaceae* in its pollen grain and secondary xylem. The resemblances between the capsular fruit and winged seed of *Ptaeroxylon* and *Swietenioideae* prove to be superficial.

Of the four subfamilies recognized here, the two largest, *Swietenioideae*, with woody capsular fruit and winged seeds, and *Melioideae*, with 'arillate' seeds or fleshy indehiscent fruits, have been recognized, in some form or other, since 1789. Their rank and circumscription, however, have frequently been debated. Adrien de Jussieu (1830) treated them as families, an opinion which Harms, as recently as 1940, suggested could be justified, though he himself had them as subfamilies, together with a third, based on *Cedrela*.

Apart from the inclusion or otherwise of *Cedrela* and the related *Toona*, the *Swietenioideae* has remained a remarkably stable taxon. Only the inclusion or otherwise of the mangrove genus *Xylocarpus* and the related *Carapa* has been seriously disputed; on the position of these two genera opinion has been evenly divided. Harms placed them in *Melioideae*, but the wood anatomist Kribs (1930), on the basis of wood anatomy alone, included them in *Swietenioideae*, where he thought *Cedrela* also belongs. Kribs produced a key to 36 genera of *Meliaceae*, implying that each genus is distinct in its wood anatomy. If this could be substantiated, xylotemy would indeed be shown to be a powerful taxonomic tool. The present study, however, based on much more material than was available to Kribs, reveals that few genera are distinct in their secondary xylem, though in some cases it provides useful confirmatory characters. In the present study, in which the secondary xylem of 230 species was examined, convincing evidence is presented which shows that *Cedrela* (and *Toona*) and *Xylocarpus* and *Carapa* have so much in common with the rest of *Swietenioideae* that their exclusion is unjustified. The secondary xylem of *Swietenioideae*, circumscribed to include these genera, is virtually uniform and constantly different from that of *Melioideae*. The pollen, on the other hand, of most *Swietenioideae* and most *Melioideae* is so similar that it confirms the decision to treat them as subfamilies, rather than as families.

Additional confirmation comes from another source. Careful study of two little-known Malagasy genera, *Capuronianthus* and *Quivisianthe*, has shown that they provide connecting links between the two larger subfamilies. They are, however, so different from each other, and, despite their intermediate position, so different from *Swietenioideae* and *Melioideae*, that it has proved necessary to establish two new subfamilies to accommodate them.

The present study is based on part of a monographic study of the family, begun by Dr. Styles in 1960, starting with the economically important genera. Shortly afterwards Dr. Pennington undertook, among other things, a generic revision of the *Melioideae*, which resulted in a doctoral thesis, parts of which are incorporated here. It was expected that Dr. Styles and Dr. Pennington would obtain posts which would enable them to complete the monograph. Because of the economic situation this did not happen and further progress has been less rapid than was hoped. It was originally intended, before publication, to undertake surveys of the chromosome cytology and germination and seedling morphology. The importance was realized of investigating the development and differentiation of the flower and fruit and seed, especially the early stages, so as to establish the homologies of the adult structures on which the classification is based. It was also intended, so far as possible, to study in the field the functional significance of the floral and fruit characters used in the classification.

Part of this programme has been achieved. Dr. Styles has germinated in Oxford the seed of representatives of most genera and has studied the seedlings. With Dr. C. Vosa (1971, and in preparation), he has made a survey of the chromosome cytology. These results are incorporated in the present study.

Much work, however, remains to be done before a comprehensive synthesis can be presented. Work has recently been resumed on the study of differentiation and development. Field studies on floral and fruit biology are planned for the near future. Since the completion of this work cannot be expected in less than three or four years it has been decided to publish this generic monograph as it stands. We believe that its publication should stimulate local floristic studies from which further syntheses could be derived.

PART I. GENERAL DISCUSSION

1. TAXONOMIC HISTORY

The first edition of Species Plantarum (1753) contains two representatives of the *Meliaceae*, *Melia azedarach* L. and *Azadirachta indica* A. Juss., which Linnaeus named *Melia azadirachta*. He placed *Melia* in the *Decandria Monogynia*. The generic name *Melia* for purposes of valid publication (Article 13 Note 3 of the International Code of Botanical Nomenclature, 1972) is associated with the subsequent description given in the 5th edition of Genera Plantarum (1754), although it had previously been described by Linnaeus in Hortus Cliffortianus (1737) and in the first edition of Genera Plantarum (1737).

A number of genera which belong to the *Meliaceae* were described before the publication of Species Plantarum, but were not accounted for by Linnaeus. They were all described by Rumphius in his Herbarium Amboinense (1741—7). This work contained descriptions and illustrations of species of six genera: *Camunium* (= *Aglaia* Lour.), *Lansium*, *Sandoricum*, *Alliaria* (= *Dysoxylum* Bl.), *Granatum* (= *Xylocarpus* Koen.) and *Surenus* (= *Toona* M. J. Roem.). Although none of Rumphius' names are valid, they are important as two of them (*Lansium* and *Sandoricum*) were taken up by later authors, and the plates of some of the others serve to typify later descriptions *(Xylocarpus)*.

During the 50 years subsequent to the publication of Species Plantarum, a number of well-known genera were described by Linnaeus and other authors. In 1756 in his Natural History of Jamaica, Patrick Browne described 4 new genera, *Cedrela*, *Trichilia*, *Barbilus*, and *Elutheria*. Because Browne used polynomials instead of binomials for some of his species, all his specific names are invalid, but this practice does not invalidate his generic names, and two of them, *Cedrela* and *Trichilia*, have continued in use to the present day.

Barbilus is synonymous with *Trichilia* and *Elutheria* is now known to be the same as *Guarea* Allam. *ex* L. (1771), which is conserved against it.

The first species of *Cedrela* and *Trichilia* to be validly published, were included by Linnaeus in the tenth edition of Systema Naturae (1759), in which, besides describing the type species of *Cedrela (C. odorata)*, Linnaeus also described *C. mahagoni*, but this plant, the true Mahogany, was transferred to *Swietenia* in the following year by Jacquin in his Enumeratio Systematica Plantarum Caribaeis. The well-known and widely distributed pantropical genus *Turraea* was not described until 1771, when Linnaeus included it in his Mantissa Plantarum. In 1781 a small South African tree, *Aitonia*, which has often been placed in the *Meliaceae*, although until recently its position has been controversial, was described by Thunberg in Physiographiska Sälskapets Handlingar. This name is antedated, however, by *Aytonia* J. R. & G. Forster, a liverwort genus in the *Marchantiaceae*. The slight difference in spelling is immaterial, since both names commemorate the same person. *Aitonia* of Thunberg is now known by its later synonym, *Nymania* of Lindberg (1868). In 1775 Aublet, in his Histoire des Plantes de la Guiane Française, described the Crabwood *(Carapa)* from French Guiana. Four years later the Swedish botanist Sparrman described *Ekebergia* from South Africa. In 1784 Koenig (Der Naturforscher 20: 3), gave a description of *Xylocarpus* which is based partly on the plates named *Granatum* in Rumphius' Herbarium Amboinense, and in 1789 Cavanilles first validly published another Rumphian name, *Sandoricum* in his seventh Dissertatio Botanica. In the same work Cavanilles described the genus *Quivisia* which is now combined with *Turraea*. Loureiro described the first species of *Aglaia*, the largest genus in the family, in his Flora Cochinchinensis (1790), and in 1807 Correa de Serra first validly published the closely related genus *Lansium* in his Vues Carpologiques (Ann. Mus. Hist. Nat. Paris 10 : 157).

The *Meliaceae* received a circumscription similar to that accepted at the present time in the Prodromus Systematis Naturalis of A. P. de Candolle in 1824, although at that time only one quarter of the genera were known. However, many authors previous to de Candolle detected the essential similarity of certain genera which belong to this group. Linnaeus himself, in a series of lectures given to his students in 1771 and published as the Praelectiones in Ordines Naturales Plantarum by one of his students, Giseke, in 1792, indicated that *Melia, Trichilia, Guarea,* and *Turraea* are closely related, and he used this group of genera to form the basis of the Ordo 23, *Trihilatae*, although he also included in it eleven other genera which do not belong to the *Meliaceae*.

Rather more Meliaceous genera were brought together into a distinct family called *Melieae* by Anton Laurent de Jussieu in his Genera Plantarum (1789). It contained sixteen genera of which ten are true *Meliaceae*. These are *Aitonia, Quivisia, Turraea, Sandoricum, Portesia* (= *Trichilia*), *Elkaja* (= *Trichilia*), *Guarea, Ekebergia,* and *Melia*. The remainder, *Canella, Symphonia, Tinus, Geruma, Ticorea,* and *Aquilicia* belong to other families. It is interesting to observe that all ten belong to the subfamily *Melioideae*. The two genera of the subfamily *Swietenioideae* at that time known to science, *Swietenia* and *Cedrela*, are placed by de Jussieu at the end of the family as '*genera affinia*'. De Jussieu placed the *Melieae* between the orders *Aurantia* (les Orangers) and *Vites* (les Vignes).

Earlier in the same year, Cavanilles, in his seventh Dissertatio Botanica, recognized a group containing fourteen monadelphous genera, of which seven belong to the *Meliaceae*. These are *Sandoricum, Turraea, Melia, Swietenia, Guarea, Quivisia,* and *Portesia*. It is interesting to note that *Swietenia* is included in this group, presumably because of its staminal tube, whereas *Cedrela* which lacks a staminal tube is not mentioned. At this time the authors of natural systems of classification were giving undue weight to the staminal tube, and this accounts for the inclusion in the *Meliaceae* of a number of genera which show this feature, but in other respects are very different from the *Meliaceae*.

Ventenat in Tableau du Règne Végétal (1799) was the first to use the name *Meliaceae*; his interpretation of the family included only eight genera: *Canella, Aitonia, Turraea, Sandoricum, Melia, Aquilicia*, and, as related genera, *Swietenia* and *Cedrela*. Of these, *Canella (Canellaceae)* and *Aquilicia (Leeaceae)* are non-Meliaceous.

De Candolle in his Prodromus (1824) clearly reveals a more detailed knowledge of the relationships of the genera of the *Meliaceae* than all other previous authors. Six genera included in the family by de Jussieu are removed: *Canella, Symphonia (Guttiferae), Tinus (Ericaceae), Aytonia, Ticorea (Rutaceae)*, and *Aquilicia*, one of them, *Aitonia*, mistakenly. Only three non-Meliaceous genera, *Geruma (Aïzoaceae), Humiria (Humiriaceae)*, and *Strigilia (Styracaceae)* are included in the family in this account.

De Candolle was the first to attempt to divide the family into tribes, which he based primarily on the number and structure of the seeds, as follows:

Tribe 1. *Melieae*, characterized by fruit with 1 or 2 seeds per loculus, and unwinged albuminous seeds with an inverted embryo and foliaceous cotyledons, contains *Geruma, Humiria, Turraea, Quivisia, Strigilia, Sandoricum*, and *Melia*.

Tribe 2. *Trichilieae*, which includes *Trichilia, Ekebergia, Guarea*, and *Heynea*, is characterized by fruit with 1 or 2 seeds per loculus, exalbuminous unwinged seeds and an inverted embryo with thick cotyledons.

Tribe 3. *Cedreleae*, which includes *Cedrela, Swietenia, Chloroxylon, Flindersia*, and *Carapa*, is characterized by having many winged seeds per loculus, with a small amount of fleshy albumen, and an erect embryo with foliaceous cotyledons.

Since the publication of the Prodromus, our knowledge of the family has increased enormously, but these three groupings can still be detected in all modern classifications, though naturally they have been somewhat modified. Authors have differed in their opinions as to the relationships of *Chloroxylon* and *Flindersia* with the *Meliaceae*; their position is discussed more fully in a later chapter.

A still more detailed account of the *Meliaceae* was published in 1830 by Adrien de Jussieu.[1] This thorough and painstaking work remained in use for a very long time. De Jussieu's classification which is based on a larger number of characters than any previous one, is a definite improvement. The characters used, in order of their importance, are:

1. Presence or absence of endosperm.
2. The ratio between the number of loculi in the ovary and the number of other parts of the flower.
3. Direction of the radicle relative to the hilum.
4. The situation of the anthers inside or on top of the staminal tube.
5. The form of the disk.

In circumscribing the family, A. de Jussieu returned to the practice of some earlier authors in excluding *Cedrela, Swietenia*, and *Carapa*, which he placed in a separate family *Cedrelaceae*, also containing *Chloroxylon* and *Flindersia*, and the new genera *Khaya, Soymida*, and *Chukrasia*. He excluded the two anomalous genera *Humiria* and *Strigilia* included in the family in the Prodromus and divided the family into two tribes.

Tribe 1. *Melieae*, characterized by an endospermous seed, contained the new genera: *Calodryum* (now united with *Turraea*), *Azadirachta* (separated from *Melia*), and *Mallea* (= *Cipadessa*).

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[1] Mém. Mus. Hist. Nat. Paris 19, ?1830: 153—304; although it is dated as '1830', there is some evidence Guillemin, Bull. Sc. Nat. Géol. 23, Nov. 1830: 234) that this did not appear until later, possibly 1831. As Guillemin gives a verbatim report of de Jussieu's classification together with the diagnoses of his new genera and species we do not feel that he intended to publish the new names there. We are therefore attributing the new taxa solely to de Jussieu and continue to cite the 'Mémoire' as the original place of their publication.

Tribe 2. *Trichilieae*, characterized by an exendospermous seed, also contains two new genera, *Cabralea* and *Synoum*.

During the first half of the nineteenth century, a number of botanical works, dealing with the floras of restricted geographical regions, were published, particularly for parts of Asia, in which genera of the *Meliaceae* were mentioned. The *Meliaceae* are well represented in India, and the first account for this country was by Roxburgh. A list of plants published in his Hortus Bengalensis (1814) included the names *Heynea*, *Walsura*, and *Andersonia*. *Heynea* was properly described and illustrated by Sims in the following year (Curtis' Bot. Mag. 41), and *Andersonia* was described and illustrated under the new name *Amoora* by Roxburgh himself, in his Plants of the Coast of Coromandel (1820). *Walsura* was given a full description in the second edition of Roxburgh's Flora Indica (1832).

Blume (1825) gave an important account of the family in Bijdragen tot de Flora van Nederlandsch Indië, in which he described seven new genera, *Aphanamixis*, *Chisocheton*, *Cipadessa*, *Dysoxylum*, and three new genera which are now regarded as synonyms of *Dysoxylum*, viz. *Didymocheton*, *Goniocheton*, and *Epicharis*.

The first herbaceous genus of *Meliaceae* to be discovered, *Naregamia*, was described by Wight and Arnott in their Prodromus Florae Peninsulae Indiae Orientalis (1834), and five years later Wight described and illustrated a plant of similar habit, *Munronia*, in his Icones Plantarum Indiae Orientalis. About this time Ecklon and Zeyher described *Ptaeroxylon* from South Africa (Enum. Fl. Afr. Austr. Extratrop. 1, 1834—35?: 54). This genus has often been placed in the *Meliaceae* but its exact relationships were doubtful. Following the studies of Leroy (1959, 1960a) and White and Styles (1966), it is now placed with the Malagasy genus *Cedrelopsis* in a separate family, the *Ptaeroxylaceae*. This is discussed more fully in a later chapter.

In 1846 M. J. Roemer published an account of the family in the first of his Synopses Monographicae, Hesperides. He followed A. de Jussieu in maintaining the *Meliaceae* and *Cedrelaceae* as distinct families. Fifty two genera were included in the *Meliaceae*, a great increase on earlier works; a few of these represented new genera, but the majority are generic splits not taken up by subsequent authors, except for one, *Toona*. The genus *Oxleya* (= *Flindersia*), included by Roemer in *Cedrelaceae*, is now placed in *Flindersiaceae* (Airy Shaw, 1966) or *Rutaceae* (Hartley, 1969).

The younger Hooker, in the Genera Plantarum of Bentham and Hooker (1862), followed A. de Candolle but differed from A. de Jussieu in uniting the *Cedrelaceae* and *Meliaceae*. All authors since then have done the same. Hooker included thirty seven genera in the *Meliaceae*, and all of them are fully and accurately described. Some of the genera he recognized have since been split into two or more and others have been subordinated to synonymy, but the majority are still accepted today. These genera are arranged in tribes as follows:

Tribe 1. *Melieae*, characterized by united filaments, biovulate loculi, unwinged albuminous seeds, and plano-convex or foliaceous cotyledons, contains *Quivisia*, *Calodryum* (= *Turraea*), *Turraea*, *Vavaea*, *Naregamia*, *Munronia*, *Melia* (including *Azadirachta*), and *Mallea* (= *Cipadessa*).

Tribe 2. *Trichilieae*, characterized by united filaments, 1- or 2-ovulate loculi, unwinged exalbuminous seeds with thick, often fused, cotyledons, contains *Dysoxylum*, *Chisocheton*, *Epicharis* (= *Dysoxylum*), *Cabralea*, *Sandoricum*, *Aglaia*, *Milnea* (= *Aglaia*), *Lansium*, *Amoora* (= *Aglaia*), *Synoum*, *Guarea*, *Dasycoleum* (= *Chisocheton*), *Ekebergia*, *Walsura*, *Heynea*, *Beddomea* (= *Aglaia*), *Moschoxylon* (= *Trichilia*), *Odontandra* (= *Trichilia*), *Trichilia*, *Owenia*, *Carapa* (including *Xylocarpus*).

Tribe 3. *Swietenieae*, characterized by united filaments, multiovulate loculi, fruit a septifragal capsule, many seeds with or without albumen and often winged. *Swietenia, Khaya, Soymida, Chukrasia ('Chickrassia'), Elutheria* (= *Schmardaea*).

Tribe 4. *Cedreleae*, characterized by free stamens, multiovulate loculi, fruit a septifragal or loculicidal capsule containing many compressed seeds, contains *Cedrela, Chloroxylon*, and *Flindersia*.

Aitonia was placed at the end of the family among '*genera affinia aut exclusa*', with the comment '*ad Sapindaceas pertinet*'.

In addition to a number of genera now regarded as synonyms, a considerable number have been described during the last one hundred years. The African genus *Turraeanthus* was described by Baillon in 1874, who in the same year published an account of the family in his Histoire des Plantes. This account was based largely on that of the younger Hooker, but contained unorthodox views on synonymy. He rightly included *Calodryum* under *Turraea*, but mistakenly combined *Vavaea* under *Quivisia, Walsura* under *Heynea, Ruagea* under *Guarea*, and *Dysoxylum* under *Epicharis*.

Four years later (1878), Casimir de Candolle, in Monographiae Phanerogamarum, resurrected *Vavaea* and *Walsura*, but reduced *Aphanamixis* to *Amoora*. C. de Candolle's circumscription of *Dysoxylum* included *Didymocheton* and *Epicharis, Guarea* included *Ruagea, Carapa* included *Xylocarpus*, and *Cedrela* included *Toona*.

In 1884 Hemsley raised to generic rank the endemic Sinhalese tree *Dysoxylum championii* Hook. *f.* & Thoms *ex* Thw. and called it *Pseudocarapa;* three years later he described an interesting Malayan endemic genus, *Megaphyllaea*. In 1893 Baillon described from Madagascar *Quivisianthe papinae*, a species which is very isolated and whose relationships are still uncertain today. A small genus, *Reinwardtiodendron*, related to *Aglaia* and *Lansium*, was described by Koorders in 1898 from Celebes.

In 1896 Harms published his first account of the *Meliaceae* in Engler and Prantl's Die Natürlichen Pflanzenfamilien. In this work he described 4 new genera, *Lovoa, Pseudocedrela, Pterorhachis*, and *Symphytosiphon* (= *Trichilia*), and included the recently described *Entandrophragma* of C. de Candolle. *Beddomea*, which had been maintained by C. de Candolle, was included under *Aglaia* by Harms, who also combined *Quivisia* with *Turraea, Heynea* with *Walsura*, and *Epicharis* and *Didymocheton* with *Dysoxylum*. *Aphanamixis* was again reinstated as a genus in this work, as were *Xylocarpus* and *Toona*.

In the same year as the publication of Harms' account of the *Meliaceae*, Pierre described the New Caledonian genus *Anthocarapa*, based on two species which C. de Candolle had placed in *Amoora*, and in 1897 he described the West African genus *Heckeldora*.

An interesting South African shrub, *Nurmonia*, which was until 1968 known only from the type gathering, was described by Harms in 1917. It is now considered to be synonymous with *Turraea*. *Urbanoguarea* was described by the same author in 1937.

In 1940 Harms published a revised account of the *Meliaceae* for the second edition of Die Natürlichen Pflanzenfamilien in which several taxa given sectional rank in the first edition were elevated to generic status. These are *Heynea, Ruagea, Didymocheton*, and *Epicharis*.

Since the publication of this important work, further genera have been described. Verdcourt (1956) described *Pseudobersama*, a monotypic African genus related to *Trichilia*, based on a plant originally placed in *Bersama (Melianthaceae)*. Leroy, more recently, working on the rich and little known Malagasy flora, has described 6 endemic genera: *Neobeguea, Calodecaryia, Capuronianthus, Malleastrum, Astrotrichilia*, and *Humbertioturraea*, and one, *Lepidotrichilia*, which occurs both in Madagascar and East Africa.

Other noteworthy taxonomic works of recent years (mainly revisions of genera or sections of genera) include those of Pellegrin (1939) on *Guarea*, Earle Smith (1960) on *Cedrela*, and Kostermans (1966) on *Lansium*.

Since the publication of Bentham and Hooker's Genera Plantarum, four comprehensive classifications of the family have been published — Casimir de Candolle (1878), two by Harms (1896 and 1940), and one based on the anatomy of the secondary xylem by Kribs (1930). This last classification is discussed in Chapter 4.

The classification of C. de Candolle (1878) is closely similar to that of the younger Hooker. He divided the family into four tribes as follows:

Tribe. 1. *Melieae*, contained those genera included by J. D. Hooker, except *Vavaea* which was removed to the *Trichilieae*. The recently described *Turraeanthus* was placed in the *Melieae* because its flowers bear a superficial resemblance to *Turraea*. At that time its fruit was unknown.

Tribe 2. *Trichilieae*, has the same circumscription as that of Hooker, except that *Carapa* was removed to the *Swietenieae*.

Tribe 3. *Swietenieae*, is that of Hooker, plus *Carapa*.

Tribe 4. *Cedreleae*, is the same as that of Hooker.

Harms' first account of the Meliaceae (1896) is also similar to those of Hooker and C. de Candolle but contains some important differences. Harms divided the *Meliaceae* into three subfamilies in the following way:

Subfamily I. *Cedreloideae*. This contains *Cedrela* and *Toona* and, in a separate tribe, *Ptaeroxylon*. *Flindersia* and *Chloroxylon* are excluded from the family.

Subfamily II. *Swietenioideae*, has the same content as C. de Candolle's *Swietenieae*, except that *Carapa* and *Xylocarpus* are removed.

Subfamily III. *Melioideae*, is subdivided into six tribes, the first of which, *Carapeae*, contains *Carapa* and *Xylocarpus*. The remaining five tribes account for all genera of C. de Candolle's *Melieae* and *Trichilieae*, plus those new genera subsequently described.

Aitonia (Nymania), which is again included by Harms in the family, is placed in the *Turraeeae*.

The contents of the tribes are as follows:

Tribe 1. *Carapeae* : *Carapa, Xylocarpus.*
Tribe 2. *Turraeeae* : *Cipadessa, Aitonia, Munronia, Turraea, Naregamia, Pterorhachis.*
Tribe 3. *Vavaeeae* : *Vavaea.*
Tribe 4. *Melieae* : *Melia.*
Tribe 5. *Azadirachtieae*: *Azadirachta.*
Tribe 6. *Trichilieae* : *Megaphyllaea, Sandoricum, Dysoxylum, Cabralea, Turraeanthus, Chisocheton, Lansium, Aphanamixis, Amoora, Pseudocarapa, Synoum, Aglaia, Guarea, Owenia, Walsura, Ekebergia, Odontandra (= Trichilia), Trichilia, Symphytosiphon (= Trichilia).*

In the second edition of Die Natürlichen Pflanzenfamilien, Harms (1940) did not alter the circumscription of the subfamilies, except to include those genera described since 1896. His division of the *Melioideae* into tribes remained virtually unchanged, except that *Azadirachta* was included with *Melia* in the tribe *Melieae*, so reducing the number of tribes to five.

During the present century, and increasingly in recent years, much information on the anatomy, structure of the pollen grain, and the chemistry of the group has been published. The taxonomic significance of characters of the secondary xylem and of pollen grain structure is discussed in later chapters. Although our knowledge of the chemistry of the *Meliaceae* and related families is rapidly increasing (see, for instance, Bevan et al., 1962, D. A. H. Taylor, 1965, and many other references cited in Grijpma and Styles, Bibliografía selectiva sobre Meliáceas, 1973) insufficient is known at present for the taxonomic value of chemical characteristics to be fully evaluated. Because of this, the chemistry of the group is not considered further.

More recently still, Styles and Vosa (1971), Styles and Khosla (in press), and Mehra et al. (1972) have published chromosome counts for most genera. Until further work is done, however, on those genera with a large number of species, the taxonomic value of this information cannot be fully assessed. Chromosome numbers are given under each relevant genus.

2. MORPHOLOGY

Almost all the species of *Meliaceae* are woody; the majority are trees, ranging from forest giants down to small treelets. In tropical Mexico and Central America they are often abundant in the upper storey of the high evergreen forest, e.g. *Swietenia*. In Africa the dominant high forest emergents, *Khaya*, *Entandrophragma*, and *Lovoa* are very important as producers of quality timber. In Malesia they form an important component of the understorey of the lowland forests, e.g. *Chisocheton*, *Aglaia*. Some members of a few genera, e.g. *Turraea*, are shrubs, whilst *Naregamia* and *Munronia* are small suffrutices with a woody rootstock.

The habit is often useful for field identification. Small unbranched trees with a dense terminal cluster of large pinnate leaves *('Schopfbaum')* are commonly found in several genera, e.g. *Chisocheton*; the leaves may be as much as three metres in length and are especially large in juvenile specimens. Other species are medium or large trees with little-branched pachycaulous twigs, as seen in *Entandrophragma*; the internodes are very short and the leaves produced in a dense terminal cluster, a habit easily recognizable at a distance in the field. One genus *(Vavaea)* has sympodial *('Terminalia')* branching.

The bark configuration does not appear to be very significant at the subfamily, tribe, or generic levels; smooth, scaly, and dippled types are present in most of the larger genera. Bark characters are probably more useful at the species level.

The extent to which a milky exudate in the bark occurs in the family is uncertain, but our observations in South East Asia, Africa, and tropical America indicate that it is often characteristic of genera. *Aglaia* is always seen to have a certain amount of such exudate, although it may be small in quantity and slow to appear, whereas in *Chisocheton* and *Dysoxylum* a milky exudate is never present. The bark frequently emits an objectionable smell when crushed or cut, for example of onions in many species of *Dysoxylum*, or of garlic *(Cedrela, Toona)*; the odour of the bark of some species of *Aglaia* in New Guinea and the Solomon Islands causes nausea and the sap is also very caustic. The wood of these species is not used commercially for this reason.

The buds of all species of the subfamily *Swietenioideae* are surrounded by a cluster of small subulate scales. This feature has not been observed in any species of the other subfamilies where the buds are naked.

The leaves are nearly always spirally inserted and very often clustered near the branch tips; they are constantly decussate only in *Capuronianthus mahafalensis* J. F. Leroy of the subfamily *Capuronianthoideae;* decussate leaves also occur very rarely in *Dysoxylum* and *Turraea* but the arrangement is usually inconstant and varies from opposite to spiral.

The majority of species have pinnate leaves. In *Melia* they are bipinnate. Bipinnate leaves also occur in juvenile specimens of *Chukrasia* and *Lovoa*. Those of *Sandoricum* are trifoliolate. Several of the genera with pinnate leaves contain species which are trifoliolate or unifoliolate. The latter differ from simple leaves by the presence of the conspicuous pulvinus at the insertion of the leaflet as in species of *Aglaia* and *Walsura*. A small number of genera have simple leaves (*Turraea, Nymania, Calodecaryia, Vavaea)*. A terminal leaflet is usually present in the majority of genera with pinnate leaves, but this is not constant in occurrence and may be present or absent within a single species (*Toona ciliata* M. J. Roem.) Rarely it is much reduced to a vestige (some species of *Cabralea* and *Carapa*). In *Amoora cucullata* Roxb. it is reduced in size and converted into an hooded structure. Occasionally a genus has exclusively paripinnate leaves, e.g. *Owenia* and *Pseudocarapa.*

Chisocheton, Megaphyllaea, and *Guarea* are characterized by pinnate leaves which show intermittent apical growth. At the leaf apex of these genera is a small curled bud (like the apex of a fern frond). This bud has intermittent growth and produces leaflets at intervals for several years (up to 11 years' growth measured in *Guarea rhopalocarpa* Radlk. from Costa Rica, cf. Skutch, 1946). Although the mature leaflets of these species are opposite, each member of a pair may develop separately. As new leaflets are produced at the leaf apex, so the older leaflets are shed from the basal portion of the rhachis. Finally the rhachis itself is shed. The leaf behaves like a shoot and has certain anatomical structures of one, e.g. a closed cambial ring. The compound leaves of many tropical plant families have a similar structure, but that of *Guarea rhopalocarpa* Radlk. differs in its greater thickness and in the presence of annual rings, together with the production of a corky bark. Some species of other genera, e.g. *Cabralea* and *Dysoxylum,* show a limited amount of apical growth, with the basal leaflets maturing before the apical ones, but there is no distinct terminal bud showing alternating periods of growth and dormancy. Growth is continuous, usually ending in the formation of a terminal leaflet.

Occasionally, the rhachis of a compound leaf is flattened and winglike as in *Pterorhachis* and *Naregamia.*

The leaflets are usually entire, less frequently dentate, serrate, or crenate, and very rarely with a prickly margin (a few species of *Trichilia*, e.g. *T. cuneifolia* (L.) Urb.).

Secretory cells of various shapes and sizes are found throughout the *Meliaceae*, usually at the boundary between the spongy and palisade mesophyll in the leaves (Metcalfe and Chalk, 1950: 351). In some genera these are visible as transparent lines or dots as in *Cabralea.* In some species of *Trichilia, Walsura,* and *Ekebergia* the cells of the lower leaf epidermis are produced into numerous papillae which give the undersurface a very characteristic glaucous appearance.

The indumentum is sometimes diagnostic of a genus, e.g. *Aglaia* is characterized by stellate hairs or peltate scales. There is no sharp distinction between these two types of indumentum and they may merge with one another within a single species. *Munronia* has a curious mixture of simple hairs with bifid or stellate hairs. This has not been observed elsewhere in the *Meliaceae.*

The inflorescence is very variable but is generally some form of panicle or thyrse. Within *Aglaia* alone this can vary from a large inflorescence, one-third to two-thirds of a metre long with profuse branching and an abundance of flowers, to a much reduced minute inflorescence 1—2 cm long. In many genera the ultimate ramifications of the inflorescence are cymose (thyrse), e.g. *Melia, Cedrela,* and *Entandrophragma.* Many genera of the *Melioideae* appear to be dioecious, although undoubtedly some species produce both hermaphrodite and ♂ flowers (polygamous) on the same plant. In *Melia* the terminal flowers of the branchlets are hermaphrodite and the lateral ones male (Lee, 1967). All the genera of *Swietenioideae* appear to be monoecious (Styles, 1972). In *Cedrela* and *Toona* and probably all other genera of *Swietenioideae* the terminal flower of a cymule is female while the other two are male.

Sex differences in inflorescence structure are often marked in the subfamily *Melioideae.*

Generally, male inflorescences are longer and more profusely-branched than the female. In some species of *Aglaia,* while the male inflorescence is 20—50 cm long and many-flowered, that of the female may be reduced to a spike 2—3 cm long with less than ten flowers.

In *Chisocheton* and *Guarea* the panicle branches are often greatly reduced in length and the main axis elongated. The resulting thyrsoid inflorescence may be up to a metre long, as in *Chisocheton penduliflorus* Planch. *ex* Hiern. Rarely the main axis of the inflorescence is reduced in length and branched from near the base to form a compound thyrse *(Pterorhachis).* In a few species of *Trichilia* and *Turraea* the inflorescence is fasciculate. *Aphanamixis* is characterized by a spicate female inflorescence, whilst the male inflorescence is usually paniculate with spicate branches. Both male and female inflorescences of this genus may be up to a metre long. *Naregamia* and *Nymania* have solitary or paired flowers.

The inflorescence is generally axillary, less frequently terminal. It is often borne above the axil of a leaf (supra-axillary) as in *Chisocheton* and *Aphanamixis.* Cauliflory and ramiflory occur sporadically throughout the subfamily *Melioideae,* e.g. in species of *Dysoxylum* and *Chisocheton. Lansium domesticum* Corr. has the inflorescence borne upon the branches. In older cauliflorous trees, the flowers are borne on large warty bulges on the trunk.

Flower size and shape vary within wide limits, from the minute globular flowers of *Aglaia* 0.05 cm in diameter to the long tubular flowers of *Turraea* over 10 cm in length. The *Swietenioideae* are characterized by having (in general) small flowers. In monoecious or dioecious species the male flowers are generally smaller and much more numerous than the female. The shape of the flower is characteristic for most genera, e.g. globular in *Aglaia,* tubular in *Chisocheton.* Although the flowers are usually inconspicuous in colour, being dull white, greenish-white, or pale yellow, they frequently emit a powerful scent. This is particularly noticeable in *Aglaia.* Other Malesian genera are also scented, though the odour varies considerably in quality and power.

Calyx form is variable and frequently important at the generic level. Free or almost free imbricate sepals are present in only a few genera, e.g. *Ruagea* and *Cabralea. Munronia* and a few species of *Turraea* have a deeply divided calyx with open aestivation and the lobes are distinctly foliaceous. The number of lobes varies from (2) 4 or 5 (7). In several genera, notably part of *Turraea, Chisocheton, Sandoricum,* and *Guarea,* there occurs a calyx with the margin only very shallowly toothed or entire (truncate). A few species of *Guarea, Chisocheton, Dysoxylum,* and *Megaphyllaea* have a calyx which is entirely closed in bud and is circumscissile. In *Megaphyllaea* and some *Chisocheton* species the calyx is greatly thickened in the lower half and round the middle there is a swollen and warty band.

A single whorl of (3) 4 or 5 (—14) free petals greatly exceeding the calyx in length is the rule in the family. Gamopetalous corollas with the petals united to halfway or more occur sporadically (e.g. some species of *Trichilia*), but petals fused at the base are fairly frequent in *Aglaia* and a few other genera. *Megaphyllaea* is unique in having a biseriate corolla (petals 8—10 in 2 whorls, fused in the lower half). In several genera, e.g. *Munronia, Turraeanthus,* and part of *Dysoxylum,* the petals are free from each other, but are fused to halfway or higher with the staminal tube. In a few species of *Munronia* the petals adhere to the staminal tube in the young flower, but appear to become free as it matures. In *Cedrela* and *Toona* the petals are adnate to the androgynophore by a median flap of tissue (carina), which prevents them spreading in open flowers. The aestivation is generally imbricate, usually one-fifth *('cochleardachig'),* but two-fifths in some species of *Aglaia.* Contorted aestivation is frequent in the subfamily *Swietenioideae* and occasional elsewhere. Valvate aestivation occurs in several genera, e.g. *Guarea, Chisocheton, Cipadessa, Malleastrum,* and *Xylocarpus.* Aestivation of the corolla is a rather unreliable character for classification as it is sometimes variable even within a single specimen. The mature petals usually reflex, especially in those species with tubular flowers, this providing a useful character for field recognition. The shape of the petals varies widely from almost orbicular in *Aglaia* and *Aphanamixis* to linear or spathulate in those genera with tubular flowers (e.g. *Dysoxylum, Turraea*). The petals of the *Meliaceae* are often rather thick and fleshy (e.g. *Chisocheton, Dysoxylum*).

The androecium provides more characters of diagnostic importance in the classification of *Meliaceae* than any other structure. The characteristic feature of the family is the partial or complete fusion of the filaments to form a staminal tube. Only two genera (*Cedrela, Toona*) have consistently free filaments. A few species of *Trichilia* and *Walsura* have free filaments but in these they are flattened dorsoventrally, giving the impression of a complete staminal tube in the mature flower. Genera with filaments united only in the lower half are *Cipadessa, Calodecaryia, Nymania,* and some species of *Entandrophragma.* In other genera there may be great variation in the degree of fusion, as in *Trichilia,* which has the complete range from free filaments to a complete staminal tube. The degree of fusion may even vary within a single species, as between male and female flowers of *Trichilia havanensis* Jacq. However, the degree of fusion of filaments is constant within genera in certain parts of the family as in *Dysoxylum* and *Chisocheton,* which are characterized by a complete staminal tube.

The shape of the androecium ranges from globular with a minute apical pore or cup-shaped as in *Aglaia,* to a long narrowly-cylindrical tube as in *Turraea* and *Dysoxylum.* In *Naregamia* and some species of *Turraea* the cylindrical tube is inflated at the apex.

The apex of the filaments or the margin of the staminal tube often bears filiform, lanceolate, deltate, truncate, emarginate, or bilobed appendages. In those species with a complete staminal tube, the appendages usually alternate with the anthers (or antherodes in female flowers) and equal them in number, whereas those with only partial fusion of the filaments usually have two or rarely 3—10 times as many appendages as anthers. The anthers are usually double the number of the petals, most commonly 8—10, but in *Aglaia* the petals and anthers are often equal in number (5) and rarely reduced to only 3. Rarely the number of anthers is very large (up to 23 in *Chisocheton macranthus* (Merr.) Airy-Shaw).

The anthers may be hairy or glabrous but this character is rarely constant within a genus and often varies within single species (*Vavaea amicorum* Benth.). The anther connective is frequently produced to form a short or sometimes long terminal appendage as in *Naregamia.* In *Schmardaea* it is much produced and thread-like. In nearly all species of *Chisocheton* and in *Megaphyllaea* the anthers differ from those of other *Meliaceae* in having transverse septa (locellate). This gives the young anthers a segmented appearance before dehiscence.

The position of insertion of the anthers in the staminal tube is often a character of generic value. The anthers may be inserted apically at the end of the filaments or on the margin of the staminal tube as in *Trichilia,* or inside the throat of the staminal tube with the anthers completely included or only partially exserted as in *Dysoxylum.* Although the insertion is constant for the majority of genera, in a number of instances it varies within a genus, for example in *Aglaia* and *Owenia.*

Various structures collectively known as disks occur between the base of the ovary and the staminal tube. These are often brightly coloured and sticky and probably function as nectaries. In a number of genera, e.g. *Aglaia, Aphanamixis,* and *Lansium,* a disk is absent, and in *Chukrasia* and *Schmardaea* it is indistinct. In *Guarea* and some species of *Chisocheton* the ovary is borne on top of a short or long stipe structure (stipitate disk.) In *Cedrela* and

Toona both ovary and stamens are supported on a columnar or swollen disk-like stipe or androgynophore which is partially fused to the inner face of the petals. In many species of the tribe *Trichilieae* (subfamily *Melioideae*) the disk is represented by a narrow ring of tissue surrounding the base of the ovary (annular disk). In other cases it may be a poorly developed saucer-shaped structure (patelliform disk) either free from, or fused to the base of the staminal tube or to the base of the ovary. In some species of *Trichilia* the patelliform disk is not only fused to the lower part of the staminal tube but is also deeply ribbed (androecial ribs). The disk reaches its greatest development in *Dysoxylum*, *Cabralea*, *Sandoricum*, and some species of *Munronia* where it is represented by a cup-shaped (cyathiform) or long tubular structure with an entire or toothed margin, often enclosing the ovary and part of the style. In most genera of the *Swietenioideae* the disk is prominent and well-developed and is often lobed or ridged.

The ovary is usually superior, but in *Sandoricum*, *Aphanamixis*, and *Cabralea* it may be partly sunken. The number of loculi varies from 1—20, but is usually 2—5. *Malleastrum*, which sometimes has a unilocular ovary, appears to be unilocular by abortion; the one extant loculus is markedly eccentric. The number of ovules in each locule provides an important subfamily distinction. Each locule may contain one or two collateral or superposed ovules (nearly all *Melioideae*) or 3— many biseriate ovules *(Swietenioideae)*. Rarely the locules contain 2 well-developed ovules and 1 or 2 vestigial ovules as in *Capuronianthus* and *Guarea thompsonii* Sprague & Hutch. The anatropous or orthotropous ovules are attached to an axile placenta or very rarely to a parietal placenta *(Heckeldora)*.

In *Aglaia* and *Aphanamixis* and several other genera with small flowers, the style is very short or absent. In those genera with tubular flowers it is usually long and slender *(Dysoxylum)*. In *Sandoricum* the style is very stout and columnar. The style-head shows great variation in form and provides valuable characters for classification. In some of the genera with very small flowers, e.g. *Aglaia*, it is like a very small pin-head (capitate). In *Aphanamixis* it is expanded into a conical structure, and in most genera of the *Swietenioideae* it is flattened and discoid, often with a central depression and stigmatic ridges. It frequently blocks the entrance to the staminal tube. The style-head is occasionally pileate (shaped like a mushroom) as in some species of *Walsura*. In *Melia*, *Azadirachta*, and *Sandoricum* the expanded style-head bears several large stigmatic lobes. The style-head reaches its greatest development in *Turraea* where it is often modified to form a variously-shaped *receptaculum pollinis*, surmounted by a small apical stigmatic area. Observation of the living plant shows that pollen is shed on to the style-head before the flower opens (White and Styles, 1963).

Sexual dimorphism within flowers of many genera in the *Meliaceae* has been fully discussed by Styles (1972).

The fruit shows wide variation in size and structure and is often a conspicuous feature in the field. The bright orange or red capsules of *Trichilia* and *Dysoxylum*, which stand out against the background of dark green foliage, contrast with the dull greyish-brown berries of *Aglaia* or *Lansium*. The fruit is most frequently a capsule, either septifragal *(Swietenioideae, Capuronianthoideae)* or loculicidal *(Quivisianthoideae, Melioideae)*. The septifragal capsules of the *Swietenioideae* are usually woody and generally contain a central columella which is angled or ridged (rudimentary in *Schmardaea*, *Xylocarpus*, and *Carapa*) and to which the seeds are attached. Dehiscence of this type of capsule may be basal, apical, or from base and apex simultaneously. The loculicidal capsules of the *Melioideae* do not have the central columella and may be woody, leathery, membraneous, or even fleshy. Dehiscence of the loculicidal capsule is always from the apex. The capsule rarely bears simple or branched appendages; in *Pseudobersama* these are stout and antler-like, whereas in some species of *Trichilia* they are slender and fimbriate. Dehiscence may be slow, and difficult to observe in dried herbarium material (especially in some species of *Guarea* and *Chisocheton*). Sutures are not always visible and dehiscence may occur only after the fruit has been shed. *Capuronianthus* is unusual in that its endocarp dehisces regularly along the septa whereas the epi-mesocarp dehisces irregularly or not at all. Further field observations are needed in many cases to determine mode and time of dehiscence.

Indehiscent fruits are also widespread in the *Melioideae*. Soft berries occur in *Aglaia, Lansium, Malleastrum*, etc., whereas in *Owenia* and *Astrotrichilia* the fruit is drupaceous. Although the distinction between a berry and drupe is not sharp, those genera with drupaceous fruits always show some differentiation of the endocarp, though this may be only a thin cartilaginous layer, as in some species of *Lepidotrichilia* and *Sandoricum*. In *Owenia* and *Astrotrichilia* the endocarp is thick and woody. One undescribed species of *Aglaia* has an indehiscent fruit in which the pericarp is entirely dry and woody (nut). In *Heckeldora* the berry is constricted between the seeds and also rostrate.

Seeds in the *Meliaceae* are of two principal types. The first has a thin dry testa and a conspicuous dry wing, which may be terminal or occur all the way round or at both ends. Seeds with terminal wings are attached to the placenta or columella either by the wing- or seed-end. This type of seed is characteristic of subfamilies *Swietenioideae* and *Quivisian-*

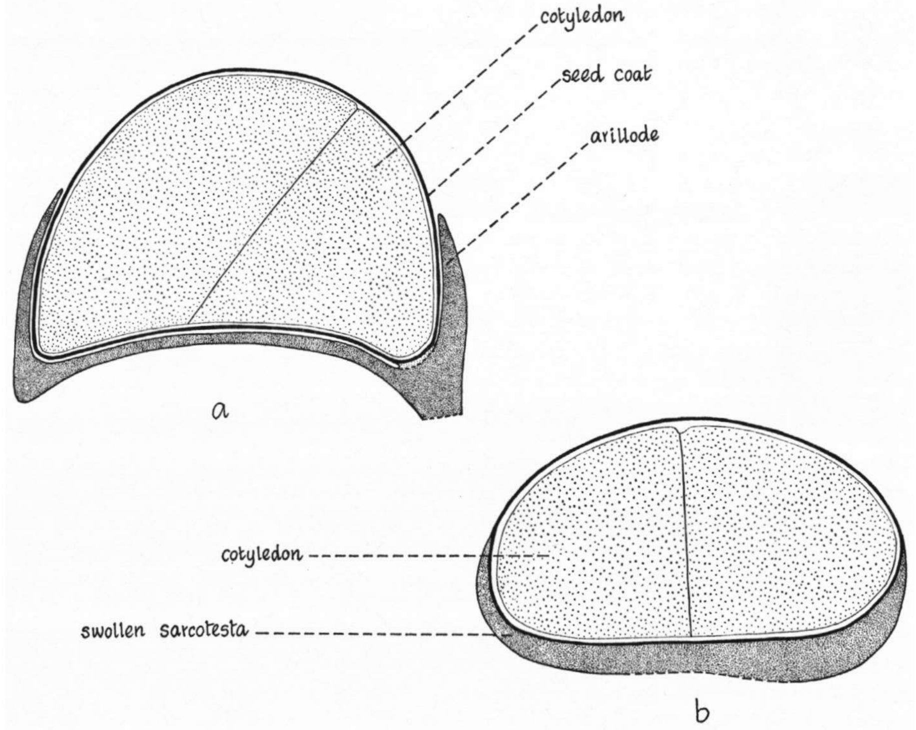

Fig. 1. a. *Aphanamixis grandifolia* Blume, T. S. of seed, showing arillode forming a free flap of tissue, attached to seed only along a line joining micropyle-raphe-chalaza. — b. *Guarea excelsa* H.B.K., L.S. of seed, with fleshy sarcotesta appearing as a localized swelling of the seed coat.

thoideae. Unwinged seeds, usually with a fleshy arillode or sarcotesta, are typical of the *Melioideae*. Studies of the arillode and sarcotesta may indicate that there is no fundamental morphological difference between them. They both appear to arise from localized or generalized meristematic activity in the outer integument. Meristematic activity may extend back to the funicle or occasionally as far as the placental tissue *(Turraea)*, but as it is never confined to these areas but always includes part of the seed coat between the raphe and the micropyle, it is thought inadvisable to use the restricted term aril for this structure. In this work the fleshy outgrowth is called an arillode if it forms a partially or completely free flap of tissue surrounding a part or the whole of the seed (fig. 1a) and a sarcotesta when the fleshy part appears as a localized or general swelling of the seed coat (fig. 1b). There is no sharp distinction between the two, and they both occur within a single genus. (e.g. *Trichilia*).

The structure of the arillode or sarcotesta is sometimes sufficiently modified to be useful as a diagnostic generic character. *Synoum* is unique in having a fleshy arillode which unites the two seeds of a valve along the abaxial surface. The sarcotesta of *Munronia* covers the adaxial surface of the seed and before maturity the fleshy inner cells disintegrate, leaving the ripe seed with a large, hollow, membraneous structure. A similar condition occurs in *Nymania*. The sarcotesta of *Ruagea* is attached to the basal (chalazal) portion of the seed and is greatly swollen. The colour of the arillode or sarcotesta is related to dehiscence of the fruit. In species with dehiscent fruit, where the arillode or sarcotesta act as visual attractants for birds or mammals, they are red or orange, often contrasting with the black undifferentiated part of the seed coat. In species with indehiscent fruit, where they cannot act by visual attraction, they are always white or colourless.

Genera of the *Turraeeae (Melioideae)* are characterized by the presence of endosperm, often quite copious. Elsewhere in the family it occurs sporadically (in species of *Trichilia* and *Astrotrichilia)* and is often very thin and rather difficult to observe *(Vavaea* and several genera in the *Swietenioideae*). The shape and structure of the embryo are correlated with the presence or absence of endosperm. Those genera with endosperm usually have thin embryos with flat collateral cotyledons and a long exserted superior radicle. Those without endosperm have larger embryos with plano-convex cotyledons and included radicle. The position of the cotyledons and radicle is usually constant within genera, e.g. *Aglaia* has superposed cotyledons and an included radicle, *Guarea* usually has an abaxial radicle. Most frequently the radicle is placed at the apex of the seed (superior).

3. WOOD STRUCTURE

Because of the great economic importance of many genera of *Meliaceae* to the timber industry, their wood anatomy has been extensively studied. Moll and Janssonius (1908), Kribs (1930), Panshin (1933), and Dadswell and Ellis (1939) have discussed the characters of the secondary xylem of the *Meliaceae* in relation to taxonomy, but only Kribs studied the whole family and attempted to produce an anatomical classification with a key to the genera.

In his investigation, Kribs examined 112 species from 36 genera. At the time this was probably the most comprehensive anatomical investigation ever carried out on a family of tropical plants of comparable size. It is significant for several reasons. First, he constructed a key to 36 genera of the *Meliaceae*, based entirely on characters of the secondary xylem and thus implied that all 36 genera could be keyed out using only anatomical characters. Second, on the basis of this knowledge, supplemented by facts from gross morphology which he obtained mainly from the literature, he suggested a new arrangement of genera which differed from those of previous authors. His conclusions were as follows:

1. *Cedrela* (including *Toona*) should be transferred to the subfamily *Swietenioideae.*
2. *Carapa* and *Xylocarpus* should also be placed in the subfamily *Swietenioideae.*
3. *Lovoa* should be placed in a subfamily of its own, the *Lovoinoideae.*
4. The genera *Flindersia*, *Chloroxylon*, and *Ptaeroxylon* resemble the *Rutaceae* more closely than the *Meliaceae* in their wood structure.
5. The *Swietenioideae* is the only subfamily which forms a homogeneous group in respect of gross morphology and wood structure. Because of this he reverts to the opinion of A. de Jussieu and M. J. Roemer that it should rank as a family, to be known as the *Swieteniaceae.*

It was clear from the start of the present study that many of the genera recognized by previous authors and dealt with by Kribs, especially those in the subfamily *Melioideae*, were very closely related, so that it was necessary to view his claims with caution. Kribs used only a small sample of species in each genus, and he did not discuss the variability of the characters.

It was our intention to study as wide a range of species as possible from all genera, to test the constancy of characters, and, for selected species, to use as many samples as possible to examine the variation of characters within species. 370 slides representing about 230 species were examined during this study. 85% of the slides were correlated with herbarium specimens. At least one slide of each species was photographed in transverse, tangential, and radial section. The collection of photographs is deposited in the Forest Herbarium, Department of Forestry, University of Oxford.

In Part II will be found descriptions of the secondary xylem of the *Melioideae* and, where this is of some taxonomic interest, it is discussed more fully in the commentary following each genus. All genera are described except *Calodecaryia*, *Sphaerosacme*, *Heckeldora*, and *Quivisianthe* for which no material was available, and for *Naregamia* and *Munronia* which have insufficient secondary xylem for meaningful comparisons to be made. The genera in *Swietenioideae* have been fully dealt with in the Forest Products Research Bulletin No. 25, Identification of Hardwoods (1960), and that information is not repeated here. New information has been added under the relevant genus.

The terms used to describe vessels, fibres, and parenchyma are defined in the International Glossary of Terms used in Wood Anatomy, Anon. (1957), and those used to describe ray tissue follow Kribs (1950).

The main conclusions concerning Kribs' work can be summarized as follows:

CIRCUMSCRIPTION OF THE FAMILY

In Chapter 5 the relationships of *Cedrelopsis*, *Ptaeroxylon*, *Flindersia*, and *Chloroxylon* with the *Meliaceae* are discussed in greater detail. Kribs only examined the last three genera, and concluded that they were more Rutaceous than Meliaceous. We have found that although the wood of *Ptaeroxylon* is definitely not Meliaceous, it is similar to that of species of both the *Rutaceae* and *Sapindaceae*; and the wood of *Flindersia* and *Chloroxylon*, in their secondary xylem, have more features in common with the *Rutaceae* than with the *Meliaceae*, but do share features of both and cannot be referred definitely to either on the basis of wood anatomy alone.

CIRCUMSCRIPTION OF THE SUBFAMILIES

This is discussed in detail in Chapter 5, but the role of the secondary xylem in circumscribing the subfamilies may conveniently be summarized here. We agree with Kribs that on the basis of the structure of their secondary xylem, *Cedrela* and *Toona*, *Carapa* and *Xylocarpus* should be placed in the *Swietenioideae*. The following combination of characters defines this subfamily: rays nearly always broad, (2)3—6(7)—seriate, and heterogeneous; crystals usually present in the marginal ray cells, often absent from wood parenchyma; paratracheal parenchyma rather sparse (vasicentric or aliform); terminal wood parenchyma in regular to irregular concentric lines (frequently absent in *Khaya*); fibres septate (non-septate in *Neobeguea*).

Kribs suggested that *Lovoa* should be placed in a subfamily of its own, due to its anomalous wood structure which lacks the heterogeneous rays and crystals in the marginal ray cells. However, he ignored the fact that *Lovoa* possesses all the characteristic morphological and palynological features of the *Swietenioideae*, as well as some of its anatomical features. If *Lovoa* is removed from the *Swietenioideae*, then *Turraeanthus*, *Cipadessa*, and *Sandoricum* could equally justifiably be removed from the *Melioideae* where on all other grounds they clearly belong. Isolating such genera on account of their anomalous wood anatomy is an impractical solution which creates more problems than it solves. *Lovoa* clearly belongs in the *Swietenioideae*, and there is little justification for removing it.

In the present work, the recently discovered Malagasy genus *Capuronianthus* is placed in a subfamily of its own, the *Capuronianthoideae*. It is intermediate in many morphological features between the *Melioideae* and *Swietenioideae*, and wood anatomical characters support this decision as they are also intermediate between the two subfamilies. The secondary xylem of this genus has crystals in both marginal ray cells and wood parenchyma, and 2 or 3-seriate rays which are partially heterogeneous.

VARIATION WITHIN SPECIES AND GENERA

Kribs did not discuss variation of the secondary xylem within species or genera. Some other authors who have studied the wood anatomy of species of *Meliaceae* from restricted geographical regions have done so.

Moll and Janssonius (1908) investigated the anatomy of several South East Asian genera, and state that variation within species often exceeds that between species, especially in *Aglaia*. We have examined infra-specific variation in three species: *Trichilia hirta* L. (six samples from the West Indies and Central America), *Dysoxylum caulostachyum* Miq. (six samples from New Guinea, New Britain, and the Solomon Islands), *Aphanamixis grandifolia* Bl. (13 samples from Malaya, Sarawak, Sabah, New Guinea, and New Britain). This has shown that certain characters previously believed to be of value in defining genera can vary within a single species, viz. (1) the amount of paratracheal and apotracheal parenchyma can vary within wide limits; (2) apotracheal parenchyma is not always constant in occurrence and may be present or absent within the same species.

Variation between species of the same genus is frequently greater than that between species of different genera. In *Aglaia* there is great variation in the amount of paratracheal parenchyma; it varies from sparse vasicentric and aliform (e.g. *A. argentea* Bl.) to almost exclusively banded (e.g. *A. shawiana* Merr.). These differences are greater than those between *A. shawiana* Merr. and *Lansium domesticum* Corr.

There appears to have been some convergence in secondary xylem characters of different genera occurring in the same geographical region. Within Madagascar the secondary xylem of several species of *Turraea*, *Malleastrum*, and *Lepidotrichilia* is closely similar. It is characterized by vessels in groups of 2 or 3 with scattered distribution, and sparse vasicentric and aliform paratracheal parenchyma, and conspicuous bands of terminal apotracheal parenchyma. In contrast, certain *Turraea* species in East Africa may differ in all these features. *T. robusta* Gürke has vessels arranged in conspicuous tangential bands, aliform and confluent parenchyma, and apotracheal terminal bands are very few or absent.

THE DISTINCTNESS OF THE GENERA IN THEIR SECONDARY XYLEM

It was found that within the subfamily *Melioideae* only nine of the genera treated by Kribs are distinct on characters of their wood anatomy alone. A further four, not examined by him, are also distinct. These are *Nymania*, *Melia*, *Azadirachta*, *Vavaea*, *Pseudobersama*, *Ekebergia*, *Astrotrichilia*, *Owenia*, *Cipadessa*, *Aphanamixis*, *Turraeanthus*, *Megaphyllaea*, *Sandoricum*. All of these except *Pseudobersama* are easily separable on morphological grounds.

Kribs' key was based on insufficient observations. Inspection of a wider range of species shows that his generic characters are not constant and frequently break down. Three characters which he uses at the generic level in this group are found to be variable within genera: homogeneous versus heterogeneous ray tissue; presence of crystals in the wood parenchyma; presence of apotracheal versus diffuse parenchyma.

The subfamily *Swietenioideae* forms a distinct homogeneous group and none of the genera can be satisfactorily distinguished on characters of their wood anatomy alone. Even in *Lovoa* which, as already mentioned, was placed by Kribs in its own subfamily, all of the anomalous anatomical characters attributed to it by him are shared by other genera in the subfamily and are not diagnostic: viz. absence of terminal parenchyma is shared with *Khaya*, homogeneous rays with some species of *Entandrophragma* and with *Chukrasia*, and non-septate fibres with *Neobeguea* and some specimens of *Chukrasia*. Kribs' observation that the secondary xylem of *Cedrela* is ring porous is based on insufficient samples as all gradations between ring and diffuse porous conditions exist. On the basis of wood anatomy *Carapa* and *Xylocarpus* belong here. Furthermore there is no single feature which adequately distinguishes the secondary xylem of *Carapa* from that of *Swietenia*.

CONCLUSIONS

(1) The secondary xylem provides good characters for the delimitation of the subfamilies.

(2) Within the subfamily *Melioideae*, two correlated anatomical characters are important (when correlated with morphological and palynological features) in arranging the genera in tribes:

(a) non-septate fibres usually with terminal bands of apotracheal parenchyma — *Turraeeae*, *Melieae*, *Trichilieae* (except *Cipadessa*), *Sandoriceae*.

(b) septate fibres usually without terminal bands of apotracheal parenchyma — *Vavaeeae*, *Aglaieae*, *Guareeae* (except *Turraeanthus*).

The presence or absence of fibre septa is very constant within genera; only two exceptions have been recorded (one sample in *Vavaea* and one in *Astrotrichilia*).

(3) In the *Meliaceae* only a few genera can be distinguished on their wood anatomy alone. They are distinct on morphological grounds.

(4) In a few cases the secondary xylem provides additional evidence for maintaining

otherwise doubtfully distinct genera, e.g. *Pseudobersama*, *Aphanamixis*, and *Ruagea*. In *Anthocarapa* the secondary xylem helps to indicate the relationships of a genus of doubtful position.

4. POLLEN

The only previous comparative account of the pollen morphology of the *Meliaceae* is that of Erdtman in Pollen Morphology and Plant Taxonomy (1952, 1966). His account of the family is based on personal observation of twenty seven species from eighteen genera, and he cites twenty one species together with the voucher herbarium specimens from which the slides were prepared.

Although Erdtman's account is based on only a small sample of the family, he had also studied related families in a similar way. On the basis of these limited observations, he was able to draw the conclusion that pollen morphology does not support Harms' suggestion that the three subfamilies should rank as families. Otherwise he follows Harms' (1940) arrangement of the family, including such anomalous genera as *Ptaeroxylon* and *Cedrelopsis* which clearly do not belong. He concludes that the *Meliaceae* is a more or less stenopalynous family.

After a preliminary study of about thirty species representing a cross-section of the family, it appeared that the pollen morphology of the family was not very variable, except for *Ptaeroxylon* and several species of *Turraea*. These latter were so different from the rest that it appeared that their characteristics might be of taxonomic value. As the pollen grains of the majority of genera in the family had never been examined, it was decided to study a selection from every genus. During the course of this investigation we have examined the pollen of two hundred species from all genera of the family except *Megaphyllaea*. For the larger genera such as *Aglaia* and *Trichilia*, we have examined up to twenty species of each, and in others which showed a large range of variation, all variable species were examined. In addition we have seen a selection of about fifty slides from related families *(Rutaceae*, *Sapindaceae*, *Burseraceae*, *Simaroubaceae*, and *Anacardiaceae)* which were kindly loaned to us by the late Professor Erdtman. Formal descriptions of the pollen characteristics of the family and genera are incorporated in Part II, and where pollen is of some taxonomic value this is discussed fully in the commentary following each genus.

The palynological terms used here are principally from Erdtman (1952, 1966). The terms describing exine patterning are also from Erdtman, except that the term 'scabrous' is used to indicate a condition intermediate between 'smooth' and 'verrucose' in which the minute protuberances are less than 1 μ m high. The sizes of grains refer to the longest axis and represent the value or range of values most frequently found in the sample examined. The pollen slides were prepared by the well-known acetolysis method.

Some general conclusions on the taxonomic value of pollen morphology in this group are given here.

CIRCUMSCRIPTION OF THE FAMILY

On the grounds of pollen morphology *Flindersia* and *Chloroxylon* belong to the *Rutaceae*, and should definitely not be included in the *Meliaceae*. The pollen grains of *Cedrelopsis* and *Ptaeroxylon* which are closely similar, differ in several important respects from the pollen grains of all known *Meliaceae*. They resemble the grains of some species of *Rutaceae*, though not closely. The relationships of these four anomalous genera are discussed in greater detail in Chapter 5.

At the beginning of this study, the taxonomic positions of *Nymania* and *Pterorhachis* were also doubtful. *Nymania* had frequently been excluded from the *Meliaceae* by previous authors, and *Pterorhachis* superficially resembles several Sapindaceous genera. The pollen grain structure of both genera confirms that they are correctly placed in the *Meliaceae*. Fuller details are given in the commentary following the formal descriptions of these genera.

CIRCUMSCRIPTION OF THE SUBFAMILIES

There are no significant differences in pollen structure between the subfamilies. The subprolate or prolate-spheroidal 4-colporate grain with a smooth exine is constant in the *Swietenioideae* (including *Cedrela*, *Carapa*, and *Xylocarpus*). For this reason it is not discussed further in Part II. This type of grain is also frequently found in the other three subfamilies, but in the *Melioideae* there are also a number of other types. Several genera, e.g. *Vavaea*, *Aglaia*, and *Lansium* are characterized by prolate or prolate-spheroidal 3-colporate grains; most species of *Guarea* and *Dysoxylum* have spheroidal 4-colporate grains, and the genera of the *Turraeeae* are characterized by oblate or oblate-spheroidal 3-colporate grains with a verrucose exine.

CIRCUMSCRIPTION OF THE TRIBES

For morphological reasons we conclude that *Pterorhachis* and *Cipadessa* do not belong in the *Turraeeae* (subfamily *Melioideae*) where they were placed by Harms (1940). Pollen grain morphology confirms that both these genera should be excluded from this tribe. The pollen of the *Turraeeae*, with these two genera excluded, differs from that of the remainder of the *Melioideae* in several well-correlated characters. Its grains are almost consistently oblate or oblate-spheroidal, 3-colporate, with a prominently scabrous or verrucose exine, a combination of characters rarely encountered elsewhere in the family. A preliminary examination of a few species of *Turraea* (*T. cornucopia* White & Styles *ined.* and *T. vogelii* Hook. *f. ex.* Benth.) revealed pollen grains so extreme that we thought the genus might be wrongly placed in the *Meliaceae*. However, further study of a greater range of species showed that others were less extreme (e.g. *T. abyssinica* Hochst. *ex* A. Rich. and *T. robusta* Gürke), and the pollen of the related genus *Munronia* is intermediate between typical *Turraeeae* and the remainder of the *Melioideae*. The pollen grains of *Munronia* are usually 4-colporate, though they retain the other distinctive features of the *Turraeeae*. The *Turraea*-type pollen has been found very rarely elsewhere in the *Melioideae* (e.g. in *Trichilia surumuensis* C. DC. from British Guiana).

RELATIONSHIPS OF THE GENERA

With few exceptions, pollen characteristics are of limited value in identifying genera in the *Melioideae*. Occasionally pairs or groups of genera are characterized by distinctive grains (e.g. *Aglaia*, *Lansium*, *Reinwardtiodendron*, with very small, usually 3-colporate, prolate grains). In one case the pollen grain structure provides additional evidence for reinstating a genus given only sectional rank by Harms (*Heckeldora*), and in three further examples (*Nymania*, *Pseudocarapa*, and *Anthocarapa*), pollen structure in combination with morphological characters helps to indicate the true relationships of genera.

5. DELIMITATION OF THE TAXA

There has been some degree of agreement among the different specialists who have worked on the group as to the circumscription of the *Meliaceae*, its subfamilies, tribes, and genera, but previous accounts are far from unanimous so that at the beginning of this investigation there were a number of taxonomic problems urgently requiring attention. In addition, since the publication of the latest comprehensive treatment (Harms, 1940), eight new genera have been described, and their positions within the family needed to be established.

With the aid of herbarium specimens borrowed from the major herbaria of the world and with many collections gathered during our own extensive fieldwork in tropical America, Africa, and South East Asia, we have been able to assemble complete material of some 300 species of *Meliaceae*, about 200 of which have correlated wood samples. Our taxonomic conclusions are based largely on the detailed examination of this morphologically complete material. Although this certainly represents more material than previous workers have used, it still only covers about half the total number of species suspected to occur in the family. We have also examined incomplete material of a further 50 species and this has not revealed any characters which extend the limits of variation recorded for each genus.

We have examined the pollen of 200 species, and as a result of this investigation have found that the characters of the pollen grain are chiefly of value in circumscribing the family, and in one case (*Turraeeae)* in delimiting a tribe, but for the most part, the differences between genera are very slight.

Our investigations of the secondary xylem revealed that it is of greater taxonomic value than the pollen grain. The secondary xylem is useful in delimiting the family and subfamilies, and to a lesser extent the tribes, and in a number of cases the genera. Separate chapters have already been devoted to a general discussion of pollen and wood structure, but further information concerning their use in solving the major taxonomic problems is given below.

By means of a critical study of all the data assembled, it has been possible to define the genera of the *Meliaceae* more clearly than before, and to produce improved generic keys. It is necessary to circumscribe the family, subfamilies, and tribes somewhat differently from Harms. In Part II, the gross morphology, pollen grain, and wood anatomy of the family are fully described. Keys to and formal descriptions of the genera are given with detailed discussions on the relationships, where relevant. In Part II most of our views on the taxonomy of the genera are recorded, but the more important taxonomic decisions are discussed at greater length below.

I. THE NUMBER OF FAMILIES INVOLVED

Should the *Meliaceae* be split into two or three separate families? A. H. L. de Jussieu (1830) recognizes *Meliaceae* and *Cedrelaceae*, and Harms (1940), although treating the *Meliaceae* as a single family, suggests that his three subfamilies, *Cedreloideae*, *Swietenioideae*, and *Melioideae* could equally well be treated as separate families.

There is little morphological, anatomical, or palynological evidence to support this suggestion. From the discussion below, it can be seen that the best division of the *Meliaceae* is into four subfamilies, but these do not deserve family rank. The *Meliaceae* fall naturally into two large subfamilies (*Melioideae* and *Swietenioideae)* which are clearly distinguished by several well-correlated morphological and anatomical characters, but the limits between these two groups are confused by the Malagasy genera *Quivisianthe* and *Capu-*

ronianthus. These share some of the characteristics of both *Melioideae* and *Swietenioideae,* but are nevertheless sufficiently isolated from them and from each other to be given subfamily rank *(Quivisianthoideae, Capuronianthoideae).* Further discussion of these two remarkable genera is given below.

2. CIRCUMSCRIPTION OF THE FAMILY

a. The taxonomic position of Flindersia and Chloroxylon

Was Harms (1896, 1940) correct in excluding them from the *Meliaceae,* where they had been frequently included by previous authors (De Candolle, 1824; Hooker *f.*, 1862; C. de Candolle, 1878)? Although both these genera lack some of the important characters of the *Meliaceae,* e.g. the staminal tube, they do share other morphological and anatomical features with both *Meliaceae* and *Rutaceae.* Engler (1877) referred them to the *Rutaceae* on account of the presence of schizogenous secretory cavities in the leaf. Secretory cells, which are found in the leaf tissue of all *Meliaceae,* are absent from the leaf of *Flindersia* and *Chloroxylon,* but present in the cortical tissue of the axis, so in this respect they appear to be intermediate between the *Meliaceae* and *Rutaceae.* Morphological evidence is conflicting. Both genera lack the characteristic staminal tube of the *Meliaceae,* and the filaments are not flattened at the base. The leaves of *Flindersia* are frequently opposite, a character hardly ever found in the *Meliaceae.* On the other hand, *Flindersia* has a septifragal capsule like that of many *Swietenioideae,* although it is warty or prickly, a feature never found in this subfamily.

The wood structure of *Flindersia* has been studied in great detail by Harrar (1937) who concluded that although it was more closely related to the *Rutaceae* than to the *Meliaceae,* the anatomical evidence did not point clearly to either, as it possesses some characters of both families. The colour and scent of the wood is typical of *Rutaceae* except for *F. brayleana* F. Muell. which resembles that of the *Meliaceae.* The large, multiseriate, homogeneous rays in combination with non-septate fibres are known in only four genera of *Meliaceae,* whereas they are frequently present in the *Rutaceae.* In contrast, *F. collina* F. M. Bail. has heterogeneous rays with crystals in the marginal cells which are present in all *Meliaceae* subfamily *Swietenioideae.* Harrar therefore favoured the formation of a distinct family, the *Flindersiaceae.* C. T. White (1931), who was familiar with the morphological features of the genus, had already reached a similar conclusion.

The secondary xylem of *Chloroxylon* also possesses features of both *Meliaceae* and *Rutaceae.* The individual characters of the wood of *Chloroxylon* are frequently found in the *Meliaceae,* but the combination of vessel type and pattern, storied rays, non-septate fibres, and sparse paratracheal parenchyma are rarely seen. The secondary xylem of *Pseudocedrela kotschyi* (Schweinf.) Harms is the most similar, differing only in the larger vessels and partially septate fibres. In the *Rutaceae, Esenbeckia leiocarpa* Engl. is very close, differing only in the absence of terminal banded parenchyma and chambered crystalliferous parenchyma. After examining the wood of many genera of the *Rutaceae,* we conclude that the features of *Chloroxylon* are more commonly found in that family than in the *Meliaceae,* but there is not sufficient evidence either way to place this genus using characters of the secondary xylem alone.

Erdtman (1952, 1966) noted that the pollen grains of *Flindersia* and *Chloroxylon* are similar to those of the *Rutaceae.* Our observations confirm this opinion, as no species of *Meliaceae* seen by us has 3-colporate grains in combination with a rather small polar area and a reticulate or prominently scabrate exine.

According to Price (1952) and Ritchie et al. (1963), there is strong phytochemical evidence for placing *Flindersia* and *Chloroxylon* in the *Rutaceae*. Both contain coumarin and the alkaloids known as furoquinolines which are absent from the *Meliaceae*. In the light of this evidence, Hartley in his recent monograph (1969) had no hesitation in placing *Flindersia* in the *Rutaceae*.

The above facts confirm that Harms was correct in excluding these two genera from the *Meliaceae*.

b. The taxonomic position of Ptaeroxylon and Cedrelopsis

Ptaeroxylon has usually been placed in either the *Sapindaceae* or *Meliaceae*. As long ago as 1860 Sonder, in Flora Capensis, gave it family rank and placed it after the *Sapindaceae*, though expressing doubt as to its true affinity. Hooker (1862) and many subsequent authors, have put it in the *Sapindaceae*. Radlkofer (1890) transferred it to the *Meliaceae*, where Harms (1896, 1940) allowed it to remain. Mauritzon (1936) has shown that the ovule structure of *Ptaeroxylon* is very similar to that of *Sapindus*, while Jenkin (1961) found that the secondary xylem of *Ptaeroxylon* was closely similar to that of *Amyris (Rutaceae)*. *Ptaeroxylon* lacks the staminal tube of the *Meliaceae* and the filaments are not flattened at the base; the capsule does contain a central columella but this differs significantly from that of the capsule in *Cedrela* and genera of the *Swietenioideae*. It does, however, possess some of the features of the *Meliaceae*, e.g. the intra-staminal disk. Recently Leroy (1959, 1960a) has discussed the relationships of *Ptaeroxylon* and *Cedrelopsis* and concluded that they should constitute a separate family, close to the *Sapindaceae*.

From our own observations we conclude that *Ptaeroxylon* has a combination of anatomical features unknown in the *Meliaceae*. These are minute vessels in long radial multiples; short, uniseriate, homogeneous rays; presence of diffuse crystalliferous parenchyma and apotracheal terminal bands only; fibres with few septa. Examination of the entire collection of slides of the *Sapindaceae* and *Rutaceae* at the Department of Forestry, University of Oxford, indicates that, although there is a close similarity between the secondary xylem of *Ptaeroxylon* and that of *Amyris*, the features shown by these two genera are unusual in the *Rutaceae*. On the other hand, although the exact combination of characters could not be found in genera of the *Sapindaceae*, the wood of *Ptaeroxylon* has many features in common with this family. Uniseriate homogenous rays, partially septate fibres, and very scarce paratracheal parenchyma are all frequently found in the *Sapindaceae*.

The Malagasy genus *Cedrelopsis* is closely related to *Ptaeroxylon* and very similar to it in morphology and in the structure of the secondary xylem. Leroy (1960b) has shown that there are greater differences between the wood of different species of *Cedrelopsis* than between *Cedrelopsis* and *Ptaeroxylon*.

Ptaeroxylon and *Cedrelopsis* also have very similar pollen morphology, the grains of both having a reticulate exine quite unlike that of any known Meliaceous pollen grain, but similar to that of some *Rutaceae* (e.g. *Calodendrum*).

This shows that although *Ptaeroxylon* and *Cedrelopsis* definitely do not belong in the *Meliaceae*, there is not sufficient evidence for placing them in either the *Sapindaceae* or *Rutaceae*. The most satisfactory solution is therefore to treat them as a separate family, the *Ptaeroxylaceae*. White and Styles (1963), who give a full account of the genus *Ptaeroxylon*, have confirmed Leroy's views on this.

c. The taxonomic position of Nymania

Nymania had formerly been placed in several other families, especially the *Sapindaceae*, because its external appearance is so unlike that of most other *Meliaceae*. The leaves are linear and sclerophyllous, the fruit is an inflated capsule, and the filaments are fused at the base and scarcely flattened. A detailed examination of its morphology, wood anatomy, and especially pollen, shows that it is closely related to *Turraea* and *Calodecaryia* in the subfamily *Melioideae*. A full discussion of its relationships is given after the generic description in Part II.

d. The taxonomic position of Pterorhachis

This genus is also superficially rather distinct from all other *Meliaceae* and resembles many *Sapindaceae*. The pollen structure had not been previously studied, but Heimsch (1942), who examined the secondary xylem, included it in the *Meliaceae* without commenting on its relationships. Any resemblance between *Pterorhachis* and the *Sapindaceae* is, however, entirely superficial, and a critical examination of morphology, wood, and pollen, shows that it definitely belongs in the *Meliaceae* and is closely related to *Trichilia*.

3. THE NUMBER AND CIRCUMSCRIPTION OF THE SUBFAMILIES

De Candolle (1824) divides the *Meliaceae* into three tribes: *Melieae*, *Trichilieae*, and *Cedreleae*, the latter containing *Cedrela*, *Swietenia*, and *Carapa* (including *Xylocarpus*). The younger Hooker (1862) divides the family into four tribes: *Melieae*, *Trichilieae* which contains *Carapa* (including *Xylocarpus*), *Swietenieae*, and *Cedreleae* containing *Cedrela* (including *Toona*). C. de Candolle (1878) follows Hooker's system but removes *Carapa* (including *Xylocarpus*) and places it in the *Swietenieae*. Kribs (1930), in an investigation of the wood structure, concludes that the *Meliaceae* should be divided into three subfamilies: the *Swietenioideae*, including *Carapa*, *Xylocarpus*, *Cedrela*, and *Toona*; the *Lovoinoideae*, including *Lovoa*; the *Melioideae*. Harms (1896, 1940) splits the *Meliaceae* into three subfamilies:

1) *Cedreloideae* (including *Cedrela* and *Toona*);
2) *Swietenioideae;*
3) *Melioideae* (including *Carapa* and *Xylocarpus*).

Clearly, the correct circumscription of these groups of genera is uncertain, and in particular there is great divergence of opinion as to the relationships of *Cedrela* and *Toona*, and *Carapa* and *Xylocarpus* with the rest of the family. Their status as separate genera is discussed in Part II.

a. The relationships of Cedrela and Toona

When *Ptaeroxylon* and *Cedrelopsis* are excluded from the family, Harms' first subfamily, the *Cedreloideae*, contains only *Cedrela* and *Toona*, and these differ from the genera of Harms' second subfamily, the *Swietenioideae*, in only one feature: their filaments are free, whereas those of the *Swietenioideae* are united. The other important morphological characters of the *Swietenioideae*, the multiovulate loculi and septifragal capsule, are also shared by *Cedrela* and *Toona*. The wood structure of the *Swietenioideae* is homogeneous, and that of *Cedrela* and *Toona* agrees with it in all important respects. It is characterized by broad heterogeneous rays, large crystals in the marginal cells of the rays, by the absence of crystals in chambered parenchyma cells, and by sparse paratracheal parenchyma. The pollen grains of the *Swietenioideae* are almost uniform, being 4-colporate, prolate, with a smooth exine. Those of *Cedrela* and *Toona* are identical with these in all important respects.

In our opinion the single morphological difference of *Cedrela* and *Toona* from the *Swietenioideae* does not warrant their separation from this subfamily, and they would be better included in it. The morphological difference between *Cedrela* and *Toona* and the *Swietenioideae*, the degree of union of the filaments, is variable within large genera of the family, e.g. *Trichilia* and *Entandrophragma*, but it must be pointed out that the filaments of *Cedrela* and *Toona* are in fact not flattened, and are fused to the disk in a manner not occurring elsewhere in the family.

b. The relationships of Carapa and Xylocarpus

Harms places *Carapa* and *Xylocarpus* in the *Melioideae* because they lack the dry winged seeds of the *Swietenioideae* and because the number of ovules in the loculus of *Carapa* is fewer than that of other genera of the *Swietenioideae*, though in general always more than two.

In our opinion Harms was mistaken in placing *Carapa* and *Xylocarpus* in *Melioideae*. By doing so, the distinction between two well-defined groups becomes confused. Apart from the seed character, *Carapa* and *Xylocarpus* agree in all important respects with *Swietenioideae*. The loculi are normally multiovulate (Harms did not realize that the flowers of these genera are unisexual and possibly based some of his observations on the 'ovary' of male flowers, which often contain fewer, abortive, ovules than the female). Furthermore, the fruit is a septifragal capsule with an, albeit rudimentary, columella. *Carapa* and *Xylocarpus* possess all the characteristic secondary xylem features as well as those of the pollen grain, of the *Swietenioideae*.

There are also strong biological grounds for including these two genera in *Swietenioideae*. The shoot borer (*Hypsipyla* spp.) which attacks most genera in this subfamily also attacks *Xylocarpus* and *Carapa*. This suggests that the group shares a group of similar biochemical compounds to which the insect is attracted. Genera in *Melioideae* are on the other hand not attacked.

These facts show clearly that *Carapa* and *Xylocarpus* were wrongly placed in the *Melioideae* and should be transferred to the *Swietenioideae*. With *Cedrela*, *Toona*, *Carapa*, and *Xylocarpus* in the *Swietenioideae*, the distinctions between the two major subfamilies become much clearer. They are summarized later in Part II.

c. The position of Capuronianthus

Leroy (1958a) who described the genus, placed it in a new subfamily the *Carapoideae* together with *Carapa* and *Xylocarpus*. Although admitting that *Capuronianthus* is extremely distinct from all known genera of *Meliaceae*, he considered it possesses all the essential characteristics of the *Carapa-Xylocarpus* pair. Minfray (1963, 1963a) supported this arrangement on cytological grounds, because both *Carapa* and *Capuronianthus* possess the same chromosome number, $2n = 58$.

We believe, however, that there are strong reasons against a) placing *Capuronianthus* with *Carapa* and *Xylocarpus* in a separate subfamily and b) placing *Capuronianthus* in the *Swietenioideae*.

We have shown above that there is overwhelming evidence, both morphological and anatomical, for including *Carapa* and *Xylocarpus* in the *Swietenioideae*. The arguments against putting *Capuronianthus* in the *Swietenioideae* are equally strong. It shares with *Carapa* and *Xylocarpus* only two characters of any significance, viz. septifragal dehiscence of the capsule and the seed with a corky sarcotesta *(Xylocarpus)*. It differs from them both in the following important characters: buds naked (protected by scales in *Carapa, Xylocarpus,* and all *Swietenioideae*); leaves decussate (spirally arranged in *Carapa, Xylocarpus,* and all *Swietenioideae*); loculi biovulate with one or two vestigial ovules (usually multiovulate in *Carapa, Xylocarpus,* and all other *Swietenioideae*); style-head capitate (discoid in *Carapa, Xylocarpus,* and nearly all *Swietenioideae*). The cytological data is inconclusive *(Capuronianthus* and *Carapa* $2n=58$; *Xylocarpus* $2n=52$). As Styles and Vosa (1971) point out, the *Meliaceae* has such a wide range of chromosome numbers that it is premature at this stage to draw any taxonomic conclusions from chromosome cytology.

Whilst acknowledging the distant relationship of *Capuronianthus* with *Carapa* and *Xylocarpus,* we consider that the only acceptable solution is to place this very distinct genus in a subfamily of its own, the *Capuronianthoideae*. This procedure emphasizes its great isolation and also preserves the unity of the *Swietenioideae*.

d. The position of Quivisianthe

Our knowledge of this exceptionally interesting genus from Madagascar is at present limited to a few herbarium specimens. In its floral structure it belongs in the *Melioideae* near *Trichilia* (where it was retained by Harms, 1940) or *Ekebergia*, though the androecium of five stamens is rarely found. even in the *Trichilieae*. The fruit structure is, however, quite unique in the family, a dry loculicidal capsule, containing dry winged seeds. These distinctive fruit and seed characters, which have already been shown to be important at the subfamily level, indicate the great isolation and antiquity of *Quivisianthe* and we have no hesitation at this stage in placing this genus in its own subfamily, the *Quivisianthoideae*. Further anatomical, cytological, or chemical data may shed light on its relationships but on the basis of information available at present it does not appear to have any close relations in the family.

4. THE NUMBER AND CONTENT OF THE TRIBES IN THE SUBFAMILY MELIOIDEAE

In previous classifications there is a tendency for certain related genera always to occur close together, but, nevertheless, there is appreciable divergence of opinion as to the number of tribes and their exact content. In Harms' latest treatment of the family, his arrangement of the *Melioideae* is based, for the most part, on the progression of a few characters which he considered of great evolutionary importance: a) the position of insertion of the anthers in the staminal tube; b) the presence and form of the intra-staminal disk; c) the presence or absence of endosperm. Harms states that anthers inserted at the ends of the filaments or on the margin of the staminal tube, represents a primitive condition and that insertion within the throat of the tube is more advanced. Similarly he recognizes an evolutionary series in the form of the disk, from the small annular structure surrounding the base of the ovary (primitive) to a shallow cyathiform disk, and finally the most advanced form is the long tubular envelope surrounding the ovary and base of the style. Harms' arrangement of the tribe *Trichilieae* is partly based on these two series.

The character states of anther insertion and disk structure may well represent evolutionary series, but it appears that they have arisen independently several times in the *Melioideae* and they are not always correlated with other progressive trends. Because of the undue weighting of these characters, Harms' tribe *Turraeeae* contains genera that do not belong there (e.g. *Cipadessa*) and his subtribes of the *Trichilieae* contain artificial groups of genera. In order to obtain an improved grouping of these genera, we have subordinated the supposed evolutionary significance of individual characters in favour of a grouping based on the correlations between the maximum number of characters of use at this level of classification and on the detection of discontinuities in the variation pattern of these characters. By basing the classification on a large number of characters, the most natural grouping of the genera is obtained and artificial assemblages resulting from the weighting of a few characters are avoided. The major changes from Harms' arrangement of the *Melioideae* are detailed below.

Tribe 1. *Carapeae.* This is excluded from the *Melioideae* for the reasons stated above.

Tribe 2. *Turraeeae.* As circumscribed by Harms this is heterogeneous because of the inclusion of *Cipadessa* and *Pterorhachis.* The former was included because of its endospermous seed, and the latter presumably because of the winged rhachis which it shares with *Naregamia.* In all other important morphological, anatomical, and palynological characters these genera are similar to various genera in the *Trichilieae,* where we have placed them.

Tribe 5. *Trichilieae.* Harms divided this into four subtribes, the contents of which are very heterogeneous.

Our new grouping of the genera, based on the principles outlined above, is summarized here. Subfamily *Melioideae*

Tribe 1. *Turraeeae: Munronia, Naregamia, Turraea, Humbertioturraea, Calodecaryia, Nymania.*

Tribe 2. *Melieae: Melia, Azadirachta.*

Tribe 3. *Vavaeeae: Vavaea.*

Tribe 4. *Trichilieae: Trichilia, Pseudobersama, Pterorhachis, Walsura, Lepidotrichilia, Malleastrum, Ekebergia, Astrotrichilia, Owenia, Cipadessa.*

Tribe 5. *Aglaieae: Aglaia, Lansium, Aphanamixis, Reinwardtiodendron, Sphaerosacme.*

Tribe 6. *Guareeae: Heckeldora, Cabralea, Ruagea, Turraeanthus, Guarea, Chisocheton, Megaphyllaea, Synoum, Anthocarapa, Pseudocarapa, Dysoxylum.*

Tribe 7. *Sandoriceae: Sandoricum.*

The first three tribes correspond fairly well with those of Harms, except that *Cipadessa* and *Pterorhachis* have been removed from the *Turraeeae,* but his tribe *Trichilieae* has been subdivided into four groups, each of which is given tribal rank. Each of the above seven tribes contains a natural assemblage of genera, but the limits between the *Trichilieae, Aglaieae,* and *Guareeae* can only be defined by reference to a number of overlapping morphological, anatomical, and palynological characters. Diagnoses of each tribe are given in Part II.

5. DELIMITATION OF THE GENERA AND THEIR RELATIONSHIPS

An examination of Harms' generic key reveals that less than half the genera in the *Melioideae* appear to be distinct on the basis of the characters used. In some cases the genera are keyed out on overlapping characters so that discontinuities in the variation pattern are not revealed. Sometimes there is a verbal distinction expressed but no corresponding morphological distinction. Also, a number of genera are keyed out by reference to their geographical distribution, and Harms has not provided evidence that they are morphologically distinct.

Within recent years there has been considerable divergence of opinion as to the status of a number of entities in the family. For instance, *Heynea, Amoora, Clemensia, Didymocheton,* and *Epicharis* have been treated as genera by some workers and as taxa of lower rank by others.

Subsequent work to that of Harms has shown that some genera, e.g. *Trichilia,* are heterogeneous, partly because a number of species formerly included were known only from imperfect material. Leroy (1958b) raised the section *Lepidotrichilia* to generic rank and combined two others, *Astrotrichilia* and *Peltotrichilia,* to form the genus *Astrotrichilia.*

Chapter 2 (Morphology of the Group) shows that there is a very wide range of morphological variation within the family, especially in the subfamily *Melioideae.* Many of the structures vary independently and because of this, well-defined sets of characters which can be used to delimit genera clearly, are difficult to find. The variation appears to be so continuous and complicated that on superficial acquaintance it might be argued that well-defined genera scarcely exist, and that the majority of species should be merged into one huge genus. If this were done, the resulting entity would contain more variation than has ever before been allowed to exist in a single genus. At the other extreme, it would be possible to create a very large number of homogeneous genera, which are constant in most, if not all, important morphological characters. If this were done, the resulting number of genera would be enormous, and a large number of unacceptable name changes would be necessary. If such a procedure is adopted, problems arise as to which characters should be used to delimit the genera. Different people would choose different characters and instability would inevitably result as in, for instance, the *Sapotaceae.* It is both desirable and possible to take the middle course, but in some cases generic delimitation presents certain difficulties.

A few genera are isolated *(Vavaea, Sandoricum),* or form an isolated pair *(Melia* and *Azadirachta).* The other genera of the *Melioideae* fall into four tribes, *Turraeeae, Trichilieae, Aglaieae,* and *Guareeae,* which all show a similar variation pattern. The majority of species in each tribe fall into a single large genus (except the *Guareeae,* where there are three large genera) which, although it contains much variation, is still definable and because of its nature cannot be satisfactorily split. The remaining species of each tribe form a number of small satellite genera which are closely related to their respective large genera. In the *Turraeeae, Turraea* contains the majority of species and *Humbertioturraea, Calodecaryia,* and *Nymania* are small, closely related genera. In the *Trichilieae, Trichilia* accounts for the majority of species and *Pterorhachis, Pseudobersama, Lepidotrichilia, Astrotrichilia, Walsura, Malleastrum,* and *Ekebergia* are closely related satellites. Generally, the large genus possesses one or more constant features (e.g. the stellate or peltate indumentum of *Aglaia)* which is lacking in its satellite genera, and in addition, the satellites possess a number of differential characters not present in the large genus.

Most of the genera we recognize differ from all others in the family in at least two characters common to all species. In other cases there is a single feature so unusual that it can justifiably be used as a generic character, e.g. the biseriate corolla of *Megaphyllaea.* In such cases the genera defined in this way are not artificial, since the species they contain resemble each other more than they do any species in any other genus.

There are a small number of genera more difficult to define. This is because, although any species of a particular genus may differ from any species of another genus in several characters, none of the defining characters are absolutely diagnostic in the sense of White (1962), so that the genera are recognized on a number of differential characters only.

In some cases, as in separating *Chisocheton* and *Guarea,* only the combined variation of several differential characters shows a discontinuity and can therefore be used to define these genera.

Applying these principles we have found it necessary to modify the treatment of Harms as follows:

(1) In the *Trichilieae.* Although we have some strong reservations, we agree with Bentvelzen (1962) that, on the basis of evidence presently available, *Heynea* should be reduced to *Trichilia* (see Part II, under the relationships of *Trichilia*). We have confirmed the conclusions reached by other authors that five of the sections of Harms' *Trichilia* should be removed from the genus. Although Hofmeyer (1925) transferred *T. pterophylla* C. DC., the type species of section *Pterotrichilia*, to *Ekebergia*, Harms (1940) allowed it to remain in *Trichilia*. The present work has shown this to be untenable.

We consider that Leroy (1958b) was fully justified in raising the section *Lepidotrichilia* to generic rank, and also in accommodating Harms' section *Pterotorhachis* within his recently-described genus *Malleastrum* (1964). Leroy (1958c) was also right to combine Harms' sections *Astrotrichilia* and *Peltotrichilia* to form the new genus *Astrotrichilia.*

(2) In the *Aglaieae.*We consider that *Amoora* should be reduced to *Aglaia.* A species provisionally called *Aglaia decandra* by Wallich, which is included under *Lansium* by Harms, should be raised to generic rank and be known as *Sphaerosacme.*

(3) In the *Guareeae.* Harms' section *Heckeldora* of *Guarea* should be reinstated as a genus, as is done by Keay (1958). On the other hand, we have failed to find evidence which would justify maintaining *Leplaea* and *Urbanoguarea* as genera, as is done by Harms. They should be reduced to *Guarea.*

Airy-Shaw (1937) was justified in reducing *Clemensia* to *Chisocheton.* Harms maintains the genus *Rhetinosperma* provisionally near *Chisocheton* and *Dysoxylum.* It has since (L. S. Smith, 1959) been reduced to *Chisocheton*, and although we have not had an opportunity of examining any material of this species, from the description of the plant it clearly belongs in this genus.

Harms (1940) maintains *Didymocheton* and *Epicharis* but we consider it is more satisfactory to include them under *Dysoxylum.*

In Part II the reasons for these changes are given in the discussion of the relationships of each genus.

PART II. THE CONSPECTUS

MELIACEAE Vent.

Meliaceae Vent., Tab. Règ. Vég. 3 (1799) 159—166; DC., Prod. 1 (1824) 619—626; A. Juss., Mém. Mus. Hist. Nat. Par. 19 (?1830) 153—304; M. J. Roem., Synops. Monogr. Hesperid. 1 (1846) 76—151; Hook. *f.* in Benth. & Hook., Gen. Plant. 1 (1862) 327—340; Miq., Ann. Mus. Bot. Lugd. Bat. 4 (1868) 1—64; C. DC., in A. & C. DC., Monog. Phan. 1 (1878) 399—758; Harms, in Engl. & Prantl, Nat. Pflanzenfam. 3, 4 (1896) 258—308; ed. 2, 19 bI (1940) 1—172; Pennington, A taxonomic study of the *Meliaceae*; unpublished D. Phil. thesis pp. 234. Bodleian Library, Oxford, (1965).

Trees, treelets or shrubs, rarely with sympodial ('*Terminalia*') branching, rarely herbs with woody rootstocks. Bark sometimes with a milky exudate. Buds protected by a cluster of scale-leaves or naked. *Leaves* spirally arranged, very rarely decussate, usually pinnate, with or without a terminal leaflet, sometimes with a dormant terminal bud, less frequently simple, rarely trifoliolate or unifoliolate, very rarely bipinnate. Leaflets usually entire, rarely lobed, dentate, serrate, or crenate. *Indumentum* usually simple, less frequently of bifid or stellate hairs or of peltate scales. *Inflorescence* usually axillary, less frequently terminal, rarely ramiflorous, cauliflorous, or epiphyllous, usually paniculate with cymose branchlets (thyrsoid), less frequently racemose, fasciculate, or spicate, or flowers in pairs or solitary. *Flowers* bisexual or unisexual (plants monoecious, dioecious, or polygamous);

rudiments of opposite sex usually well-developed in unisexual flowers. *Calyx* usually shallowly or deeply (2)3—5(7)—lobed, less frequently truncate or with free sepals, rarely closed in bud and circumscissile at the base; aestivation open or imbricate. *Petals* 3—6(14), free or less frequently united below, often partially fused to the staminal tube; aestivation imbricate or contorted, less frequently valvate. *Filaments* rarely completely free, usually partly or completely united to form a staminal tube, with or without appendages. Staminal tube 0.05—14 cm long, globose, urceolate, campanulate, cyathiform, or cylindrical and then sometimes curved or inflated distally, rarely ribbed; throat open or constricted; margin entire, crenate, lobed, or toothed, or bearing appendages; appendages very variable in shape, free or partly or completely united, as many as or twice as many as, rarely 3(—10) times as many as, the anthers. Anthers (3)5—10(23), hairy or glabrous, sometimes locellate, inserted apically on the filaments or on the margin of the staminal tube, or within the throat of the staminal tube and partially or completely included, usually alternate with the appendages, rarely opposite them; usually in a single whorl, rarely in two alternating whorls; connective sometimes produced to form a short or long appendage. Antherodes in ♀ flowers smaller, not dehiscing or producing pollen. *Disk* intrastaminal, stipitate, patelliform, cyathiform, tubular, or absent, free from or partly or completely fused to the base of the staminal tube or ovary. *Ovary* (1)2—6(20)—locular; loculi uniovulate, biovulate, or multiovulate. Placentation axile or very rarely parietal. Ovules collateral, superposed, or biseriate. Style-head capitate or discoid, less frequently conical, pileate, or deeply lobed, or forming an ovoid, globose, fusiform, cylindrical, conical, or obconical *receptaculum pollinis*. Pistillode in ♂ flowers narrower with a longer, more slender style, less glandular style head, and very small abortive ovules. *Fruit* a loculicidal or septifragal capsule, a berry, drupe, or very rarely a nut. *Seed* either winged and then usually attached to a large woody columella, or unwinged and then usually with a fleshy arillode or sarcotesta, rarely with a corky or woody sarcotesta, or exarillodiate and without a sarcotesta; seed sometimes endospermous, usually exendospermous. *Embryo* with plano-convex or flat, collateral, superposed, or rarely oblique cotyledons; radicle usually superior, less frequently abaxial, rarely adaxial; included, or extending to the surface, or long exserted.

Germination[1]: Cotyledons emergent (phanerocotylar) or not (cryptocotylar), sometimes becoming green and photosynthetic. Hypocotyl elongating or not, sometimes swollen. Scale-leaves (cataphylls) sometimes produced before the first foliage leaves (eophylls). First foliage leaves opposite or spirally arranged, simple, pinnatisect, trifoliolate, or imparipinnate, the margin entire, toothed, or deeply lobed. Rhachis often winged.

Pollen: Pollen grains nearly always shed singly, very rarely in rhomboidal tetrads. Grains oblate-spheroidal, spheroidal, prolate-spheroidal, subprolate, or prolate, 10—80 (130) μm, amb rounded or angular. Apocolpium small, medium, or large. Colpi sometimes shortly bifurcate. Ora circular, lalongate, or rarely lolongate, sometimes crassimarginate, very rarely zonorate. Exine usually smooth or minutely scabrous, less frequently verrucose, rugulose, or reticulate, usually thickened at the apertures.

Secondary Xylem: The secondary xylem is usually diffuse porous, rarely ring porous. Silica deposits are frequent in a small number of genera and occasional elsewhere. *Vessels* most frequently solitary and in radial groups of up to 10(—15), occasionally with tangential or oblique arrangement; pore clusters rare, 5—40(110) per sq mm, tangential diameter

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[1] In the following description of the mode of germination and morphology of the seedlings we are following the terminology in Duke (1965).

(20) 60—160(320) μm; intervascular pitting alternate, sometimes with coalescent apertures; pits 2.25—7.5 μm diameter; vessel to ray pitting similar; vessel perforations exclusively simple; spiral thickening rarely present; tyloses absent; gum usually present. *Ray tissue* usually heterogeneous Kribs Type 3, or homogeneous Kribs Type 1, or uniseriate-homogeneous or -heterogeneous, less frequently heterogeneous Kribs Type 1 or 2, or homogeneous Kribs Type 2; rays 1—6(7)-seriate, 15—50(100) cells high; the heterocellular with 1(6) marginal rows; homocellular rays composed entirely of square or upright cells occasionally present. Crystals in marginal ray cells present or absent. Rays sometimes storied. *Fibres* septate or non-septate; fibre-pits predominantly on the radial walls, usually simple or with narrow borders, occasionally with conspicuous borders; walls thick to very thick; lumen open or plugged with gum. *Parenchyma*. Paratracheal: varying from sparcely scattered cells to vasicentric, aliform, confluent, and banded in various combinations; bands 1—7(11) cells wide, (1)3—7(13) per mm, usually containing crystals in chambered cells. Apotracheal: terminal bands present or absent, with or without crystals in chambered cells. Diffuse parenchyma occasionally present, usually chambered and containing crystals.

A medium-sized family of woody plants in the tropics and subtropics of both hemispheres, comprising 51 genera and probably no more than 550 species.

FAMILY — MELIACEAE

SUBFAMILY I MELIOIDEAE

Tribe 1 TURRAEEAE
Munronia, Naregamia, Turraea, Humbertioturraea, Calodecaryia, Nymania
Tribe 2 MELIEAE
Melia, Azadirachta
Tribe 3 VAVAEEAE
Vavaea
Tribe 4 TRICHILIEAE
Trichilia, Pseudobersama, Pterorhachis, Walsura, Lepidotrichilia, Malleastrum, Ekebergia, Astrotrichilia, Owenia, Cipadessa
Tribe 5 AGLAIEAE
Aglaia, Lansium, Aphanamixis, Reinwardtiodendron, Sphaerosacme
Tribe 6 GUAREEAE
Heckeldora, Cabralea, Ruagea, Turraeanthus, Guarea, Chisocheton, Megaphyllaea, Synoum, Anthocarapa, Pseudocarapa, Dysoxylum
Tribe 7 SANDORICEAE
Sandoricum

SUBFAMILY II QUIVISIANTHOIDEAE

Quivisianthe

SUBFAMILY III CAPURONIANTHOIDEAE

Capuronianthus

SUBFAMILY IV SWIETENIOIDEAE

Tribe 1 CEDRELEAE
Cedrela, Toona

Tribe 2 SWIETENIEAE
Khaya, Neobeguea, Soymida, Entandrophragma, Chukrasia, Pseudocedrela, Schmardaea, Swietenia, Lovoa
Tribe 3 XYLOCARPEAE
Carapa, Xylocarpus

SUBFAMILY I. MELIOIDEAE

Buds naked. Leaves nearly always spirally arranged. Plants dioecious, or flowers hermaphrodite, or polygamous. Loculi uni- or bi-ovulate, or bi-ovulate with a third vestigial ovule, very rarely multi-ovulate; ovules collateral or superposed. Style-head variable. Fruit a fleshy or leathery loculicidal capsule, berry, drupe, or very rarely a nut. Seed never winged, never with a woody or corky testa, usually with a fleshy arillode or sarcotesta. Endosperm present or absent.

Secondary Xylem. Rays usually 1 or 2-seriate, rarely broader, homogeneous or heterogeneous. Crystals never present in marginal ray cells, usually present in wood parenchyma. Paratracheal parenchyma often abundant (confluent or banded).

Tribe 1. TURRAEEAE[1]

Leaves usually simple. Indumentum of simple or stellate hairs. Flowers hermaphrodite Staminal tube nearly always cylindrical, usually complete, or less frequently, filaments connate in the upper or lower half only. Anthers usually inserted on the margin of the staminal tube or apically on the filaments. Disk, when present, usually poorly developed, usually annular, patelliform and fused to the base of the staminal tube. Style-head often characteristically modified to form a *receptaculum pollinis*. Fruit nearly always a capsule. Seed usually with an adaxial fleshy arillode; endospermous.
Cotyledons flat, collateral; radicle superior, exserted.

Pollen. Oblate to spheroidal; 3(5)-colporate; exine usually verrucose or rugulose.

Secondary xylem. Fibres non-septate.

1. Indumentum a mixture of simple and stellate or bifid hairs; petals fused to staminal tube below, rarely becoming free; disk, when present, tubular; sarcotesta adaxial, membraneous, swollen and hollow . . . . 1. *Munronia*
1a. Indumentum of simple hairs; petals free from staminal tube; disk, when present, never tubular; seed usually with a fleshy arillode; sarcotesta, when present, never membraneous.
    2. Filaments completely united or partly free at the apex for not more than one third of their length.
        3. Fruit a capsule.
            4. Leaves 3-foliolate, leaflets shallowly lobed or entire, rhachis with a conspicuous wing to the base; staminal tube without appendages; style-head sometimes modified to form a *receptaculum pollinis*; seed curved, truncate at base and apex, testa with irregular transverse ridges, puberulent; arillode fleshy, free except for attachment along raphe 2. *Naregamia*

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[1] We gratefully acknowledge the assistance of Prof. J. F. Leroy, Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris, who has provided us with much material and information on the new Malagasy genera in this and other tribes in the family.

4a. Leaves simple (or in one species compound, but then leaflets deeply lobed to partite, rhachis unwinged at the base, and staminal tube with appendages); staminal tube appendages present or absent; style-head usually modified to form a *receptaculum pollinis*; seeds 0.2—0.8 cm long, not truncate at base and apex, nearly always smooth, glabrous; arillode fleshy, usually free except for a narrow attachment along adaxial surface below micropyle: cotyledons nearly always narrow; radicle long exserted . . . . 3. *Turraea*

3a. Fruit indehiscent; leaves simple; staminal tube complete, with appendages; fruit large, seeds 1.3—1.5 cm long; sarcotesta adaxial; hilum large; cotyledons broad; radicle very short, slightly exserted . . . . 4. *Humbertioturraea*

2a. Filaments usually united only at the base, always free for more than half of their length.

5. Capsule not inflated, not deeply 4-lobed; anthers basifixed, not versatile; seed glabrous, smooth . . . . 5. *Calodecaryia*

5a. Capsule inflated, deeply 4-lobed; anthers dorsifixed, versatile; seed puberulent, minutely verrucose . . . . 6. *Nymania*

1. MUNRONIA

Munronia Wight, Illustr. 1 (1831) 147, t. 54; Icones Pl. Ind. 1 (1838) Explanation of plates 5, t. 91; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 91, t. 21, fig. E, F, t. 22. — **Fig. 2a, b.**
Philastrea Pierre, Bull. Soc. Linn. Paris 1 (1885) 475.

Small shrubs or herbs with woody rootstocks. *Leaves* simple, trifoliolate or imparipinnate, often repand or remotely crenate or serrate. *Indumentum* a mixture of simple and bifid or stellate hairs. *Flowers* bisexual, solitary or in few-flowered axillary panicles. *Calyx* 5-lobed to near the base, lobes somewhat foliaceous. *Petals* 5, fused to the staminal tube below, rarely becoming free later. *Staminal tube* 1.5—5.5 cm long, narrowly cylindrical, the margin with 10 narrow, entire or bilobed appendages, rarely with 10 reflexed filiform appendages arising some distance below the margin. Anthers 10, hairy, inserted on the rim of the staminal tube, alternating with the appendages; connective often produced apically to form a short or long or rarely filiform appendage. *Disk* tubular, free, or fused at the base to the staminal tube, or absent. *Ovary* 5-locular; loculi with 2 superposed ovules. Style slender; style-head capitate, sometimes with 5 minute stigmatic lobes. *Fruit* a 5-valved loculicidal capsule; loculi 1 or 2-seeded. *Seed* plano-convex with a pergamentaceous testa and a large, membraneous, swollen sarcotesta covering the adaxial surface of the seed and surrounding the hilum. *Embryo* embedded in thin endosperm; cotyledons flat, collateral; radicle superior, short, exserted.

Germination: phanerocotylar; eophylls opposite, pinnatisect; metaphylls pinnate and spirally arranged (*M. pumila* (Moon) Wight).

Chromosome number: 2n=50 (*M. pinnata* (Wall.) Harms).

Pollen: Pollen grains (3)4(5)-colporate, oblate-spheroidal or spheroidal (70—85 μm, amb rounded). Apocolpium large. Ora circular or lalongate, sometimes crassimarginate. Exine scabrous or rugulose, thickened at the apertures.

Distribution: About 10 species from India eastwards to Malesia.

Type species: *M. pumila* (Moon) Wight (here chosen as lectotype).

Relationships: *Munronia* is a clearly defined genus, easily separable from all other genera of the *Turraeeae*. It differs from *Turraea* in the following characters: indumentum

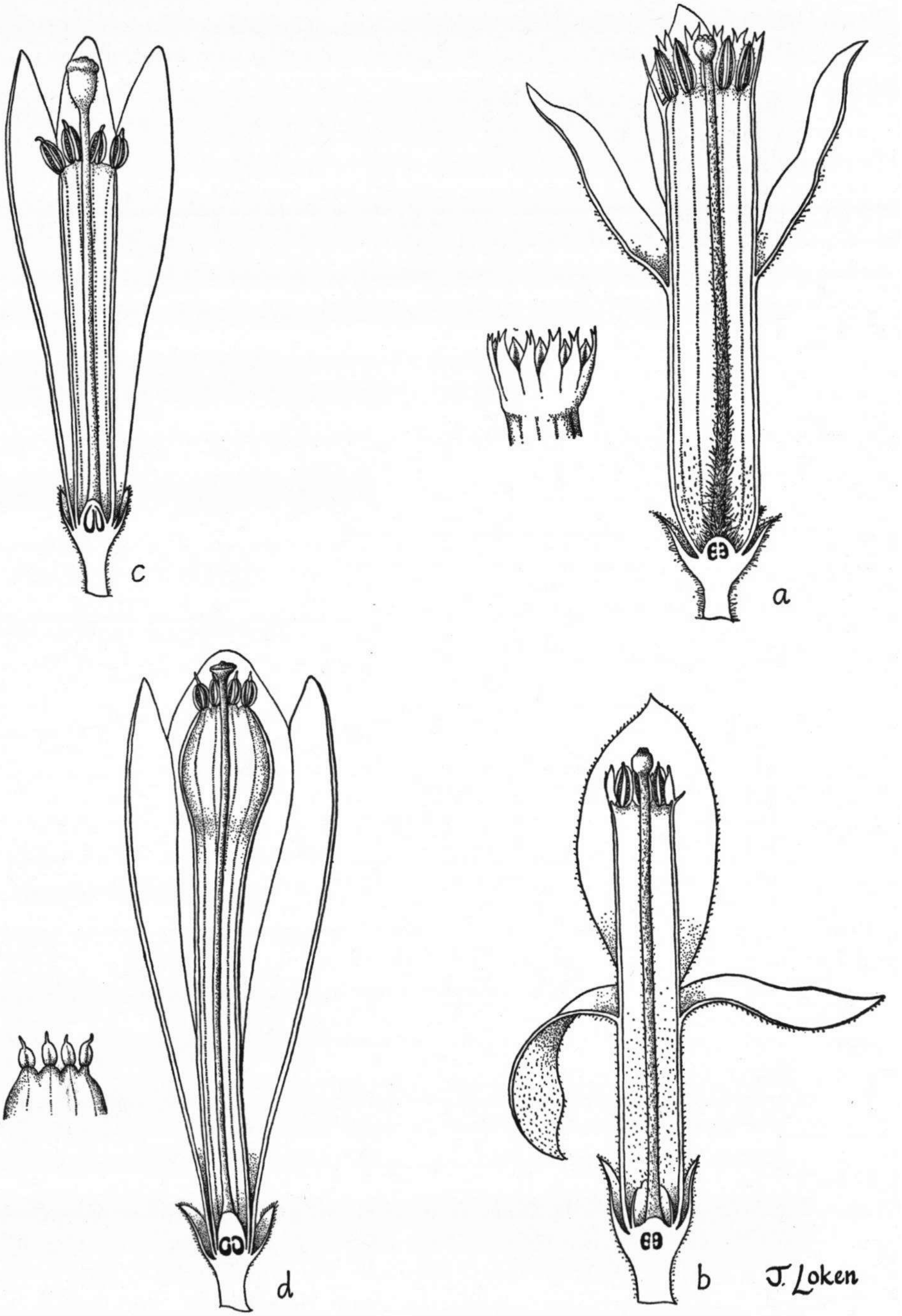

Fig. 2. a. *Munronia unifoliolata* Oliv., ☿, ×5. — b. *M. pumila* (Moon) Wight, ☿, ×5. — c. *Naregamia africana* (C. DC.) Exell, ☿, ×2.5 — d. *N. alata* Wight & Arnott, ☿, ×2.5. (a. *Henry 3963*; b. *Walker s.n.*; c. *Gossweiler 10434*; d. *Johnson s.n.*).

a mixture of simple and bifid or stellate hairs (hairs simple in *Turraea*); petals fused to the staminal tube, rarely becoming free later (free in *Turraea*); in the shape and structure of the sarcotesta which is membraneous and covers the adaxial surface of the seed. The fleshy inner part disintegrates at maturity, leaving a hollow membraneous structure. *Nymania* is the only other genus in the *Meliaceae* with a similar adaxial sarcotesta, but in this case it is relatively poorly developed.

The characters mentioned above distinguish *Munronia* from all other genera of the *Turraeeae* and in addition, *Munronia* frequently has a free tubular disk and its pollen grains are nearly always 4-colporate; the former character is unknown and the latter very rare in *Turraea.*

The relationship between *Munronia* and *Naregamia* is considered in detail under the latter.

2. NAREGAMIA

Naregamia Wight & Arn., Prod. Fl. Pen. Ind. Or. 1 (1834) 116, *nom. cons.*; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 90, t. 21, figs. G, H. — **Fig. 2 c, d.**
Nelanaregam Adanson, Fam. Pl. 2 (1763) 343., *nom. rejic.*

Small shrubs or herbs with a woody rootstock. *Leaves* trifoliolate, leaflets shallowly lobed or entire, the rhachis broadly winged. *Indumentum* of simple hairs. *Flowers* bisexual, solitary or paired, axillary. *Calyx* 4 or 5-lobed to the middle. *Petals* 4 or 5, free, imbricate. *Staminal tube* 2—3.5 cm long, narrowly cylindrical, sometimes inflated at the apex, the margin entire or with small crenations bearing the anthers. Anthers 8 or 10, glabrous; connective produced apically to form an appendage shorter than or as long as the anther. *Disk* absent. *Ovary* 3- or 4-locular; loculi with 2 collateral ovules. Style slender; style-head thinly discoid or modified to form an obconical to ovoid-cylindrical *receptaculum pollinis.Fruit* a 3- or 4-valved loculicidal capsule; loculi 1- or 2-seeded. *Seed* curved, truncate at base and apex; testa thick and bony, with irregular transverse ridges, puberulent; arillode small, thin, fleshy, free except for attachment along the adaxial raphe. *Embryo* slightly curved, embedded in thick endosperm; cotyledons flat, collateral; radicle superior, long exserted, almost as long as the cotyledons.

Germination: phanerocotylar (*N. alata* Wight & Arn.)

Chromosome number: 2n=46 (*N. alata* Wight & Arn.)

Pollen: Pollen grains 3(4)-colporate, suboblate (75—80 μm, amb rounded). Apocolpium large. Ora circular. Exine scabrous or verrucose, thickened at the apertures.

Distribution: Probably two species: one on the west coast of India, the other in Angola.

Type species: *N. alata* Wight & Arn.

Relationships: *Naregamia* has obvious affinities with *Munronia* and *Turraea*, but is more closely related to the latter. It is, however, easily distinguished from *Turraea* by a number of characters.

Naregamia has trifoliolate leaves. Those of *Turraea* are simple, except for those of one recently discovered species (allied to **Turraea pulchella** (Harms) Pennington *comb. nov.**) from Natal. This species has a mixture of trifoliolate and imparipinnate leaves, with deeply lobed or partite leaflets (shallowly lobed or entire in *Naregamia*), the rhachis unwinged at the base (broadly winged in *Naregamia*), a staminal tube with prominent

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* *Basionym : Nurmonia pulchella* Harms, Ber. Deutsch. Bot. Ges. 35 (1917) 80, t. 1.

appendages (appendages absent in *Naregamia*). In addition, the characteristic seed structure of *Naregamia* immediately separates it from *Turraea*. It is slender, curved, prominently truncate at the base and apex, and the thick bony testa has large, irregular, transverse ridges and is puberulent. The seed of all species of *Turraea* is rather swollen and rounded, not truncate at base and apex, usually with a smooth shining testa, and always glabrous.

Naregamia can be distinguished from *Munronia* by its simple hairs (simple and bifid or stellate in *Munronia*), free petals (fused to staminal tube in *Munronia*), glabrous anthers (hairy in *Munronia*), 3- or 4-locular ovary with collateral ovules (5-locular with superposed ovules in *Munronia*), and the characteristic shape and structure of its seed and arillode. The tubular disk, frequently present in *Munronia*, is not known in *Naregamia*.

3. TURRAEA

Turraea L., Mant. Pl. 2 (1771) 150, 237; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 85, t. 20. — **Fig. 3 a—e.**

Quivisia Cav., Dissert. 7 (1789) 367; Comm. *ex.* Jussieu, Gen. Pl. (1789) 264.

Gilibertia J. F. Gmel., Syst. Nat. 2 (1791) 682, *non* Ruiz & Pav. (1794).

Calodryum Desv., Ann. Sc. Nat. 9 (1826) 401, t. 51.

Ginnania M. J. Roem., Synops. Hesp. Monogr. 1 (1846) 79, 91, *nom. illeg.*, *non* Scop. (1777), *nec* F. G. Dietr. (1804).

Scyphostigma M. J. Roem., tom. cit. 80, 94.

Rutaea M. J. Roem., tom. cit. 80, 93.

Payeria Baill., Adansonia 1 (1860) 50, t. 3.

Grevellina Baill., Bull. Soc. Linn. Paris 2 (1894) 1160.

Nurmonia Harms, Ber. Deutsch. Bot. Ges. 35 (1917) 80, t.l.

Small trees or shrubs. *Leaves* simple, entire or less frequently with a repand, sinuate, or crenate margin, or very rarely (1 species) leaves compound. Indumentum of simple hairs. *Flowers* bisexual, solitary, or fasciculate, or in short axillary or terminal cymes or panicles, rarely paired, very rarely ramiflorous. *Calyx* (3)4 or 5(6)-lobed or -toothed to above or below the middle, rarely almost entire, or with foliaceous lobes. *Petals* (3)4 or 5, free, imbricate or contorted, rarely valvate at the apex. *Staminal tube* 0.1—14 cm long, complete or filaments free at the apex for one third or less of their length; tube cylindrical or rarely cyathiform, sometimes curved or inflated distally; terminated by simple or bilobed, free or partly or completely fused, often reflexed appendages, as many as or twice as many as the anthers, or margin shallowly lobed or entire. Anthers (7)8—10(20), glabrous or less frequently hairy, inserted on the margin of the staminal tube or inside below the margin, opposite to or alternating with the appendages, or apically on the filaments; apiculate or connective produced apically or basally to form a long or short appendage. *Disk* small, annular, patelliform, cyathiform, or absent; when annular then sometimes free, when patelliform or cyathiform then always fused to the base of the ovary or staminal tube, sometimes ribbed and with the margin lobed. *Ovary* (3)4—10(20)-locular; loculi with 2 collateral, oblique or superposed ovules. Style usually expanded apically to form an ovoid, globose, fusiform, cylindrical, conical, or obconical style-head *(receptaculum pollinis)*, surmounted by a discoid or rounded stigmatic area; less frequently only slightly or not expanded and then capitate or narrowly discoid and often with 4 or 5 small stigmatic lobes. *Fruit* a (3)4—10(20)-valved, leathery or woody, usually rather thin-walled, loculicidal capsule; loculi 1 or 2-seeded. *Seed* 0.2—0.8 cm long, plano-convex, slightly pointed at the apex; testa hard, shining, nearly always smooth, glabrous; arillode present, fleshy, usually free except along the narrow adaxial line of attachment to just below the micropyle, rarely partially fused to the seed. *Embryo* embedded in

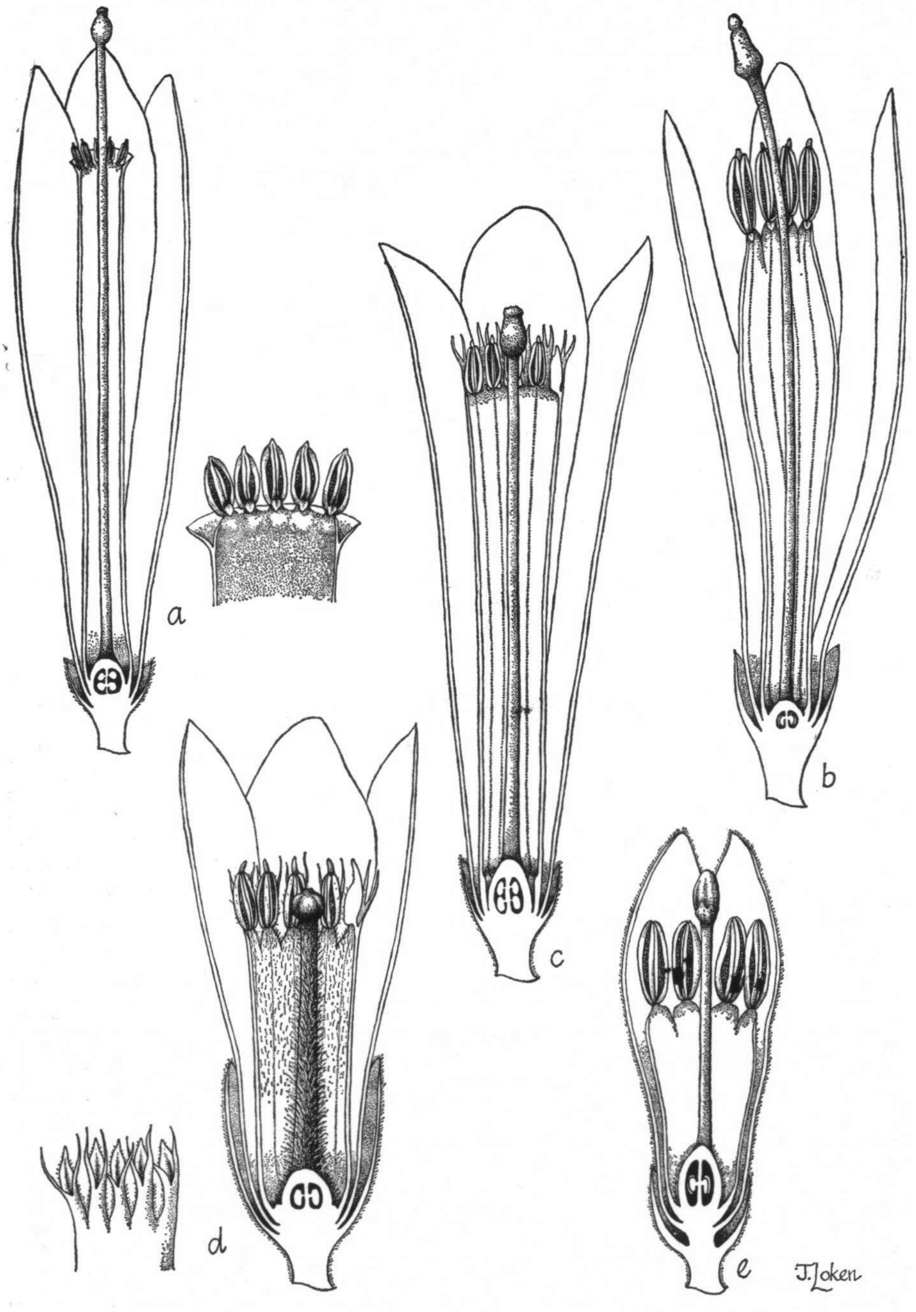

Fig. 3. a. *Turraea cabrae* De Wildem. & Th. Dur., ☿, ×2.5. — b. *T. pubescens* Benth., ☿, ×5. — c. *T. pervillei* Baill., ☿, × 2.5. — d. *T. pulchella* (Harms) Pennington, ☿, ×7.5. — e. *T. heterophylla* (Cav.) Harms, ☿, ×7.5. (a. *Cabra s.n.*; b. *Brown s.n.*; c. *Perrier de la Bâthie 965*; d. *Pegler 730*; e. *Herb. Richard s.n.*).

thick endosperm, straight or curved; cotyledons flat, rather narrow, collateral; radicle superior, long exserted.

Germination: phanerocotylar; eophylls spirally arranged, simple, margin sinuate to coarsely toothed (*T. nilotica* Kotschy & Peyr., *T. obtusifolia* Hochst.).

Chromosome numbers: 2n=50 (7 species), 2n=36 (*T. sp. nov.*).

Pollen: Pollen grains 3(4)-colporate, oblate, suboblate, or oblate-spheroidal, very rarely spheroidal; (30—105 μm; amb rounded or triangular). Apocolpium medium or large. Ora circular or lalongate, rarely lolongate, sometimes crassimarginate. Exine scabrous, verrucose, rugulose, or reticulate, very rarely smooth, sometimes thickened at the apertures.

Secondary xylem: *Vessels* solitary and in radial groups of 2—5(15), sometimes with pore clusters, sometimes showing oblique or tangential patterns; tangential diameter (15)20—140μm; intervascular pits 3—6μm; gum usually absent. *Ray tissue* heterogeneous Kribs Type 3, homogeneous Kribs Type 1, or uniseriate-homogeneous or -heterogeneous; rays 1 or 2 (3)-seriate, up to 40 cells high, the heterocellular rays with 1(2) marginal rows. *Fibres* non-septate. *Parenchyma*. Paratracheal: vasicentric, aliform, confluent and banded in various combinations, rarely absent; crystals usually absent. Apotracheal: terminal bands present or absent. Diffuse cells present or absent.

Distribution: About 24 species in tropical Africa, perhaps 35 in Madagascar, Mauritius, and the Comores, and about 6 in tropical Asia and Australia.

Type species: *T. virens* L.

Relationships: *Turraea* as defined here includes four genera formerly recognized by other authors, viz. *Quivisia*, *Calodryum*, *Grevellina*, and *Nurmonia*. Harms, in his latest treatment of the *Meliaceae* (1940), placed all these, except *Nurmonia*, in synonymy with *Turraea*.

Typical *Turraea* as illustrated by the majority of African and Asiatic species, is characterized by a long, cylindrical, complete staminal tube, usually with terminal appendages, and a style-head strongly modified to form a *receptaculum pollinis*. The four synonymous genera mentioned above were based on the following characters:

Size of flower and shape of staminal tube (small flowers and staminal tube sometimes cyathiform in *Quivisia*).

Degree of fusion of the filaments (filaments free at the apex in *Calodryum* and *Nurmonia*).

Presence or absence of staminal tube appendages (no appendages in *Grevellina*, *Calodryum*, *Quivisia*).

Presence or absence of the *receptaculum pollinis* (absent in *Nurmonia* and *Quivisia*).

Leaf-shape (*Grevellina* has very slender leaves).

Although the extremes are different there are many intermediate conditions. The size of flower and shape of staminal tube ranges from the minute flower of *Quivisia oppositifolia* Cav. with its cyathiform staminal tube less than 0.5 cm long, through species with a shortly cylindrical staminal tube (e.g. *T. robusta* Gürke) to the other extreme of *T. macrantha* Danguy whose staminal tube is 12 cm long. There is no sharp discontinuity between the partly free filaments of some *Quivisia* or *Calodryum* and the complete staminal tube of typical *Turraea*. Among the Malagasy species there is much variation in the form of the style-head, from the pronounced *receptaculum pollinis* to the simple capitate style-head of *Quivisia*. *Grevellina* is similar in all respects to typical *Turraea*, except for the lack of staminal tube appendages and leaf shape which is not a generic character. Apart from the characters mentioned above, *Nurmonia* is also unusual in having foliaceous calyx lobes, but this condition is approached in some Malagasy *Turraea* (e.g. *Calodryum tubiflorum* Desv. = *T. lanceolata* Cav.).

The presence or absence of staminal tube appendages is the only character showing a clear discontinuity, but as this feature is not correlated sufficiently highly with any other, it cannot be used to divide *Turraea* in any natural way.

Turraea is a very variable genus with extreme species widely different, but linked by many intermediates. The variable characters are not correlated or are insufficiently correlated to give discontinuities between groups of species. A similar pattern of variation occurs in other large genera of the *Meliaceae*, e.g. *Trichilia*. In *Turraea*, as in *Trichilia*, there are a small number of unifying features common to all or nearly all species. These are the simple leaves (all species except one) and the structure of the fruit, seed, and embryo. The fruit is always a loculicidal capsule, generally with rather thin-walled valves. The seeds are small in proportion to the size of the fruit, have a hard, shining, glabrous testa with a fleshy adaxial arillode. The seeds of all species have copious endosperm and a straight or curved embryo with thin, rather narrow, collateral cotyledons and a long exserted radicle. It is the fruit, seed, and arillode characters which distinguish *Turraea* from its satellite genera *Humbertioturraea*, *Calodecaryia*, and *Nymania*. The relationships of these will be discussed in detail under the respective genera.

Note: *Turraea breviflora* Ridley. The relationships of this endemic Malayan species are uncertain. It differs from all known *Turraea* species in several important characters: stellate indumentum, valvate corolla, shortly tubular disk, uniovulate loculi. It also lacks the modified style-head present in most species of *Turraea*. The sparse field data available indicates that the species is dioecious (all known *Turraea* species are hermaphrodite). The 3 or 4 colporate suboblate pollen grains are similar to those of *Turraea* and *Munronia*.

The vegetative and floral structure suggests that this species has almost equal affinities with both *Turraea* and *Munronia*, but it is nevertheless quite distinct from both. Until the fruit is collected it is not possible to place it with any greater accuracy.

4. HUMBERTIOTURRAEA

Humbertioturraea J. F. Leroy, Compt. Rend. Acad. Sci. Paris 269 (1969) 2322. — **Fig. 4a.**

Small trees or shrubs. *Leaves* simple, entire. *Indumentum* of simple hairs. *Flowers* bisexual, solitary, paired, or in small axillary fascicles. *Calyx* 4- or 5-lobed to halfway. *Petals* 4 or 5, free, imbricate. *Staminal tube* 3—8 cm long, ± complete, cylindrical or sometimes slightly expanded at the apex, terminated by emarginate to deeply bifid, sometimes partly fused, often reflexed appendages alternating with the anthers. Anthers 10—12, sparsely hairy or glabrous, inserted on the very short free portion of the filaments; connective produced apically or basally to form a short, sparsely hairy or glabrous appendage. *Disk* small, patelliform or cyathiform, partly or completely fused to the base of the staminal tube, often ribbed and the margin lobed. *Ovary* 5—15-locular; loculi with 2 superposed ovules. Style expanded apically to form a globose, conical, or discoid *receptaculum pollinis* surmounted by a rounded or discoid, papillose stigmatic area. *Fruit* indehiscent with a thick leathery-fleshy pericarp, 5—10-locular, loculi usually with 2 superposed seeds. *Seed* 1.3—1.5 cm long, plano-convex, with a thick, woody, smooth, glabrous testa; sarcotesta adaxial, hilum large. *Embryo* embedded in thick endosperm, almost straight; cotyledons flat, broad, collateral; radicle superior, very short, slightly exserted.

Pollen: Pollen grains 3-colporate, suboblate (85—90 μm; amb rounded or triangular). Apocolpium medium. Ora circular or lalongate. Exine scabrous.

Distribution: 3 or 4 species in Madagascar.

Type species: *H. seyrigii* J. F. Leroy.

Relationships: In its floral features *Humbertioturraea* is similar in all respects to typical *Turraea*, but it differs in its completely indehiscent fruit. It is difficult to decide from dried material whether the fruit is a berry or drupe, but it appears to be leathery-fleshy in texture, and from field observation it is known to rot on the ground where it falls. *Humbertioturraea* is the only genus in the tribe with an indehiscent fruit.

It also differs from *Turraea* in some minor characters. The size of the seed relative to that of the fruit is far greater in *Humbertioturraea* than in the few species of *Turraea* which have an equally large fruit. The adaxial sarcotesta which leaves a large scar is unknown in *Turraea* which has an arillode. Here the arillode is usually free except for a narrow line along the adaxial side and leaves a narrow scar, except in a few species *(Quivisia)*, where it may be broadened slightly. The embryo also differs from that of *Turraea*. It has broad flat cotyledons and a very shortly exserted radicle; the cotyledons of *Turraea* are slender, often parallel-sided, and the radicle is much longer in proportion to the size of the cotyledons.

5. CALODECARYIA

Calodecaryia J. F. Leroy, Compt. Rend. Acad. Sci. Paris 250 (1960) 4026; Journ. Agric. Trop. Bot. Appl. 7 (1960) 379. — **Fig. 4b.**

Small trees or shrubs. *Leaves* simple, entire. *Indumentum* of simple hairs. *Flowers* bisexual, in small axillary panicles or fascicles. *Calyx* 4- or 5-lobed to the middle. *Petals* 4 or 5, free, contorted. *Filaments* 0.6—1.1 cm long, connate in the lower half only, often free almost to the base, without appendages. Anthers 8—10, glabrous, basifixed. *Disk* annular or patelliform, often indistinct, fused to the base of the staminal tube. *Ovary* 4- or 5-locular; loculi with 2 collateral ovules. Style usually slightly expanded below the capitate to discoid style-head, usually with 4 or 5 minute stigmatic lobes. *Fruit* a 2—5-valved, leathery, loculicidal capsule; loculi 1 or 2-seeded. *Seed* plano-convex to reniform, rounded at both ends; testa thick, hard, smooth, projecting inwards deeply on the adaxial side, glabrous; small fleshy sarcotesta on the adaxial surface and surrounding the minute hilum. *Embryo* strongly curved, surrounded by thick endosperm; cotyledons flat, slender, collateral; radicle superior, rather long, exserted.

Germination: phanerocotylar; eophylls spirally arranged, simple; axillary buds sometimes develop from the cotyledons (*C. crassifolia* J. F. Leroy)

Chromosome number: 2n=36 (*C. crassifolia* J. F. Leroy)

Pollen: Pollen grains 3-colporate, oblate (58—65 μm; amb triangular). Apocolpium large. Ora lalongate. Exine scabrous or smooth.

Secondary xylem: *Vessels*: solitary and in radial groups of up to 15; tangential diameter 15—32 μm; intervascular pits 2—3 μm; gum absent. *Ray tissue*: uniseriate-homogeneous; rays up to 15 cells high. *Fibres*: non septate. *Parenchyma*: Paratracheal: absent. Apotracheal: thin terminal bands numerous. Crystals absent.

Distribution: One or two species in Madagascar.

Type species: *C. pauciflora* J. F. Leroy.

Relationships: *Calodecaryia* is closely related to *Turraea*, particularly to those species formerly included under *Calodryum*. It differs from *Turraea* in the degree of fusion of the filaments and in the characteristics of the seed and sarcotesta. In *Turraea* the filaments are completely or almost completely fused whereas in *Calodecaryia* they are never fused to more than halfway.

The seed differs from that of *Turraea* in its much greater degree of curvature, so that the micropyle, hilum, and chalaza approach one another very closely. There is also a peculiar inward projection of the testa on the adaxial side which is unknown in *Turraea*. The hilum is surrounded by a small fleshy sarcotesta which has not been observed in any species of *Turraea*. The embryo is very strongly curved, resembling that of *Nymania*. The relationship of *Calodecaryia* with *Nymania* is discussed under the latter.

6. NYMANIA

Nymania S. O. Lindb., in nota sub *Aitonia* J. & G. Forst., Notis. Sällsk. Fl. Fenn. Förhandl. 9 (1868) 290; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 94, t. 24; *non Nymania* K. Schum. (1905) (*Euphorbiaceae*) (*nom. illegit.*). — **Fig. 4c.**

Aitonia Thunb., Phys. Sällsk. Handl. Stockh. (Act. Lund.) 1 (1781) 166, *nom. illegit*; non *Aytonia* J. & G. Forst., Charact. Gen. Fl. (1776) 147 (*Marchantiaceae*).

Aytonia L. *f.* Suppl. Pl. (1781) 49, 303 (emend. *Aitonia*, 468) *nom. illegit.*.

Carruthia O. Kuntze, Rev. Gen. 1 (1891) 141.

Shrub with simple *leaves* spirally arranged and fasciculate on short lateral shoots. *Indumentum* of simple hairs. *Flowers* bisexual, solitary, axillary. *Calyx* 4-lobed to near the base. *Petals* 4, free, imbricate. *Filaments* 1.6—2.3 cm long, distinctly curved, fused near the base. Anthers 8 or 9, glabrous, fixed dorsally towards the base, versatile. *Disk* thin, patelliform, partly fused to the base of the staminal tube. *Ovary* 4(5)-locular; loculi with 2 collateral ovules. Style long, slender, with a simple, minute, capitate style-head. *Fruit* an inflated, deeply 4(5)-lobed, thinly membraneous, loculicidal capsule; loculi 1(2)-seeded. *Seed* reniform, with a thick, rather woody, minutely verrucose, puberulent testa, the adaxial depression filled with a fleshy sarcotesta which surrounds the hilum. *Embryo* strongly curved, embedded in thin endosperm; cotyledons flat, slender, collateral; radicle superior, rather short, exserted.

Germination: phanerocotylar; eophylls opposite, simple, growth of apical shoot soon stops and axillary buds develop from first and second pairs of eophylls. Eophylls on axillary shoots spirally arranged and opposite.

Chromosome number: $2n=40$.

Pollen: Pollen grains 3-colporate, suboblate (65—70 μm; amb triangular). Apocolpium large. Ora lolongate, usually crassimarginate. Exine scabrous or rugulose.

Secondary xylem: *Vessels*: in radial groups of 2—8 and with some pore clusters; tangential diameter 20—40 μm; intervascular pits *c.* 6 μm; gum absent. *Ray tissue*: homogeneous Kribs Type 1; rays 1 or 2-seriate, up to 20 cells high. *Fibres*: non-septate. *Parenchyma*. Paratracheal: very sparse, vasicentric, consisting mainly of scattered cells; crystals absent.

Distribution: One species in South Africa.

Type species: *N. capensis* (Thunb.) Lindb.

Relationships: This genus, which was originally placed by Thunberg (1781) in the *Monadelphia '8-andria'*, and by the younger Linnaeus (1781) in *Octandria Monogyna*, was recognized as belonging to the *Meliaceae* by both De Jussieu (1789) and Ventenat (1799). Some subsequent authors have not agreed with this conclusion and it has been placed in no fewer than six families: *Malvaceae* (Cavanilles, 1788), *Hesperideae* (Batsch, 1802), *Rutaceae* (D. Don, 1832), *Zygophyllaceae* (Harvey, 1838), *Aitonieae* (Harvey, 1860), *Sapindaceae* tribe *Dodonaeae* (Hook *f.* in Bentham & Hooker, 1862), in *Sapindaceae* tribe *Aitonieae* (Baillon, 1874/5), and *Aitoniaceae* (Airy Shaw, 1966).

Radlkofer (1890) discusses the affinities of this genus at some length and shows con-

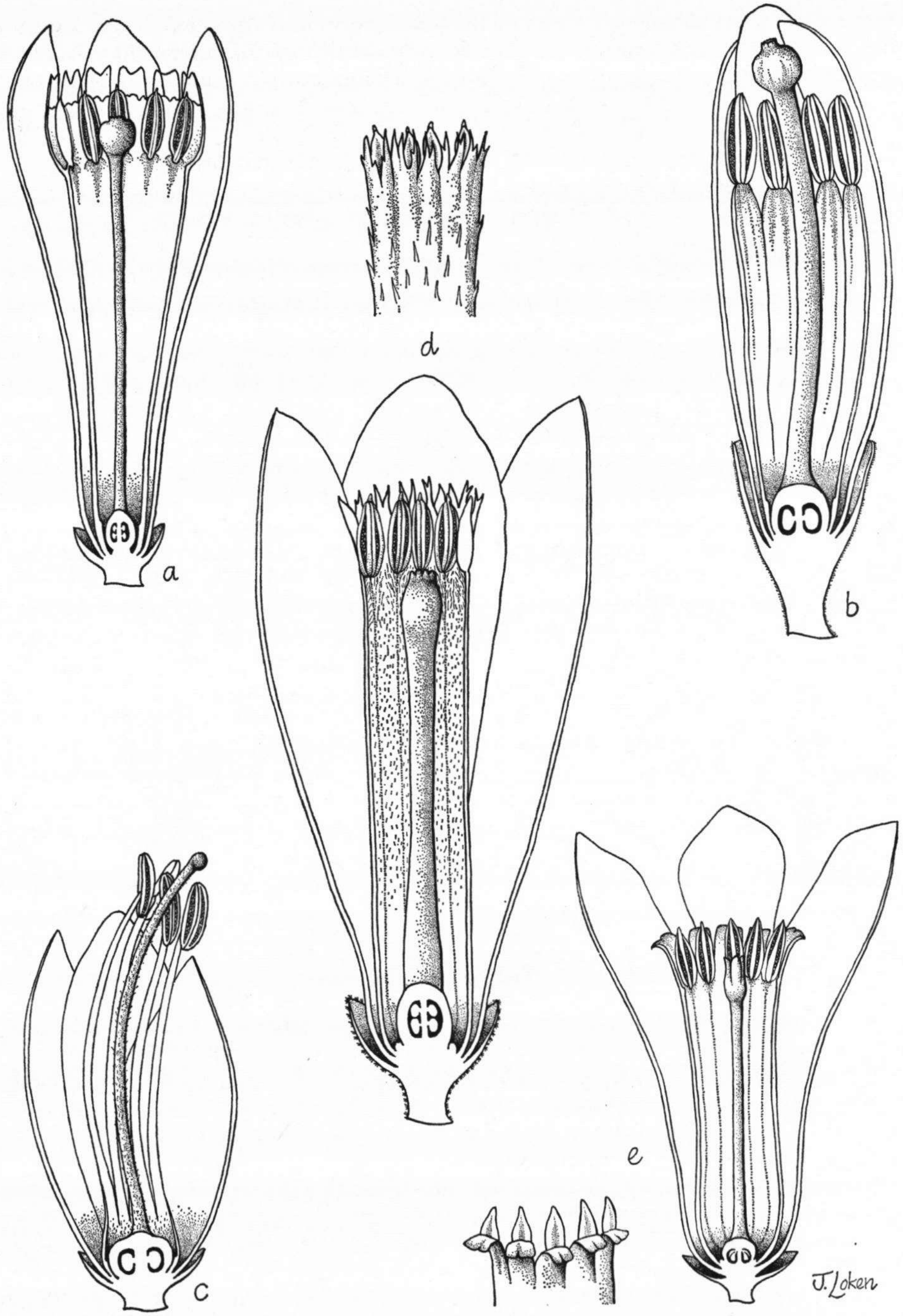

Fig. 4. a. *Humbertioturraea sp.*, ⚥, ×2.5. — b. *Calodecaryia crassifolia* J. F. Leroy, ⚥, ×7.5. — c. *Nymania capensis* (Thunb.)Lindberg, ⚥, ×3. — d. *Melia azedarach* L., ⚥, ×10. — e. *Azadirachta indica* A. Juss., ⚥, ×10. (a. *R. F. 7225*; b. *S. F. 8194*; c. *von Breda 4132*; d. *Pennington 8099*; e. *Pennington 7833*).

vincingly that the relationship with the *Meliaceae* is very close. Although there is a superficial resemblance between the fruit of *Nymania* and that of *Melianthus (Melianthaceae*, a satellite genus of the *Sapindaceae)* or *Dodonaea (Sapindaceae)*, many other characters, notably the 4-merous flowers, antisepalous position of the carpels, endospermous seed, curved embryo, and intra-staminal disk would not exclude it from the *Meliaceae*. Radlkofer also supports his conclusion with anatomical characters; in particular he notes that the continuous ring of sclerenchymatous tissue, which is present in the bark of the twigs of the *Sapindaceae* is absent from *Nymania*, as it is from all other *Meliaceae*.

In general appearance, largely because of the linear sclerophyllous leaves in fascicles on the stems and the large inflated capsule, *Nymania* differs markedly in appearance from other *Meliaceae*, except *Calodecaryia* and a few Malagasy species of *Turraea* which have similar foliage.

The inflated capsule is not known elsewhere in the *Meliaceae* and *Nymania* lacks some of the distinctive features of the family e.g. the complete staminal tube and expanded style-head. The pollen grains, which are 3-colporate with meridionally elongate pores, suboblate and with a scabrous or rugulose exine, look different from typical *Meliaceae*, but are similar to those of *Humbertioturraea* and some species of *Turraea*. In its morphology *Nymania* differs from *Turraea* in having staminal filaments fused only at the base, in the dorsifixed versatile anthers (basifixed and not versatile in *Turraea*), and in its seed structure. The seed of *Nymania* is strongly curved, with a minutely verrucose, puberulent testa; that of *Turraea* is straight or less curved, with a usually smooth, glabrous testa. The inner layer of the testa is strongly concave on the adaxial side, and the concavity filled by a fleshy sarcotesta which distintegrates when the seed is mature leaving a cavity, a condition unknown in *Turraea*, but approached in *Calodecaryia*. The latter genus provides a connecting link between *Nymania* and *Turraea*. It differs from *Nymania* in its basifixed non-versatile anthers, in its larger style-head, and in its capsule which is not inflated. The seed of *Calodecaryia* is strongly curved like that of *Nymania*, but with a smooth glabrous testa (verrucose and puberulent in *Nymania*). The testa projects inwards deeply on the adaxial side, but is not strongly concave as in *Nymania*.

The secondary xylem of *Nymania* confirms its position in the *Meliaceae*: it is very similar to that of *Calodecaryia* and some species of *Turraea (Calodryum)*. The very small vessels and sparse or absent paratracheal parenchyma give a characteristic combination of characters not found elsewhere in the family.

Tribe 2. MELIEAE

Leaves pinnate or bipinnate. Petioles with paired sunken glands at the base. Indumentum of simple or stellate hairs. Flowers hermaphrodite or male. Staminal tube cylindrical, complete, with appendages. Disk annular. Style-head 3—8-lobed. Fruit a drupe. Seed exarillodiate, with thin endosperm. Cotyledons collateral; radicle superior, exserted.

Pollen. Prolate-spheroidal or subprolate, less frequently oblate-spheroidal; 3 or 4-colporate; exine smooth or minutely scabrous.

Secondary xylem. Minute vessels present with spiral thickening; fibres non-septate; apotracheal terminal parenchyma present.

1. Leaves 2—3-pinnate; innovations with stellate indumentum; ovary 4—8-locular; loculi with 2 superposed ovules; style-head 4—8-lobed; drupe 3—8-seeded, with a thick bony endocarp . . . . 7. *Melia*

1a. Leaves pinnate; indumentum simple; ovary 3-locular; loculi with 2 collateral ovules; style-head 3-lobed; drupe 1(2)-seeded; endocarp thin . . . . 8. *Azadirachta*

7. MELIA

Melia L. [Gen. Pl. ed. I. (1737) 127] Sp. Pl. 1 (1753) 384; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 99, t. 26, figs. A—L, t. 27. — **Fig. 4d.**
Azedarach Mill., Gard. Dict. Abr. ed. 4 (1754).
Zederachia Heist. *ex* Fabr., Enum. Meth. Pl. (1759) 221.
Antelaea Gaertn., Fruct. Sem. Pl. 1 (1788) 277, t. 58.

Monopodial trees or treelets. *Indumentum* a mixture of simple and tufted-stellate hairs. *Leaves* 2—3-pinnate. *Inflorescence* a many-flowered axillary panicle, the ultimate branchlets often cymose. *Flowers* bisexual and male on the same individual (polygamous). *Calyx* 5(6)-lobed to near the base, sepals sometimes imbricate at the base. *Petals* 5(6), free, imbricate. *Staminal tube* 0.4—1 cm long, narrowly cylindrical, slightly expanded at the mouth, 10—12-ribbed, terminated by slender, filiform, truncate, or 2—4-lobed appendages, as many as or up to twice as many as the anthers. Anthers 10(12), hairy or glabrous, apiculate or acute; inserted on the margin of the staminal tube or just inside, alternate with or opposite to the appendages. *Disk* small, annular or patelliform, free, surrounding the base of the ovary. *Ovary* 4—8-locular; loculi with 2 superposed ovules. Style-head capitate to coroniform, with 4—8 short erect or incurved stigmatic lobes. *Fruit* a 3—8-locular drupe; endocarp thick, bony, hollowed out at base and apex; loculi 1(2)-seeded. *Seed* oblong, laterally compressed, exarillodiate; testa leathery, sometimes slightly swollen and fleshy round the hilum. *Embryo* embedded in thin endosperm; cotyledons flat, collateral; radicle superior, short, projecting from the cotyledons.

Germination: phanerocotylar; eophylls opposite, pinnatisect or trifoliolate (*M. azedarach* L.).

Chromosome numbers: n=14, 2n=28 (5 species).

Pollen: Pollen grains (3)4-colporate, prolate-spheroidal, subprolate, or oblate-spheroidal (50—60 µm; amb rounded). Apocolpium medium. Ora circular. Exine smooth or minutely scabrous, thickened at the apertures.

Secondary xylem: ring porous. *Vessels*: in clusters; minute vessels with spiral thickening are also present, often in more or less tangential rows; tangential diameter 40—240 µm; intervascular pits 6 µm; gum present. *Ray tissue*: homogeneous Kribs Type 2; rays 5—7-seriate, up to 40 cells high, a few heterocellular with 1 marginal row. *Fibres*: non-septate. *Parenchyma*. Paratracheal: vasicentric and confluent. Apotracheal: terminal bands present with crystals. Diffuse crystalliferous cells abundant.

Distribution: *c.* 5 confused species in the Old World tropics. Introduced elsewhere.

Type species: *M. azedarach* L.

Relationships: *Melia* and *Azadirachta* are closely related both morphologically and anatomically. The morphological differences are enumerated in the key.

Jacobs (1961) mentions a useful field character for separating sterile specimens of these two genera. Both have glands at the base of the petiole. In *Melia* there is a pair of orbicular glands, while in *Azadirachta* there is in addition a pair of linear glands below these. This is a good field character, but the glands are often difficult to observe in herbarium material.

Both genera share a number of interesting anatomical characters not recorded elsewhere in the *Meliaceae*, in particular the clusters of minute vessels with spiral thickening of the walls. *Melia* differs anatomically from *Azadirachta* in having ring porous secondary xylem.

8. AZADIRACHTA

Azadirachta A. Juss., Mém. Mus. Hist. Nat. Par. 19 (?1830) 220, t. 2, n. 5; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 102, t. 26, figs. M-S. — **Fig. 4e.**
Antelaea auct., non Gaertn.: Adelb., Blumea 6 (1948) 315.

Trees with pinnate leaves. *Indumentum* of simple hairs. *Panicles* axillary, many-flowered. *Flowers* bisexual and male on the same individual (polygamous). *Calyx* 5-lobed to the lower half, the lobes imbricate. *Petals* 5, free, imbricate. *Staminal tube* 0.3—0.5 cm long, cylindrical, slightly expanded at the mouth, terminated by 10 rounded, truncate, emarginate, or bilobed appendages, often partially united to form a frill. Anthers 10, glabrous, tapering to a short point, inserted at the base of, and opposite to, the appendages. *Disk* annular, fused to the base of the ovary. *Ovary* 3-locular; loculi with 2 collateral ovules. Style-head expanded to form a ring bearing 3 acute, partially fused, papillose stigmatic lobes. *Fruit* a 1(2)-seeded drupe with a thin cartilaginous endocarp. *Seed* ovoid, pointed above, with a thin membraneous testa; exarillate, with a small adaxial sarcotesta. *Embryo* surrounded by very thin endosperm; cotyledons plano-convex, collateral; radicle superior, short, projecting from the cotyledons.

Germination: phanerocotylar; eophylls opposite, trifoliolate, leaflets deeply incised, pinnatifid, or partite.

Chromosome numbers: 2n=28, 30; n=14 (*A. indica* A. Juss.).

Pollen: Pollen grains 3- or 4-colporate, prolate-spheroidal or subprolate (55—65 μm; amb rounded). Apocolpium medium. Ora circular. Exine smooth, slightly thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial pairs, with pore clusters; minute vessels with spiral thickening also present; tangential diameter 40—240 μm; intervascular pits 4.5—7.5 μm; gum present. *Ray tissue:* heterogeneous Kribs Type 3, or homogeneous Kribs Type 2; rays 2—7 seriate, up to 20 cells high, the heterocellular with 1 marginal row. *Fibres:* non-septate. *Parenchyma:* Paratracheal: vasicentric. Apotracheal: terminal bands present with crystals. Diffuse crystalliferous cells present or absent. Silica deposits present or absent.

Distribution: Two species in the Indo-Malesian region.

Type species: *A. indica* A. Juss.

Relationships: The affinites of this genus with *Melia* are discussed in detail under the latter.

Tribe 3. VAVAEEAE

Trees or treelets with sympodial (*'Terminalia'*) branching. Leaves simple. Indumentum of simple hairs. Flowers mostly bisexual. Staminal tube cylindrical or cyathiform; filaments partly free; appendages absent. Disk poorly developed or absent. Loculi uniovulate, biovulate, or multiovulate. Fruit a berry. Seed with a thin sarcotesta; sometimes with thin endosperm. Cotyledons plano-convex, collateral.

Pollen: Prolate, subprolate, or prolate-spheroidal; 3(4)-colporate; ora lalongate to zonorate.

Secondary xylem: Vessels solitary or paired; rays very heterogeneous (Kribs Type 1, 2, or 3); fibres nearly always septate.

9. VAVAEA

Vavaea Benth. in Hook., Lond. Journ. Bot. 2 (1843) 212; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 97, t. 21, fig. J, K, t. 25; Pennington, Blumea 17 (1969) 351. — **Fig. 5a, b.**
Lamiofrutex Lauterbach, Nova Guinea 14 (1924) 147.

Trees or treelets with sympodial ('*Terminalia*') branching. *Leaves* simple, clustered at the ends of branchlets. *Inflorescence* usually axillary, rarely extra-axillary, a panicle or less frequently a cyme. Plants sometimes polygamous. *Calyx* shallowly or deeply 4 or 5(7)-lobed, with open or rarely imbricate aestivation. *Petals* (3)4—6, free, imbricate or rarely contorted. *Filaments* 0.2—6.7 cm long, fused in the lower half or beyond, the staminal tube cyathiform, shortly tubular or long tubular and then sometimes slightly curved; appendages absent, rarely represented by a pair of short rounded lobes. Anthers 9—23, hairy or glabrous, attached at the ends of the filaments. *Disk* patelliform or cyathiform, fused to the base of the staminal tube, or forming androecial ribs, or absent. *Ovary* 2—6-locular, loculi uniovulate or with 2(3) collateral ovules or with 4—10 ovules in 2 rows. Style-head capitate or discoid. *Fruit* a berry with a thin and fleshy or thick and rather woody pericarp,c ontaining 1—3(7) seeds. *Seed* ovoid or plano-convex; seed coat cartilaginous, surrounded by a thin sarcotesta. *Embryo* sometimes surrounded by a thin layer of residual endosperm; cotyledons plano-convex, rather thick, collateral; radicle superior, small, included or extending to the surface.

Germination: cryptocotylar; eophylls opposite, simple (*V. amicorum* Benth.).

Pollen: Pollen grains 3(4)-colporate, prolate-spheroidal, subprolate, or prolate (longest axis 45—130 μ m; amb rounded to triangular). Apocolpium medium to large. Ora lalongate to zonorate. Exine usually scabrous, less frequently smooth, thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial pairs, rarely with pore clusters,

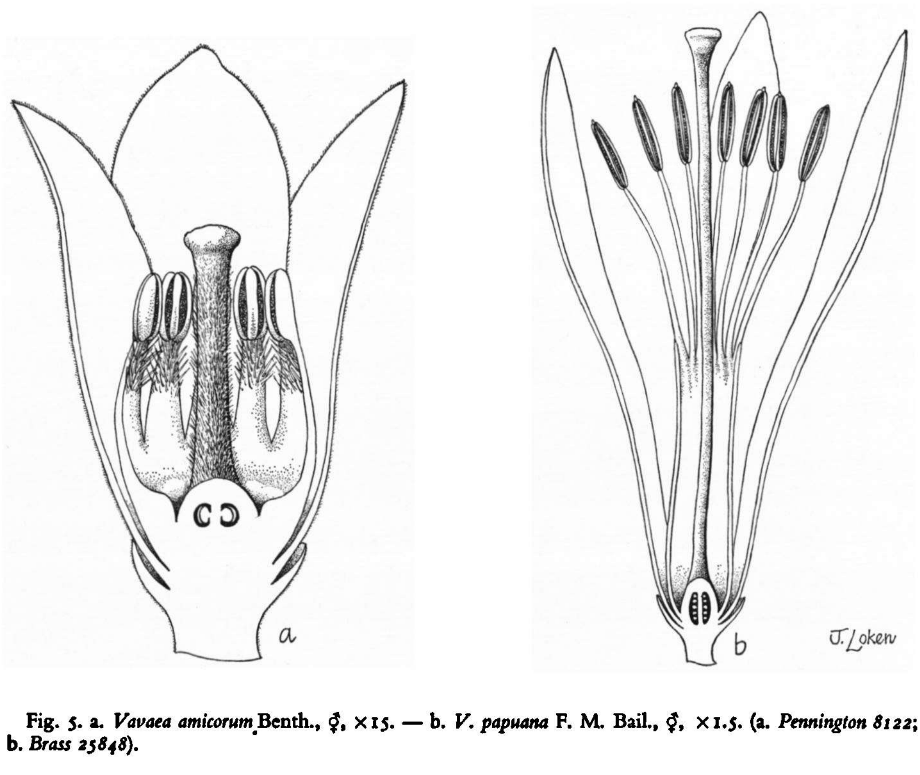

Fig. 5. a. *Vavaea amicorum* Benth., ☿, ×15. — b. *V. papuana* F. M. Bail., ☿, ×1.5. (a. *Pennington 8122*; b. *Brass 25848*).

rarely showing local oblique patterning; tangential diameter 40—160 μm; intervascular pits 3.75—6 μm; gum absent. *Ray tissue:* heterogeneous Kribs Type 1, 2, or 3; rays 1- or 2-seriate, up to 40 cells high, the heterocellular with 1—3 marginal rows. *Fibres:* septate or partially septate, very rarely non-septate. *Parenchyma:* Paratracheal; vasicentric, aliform, confluent, with crystals. Apotracheal: terminal bands rarely present. Diffuse crystalliferous parenchyma frequent.

Distribution: 4 species from Sumatra eastwards through Malesia to northern Australia, Melanesia, and Polynesia.

Type species: *V. amicorum* Benth.

Relationships: *Vavaea* occupies an isolated position within the *Melioideae* (Pennington, l.c.). It possesses most of the individual morphological, anatomical, and palynological characters of the subfamily but in a distinctive combination enabling it to be easily distinguished from all other genera. Its relationships are with the *Turraeeae* and *Trichilieae*, especially the latter. It has the simple leaves of the *Turraeeae*, but has the baccate fruit, seed with sarcotesta, and embryo structure of some *Trichilieae*. The poorly developed disk is present in both these tribes.

The wood anatomy of *Vavaea* is very distinct and unlike that of the *Turraeeae* or *Trichilieae*. It resembles that of *Sandoricum (Sandoriceae)*, sharing with this genus the predominantly solitary vessels and very heterogeneous ray tissue. It differs, however, in having narrower rays and septate fibres.

The 3-colporate pollen grains differ from those of the majority of genera in the *Meliaceae* which are 4-colporate. Only *Vavaea*, *Aglaia*, *Sandoricum*, and certain species of a few other genera have 3-colporate, prolate to prolate-spheroidal grains. The pollen grains of *V. papuana* F. M. Bail. and *V. tubiflora* Pennington differ from all others in the *Meliaceae* in being zonorate.

Tribe 4. TRICHILIEAE

Leaves usually pinnate, rarely trifoliolate or unifoliolate. Indumentum of simple or stellate hairs. Either flowers hermaphrodite or plants dioecious. Staminal tube usually complete, or filaments connate in the upper or lower half or rarely free. Anthers nearly always inserted apically on the margin of the staminal tube or on the filaments. Disk poorly developed, usually annular or patelliform. Fruit a capsule, berry, or drupe. Seed usually arillodiate or with a sarcotesta; usually without endosperm. Cotyledons usually plano-convex and collateral, with superior radicle.

Pollen: Usually prolate-spheroidal or prolate; 3—5-colporate; exine nearly always smooth or scabrous.

Secondary xylem: Fibres nearly always non-septate; apotracheal terminal parenchyma usually present; paratracheal parenchyma usually vasicentric, aliform and confluent.

1. Fruit a capsule.
    2. Filament appendages (3)4—6(10) times as many as the anthers in male flowers, 2—3(4) times as many in the female; leaf-rhachis winged; indumentum stellate; filaments free in upper half; anthers hairy; disk thick, fleshy, annular 12. *Pterorhachis*
    2a. Filament appendages absent or not more than twice as many as the anthers:
        3. Capsule (4)5-valved; valves thick, woody, rugulose, bearing branched antler-like appendages; petals free, imbricate; filaments partly free, without appendages; seed small, with thin endosperm. . . . . 11. *Pseudobersama*

3a. Capsule 2 or 3(4)-valved without antler-like appendages; petals free or united at the base, imbricate or valvate; staminal tube complete, or filaments partly or completely free, with or without appendages; seed usually without endosperm. . . . . 10. *Trichilia*

1a. Fruit a berry (see also 1b. below).

4. Style-head well-developed, capitate, truncate, or pileate; petiolules usually pulvinate; petals usually imbricate; filaments partly or completely free; ovary 2—4-locular, loculi uniovulate or with 2 collateral ovules; seed usually arillodiate 13. *Walsura*

4a. Style-head minute, capitate; petiolules not pulvinate; petals valvate; staminal tube complete, or filaments partly free; ovary often unilocular, rarely 2- or 3-locular, loculi with 2 superposed ovules; seed exarillodiate and without a sarcotesta . . . . 15. *Malleastrum*

1b. Fruit a drupe.

5. Indumentum stellate.

6. Corolla valvate; loculi uniovulate; style-head capitate; endocarp thin, membraneous or cartilaginous . . . . 14. *Lepidotrichilia*

6a. Corolla imbricate; loculi bi -ovulate; style-head thick, discoid; endocarp very thick and woody . . . . 17. *Astrotrichilia*

5a. Indumentum simple.

7. Corolla with imbricate aestivation.

8. Staminal tube with lobes or appendages; sepals free, imbricate; loculi uniovulate; style-head discoid, bearing a large, conical, 2 or 3-lobed stigma; endocarp very thick and woody; seed with thin sarcotesta 18. *Owenia*

8a. Staminal tube without appendages; calyx shallowly lobed; loculi with 2 superposed ovules; style-head capitate or thick discoid, without a conical stigma; endocarp thin; seed exarillodiate, without a sarcotesta 16. *Ekebergia*

7a. Corolla with valvate aestivation; filaments united only near the base, with appendages; endocarp bony; seed exarillodiate, without a sarcotesta 19. *Cipadessa*

10. TRICHILIA

Trichilia P. Browne, Hist. Jamaica (1756) 278; Harms in Engl. & Prantl. Nat. Pflanzenfam. ed. 2, 19 bI (1940) 104, t. 28, figs. H-S; t. 31 E, F; J. J. F. E. De Wilde, Revision of the species of *Trichilia* on the African Continent, (1968) 207 pp. — **Fig. 6a—f.**

Barbilus P. Browne, Hist. Jamaica (1756) 216.

Barola Adans., Fam. Pl. 2 (1763) 344, 524, *nom. illeg.*

Elcaja Forsk., Fl. Aegypt.-Arab. (1775) 127.

Portesia Cav., Diss. 7 (1789) 369, t. 215, 216.

Heynea Roxb. *ex* Sims in Curt., Bot. Mag. 41 (1815) t. 1738; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 117, t. 31, figs E, F.

Odontandra Willd. *ex* M. J. Roem. & Schultes, Syst. Veg. 5 (1819) 511.

Moschoxylum A. Juss., Mém Mus. Hist. Nat. Par. 19 (?1830) 237.

Trichilia sect. *Torpesia* Endl., Gen. Pl. (1840) 1051.

[*Geniostephanus* Fenzl, Flora 27 (1844) 312, *nom. nud.*]

[*Heynichia* Kunth, Index Sem. Hort. Berol. (1844) 8; Linnaea 18 (1844) 504, *nom. nud.*]

Odontosiphon M. J. Roem., Synops. Monog. Hesperid. 1 (1846) 85, 106.

Torpesia (Endl.) M. J. Roem., tom. cit. 86, 116.

Rochetia Delile in Rochet, Sec. Voy. Adels et Choa (1846) 344.

Mafureira Bertol., Mem. Accad. Sci. Bologna 2 (1850) 269.

Acrilia Griseb., Fl. Brit. West Ind. Isl. (1864) 129.
Pholacilia Griseb., loc. cit.
Symphytosiphon Harms, Bot. Jahrb. 23 (1896) 165.
Trichilia sect. *Acanthotrichilia* Urb., Symb. Antill. 1 (1899) 328.
Acanthotrichilia (Urb.) Cook & Collins, Contrib. U.S. Nat. Herb. 8 (1903) 65, 258.
Ailantopsis Gagnep,. Not. Syst. 11 (1944) 163.
Picroderma Thorel *ex* Gagnep., tom. cit. 165.

Trees, treelets, or rarely suffrutices. *Indumentum* usually of simple, rarely of stellate hairs. *Leaves* pinnate, rarely trifoliolate or unifoliolate. *Flowers* unisexual (plants dioecious), in axillary or rarely terminal panicles, rarely fasciculate or cymose. *Calyx* shallowly or deeply 4 or 5(7)-lobed, rarely entire or of free imbricate sepals. *Petals* 4 or 5 (7), free or united below, imbricate or valvate. *Filaments* 0.1—2 cm long, completely united to form a cyathiform, urceolate, globose, or cylindrical staminal tube, the margin entire, toothed, lobed, or with simple or bilobed appendages; or filaments partly (rarely completely) free, and then with or without 2 terminal appendages. Anthers 5—10(13), hairy or glabrous, inserted between the teeth or appendages on the margin of the staminal tube, or apically on the filaments; antherodes narrower than the anthers, not dehiscing, without pollen. *Disk* a fleshy annulus surrounding the base of the ovary, or broadly stipitate, or patelliform, or cyathiform, free from, or partly or completely fused to, the base of the staminal tube or ovary, or forming androecial ribs, or absent; often less distinct in the female flower. *Ovary* 2—4(6)-locular; loculi with 1 or 2 collateral or less frequently superposed ovules; pistillode smaller but often with well-developed abortive ovules. Style-head capitate or rarely annular, surmounted by a conical or deeply 2—6-lobed stigmatic area. *Fruit* an ellipsoid, ovoid, or globose 2 or 3(4)-valved loculicidal capsule; valves leathery or woody, loculi 1 or 2-seeded. *Seed* plano-convex, partly or completely surrounded by a thin or fleshy arillode, or occasionally with a partial or complete sarcotesta; exendospermous or occasionally with thick endosperm. *Embryo* with plano-convex or less frequently flat, collateral cotyledons; radicle superior, included or occasionally exserted; rarely with oblique or superposed cotyledons and abaxial radicle.

Germination: cryptocotylar or phanerocotylar; eophylls opposite, soon becoming spirally arranged, simple, entire; cataphylls present in *T. connaroides* (Wight & Arn.) Bentv., followed by spirally arranged, simple eophylls.

Chromosome numbers: n= 14, 2n= 24, 28, 46, 50, 92, *c.* 360.

Pollen: Pollen grains 3 or 4(5)-colporate, prolate-spheroidal, subprolate, or prolate, rarely spheroidal or oblate-spheroidal (30—55 μm; amb rounded or rarely quadrangular). Apocolpium large or medium. Ora circular or lalongate. Exine smooth or rarely scabrous or verrucose, thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial groups of 2—4(8), very rarely with pore clusters; tangential diameter (20)40—220 μm; intervascular pits 2.25—4.5(6) μm; gum present or absent. *Ray tissue:* heterogeneous Kribs Type 3, uniseriate homogeneous or heterogeneous, rarely homogeneous Kribs Type 1; rays 1 or 2(5)-seriate, up to 35(50) cells high, the heterocellular with 1 marginal row. *Fibres:* non-septate. *Parenchyma:* Paratracheal: vasicentric, aliform, and confluent, sometimes with bands, in various combinations. Apotracheal: terminal bands usually present, with crystals. Diffuse cells often present, usually crystalliferous. Silica deposits present or absent.

Distribution: Tropical America (*c.* 50 species) and Africa (*c.* 14 species) with two species in the Indo-Malayan region.

Type species: *T. hirta* L.

Relationships: Harms divided *Trichilia* into ten sections, some of which were based on imperfect material and do not show the generic characters. Thus section *Pterotrichilia* contained one species which has been justifiably transferred to *Ekebergia*; section *Pterotorhachis* is now accommodated within the recently described Malagasy genus *Malleastrum*; section *Lepidotrichilia* has been elevated to generic rank by Leroy; the section *Astrotrichilia* is also treated as a genus by Leroy who includes in it section *Peltotrichilia.* In all these cases the fruit is indehiscent. When they are removed, *Trichilia* is a much more natural entity, still variable, but the fruit is always a capsule and the seed always has an arillode or sarcotesta. The remaining five sections of Harms are unsatisfactory. They are based on the degree of fusion of the staminal filaments, the structure of the disk, and the presence or absence of stellate hairs, all characters which are variable within the genus but uncorrelated. The degree of fusion of the filaments can vary within wide limits in a single species (e.g. between male and female flowers of *T. havanensis* Jacq.) and there is no clear-cut distinction between the condition with partially fused filaments and that with completely fused filaments.

In the first edition of Die Natürlichen Pflanzenfamilien (1896) Harms, following Kurz, combined *Heynea* with *Walsura,* but kept it separate in the second edition (1940). More recently (1962) Bentvelzen has combined it with *Trichilia,* an opinion we would provisionally accept. Since, however, both *Heynea* and *Walsura* have a haploid chromosome number of 14 (Rao, 1969, and *Mehra* et al, 1969), which is so far unknown in *Trichilia,* we believe the matter is worthy of further study.

11. PSEUDOBERSAMA

Pseudobersama Verdcourt, Journ. Linn. Soc., Bot. Lond. 55 (1956) 504, t. 1, — **Fig. 6g.**

Trees with pinnate leaves. *Indumentum* of simple hairs. *Flowers* unisexual (plant dioecious), in axillary thyrses. *Calyx* 5(6)-lobed to the middle. *Petals* 5, free, imbricate. *Filaments c.* 0.35 cm long, connate at the base for one-third to two-thirds of their length; without appendages. Anthers 11 or 12, hairy, inserted at the end of the filaments; antherodes not dehiscing, without pollen. *Disk* patelliform, partly fused to the base of the ovary. *Ovary* (4)5-locular; loculi with 2 collateral ovules; pistillode much narrower, 3-locular, sometimes with vestigial ovules. Style-head scarcely broader than the style, capitate, obscurely 4- or 5-lobed. *Fruit* a (4)5-valved loculicidal capsule; the very thick, woody, valves prominently rugulose, the ridges in places developed into branched antler-like appendages; loculi 2-seeded. *Seed* small, ovoid to globose, partly surrounded by a fleshy arillode. *Embryo* surrounded by thin endosperm; with collateral, plano-convex cotyledons; radicle superior, slightly exserted or extending to the surface.

Germination: cryptocotylar; eophylls opposite, simple, entire; subsequent eophylls become spirally arranged, with a deeply and irregularly toothed margin.

Chromosome number: 2n= 46.

Pollen: Pollen grains 4-colporate, subprolate (45—50 μm; amb rounded). Apocolpium medium. Ora circular. Exine smooth or scabrous, thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial rows of 2—5, with occasional pore clusters; tangential diameter 20—40 μm; intervascular pits 3 μm; gum present. *Ray tissue:* uniseriate-homogeneous or -heterogeneous; rays up to 30 cells high, the heterocellular with 1 marginal row. *Fibres:* non-septate. *Parenchyma:* Paratracheal: aliform and confluent. Apotracheal: terminal bands present, with crystals.

Distribution: One species on the East coast of Africa, from Kenya to Natal.

Type species: *P. mossambicensis* (Sim) Verdcourt.

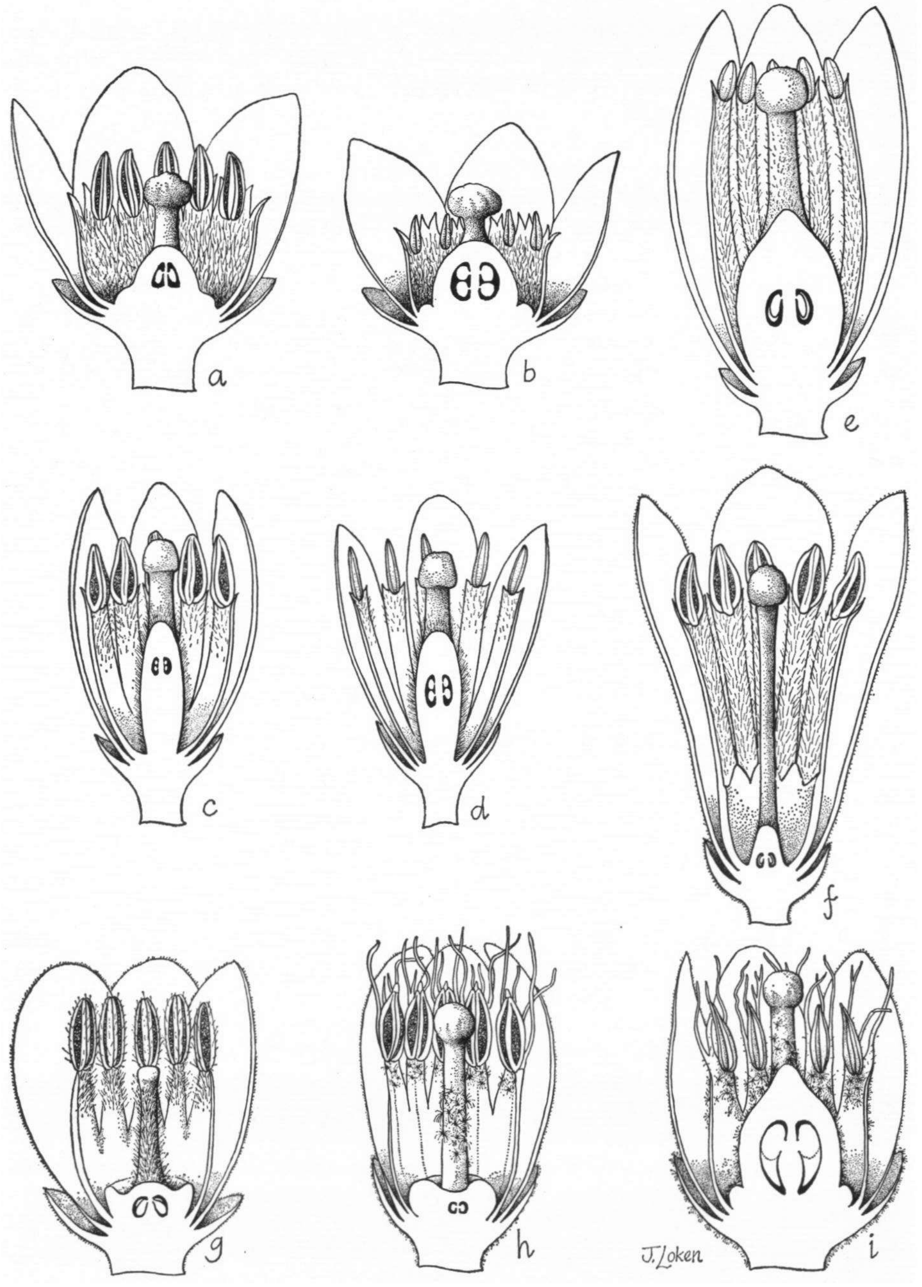

Fig. 6. a. *Trichilia havanensis* Jacq., ♂, ×7; b. ditto, ♀, ×7. — c. *T. hirta* L., ♂, ×7; d. ditto, ♀, ×7. — e. *T. martineaui* Aubrév. & Pellegrin, ♀, ×5; f. ditto, ♂, ×4. — g. *Pseudobersama mossambicensis* (Sim) Verdcourt, ♂, ×7. — h. *Pterorhachis zenkeri* Harms, ♂, ×7; — i. ditto, ♀, ×7. (a. *Pennington & Sarukhán 9546*; b. *Pennington & Sarukhán 9571*; c. *Scott Gentry 1647*; d. *Pringle 6394*; e. *de Wilde 3620-A*; f. *King 299*; g, h. *Cult. Wageningen s.n.*; i. *de Wilde s.n.*).

Relationships: This monotypic genus differs from *Trichilia* in possessing a very woody 5-valved capsule bearing conspicuous ridges which are in places developed into short antler-like appendages. The fruit contains seeds which are rather small in relation to the size of the capsule.

The secondary xylem of *Pseudobersama* can be readily distinguished from that of African species of *Trichilia* by the very large number (80—110 per sq mm) of small (20—40 μ m diameter) vessels arranged in radial rows of 2—5 and the rather sparse aliform and confluent parenchyma. African species of *Trichilia* have up to 30 vessels per sq mm with a tangential diameter ranging from 40—220μ m. However, several American species of *Trichilia*, e.g. *T. surumuensis* C. DC., *T. trifolia* L., have sparse parenchyma, combined with more numerous vessels per sq mm (50—70) than the African species, but fewer than *Pseudobersama*.

In our opinion *Pseudobersama* can be maintained as a genus distinct from *Trichilia*, but only just. The type species, based on fruiting material, was first described as a *Bersama (Melianthaceae)*. Verdcourt, who recognized it as *Meliaceae*, placed it in a new genus. Of the characters which serve to distinguish *Pseudobersama* from the African species of *Trichilia*, some occur sporadically in American species. Had Verdcourt studied the whole of *Trichilia* before creating the genus, he might equally have justifiably placed it in *Trichilia*.

12. PTERORHACHIS

Pterorhachis Harms, Bot. Jahrb. 22 (1895) 155; in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 94, t. 23. — Fig. 6h, i.

Treelet with stellate indumentum. *Leaves* imparipinnate or trifoliolate; rhachis winged. *Inflorescence* axillary, thyrsoid. *Flowers* unisexual (plant dioecious). *Calyx* 5-lobed to near the base, with open or slightly imbricate aestivation. *Petals* 5, free, imbricate. *Staminal tube* 0.35—0.45 cm long, urceolate or shortly cylindrical, filaments free in the upper half and terminated by (3)4—6(10) unequal filiform appendages, the outer pair longer than the others and 1.5—3 times as long as the anthers. Anthers (9)10, with a few hairs on the back, inserted just below the terminal appendages; connective produced to form a point or short slender appendage. Filament appendages in female flowers 2 or 3(4); antherodes very slender, not dehiscing, without pollen. *Disk* a swollen annulus fused to the base of the ovary. *Ovary* 3-locular; loculi with 1 or 2 superposed ovules; style-head capitate with 3(4) minute obtuse lobes. Pistillode very slender, scarcely expanded at the base, 3(4)-locular, loculi with 1 or 2 vestigial ovules. *Fruit* a 3(4)-valved loculicidal capsule; loculi 1(2)-seeded. *Seed* plano-convex with a flattened base; testa leathery. Arillode thin-fleshy, surrounding the basal ⅓ to ½ of seed. Endosperm absent. *Embryo* with plano-convex, collateral cotyledons; radicle superior, included or extending to the surface.

Chromosome number: n= 14 (*P. zenkeri* Harms).

Pollen: Pollen grains 3 or 4(5)-colporate, oblate-spheroidal or spheroidal (*c.* 60 μ m; amb rounded). Apocolpium large. Ora circular. Exine smooth.

Secondary xylem: solitary and in radial rows of 2—6, with a few pore clusters; tangential diameter 20—60 μm; intervascular pits 3 μm; gum present. *Ray tissue*: heterogeneous Kribs Type 3, but some rays are homocellular; rays 1- or 2-seriate, up to 25 cells high, the heterocellular with 1 marginal row. *Fibres*: non-septate. *Parenchyma*: Paratracheal: vasicentric. Apotracheal: terminal bands present.

Distribution: One or possibly two species in Cameroun and Gabon.

Type species: *P. zenkeri* Harms.

Relationships: Harms, who had not examined mature fruit, unaccountably placed *Pterorhachis* in the *Turraeeae* next to *Cipadessa*. The only important morphological feature *Pterorhachis* shares with true members of this tribe is the winged rhachis (shared by *Naregamia* which is, however, different in all other respects). In gross morphological features *Pterorhachis* is very similar to *Trichilia* from which it differs principally in having more numerous filament appendages. The appendages are more numerous in the male flowers than in the female, but in the latter a high proportion of the filaments of every flower bears 3 appendages. This immediately distinguishes *Pterorhachis* from *Trichilia* whose filaments never have more than two appendages.

The secondary xylem of *Turraea*, *Pterorhachis*, and *Trichilia* is so similar that it is of no assistance in determining their relationships. However, the pollen of *Pterorhachis* is quite different from that of the *Turraeeae*, and in all essential features confirms its close relationship with *Trichilia*. *Pterorhachis* does, however, differ from most species of *Trichilia* in its spheroidal grains, but this feature occurs occasionally in *Trichilia*, as in *T. hirta* L.

13. WALSURA

Walsura Roxb. [Hort. Beng. (1814) 32, *nom. nud.*], Fl. Ind. ed. 2, 2 (1832) 387; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 118, t. 31, figs. A—D. — **Fig. 7a, b.**
[*Monocyclis* Wall. *ex* Voigt, Hort. Suburb. Calc. (1845) 135, *nom. nud.*]
Surwala M. J. Roem., Synops. Hesp. Monogr. 1 (1846) 85, 108.
[*Scytalia* Ham. *ex* Wall., Cat. (1847) 8048 E, *nom. nud.*, *non* Gaertn. (1788).]
[*Melospermum* Scortech. *ex* King, Journ. As. Soc. Bengal 64 (2) (1895) 83, *nom. nud.*]
Napeodendron Ridley, Journ. Roy. As. Soc. Straits Branch 82 (1920) 179.

Trees or treelets. *Indumentum* of simple hairs. *Leaves* imparipinnate, trifoliolate, or unifoliolate; lower epidermis usually papillose; petiolules usually pulvinate. *Inflorescence* either axillary, or subtended by a small caducous scale-leaf and then crowded and apparently terminal, or borne on short axillary or lateral shoots; panicles usually large, rarely much reduced and subfasciculate; ultimate ramifications often cymose. *Flowers* bisexual and male or unisexual (then plants dioecious). *Calyx* deeply (4)5(6)-lobed or of free sepals, aestivation imbricate or open. *Petals* (4)5(6), free, usually imbricate, less frequently valvate, rarely contorted. *Stamens* 0.1—0.4 cm long, filaments usually fused in the lower half or to half or three quarters of their length, less frequently free; often terminated by a pair of lanceolate or deltate appendages or teeth. Anthers (7)10(14), hairy or glabrous, inserted apically on the filaments between the appendages (when present); connective often produced to form a short acute appendage; antherodes smaller, not dehiscing, without pollen. *Disk* in male and hermaphrodite flowers annular or patelliform; in female flowers represented by a small swelling at the base of the enlarged ovary. *Ovary* 2(3)-locular, loculi with 2 collateral ovules, or incompletely 4-locular and then the loculi uniovulate, ovoid and swollen in female and hermaphrodite flowers; style very short or absent; style-head capitate, or stout and truncate, or pileate, often with 2 or 3 short apiculi. Pistillode with a small flattened ovary immersed in the disk containing vestigial ovules, style present, style-head broader than in the female and hermaphrodite flowers. *Fruit* a 1 or 2-seeded berry with a fleshy or fibrous-fleshy pericarp. *Seed* partially or completely surrounded by a fleshy arillode, or exarillodiate. Endosperm absent. *Embryo* with plano-convex, collateral cotyledons; radicle superior, included or extending to the surface.

Germination: cryptocotylar; cataphylls minute, followed by spirally arranged, simple, entire eophylls.

Chromosome numbers: $n = 14$, $2n = 28$.

Pollen: Pollen grains 4(5)-colporate, prolate-spheroidal, subprolate or prolate

(35—85 µm; amb rounded or quadrangular). Apocolpium small to medium. Ora circular or lalongate. Exine smooth or scabrous, thickened at the apertures.

Secondary xylem: *Vessels:* solitary or in radial groups of 2(3); tangential diameter 60—120 µm; intervascular pits 3 µm; gum present or absent. *Ray tissue:* heterogeneous Kribs Type 3, or homogeneous Kribs Type 1 or 2, or uniseriate heterogeneous; rays 1—4-seriate, up to 40 cells high, the heterocellular with 1(2) marginal rows. *Fibres:* non-septate. *Parenchyma:* Paratracheal: vasicentric, aliform, confluent, and sometimes banded; crystals present or absent. Apotracheal: terminal bands present or absent. Diffuse cells present or absent. In some cases the parenchyma cells in radial section are partially storied and very short (only 1—3 times as tall as broad).

Distribution: About seven species in the Indo-Malesian region.

Type species: *W. piscidia* Roxb. (equals *W. trifolia* (A. Juss.) Harms).

Relationships: The relationships of *Walsura* with *Trichilia*, *Malleastrum*, and *Cipadessa* are discussed under these genera.

14. LEPIDOTRICHILIA

Lepidotrichilia (Harms) J. F. Leroy, Comp. Rend. Acad. Sci. Paris. 247 (1958) 1025; Journ. Agr. Trop. Bot Appl. 5 (1958) 673. — **Fig. 7c.**

Trichilia sect. *Lepidotrichilia* Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 1, 3 (4) (1896) 306; ed. 2, 19bI (1940) 112, t. 28, figs. T-V.

Trees with imparipinnate leaves. *Indumentum* stellate. *Flowers* bisexual or sometimes unisexual, in axillary thyrses. *Calyx* shallowly 5(6)-lobed. *Petals* 5, free, valvate. *Filaments* 0.3—0.7 cm long, connate in the lower half or to above half way, terminated by a pair of narrowly lanceolate to deltate-acuminate appendages, or completely fused to form a shortly cylindrical staminal tube with a toothed margin. Anthers 10, hairy or glabrous, inserted between the teeth or appendages. Antherodes similar, rather slender, not dehiscing, without pollen. *Disk* absent. *Ovary* 2—5-locular; loculi uniovulate. Style-head capitate, surmounted by 3—5 obscure or erect stigmatic lobes. *Fruit* a 1—5-seeded drupe with a thin membraneous or cartilaginous endocarp. *Seed* oblong to globose, exarillodiate; testa thin and membraneous or slightly fleshy. Endosperm absent. *Embryo* with plano-convex, collateral or oblique cotyledons; radicle superior or abaxial, included or slightly projecting.

Germination: cryptocotylar; eophylls opposite, simple, entire, becoming trifoliolate.

Chromosome number: 2n= 38 (*L. volkensii* (Harms) Leroy).

Pollen: Pollen grains 4-colporate, prolate-spheroidal (33—45 µm; amb rounded or quadrangular). Apocolpium medium. Colpi often shortly bifurcate; short colpi transversales sometimes present. Ora circular or lalongate. Exine medium or thick, smooth thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial rows of 2—5; tangential diameter 40—140 µm; intervascular pits 3—4.5 µm; gum present or absent. *Ray tissue:* a mixture of uniseriate-homogeneous and -heterogeneous; rays rarely partly biseriate, up to 20 cells high, the heterocellular with 1 marginal row. *Fibres:* non-septate. *Parenchyma:* Paratracheal: vasicentric, often of scattered cells, sometimes aliform. Apotracheal: bands present, with crystals.

Distribution: One species in east Africa and three in Madagascar.

Type species: *L. convallariaeodora* (Baill.) J. F. Leroy.

Relationships: *Lepidotrichilia* may be distinguished from all species of *Trichilia* by its fleshy indehiscent fruit. Valvate aestivation of free petals is known from only one

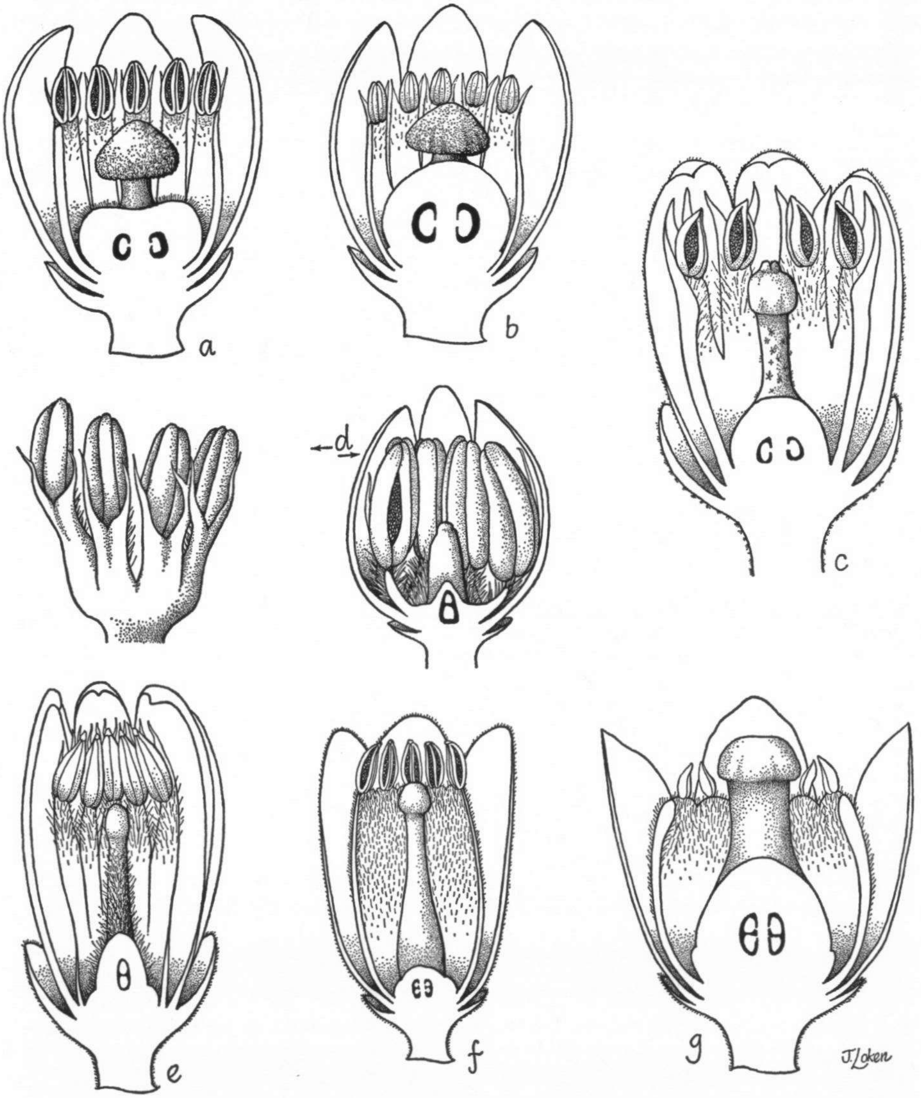

Fig. 7. a. *Walsura chrysogyne* (Miq.) Bakh., ♂, ×10; b. ditto, ♀, ×10. — c. *Lepidotrichilia volkensii* (Gürke) J. F. Leroy, ♀, ×10. — d. *Malleastrum gracile* J. F. Leroy, ♂, ×20. — e. *M. sp.* ♀, ×15. — f. *Ekebergia capensis* Sparrm., ⚥, ×7.5; g. ditto, ♀, ×15. (a. *Pennington 7907*; b. *Pennington 7831*; c. *Styles 180*; d. *Decary 1573*; e. *R.N. 2930*; f. *White 8212*; g. *White 8146*).

species of *Trichilia*, *T. cuneifolia* (L.) Urb. from the West Indies, and stellate indumentum occurs in only a few species of *Trichilia*.

The relationship of *Lepidotrichilia* with *Astrotrichilia* is discussed under the latter.

15. MALLEASTRUM

Malleastrum (Baill.) J. F. Leroy, Journ. Agr. Trop. Bot. Appl. 11 (1964) 128. — **Fig. 7d, e.**
Cipadessa sect. *Malleastrum* Baill., Adansonia 11 (1874) 256.
Trichilia sect. *Eutrichilia* C. DC., Bull. Herb. Boiss. II, 1 (1901) 563, *pro parte, quoad T. mocquersii* C. DC., *T. obtusifolia* C. DC. *tantum*.
Trichilia sect. *Pterotorhachis* Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 116.

Trees or shrubs. *Indumentum* of simple hairs. *Leaves* imparipinnate, trifoliolate, or unifoliolate, the rhachis sometimes winged. *Flowers* bisexual or unisexual, in small axillary panicles. *Calyx* 4—6-lobed to halfway or below, or almost truncate. *Petals* (3)5 or 6, free, valvate. *Filaments* 0.125—0.7 cm long, connate in the lower half or to above halfway, terminated by a pair of narrowly lanceolate or filiform appendages, or completely fused to form a cyathiform or shortly cylindrical staminal tube, the margin with (8)10 lanceolate, filiform, or shallowly to deeply bifid appendages alternating with the anthers. Anthers (8)10, hairy or glabrous, inserted between the appendages. Antherodes narrower, rather shrunken, not dehiscing, without pollen. *Disk* annular, hairy or rarely glabrous, fused to the base of the ovary, or absent. *Ovary* 1—3(5)-locular; loculi with 2 superposed or slightly oblique ovules. Style-head capitate, surmounted by a minute stigma with an apical depression. *Fruit* a 1—3(5)-locular berry, often asymetrical, the loculi 1-seeded; pericarp thin-fleshy. *Seed* oblong or spheroidal, exarillodiate. Testa thin and membraneous or sometimes thickened and rather hard. Endosperm absent. *Embryo* with plano-convex, collateral or oblique cotyledons. Radicle superior, included or extending to the surface.

Pollen: Pollen grains (3)4-colporate, spheroidal, prolate-spheroidal, or subprolate (30—40 μm; amb rounded or quadrangular). Apocolpium medium to large. Short colpi transversales sometimes present. Ora circular or lalongate. Exine thick or medium, smooth to slightly scabrous, thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial rows of 2—5; tangential diameter 20—60 μm; intervascular pits 3 μm; gum present. *Ray tissue:* uniseriate-homogeneous or -heterogeneous; rays up to 20 cells high, the heterocellular with 1 marginal row. *Fibres:* non-septate. *Parenchyma.* Paratracheal: vasicentric, of mainly scattered cells, occasionally aliform. Apotracheal: bands present, with crystals. Diffuse cells present, usually crystalliferous.

Distribution: About 12 species in Madagascar and the Comores.

Type species: *M. boivinianum* (Baill.) J. F. Leroy.

Relationships: Baillon (1874), who was unaware of the nature of the fruit, placed the first two species to be described, *M. boivinianum* (Baill.) Leroy and *M. depauperatum* (Baill.) Leroy, in the section *Malleastrum* of *Cipadessa*. C. de Candolle (1878) followed Baillon, but later described three further species under *Trichilia*. In the first edition of Die Natürlichen Pflanzenfamilien (1896) Harms followed Baillon, but in the second (1940) largely followed De Candolle, although he created a new section *Pterotorhachis* for *Trichilia ramiflora* C. DC.

Malleastrum differs from *Cipadessa* in the following characters: loculi with superposed ovules (loculi uniovulate or rarely with 2 collateral ovules in *Cipadessa*); the fruit is a 1—3(5)-seeded berry with a thin fleshy pericarp (a drupe with 5 pyrenes, endocarp bony, in *Cipadessa*); the seed is exendospermous (endospermous in *Cipadessa*); the embryo has plano-convex cotyledons with a short included radicle (cotyledons thin, flat; radicle long exserted in *Cipadessa*). In addition to these diagnostic characters, *Malleastrum* differs in the structure of the disk, when present, and the ovary, which is usually 1—3-locular compared with 5-locular in *Cipadessa*; the fruit of *Malleastrum* is generally 1-seeded, (5 pyrenes, each 1(2)-seeded in *Cipadessa*).

Cipadessa has very distinct secondary xylem and differs from *Malleastrum* in having very heterogeneous ray tissue (rays with 1—6 rows of marginal cells), septate fibres, and no diffuse parenchyma cells.

Malleastrum can be distinguished from *Trichilia* by its baccate fruit with an exarillodiate seed. The free valvate corolla lobes, constant in *Malleastrum*, are known only from one species of *Trichilia* (*T. cuneifolia* (L.) Urb.).

In gross morphology this genus appears to be closer to *Lepidotrichilia*, from which it differs in the simple indumentum and two superposed ovules in each locule (locule uniovulate in *Lepidotrichilia*). Differential characters often occurring in *Malleastrum* but never in *Lepidotrichilia* are the usually unilocular ovary and well marked annular disk. The structure of the secondary xylem also confirms that *Malleastrum* is closely related to *Lepidotrichilia*.

Malleastrum differs from *Walsura* in having loculi with 2 superposed ovules (loculi uniovulate or with two collateral ovules in *Walsura*). A character often present in *Malleastrum* but never in *Walsura* is the unilocular ovary. *Malleastrum* always has valvate aestivation of the corolla, whereas in *Walsura* it is imbricate or rarely contorted except in *W. robusta* Roxb. and very rarely in *W. pinnata* Hassk. The style-head of *Malleastrum* is always minute-capitate, usually no broader than the style, whereas that of *Walsura* is more developed and generally truncate or pileate. The seed of *Malleastrum* is always exarillodiate, while that of *Walsura* usually has an arillode. All species of *Walsura* except *W. chrysogyne* (Miq.) Bakh. *f.* have pulvinate petiolules, a character never present in *Malleastrum*.

16. EKEBERGIA

Ekebergia Sparrm., Svenska Vet. Akad. Handl. Stockh. 40 (1779) 282, t. 9; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 119, t. 29. — **Fig. 7 f, g.**

Charia C. DC., Bull. Soc. Bot. France Mém. 8 (1907) 9.

Trichlia sect. *Pterotrichilia* Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 1, 3(4) (1896) 307.

Trees or shrubs. *Indumentum* of simple hairs. *Leaves* imparipinnate. *Flowers* unisexual (plant dioecious), in axillary or supra-axillary thyrses. *Calyx* 4- or 5(6)-lobed in the upper half. *Petals* 4—6, free, imbricate. *Staminal tube* 0.15—0.5 cm long, urceolate to shortly cylindrical, filaments completely fused or connate just below the apex; margin of staminal tube without appendages. Anthers 8—10(13), hairy or glabrous, inserted on the rim of the staminal tube; antherodes very slender, not dehiscing, without pollen. *Disk* in male flowers annular or patelliform, partially fused to the base of the staminal tube and ovary; in female flowers represented by a small swelling fused to the base of the swollen ovary. *Ovary* 2—5(6)-locular; loculi with 2 superposed ovules; style short and stout; style-head capitate or thick discoid, with 2—5(6) small incurved stigmatic lobes and a central depression; pistillode with a slender vestigial ovary containing loculi and small ovules; style longer. *Fruit* a drupe with 2—5(6) pyrenes, each 1(2)-seeded; endocarp thin, woody or cartilaginous. *Seed* shaped like the segment of an orange; exarillodiate; testa thin. *Embryo* surrounded by fleshy endosperm or seed exendospermous; cotyledons plano-convex, collateral; radicle superior, short, slightly exserted.

Germination: phanerocotylar or cryptocotylar; eophylls opposite, trifoliolate or pinnate, the rhachis winged.

Chromosome numbers: 2n= 46, 50.

Pollen: Pollen grains 4(5)-colporate, oblate-spheroidal, spheroidal, prolate-spheroidal, or subprolate (25—40 μm; amb rounded). Apocolpium medium to small. Colpi often shortly bifurcate. Ora circular or lalongate. Exine smooth to scabrous, slightly thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial groups of 2(3); tangential diameter 100—140 μm; intervascular pits 7.5 μm; gum present. *Ray tissue:* homogeneous Kribs Type I; rays 2 or 3-seriate, up to 30 cells high. *Fibres:* non-septate. *Parenchyma.* Paratracheal: vasicentric. Apotracheal: terminal bands present. Diffuse crystalliferous cells present. The amount of apotracheal parenchyma varies from widely spaced, narrow terminal bands to abundant broad bands.

Distribution: 4 species in Africa.

Type species: *E. capensis* Sparrm.

Relationships: *Ekebergia* differs from *Trichilia* in its indehiscent drupaceous fruit which contains exarillodiate seeds without a sarcotesta. *Ekebergia* may be distinguished from *Lepidotrichilia* by the simple indumentum (stellate in *Lepidotrichilia*); imbricate aestivation of the corolla (valvate in *Lepidotrichilia*); annular or patelliform disk (disk absent in *Lepidotrichilia*); biovulate loculi (uniovulate in *Lepidotrichilia*.)

The secondary xylem of *Ekebergia* differs from that of *Trichilia* and *Lepidotrichilia* in its large intervascular pits (7.5 μm diameter). The rays are also broader (2- or 3-seriate) than in these two genera except for those of the two Asiatic species of *Trichilia.*

17. ASTROTRICHILIA

Astrotrichilia (Harms) J. F. Leroy, Compt. Rend. Acad. Sci. Paris 247 (1958) 1889; Journ. Agr. Trop. Bot' Appl. 5 (1958) 861. — **Fig. 8a.**

Trichilia sect. *Astrotrichilia* Harms in Engl. & Prantl, Nat. Pflanzenfam. ed 1, 3 (4) (1896) 306.

Trichilia sect. *Peltotrichilia* Harms, op. cit. ed. 2, 19 bI (1940) 111.

Trees with stellate indumentum at least on the young parts. *Leaves* pinnate or trifoliolate. *Flowers* bisexual or unisexual, in axillary thyrses or panicles. *Calyx* shallowly to deeply 5-lobed; aestivation open or imbricate. *Petals* 5, free, imbricate. *Staminal tube* 0.05—0.15 cm long, cyathiform, the margin almost entire or with 10(11) narrow lanceolate teeth bearing the anthers. Anthers 10(11), hairy or glabrous. Antherodes similar, not dehiscing, without pollen. *Disk* patelliform, fused to the base of the staminal tube, or absent. *Ovary* 2—5-locular; loculi with 2 usually superposed or rarely collateral ovules. Style-head thick, discoid. *Fruit* a 1—3-locular drupe; loculi 1-seeded; mesocarp thin and fleshy; endocarp thick, woody, with a cartilaginous inner face, sometimes with loculicidal dehiscence. *Seed* radially compressed, exarillodiate, with an indistinct sarcotesta. *Embryo* surrounded by thick endosperm; cotyledons thin, flat, collateral; radicle abaxial, small, slightly projecting.

Pollen: Pollen grains 4(5)-colporate, prolate-spheroidal or subprolate (*c.* 45 μm; amb rounded or angular). Apocolpium medium to large. Ora lalongate. Exine smooth or scabrous, thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial rows of 2—4(7); tangential diameter 40—160 μm; intervascular pits 4.5—6 μ m; gum present. *Rays tissue:* homogeneous Kribs Type I or uniseriate homogeneous; rays 1 or 2-seriate, up to 25 cells high. *Fibres:* non-septate or occasionally septate; with prominent bordered pits in the radial walls. *Parenchyma:* Paratracheal: sparse vasicentric, consisting entirely of scattered cells. Apotracheal: bands present with abundant crystals. Diffuse crystalliferous cells present.

Distribution: About 14 species in Madagascar.

Type species: *A. asterotricha* (Radlk.) J. F. Leroy.

Relationships: In its morphology and anatomy this genus is most closely allied to the endemic Australian genus *Owenia*, under which the relationships are discussed. It is also related to *Ekebergia* and *Lepidotrichilia*, though not so closely. It differs from *Ekebergia* in its stellate indumentum (simple in *Ekebergia*); thick woody endocarp (thin in *Ekebergia*), and its radially compressed seeds with a sarcotesta (seeds shaped like the segment of an orange and without a sarcotesta in *Ekebergia*). The embryo is surrounded by copious endosperm, which is known for only one species of *Ekebergia*. All these characters except the stellate indumentum, also distinguish *Astrotrichilia* from *Lepidotrichilia*, and in addition the latter genus has valvate aestivation of the corolla.

The secondary xylem of *Astrotrichilia* is similar to that of *Lepidotrichilia*, but can be distinguished by the large bordered pits in the radial walls of the fibres. The broader rays and larger intervascular pits of *Ekebergia* are sufficient to distinguish this genus.

18. OWENIA

Owenia F. Muell. in Hook. Kew Journ. Bot. 9 (1857) 303; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 122 — **Fig. 8b, c.**

Trees with paripinnate leaves. *Indumentum* of simple hairs. *Flowers* unisexual (plant dioecious), in axillary panicles. *Calyx* of 5 free imbricate sepals. *Petals* 5, free, imbricate. *Staminal tube* 0.1—0.3 cm long; margin irregularly lobed, the lobes forming a frill, or filaments free in the upper half and terminated by 2 narrowly lanceolate appendages. Anthers 10, glabrous, inserted inside the margin of the staminal tube or apically between the filament appendages; antherodes slender, indehiscent, without pollen. *Disk* small, annular, fused to base of ovary. *Ovary* 2- or 3(4)-locular; loculi uniovulate; in male flowers ovary smaller, not at all swollen, with vestigial ovules. Style abruptly expanded at the apex to form a shallow disk bearing a large conical 2- or 3-lobed stigma. *Fruit* a 2- or 3-locular drupe; mesocarp thin, leathery or fleshy, endocarp very thick, hard, and woody. *Seed* shaped like the segment of an orange, depressed or ovoid, exarillodiate, with a complete thin sarcotesta. *Embryo* surrounded by thin endosperm; cotyledons plano-convex, collateral; radicle superior, short, slightly exserted or extending to the surface.

Germination*: phanerocotylar; eophylls opposite, pinnate; rhachis winged (*O. reticulata* F. Muell., *O. vernicosa* F. Muell.).

Chromosome number: 2n= 28 (*O. acidula* F. Muell.) (Styles & Khosla, in press).

Pollen: Pollen grains 4- or 5-colporate, subprolate or prolate (30—40 μm; amb rounded). Apocolpium large or medium. Ora circular or lalongate. Exine smooth or scabrous, usually slightly thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial rows of 2 or 3(8), sometimes with pore clusters; tangential diameter 60—160 μm; intervascular pits 3.75—4.5 μm; gum present. *Ray tissue:* heterogeneous Kribs Type 3 or homogeneous Kribs Type 1 or 2; rays (1)2—5-seriate, up to 35 cells high, the heterocellular with 1 marginal row; sometimes the rays are almost storied. *Fibres*: non-septate. *Parenchyma:* Paratracheal: vasicentric and aliform, sometimes confluent. Apotracheal: terminal bands present, with crystals. Diffuse crystalliferous cells abundant.

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* Information kindly supplied by David Symon Esq., Waite Agricultural Research Institute, Glen Osmond, S. Australia.

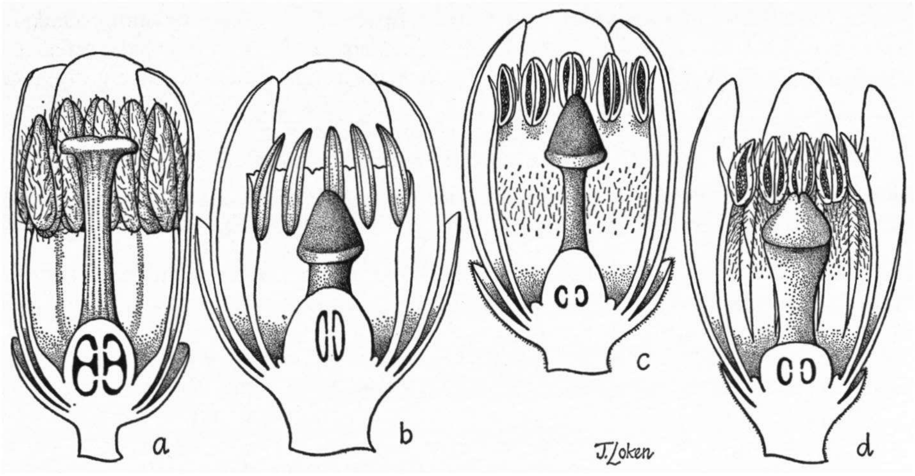

Fig. 8. a. *Astrotrichilia sp.*, ♀, ×15.— b. *Owenia acidula* F. Muell., ♀, ×15. — c. *O. reticulata* F. Muell., ♂, ×15. — d. *Cipadessa fruticosa* Bl., ⚥, ×25. (a. *Capuron 11319*; b. *Smith s.n.*; c. *Borden s.n.*; d. *Rao 18604*).

Distribution: About six species in eastern Australia.

Type species: *O. acidula* F. Muell. (here chosen as lectotype).

Relationships: This genus is closest to *Astrotrichilia*. It can, however, be distinguished on a number of characters. These are the simple indumentum, the form of the staminal tube with appendages, the uniovulate loculi, the form of the stigmatic lobes, and the plano-convex fleshy cotyledons with a superior radicle. The shape of the disk also provides distinction between these two genera.

The seeds of species in the genus have proved almost impossible to germinate.

19. CIPADESSA

Cipadessa Blume, Bijdr. (1825) 162; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 93, t. 21, figs. A-D. — **Fig. 8d.**
Mallea A. Juss., Mém. Mus. Hist. Nat. Par. 19 (1830) 221.

Small trees or treelets with imparipinnate leaves. *Indumentum* of simple hairs. *Flowers* bisexual and unisexual on the same individual (polygamous), in axillary panicles. *Calyx* 5-lobed in the upper half. *Petals* 5, free, valvate. *Filaments* 0.15—0.25 cm long, connate near the base, terminated by a pair of narrowly lanceolate to filiform appendages. Anthers 10, hairy, acute or apiculate, inserted between the appendages. *Disk* patelliform, fused to the base of the staminal tube. *Ovary* 5(6)-locular; loculi with 1(2) collateral ovules. Style short, stout, columnar, terminated by a swollen capitate style-head with 5 small, stigmatic lobes. *Fruit* a small globular drupe with 5 pyrenes, each 1(2)-seeded. Endocarp bony. *Seed* shaped like the segment of an orange, exarillodiate; testa thin, membraneous. *Embryo* surrounded by copious endosperm; cotyledons thin, flat, collateral; radicle superior, long exserted.

Germination: phanerocotylar; eophylls opposite or subopposite, ternate or trifoliolate. (*C. baccifera* (Roth) Miq.)

Chromosome numbers: 2n= 28, 56.

Pollen: Pollen grains 4(5)-colporate, prolate-spheroidal (30—40 µm; amb rounded). Apocolpium large. Ora lalongate. Exine smooth, slightly thickened at the apertures.

Secondary xylem: *Vessels:* in radial rows of 2—4; tangential diameter 60—120 µm; intervascular pits 3.75 µm; gum present. *Ray tissue:* uniseriate-heterogeneous; rays 1(2)-seriate, up to 30 cells high, the heterocellular with 1—6 marginal rows; often composed entirely of upright cells. *Fibres:* septate. *Parenchyma:* Paratracheal: sparse vasicentric. Apotracheal: terminal bands present, with crystals.

Distribution: One or two species in the Indo-Malayan region.

Type species: *C. fruticosa* Bl. (equals *C. baccifera* (Roth.) Miq.).

Relationships: Harms placed *Cipadessa* in the tribe *Turraeeae* next to *Munronia*, on account of the endospermous seed and embryo with exserted radicle. Endospermous seeds are now known to occur sporadically in other genera of the *Melioideae*, e.g. in *Ekebergia pterophylla* (C.DC.) Hofm. and some species of *Trichilia*. This fact alone would not provide sufficient ground for removing *Cipadessa* from the *Turraeeae*, but other vegetative, floral, fruit, and pollen characters indicate that it is incorrectly placed there and that it is more closely related to *Ekebergia*, *Astrotrichilia*, and *Walsura* in the *Trichilieae*.

The secondary xylem, however, is very distinctive and unlike that of any other member of the *Trichilieae* in having septate fibres correlated with very heterogeneous ray tissue, and in this respect it is similar to *Vavaea*.

Walsura is similar to *Cipadessa* in the structure of the androecium, but differs in the annular disk surrounding the 2—4-locular ovary and in the fruit which is a fleshy berry.

Ekebergia differs in several characters. These are the imbricate aestivation of the corolla, the entire staminal tube without appendages, and the superposed ovules.

Both *Owenia* and *Astrotrichilia* differ in having imbricate corolla lobes, filaments which are fused in the upper half or completely, in the shape of the style-head, and in the extremely thick bony endocarp of the fruit.

The relationships of *Cipadessa* with *Malleastrum* are discussed under the latter.

Tribe 5. AGLAIEAE

Tribus **Aglaieae,** *tribus nova.*

Folia fere pinnata. Indumentum fere stellatum vel ex squamis peltatis constans. Tubus stamineus fere globularis vel cyathiformis, semper appendicibus carens. Discus nullus. Fructus fere baccatus. Semina fere sarcotesta, rarius arillodio praedita; endospermium nullum. Cotyledones fere superpositae; radicula inclusa.

Typus tribus: *Aglaia.*

Leaves usually pinnate, rarely trifoliolate or unifoliolate. Indumentum usually of stellate or simple hairs or of peltate scales. Flowers hermaphrodite or unisexual (plants dioecious). Staminal tube usually globular or cyathiform, always without appendages. Disk absent. Fruit usually a berry. Seeds usually with a sarcotesta, less frequently arillodiate; without endosperm. Cotyledons usually superposed; radicle included.

Pollen: Usually subprolate or prolate, very small (10—30(35) µ m); usually 3-colporate; exine usually smooth.

Secondary xylem. Fibres septate; apotracheal terminal bands usually absent; paratracheal parenchyma aliform, confluent, and banded.

1. Anthers in a single whorl; indumentum of stellate or simple hairs or peltate scales.
    2. Cotyledons free, nearly always superposed.
        3. Indumentum of stellate hairs or peltate scales; inflorescence nearly always axillary, usually a panicle; petals 3—6; ovary 1—3(4)-locular; style very short or absent, style-head small, capitate, clavate, or conical, sometimes lobed; fruit usually a berry, less frequently a nut or capsule . . . . . . 20. *Aglaia*

3a. Indumentum of simple hairs; flowers cauliflorous or ramiflorous; inflorescence nearly always a simple or compound spike, rarely a raceme; petals 5; ovary 5-locular; style long and broad-columnar, gradually tapering to the truncate style-head; fruit a berry . . . . 21. *Lansium*

Cotyledons completely fused, collateral; indumentum usually of simple hairs (stellate in one species); inflorescence nearly always a long spike or panicle with spicate branches; petals 3; ovary 3(4)-locular, loculi mostly biovulate; fruit a capsule . . . . 22. *Aphanamixis*

1a. Anthers in 2 alternating whorls of 5; indumentum of simple hairs.

4. Fruit a berry; petals fused to staminal tube at the base; anthers of lower whorl with short acute connective appendages; seed exarillodiate, usually with a sarcotesta; cotyledons superposed, free . . . . 23. *Reinwardtiodendron*

4a. Fruit a capsule; petals free from staminal tube; anthers without connective appendages; seed arillodiate; cotyledons collateral, completely fused 24. *Sphaerosacme*

20. AGLAIA

Aglaia Lour., Fl. Cochinch. (1790) 173, *nom. conserv.* (*Aglaia* Lour. is conserved against *Aglaia* Allamand• Nova Act. Acad. Leop. – Carol 4, 1770, 93, *Cyperaceae*); Harms in Engl. & Prantl, Nat. Pflanzenfam., ed, 2, 19 bI (1940) 140, t. 31, figs. A-Q — Fig. 9a—f.

Camunium Rumph. [Herb. Amb. 5 (1747) 26, t. 18 f. 1] *ex* Roxb., Fl. Ind. 2 (1824) 425, *non* Adans. (1763) (=*Murraya* Koen. *ex* L.).

Amerina Noronha, Verh. Bat. Gen. 5(2) (1790) 64, *nom. nud.*, *non* Rafin. (1838) *nec* DC. (1840).

Andersonia Roxb., Hort. Beng. (1814) 87, *nom. nud.*, *pro parte quoad A. cucullata* Roxb. *tantum*; Fl. Ind. ed. 2, 2 (1832) 212, *pro parte.*, *non* R. Br. (1810) *nec* Willd. *ex* Roem. & Schult. (1819).

Milnea Roxb. [op. cit. (1814) 18, *nom. nud.*] Fl. Ind. ed. Carey & Wall. 2 (1824) 430, *non* Rafin. (1838).

?*Nyalelia* Dennst., Schlüssel Hort. Malabar. (1818) 30.

Amoora Roxb., Pl. Coromandel 3 (1819) 54, t. 258; Harms tom. cit. 128.

Nemedra A. Juss., Mém. Mus. Hist. Nat. Par. 19 (?1830) 223.

Argophilum Blanco, Fl. Filip. (1837) 186 ('*Argopyilum*'), *non Argophyllum* Forst. (1776).

Selbya M. Roem., Synops. Hesp. Monogr. 1 (1846) 89, 126.

Nimmoia Wight, Calc. Journ. Nat. Hist. 7 (1847) 13, *non* Wight (1837).

Euphora Griff., Notul. 4 (1854) 547.

Oraoma Turcz., Bull. Soc. Nat. Mosc. 31 (1858) 411.

Beddomea Hook. *f.* in Benth. & Hook. *f.*, Gen. Pl. 1 (1862) 336.

Hearnia F. Muell., Fragm. 5 (1865) 55.

Aglaiopsis Miq., Ann. Mus. Bot. Lugd. Batav. 4 (1868) 58.

Lepiaglaia Pierre, Fl. Forest. Cochinch. sub t. 334 (1895), sub t. 352 (1896).

Merostela Pierre, op. cit. sub t. 334 (1895), sub t. 342 (1896).

Trees or treelets with pinnate or rarely trifoliolate or unifoliolate leaves. *Indumentum* of stellate hairs or peltate scales at least on the young parts. *Flowers* unisexual (plants dioecious), usually in axillary panicles, rarely cauliflorous; male inflorescence large and many-flowered, female smaller, fewer-flowered and sometimes reduced to a short spike. Female flowers often much larger than the male. *Calyx* shallowly or deeply (2)3—5-lobed; aestivation open or imbricate. *Petals* 3—6, free or united below, free from the staminal tube or partially united to it, imbricate. *Staminal tube* 0.05—0.55 cm long, globose, urceolate, campanulate, cyathiform, or rarely shortly cylindrical, the throat open or constricted, with an entire or crenate or rarely lobed margin. Anthers (3)5—10(19), glabrous or rarely hairy, inserted in a single whorl in the lower or upper half of the staminal tube or on the margin. Antherodes similar, without pollen. *Disk* absent. *Ovary* 1—3(4)-locular; loculi with 1 or 2-collateral or superposed ovules. Style short or absent. Style-head usually small, capitate, conical, or clavate, sometimes with 3 or 4 small lobes. Pistillode usually minute, ovules very small or absent. *Fruit* a 1—4(6)-seeded berry, nut, or less frequently a 2- or 3-valved loculicidal capsule. *Seed* arillodiate or less frequently with a sarcotesta; arillode fleshy, free or partly fused, partly or completely surrounding the seed; sarcotesta fleshy, often vascularized. *Embryo* with thick, plano-convex, superposed or very rarely oblique to collateral, free cotyledons; radicle included.

Germination: cryptocotylar, eophylls usually opposite, sometimes spirally arranged, simple or trifoliolate, margin entire (*A. sp., KEP FRI. 15187*, Malaya; *A. odoratissima* Bl., *A. eusideroxylon* Koord. & Valet. (Burger, 1972)).

Chromosome numbers: n= 20, 40; 2n= 92.

Pollen: Pollen grains 3(4)-porate or-colporate, subprolate or prolate, rarely spheroidal (10—30 μm; amb rounded or triangular). Apocolpium large. Ora circular or lalongate, rarely crassimarginate. Exine smooth or rarely minutely scabrous, thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial groups of 2—8, rarely showing an oblique pattern; tangential diameter 40—300 μm; intervascular pits 1.5—4.5 μm; gum present or absent. *Ray tissue:* usually heterogeneous Kribs Type 3, homogeneous Kribs Type 1, or uniseriate-heterogeneous, more rarely heterogeneous Kribs Type 2, homogeneous Kribs Type 2 or uniseriate homogeneous; rays 1 or 2(4)-seriate, up to 40 cells high, the heterocellular with 1(3) marginal rows. *Fibres:* septate. *Parenchyma.* Paratracheal: vasicentric, aliform, confluent and often banded, with crystals (the latter very rarely absent). Apotracheal: terminal bands usually absent, very rarely present. Diffuse crystalliferous cells occasionally present.

Distribution: About 100 species in the Indo-Malesian region, Australia, Melanesia, and Polynesia.

Type species: *A. odorata* Lour.

Relationships: *Aglaia* has more synonyms than most genera in the *Melioideae*, due to the considerable variation within it. The majority of species are similar to the type *A. odorata* Lour. in having the following combination of characters: 5 petals; 5 anthers inserted within the throat of the staminal tube; a bilocular ovary; a baccate fruit. Since Loureiro described the type species, a number of closely related genera have been described which differ from typical *Aglaia* in single features, e.g. *Milnea* has a 3-locular ovary; *Hearnia* has the anthers inserted on the margin of the staminal tube; *Beddomea* has a capsular fruit. It can be easily demonstrated that intermediates exist, e.g. many species have a 2 or 3-locular ovary, and that there is no justification for maintaining these genera.

The type of *Amoora*, *A. cucullata* Roxb., differs from typical *Aglaia* in more respects; it has 3 petals, 6—8 anthers, a 3-locular ovary, and a capsular fruit. Since *A. cucullata* was described, other, less extreme species have been discovered which provide connecting links, so that it is now impossible to recognize *Amoora* as a distinct entity. Various authors have maintained *Amoora* on the basis of single characters. C. de Candolle (1878) emphasized the number of anthers, King (1895) the number of petals, and Harms (1940) considered dehiscence of the fruit to be most important. Because these characters are not completely correlated, the circumscription of *Amoora* differs according to which character is emphasized, and none is satisfactory. Pellegrin (1909), one of the few authors who has united *Amoora* with *Aglaia*, gives a detailed account of the gradation of morphological characters between the two groups, though later (1946: 48) he apparently had second thoughts, again without stating his reasons.

Characters of the secondary xylem show similar intergradation. Typical *Aglaia* has 1 or 2-seriate rays and a mixture of confluent and banded parenchyma, whereas typical *Amoora* has 2- or 3-seriate rays with vasicentric and aliform parenchyma. *Aglaia argentea* Bl. has 2-seriate rays with aliform parenchyma; *Amoora cucullata* Roxb. has 1- or 2-seriate rays with aliform and confluent parenchyma.

The relationships of *Aglaia* with *Lansium*, *Reinwardtiodendron*, and *Aphanamixis* are discussed under those genera.

21. LANSIUM

Lansium Rumph. [Herb. Amb. 1 (1741) 151, t. 54] *ex* Corr., Ann. Mus. Hist. Nat. Paris 10 (1807) 157, t. 10 fig. 1; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 123, t. 30, figs. J-P, *pro parte quoad sectio Eulansium tantum*. — **Fig. 9g, h.**

[*Plutea* Noronha, Verh. Batav. Gen. 5 (2) (1790) 64, *nom. nud.*]

[*Lachanodendron* Reinw. *ex* Blume, Cat. Gew. Buitenzorg (1823) 70, *nom. nud.*]

Aglaia sect. *Lansium* (Corr.) Kosterm., Reinwardtia 7 (1966) 221 *pro parte.*

Trees with pinnate leaves. *Indumentum* of simple hairs. Ramiflorous; or occasionally cauliflorous, the flowers in spikes, or slender racemes, or panicles branched from the base with spicate branches. *Flowers* unisexual (plants dioecious) and bisexual, perfect flowers, larger than the male. *Calyx* deeply 5-lobed; lobes imbricate. *Petals* 5, free from each other, but fused to the staminal tube in the lower half; imbricate. *Staminal tube* 0.2—0.4 cm long, globular to cyathiform, with an undulate or crenate margin. Anthers (8)10, glabrous, inserted in a single whorl inside the throat of the tube and scarcely exserted beyond the rim. *Disk* absent. *Ovary* 5-locular; loculi uniovulate. Style long and broad-columnar, not or only slightly expanded at the truncate style-head, the margin ribbed with the impression of the surrounding anthers. Pistillode more slender, (3)5-locular; ovules smaller. *Fruit* a 1—5-seeded berry with soft pericarp. *Seeds* with a thick, fleshy, whitish arillode closely applied but not fused to the testa. *Embryo* with thick, plano-convex, superposed, free cotyledons; radicle included.

Chromosome number: n= 72 (*L. domesticum* Corr.)

Pollen: Pollen grains 3—5-colporate, oblate-spheroidal (20—28 μm; amb rounded). Apocolpium large. Ora circular. Exine smooth or finely scabrous, thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial rows of 2 or 3; tangential diameter 60—120 μm; intervascular pits 3.75 μm; gum absent. *Ray tissue:* heterogeneous Kribs Type 3; rays 1- or 2-seriate, up to 20 cells high, the heterocellular with 1 marginal row. *Fibres:* septate. *Parenchyma.* Paratracheal: confluent and banded, with crystals.

Distribution: Probably 1—5 variable species in western Malesia.

Type species: *L. domesticum* Corr.

Relationships: *Lansium* as accepted by Harms is heterogeneous, and his first section *Eulansium*, containing *L. domesticum* Corr. and its varieties, occupies an isolated position within it. Harms' second section, *Neolansium* (containing *L. humile* Hassk., *L. cinereum* Hiern, *L. anamallayanum* Bedd., and *L. dubium* Merr.) differs from *Eulansium* in the following characters: inflorescence axillary (ramiflorous or cauliflorous in *Eulansium*); anthers in two alternating whorls of five, the lower whorl with a short connective appendage (one whorl of 10 anthers without appendages in *Eulansium*); style very short with a small, capitate, and obscurely-lobed style-head (style long, columnar, not or only slightly expanded at the truncate style-head in *Eulansium*); corolla fused to the staminal tube at the base only (corolla fused for almost half its length to the staminal tube in *Eulansium*). As all the characteristics of section *Neolansium* mentioned above are shared by the genus *Reinwardtiodendron*, the species of this section are therefore transferred to the latter genus.

Harms' third section *Pseudolansium* contains the single species *L. decandrum* (Wall.) Harms which differs from the type in many floral and fruiting characters. In the present

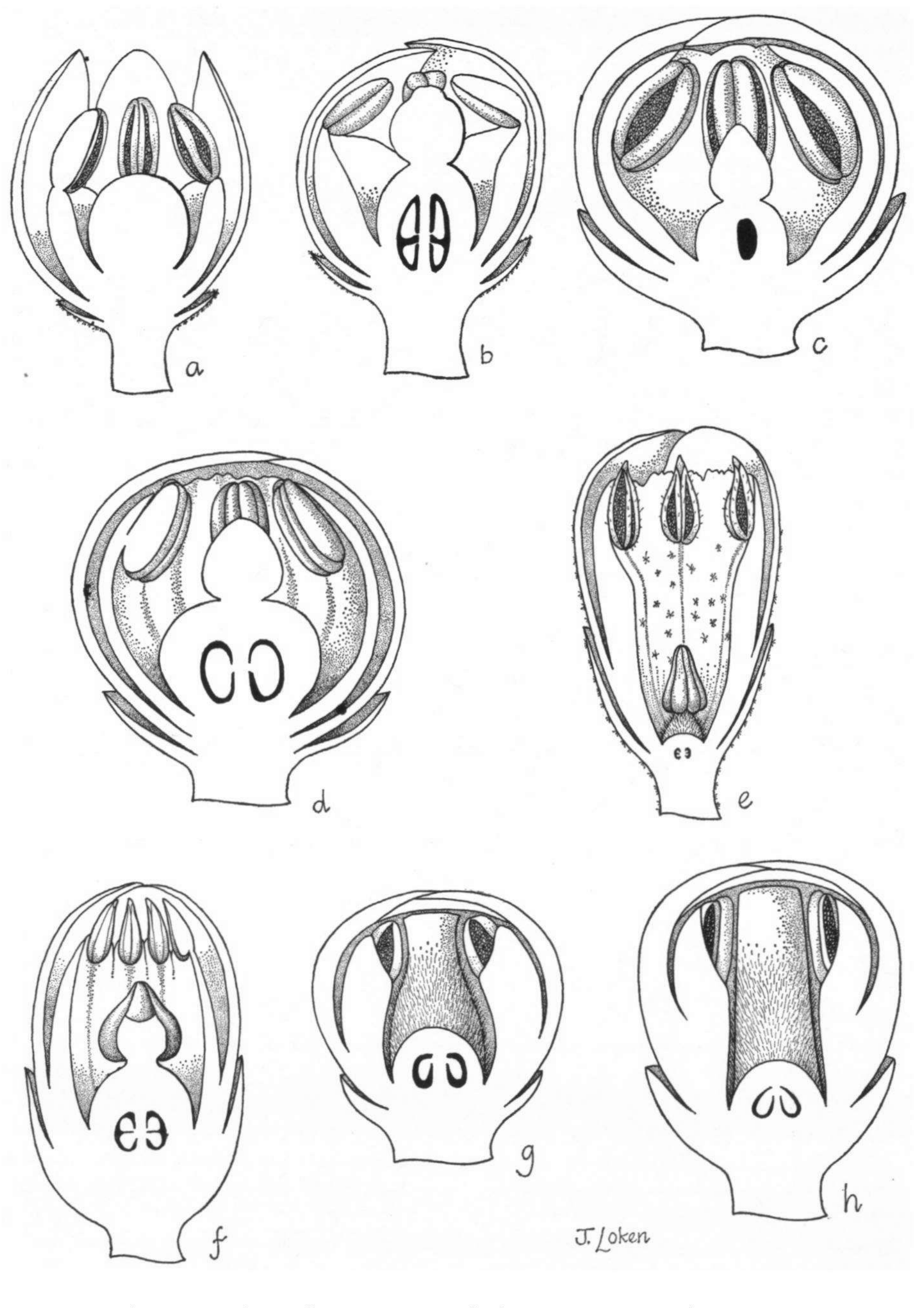

Fig. 9. a. *Aglaia sapindina* (F. Muell.) Harms, ♂, ×35; b. ditto, ♀, ×25 — c. *A. elaeagnoidea* (A. Juss.) Benth., ♂, × 50; d. ditto, ♀, ×35. — e. *A. sp.*, ♂, × 10; f. *A. sp.*, ♀, ×5. — g. *Lansium domesticum* Corr., ♂, ×10; h. ditto, ⚥, ×7.5. (a. *Hollrung 25*; b. *N.G.F. 3133*; c. *Rahman 2694*; d. *Pennington 8130*; e. *Pennington 7903*; f. *Pennington 7902*; g. *Pennington 7972*; h. *Pennington 7989*).

work it is elevated to generic rank *(Sphaerosacme)*. Its relationships are discussed in detail after the description.

Aglaia section *Lansium* of Kostermans (1966) is also heterogeneous and those species of it whose floral characters are known, can be confidently placed in either *Lansium* (*A. steenisii* Kosterm., *A. aquea* (Jack) Kosterm., *A. dookkoo* Griff., *A. domestica* (Corr.) Pellegr., *A. sepalina* (Kosterm.) Kosterm. or *Reinwardtiodendron* (*A. reinwardtiana* Kosterm., *A. pseudolansium* Kosterm., *A. kinabaluensis* Kosterm., *A. dubia* (Merr.) Kosterm., *A. anamallayana* (Bedd.) Kosterm.). Flowering material is needed before the remaining five species described in Kosterman's monograph can be placed with certainty.

Lansium, as defined in the present work, is distinguished from *Aglaia* by its simple indumentum (not stellate or peltate); its 5-locular ovary (1—4-locular in *Aglaia*), and by the structure of its style and style-head. Other features of *Lansium* which are rarely found in *Aglaia* are the ramiflory or cauliflory and the spicate inflorescence.

The secondary xylem of *Lansium* cannot be distinguished from that of some species of *Aglaia*. Its pollen morphology is, however, quite distinct, the 3—5-colporate, oblate-spheroidal pollen grains differ from those of all known *Aglaia* species which are 3(4)-colporate and nearly always prolate or prolate-spheroidal.

22. APHANAMIXIS

Aphanamixis Blume, Bijdr. (1825) 165; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 126 t. 30, fig. Q — **Fig. 10a, b.**

Andersonia Roxb. [Hort. Beng. (1814) 87 *nom. nud.*, *pro parte quoad A. rohituka* Roxb. *tantum*] Fl. Ind. 2, (1832) 212, *non* R. Br. (1810) *nec* Willd. *ex* R. & S. (1819).

[*Sphaerosacme* Wall., Num. List (1829) n. 1277 *nom. nud.*, *pro parte quoad S. polystachya* Wall. *tantum.*]

Aphanomyxis DC., Prod. 7 (2) (1839) 766.

[*Chuniodendron* Hu, Journ. Roy. Hort. Soc. 63 (1938) 387 in obs., *nom. nud.*]

Trees or treelets with pinnate leaves. *Indumentum* of simple or very rarely stellate hairs. *Flowers* unisexual (plant dioecious) or bisexual. *Inflorescence* axillary or supra-axillary, the male flowers in large panicles with spicate or rarely racemose branches, the female and hermaphrodite ones in long spikes or rarely in large panicles with spicate branches. Male flowers smaller than female and hermaphrodite. *Calyx* deeply 5-lobed; lobes imbricate. *Petals* 3, free, fused in the lower half to the staminal tube, imbricate. *Staminal tube* 0.15—0.45 cm long, globose or deeply cyathiform, the throat narrow or wide; margin entire or slightly crenate. Anthers 3—8, glabrous, inserted within the throat in the upper or lower half of the staminal tube, completely included or partly exserted; connective sometimes produced to form a short terminal appendage. Antherodes indehiscent, without pollen. *Disk* absent. *Ovary* 3(4)-locular; loculi with (1)2 collateral to superposed ovules. Style very short and broad, terminated by a large, conical, 3-angled stigma, or style longer, stout, and then terminated by a truncate stigma, the margin ribbed with the impression of the surrounding anthers. Pistillode with rudimentary ovules present or absent. *Fruit* a 2 or 3(4)-valved loculicidal capsule; loculi 1- or 2-seeded. *Seeds* partly or completely surrounded by a free fleshy arillode. *Embryo* with plano-convex, collateral, fused cotyledons; radicle small, superior, included.

Germination: cryptocotylar, eophylls opposite, simple, toothed (*A. polystachya* (Wall.) R. N. Parker)

Chromosome numbers: n= 18, 2n= 76, *c.* 150.

Pollen: Pollen grains 4-colporate, subprolate or prolate (20—35 μm; amb rounded or quadrangular). Apocolpium large. Ora circular or lalongate. Exine smooth or more frequently scabrous, thickened at the apertures.

Secondary xylem: *Vessels:* solitary and in radial rows of 2—4(5), rarely with some pore clusters; tangential diameter 60—180 μm; intervascular pits (4.5)6—7.5 μm; gum present or absent. *Ray tissue:* heterogeneous Kribs Type 3 or uniseriate-heterogeneous or -homogeneous; rays 1- or 2-seriate, up to 35 cells high, the heterocellular with 1 marginal row. *Fibres:* septate. *Parenchyma.* Paratracheal: confluent and banded, often exclusively banded, with or without crystals. Diffuse crystalliferous cells present or absent. Silica deposits were present in the ray tissue of all species examined.

Distribution: About four species from the Indo-Malayan region to New Guinea and the Solomon Islands.

Type species: *A. grandifolia* Bl.

Relationships: This genus is allied to *Aglaia*, but is easily distinguished from it by a number of morphological, palynological, and anatomical characters. The embryo of *Aphanamixis* has cotyledons which are fused throughout their length, a condition unknown elsewhere in the subfamily, except in *Sphaerosacme*. A differential character never occurring in *Aglaia* is the simple indumentum, present in all species of *Aphanamixis* except *A. cumingiana* (C. DC.) Harms. Other characters found in *Aphanamixis* but very rarely in *Aglaia* are the long spicate inflorescence and collateral cotyledons. In the field, the characteristic long, spicate female inflorescence enables *Aphanamixis* to be identified without difficulty.

The pollen of *Aphanamixis* differs from that of *Aglaia* in being consistently 4-colporate, a feature recorded in only one species in *Aglaia*. In addition, the pollen grains of *Aphanamixis* are frequently distinctly scabrous while those of *Aglaia* are always smooth.

In its secondary xylem *Aphanamixis* is homogeneous and distinct from *Aglaia*. It differs in the presence of silica deposits in the ray tissue, from *Aglaia sensu stricto* by the larger intervascular pits (4.5—7.5 μ m), and from those species of *Aglaia* formerly included in *Amoora* by the confluent and banded paratracheal parenchyma, in addition to the usually larger intervascular pits.

Aphanamixis is also fairly close to *Lansium* and *Reinwardtiodendron* but may be readily distinguished from them by its corolla of 3 petals (5 in *Lansium* and *Reinwardtiodendron*), its capsular fruit, and the structure of the seed. The large intervascular pits and presence of silica deposits also distinguish the wood anatomy of *Aphanamixis* from that of *Lansium* and *Reinwardtiodendron*.

In view of the very distinct morphology, palynology, and wood anatomy of this genus, it is surprising that *Aphanamixis* has so frequently been confused with other members of the *Aglaieae*.

23. REINWARDTIODENDRON

Reinwardtiodendron Koord., Meded. van s'Lands Plantentuin Buitenzorg 19 (1898) 389; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 125. — **Fig. 10c.**

Lansium sect. *Neolansium* Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 124.

Aglaia sect. *Lansium* (Corr.) Kosterm., Reinwardtia 7 (1966) 221 *pro parte.*

Trees with pinnate, trifoliolate, or unifoliolate leaves. *Indumentum* of simple hairs. *Flowers* bisexual, in axillary spikes or panicles with spicate branches. *Calyx* deeply 5-lobed; lobes imbricate. *Petals* 5, free from each other but fused to the staminal tube at the base. *Staminal tube* 0.15—0.3 cm long, globose, cyathiform, or ovoid, with an undulate or toothed margin. Anthers 10, glabrous, in 2 whorls of 5, the upper partly exserted, the lower alternating with the upper and completely included; anthers of the lower whorl with connective produced to form a short acute appendage. *Disk* absent. *Ovary* (3)5-locu-

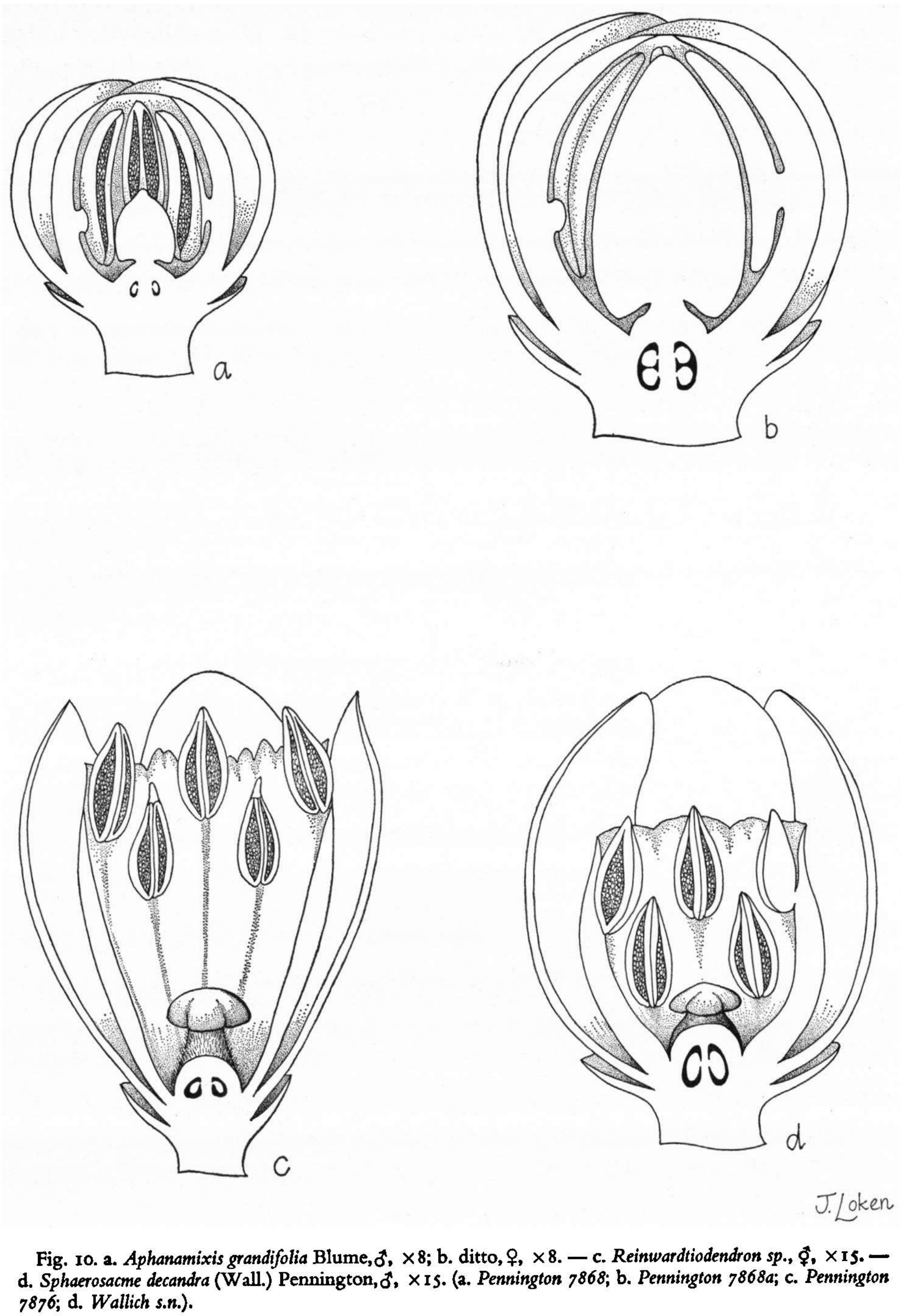

Fig. 10. a. *Aphanamixis grandifolia* Blume, ♂, ×8; b. ditto, ♀, ×8. — c. *Reinwardtiodendron sp.*, ⚥, ×15. — d. *Sphaerosacme decandra* (Wall.) Pennington, ♂, ×15. (a. *Pennington 7868*; b. *Pennington 7868a*; c. *Pennington 7876*; d. *Wallich s.n.*).

lar; loculi with 1(2) collateral ovules. Style very short, with a small capitate or pileate and obscurely lobed style-head. *Fruit* a 1- or 2-seeded berry. *Seed* exarillodiate, usually with a sarcotesta. *Embryo* with thick, plano-convex, superposed, free cotyledons; radicle included.

Pollen: Pollen grains 3- or 4-colporate, prolate-spheroidal or subprolate (22—26 μm; amb rounded). Apocolpium medium. Ora circular or lalongate. Exine smooth, thickened at the apertures.

Secondary xylem: *Vessels*: solitary and in radial rows of 2 or 3(5), rarely with some pore clusters; tangential diameter 40—100 μm; intervascular pits 2.25 μm; gum present. *Ray tissue*: homogeneous Kribs Type 1 or uniseriate-homogeneous; rays 1- or 2-seriate, up to 20 cells high. *Fibres* septate. *Parenchyma*. Paratracheal: aliform, confluent and banded, with crystals.

Distribution: 4 or 5 species in the Indo-Malesian region.

Type species: *R. celebicum* Koord.

Relationships: *Reinwardtiodendron* is related to *Aglaia* and *Lansium* but can be distinguished from both these genera by a number of characters. It differs from all species of *Aglaia* in its simple indumentum and in its anthers which are arranged in 2 alternating whorls of 5, the anthers of the lower whorl with the connective produced to form a short acute appendage (anthers of *Aglaia* in a single whorl without appendages). In addition, the ovary of *Reinwardtiodendron* is usually 5-locular (1—4-locular in *Aglaia*). The spicate inflorescence is rarely found in *Aglaia*.

Reinwardtiodendron is very similar to *Aglaia* in its pollen morphology and in the structure of its secondary xylem.

It can be distinguished from *Lansium* by its axillary inflorescence (ramiflorous or cauliflorous in *Lansium*), the corolla free from the staminal tube almost to the base (fused almost to half way in *Lansium*), its anthers arranged in 2 whorls of 5, the lower whorl with a connective appendage (1 whorl of 10 without connective appendages in *Lansium*).

The pollen grains of *Reinwardtiodendron* are 3- or 4-colporate, prolate-spheroidal or subprolate, differing from those of *Lansium* which are 3—5-colporate, oblate-spheroidal.

The secondary xylem of both genera is very similar, but the ray tissue of *Lansium* (heterogeneous Kribs Type 3) is slightly more heterogeneous than that of *Reinwardtiodendron* (homogeneous Kribs Type 1 or uniseriate homogeneous).

Note: *Lansium humile* Hassk. This species, placed by Harms with some reservations in his section *Neolansium*, cannot be placed with certainty until the nature of the fruit is known. The floral structure is similar in all respects to that of *Reinwardtiodendron*. Its pollen morphology and the structure of its secondary xylem also agree very closely with that of *Reinwardtiodendron*. Although Hasskarl described the fruit as a berry, some later authors (e.g. Koorders) have mentioned a loculicidal capsule. Kostermans (1966) has described a large capsular fruit collected by Koorders with 5 large exarillate seeds. Until mature fruit correlated with leaves and flowers is obtained, it is not possible to place this species with certainty, but the floral, pollen, and wood characters alone are sufficient to exclude it from *Aglaia*, *Lansium*, *Aphanamixis*, and *Sphaerosacme*, but indicate a close relationship with *Reinwardtiodendron*.

24. SPHAEROSACME

Sphaerosacme Wall. [in Roxb., Fl. Ind. (ed. Carey) 2 (1824) 429, in obs., *nomen provisorium*] *ex* M. J. Roem., Synops. Monog. Hesperid. 1 (1846) 98. — **Fig. 10d.**

Lansium sect. *Pseudolansium* Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 125.

Trees with imparipinnate leaves. *Indumentum* of simple hairs. *Flowers* unisexual (plant dioecious). *Inflorescence* axillary or supra-axillary; male flowers (female flowers not seen by us) in panicles with racemose branches. *Calyx* deeply 4- or 5-lobed; aestivation open or imbricate. *Petals* 5, free, imbricate. *Staminal tube c.* 0.2 cm long, almost globose, margin undulate. Anthers 10, glabrous, lacking connective appendages, in 2 whorls of 5, the upper partly exserted, the lower alternating with the upper and completely included. *Disk* absent. *Ovary* with 5 uniovulate loculi. Style absent; style-head broad, pileate, 5-lobed. *Fruit* a 2—5-valved loculicidal capsule. *Seed* partly or completely surrounded by an arillode. *Embryo* with plano-convex, collateral, completely fused cotyledons; radicle small, superior, included.

Pollen: Pollen grains 4-colporate, prolate (25—30 μm; amb quadrangular). Apocolpium large. Ora lalongate. Exine smooth or scabrous, thickened at the apertures.

Secondary xylem: not seen.

Distribution: One species in Sikkim, Bhutan, and Nepal.

Type species: **S. decandra** (Wall.) Pennington. *comb. nov.* (Basionym: *Aglaia*? *decandra* Wall. in Roxb., Fl. Ind. (ed. Carey) 2 (1824) 427).

Relationships: The rank and relationships of this plant have been in doubt since it was first described. Wallich tentatively placed it in *Aglaia* as *Aglaia*? *decandra* (1824). He did not have ripe fruiting material available for study and in his observation after the description states "the fruit is decidedly 5-seeded. I have not had the opportunity of examining the latter in the ripe state and have therefore preferred placing the tree here, to forming it into a new genus. Should it prove the latter, the name which I originally gave it, *Sphaerosacme*, might be adopted." Wight and Arnott (1834) and Hooker *f.* (1862) referred it to *Lansium* on account of the 10 stamens in 2 whorls of 5, but Hiern (1875), who saw the ripe capsular fruit, placed it in *Amoora*.

It appears that this genus has almost equal affinities with *Reinwardtiodendron* and *Aphanamixis* but is quite distinct from both, and that Roemer (1846) was fully justified in taking up Wallich's provisional name. It possesses the floral characters of *Reinwardtiodendron* and the fruit and seed characters of *Aphanamixis*. The following characters separate it from *Aphanamixis*: petals 5, free from the staminal tube; anthers 10, in 2 whorls; ovary 5-locular with a single ovule in each locule.

The differences from *Reinwardtiodendron* are: petals free from the staminal tube; fruit a loculicidal capsule; seed with a free arillode; cotyledons collateral, fused.

The pollen grains are similar to those of *Aphanamixis* being 4-colporate with a scabrous exine.

Sphaerosacme is less closely related to *Lansium*, and differs from it in floral, fruit, and seed characters. It may be distinguished by its petals which are free from the staminal tube (fused in the lower half in *Lansium*), its anthers in 2 whorls of 5 (1 whorl of 10 in *Lansium*), the fruit which is a loculicidal capsule (berry in *Lansium*), and its fused collateral cotyledons (free, superposed in *Lansium*). In addition the prolate pollen grains of *Sphaerosacme* differ from those of *Lansium* which are oblate-spheroidal.

Tribe 6. GUAREEAE

Tribus Guareeae, *tribus nova.*

Folia pinnata. Tubus stamineus integer, paene semper cylindricus, cum vel sine appendicibus. Antherae paene semper intra fauces insertae. Discus fere evolutus, stipitatus, cyathiformis vel tubularis. Caput styli fere discoideum. Fructus paene semper capsularis, loculicide dehiscens. Semen arillodio vel sarcotesta praeditum, sine endospermio.

Typus tribus: *Guarea.*

Leaves pinnate. Indumentum of simple or rarely stellate hairs. Flowers hermaphrodite or unisexual (plants dioecious). Staminal tube complete, nearly always cylindrical, with or without appendages. Anthers nearly always inserted within the throat. Disk usually well-developed, stipitate, cyathiform or tubular. Style-head usually discoid, rarely capitate. Fruit nearly always a loculicidal capsule. Seed arillodiate or with a sarcotesta, exendospermous. Cotyledons plano-convex, collateral or superposed, rarely oblique.

Pollen: Usually suboblate, oblate-spheroidal, or spheroidal, 3—5-colporate, exine usually smooth.

Secondary xylem: Fibres nearly always septate; apotracheal terminal bands of parenchyma usually absent; paratracheal parenchyma usually confluent and banded.

1. Disk cyathiform or tubular.
    2. Leaflets with pellucid lines and dots; calyx lobed, with imbricate aestivation; petals imbricate, free from the staminal tube; seed arillodiate. . . . . . 26. *Cabralea*
    2a. Leaflets without pellucid lines or dots; calyx entire or lobed, aestivation open or imbricate; petals imbricate or valvate, free from, or fused to, the staminal tube; seed arillodiate or with a sarcotesta . . . . 35. *Dysoxylum*

1a. Disk annular or stipitate, rarely patelliform or absent.
    3. Sarcotesta surrounding the base of the seed, greatly swollen; disk short, stipitate; fruit a capsule; cotyledons collateral . . . . 27. *Ruagea*
    3a. Sarcotesta absent or, when present, not swollen or basal.
        4. Ovary unilocular with 2(3) parietal placentas; disk long, slender, stipitate, expanded at the apex; fruit a narrow rostrate berry; seed with a vascularised sarcotesta; cotyledons collateral . . . . 25. *Heckeldora*
        4a. Ovary bi- or multi-locular, with axile placentas; fruit a capsule.
            5. The two seeds of a locule united by a common arillode; petals imbricate, free; staminal tube cyathiform; disk a swollen annulus; cotyledons collateral . . . . 32. *Synoum*
            5a. Seeds not united by a common arillode.
                6. Petals fused to the staminal tube for the greater part of its length, valvate; staminal tube long cylindrical; disk absent; seed with a non-vascularised sarcotesta; cotyledons superposed . . 28. *Turraeanthus*
                6a. Petals free from or rarely fused at the base to the staminal tube; disk mostly present.
                    7. Leaves paripinnate.
                        8. Petals 3 or 4, valvate at least in the lower half; staminal tube cylindrical; loculi with 2 collateral ovules; seed with an arillode . . . . 34. *Pseudocarapa*
                        8a. Petals 5, imbricate; staminal tube cyathiform; loculi uniovulate; fruit a capsule; seed with a non-vascularised sarcotesta 33. *Anthocarapa*
                    7a. Leaves with a dormant terminal bud or more rarely a terminal leaflet.
                        9. Petals in 2 whorls, united below; seed with a sarcotesta 31. *Megaphyllaea*
                        9a. Petals in a single whorl.
                            10. Anthers nearly always locellate; style-head often capitate; seed often scutiform (ovules orthotropous), arillodiate or with a sarcotesta, the latter often mealy white 30. *Chisocheton*

10a. Anthers never locellate; style-head always discoid; seed never scutiform, exarillodiate, with a fleshy, mealy, or vascularised sarcotesta . . . . 29. *Guarea*

25. HECKELDORA

Heckeldora Pierre, Bull. Soc. Linn. Paris 2 (1897) 1286. — **Fig. 11 a.**
Guarea sect. *Heckeldora* (Pierre) Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 135.

Small trees or treelets with imparipinnate leaves. *Indumentum* of simple hairs. Leaflets without pellucid lines or dots. *Flowers* unisexual (plants dioecious) in narrow axillary panicles or racemes. *Calyx* shallowly 3—5-lobed. *Petals* 4, free, imbricate. *Staminal tube* 0.65—0.9 cm long, cylindrical, the margin with shallow, rounded lobes. Anthers 8, glabrous, inserted within the throat of the staminal tube and sometimes partly exserted. *Disk* long, slender, stipitate, expanded at the apex to form a collar beneath the constricted base of the ovary. *Ovary* unilocular with 2(3) parietal placentas, each with 2 collateral ovules. Style-head discoid, flat or with a slight central depression. *Fruit* a narrow, rostrate, 2—4-seeded berry, with conspicuous constrictions between the seeds. *Seed* with a vascularised sarcotesta. *Embryo* with thick, plano-convex, collateral cotyledons; radicle superior, extending to the surface.

Pollen: Pollen grains 3 or 4(5)-colporate, oblate-spheroidal (40—45 μm; amb rounded). Apocolpium large. Ora circular, crassimarginate. Exine scabrous to verrucose.

Distribution: One very variable species in tropical West Africa.

Type species: *H. latifolia* Pierre (here chosen as lectotype); equals *H. staudtii* (Harms) Staner (*Guarea staudtii* Harms).

Relationships: Harms treated this genus as a section of *Guarea*, which is surprising as it differs significantly from that genus in several respects. The unilocular ovary with parietal placentas is a condition unique in the family. Other differences from *Guarea* are the berry and the embryo with collateral cotyledons and superior radicle, though the latter does occur rarely in *Guarea*.

The pollen grains of *Heckeldora* also show several differences from those of all species of *Guarea* examined so far. The pores protrude (crassimarginate) and the exine is prominently scabrous or verrucose, whereas in *Guarea* the pores do not protrude and the exine is smooth and rarely scabrous.

26. CABRALEA

Cabralea A. Juss., Mém. Mus. Hist. Nat. Par. 19 (?1830) 229, t. 16; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 158, t. 35 figs R, S. — **Fig. 11b.**

Trees or shrubs. *Indumentum* of simple hairs. *Leaves* pinnate with limited apical growth; leaflets with pellucid lines and dots. *Flowers* unisexual (plants dioecious), in axillary panicles. *Calyx* deeply 5-lobed, lobes imbricate. *Petals* 5, free, imbricate. *Staminal tube* 0.3—0.5 cm long, cylindrical, terminated by 9—12 short truncate, emarginate, or bilobed appendages. Anthers glabrous, alternate with the appendages, inserted within the throat of the staminal tube and completely included. *Disk* cyathiform. *Ovary* 4 or 5-locular; loculi with 2 superposed ovules, placentation axile. Style-head discoid, with a small central depression. *Fruit* a tardily dehiscent 4- or 5-valved loculicidal capsule, pericarp rather fleshy; loculi 1- or 2-seeded. *Seed* partly or completely surrounded by a thin arillode. *Embryo* with thick collateral cotyledons; radicle superior, slightly projecting or extending to the surface.

Pollen: Pollen grains (3)4(5)-colporate, spheroidal or prolate-spheroidal (35—50 μm; amb rounded or quadrangular, rarely triangular). Apocolpium large or rarely medium. Ora circular. Exine smooth or rarely scabrous.

Secondary xylem: *Vessels* solitary and in radial groups of 2 or 3; tangential diameter 80—160 μm; intervascular pits 4.5 μm; gum present. *Ray tissue* heterogeneous Kribs Type 2 or 3 or uniseriate heterogeneous; rays 1- or 2-seriate, up to 30 cells high, the heterocellular with 1 or 2 marginal rows. *Fibres:* septate. *Parenchyma.* Paratracheal: vasicentric, aliform, confluent and sometimes banded, in various combinations; crystals present or absent.

Distribution: About 6 species in southern Brazil and neighbouring countries in S. America.

Type species: *C. polytricha* A. Juss.

Relationships: Harms, on the basis of morphological information alone, considered *Cabralea* to be most closely related to the Asiatic genus *Didymocheton* (included under *Dysoxylum* in the present work) on account of the free cyathiform disk surrounding the ovary, a structure to which he attached great importance. It also shares many features with the South American genus *Ruagea*, and the secondary xylem of the latter has a combination of characters very close to that of *Cabralea*.

Cabralea differs from *Didymocheton* in the following characters: leaves with pellucid lines or dots; in *Cabralea* the petals are always free whereas in *Didymocheton* they are generally fused to the staminal tube.

The leaves with pellucid lines and dots also distinguish *Cabralea* from *Ruagea*. *Cabralea* also has a cyathiform disk (not stipitate); 4- or 5-locular ovary (not 3 or 4-locular); an arillodiate seed (not a basal swollen sarcotesta).

The secondary xylem of *Cabralea* more closely resembles that of *Ruagea* than that of *Didymocheton*. It lacks the exclusively banded paratracheal parenchyma of *Didymocheton*. The following combination of characters — thin-walled fibres, small number of vessels per sq mm (8—12), and sparse parenchyma — is characteristic of *Ruagea*.

27. RUAGEA

Ruagea Karsten, Fl. Columb. 2 (1863) 51, t. 126; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 137, t. 31 fig. Z. — **Fig. 11c.**

Guarea sect. *Ruagea* C. DC. in A. & C. DC., Monog. Phan. 1 (1878) 577.

Trees with imparipinnate leaves. *Indumentum* of simple hairs. *Leaflets* sometimes with pellucid lines or dots. *Flowers* ?bisexual, in axillary panicles or occasionally ramiflorous. *Calyx* deeply 5-lobed, lobes imbricate. *Petals* 5, free, imbricate. *Staminal tube* 0.175—0.9 cm long, cylindrical, margin undulate, crenate, or with shallow emarginate lobes. Anthers 9 or 10, glabrous, inserted within the throat of the staminal tube, included or partly exserted. *Disk* short, broad, stipitate, sometimes expanded to form a collar at the base of the ovary. *Ovary* 3(4)-locular; loculi with 2 superposed ovules, placentation axile. Style-head discoid with a small central depression. *Fruit* a 1—3-valved loculicidal capsule, loculi 1(2)-seeded; pericarp thin and leathery or rather woody. *Seed* with a large, swollen, fleshy, basal sarcotesta. *Embryo* with thick, plano-convex, collateral cotyledons; radicle superior, included or extending to the surface.

Pollen: Pollen grains 4-colporate, suboblate, oblate-spheroidal, spheroidal, or prolate-spheroidal (45—55 μm; amb rounded). Apocolpium large or medium. Ora circular or lalongate. Exine smooth, thickened at the apertures.

Secondary xylem: *Vessels* solitary and in radial pairs; tangential diameter

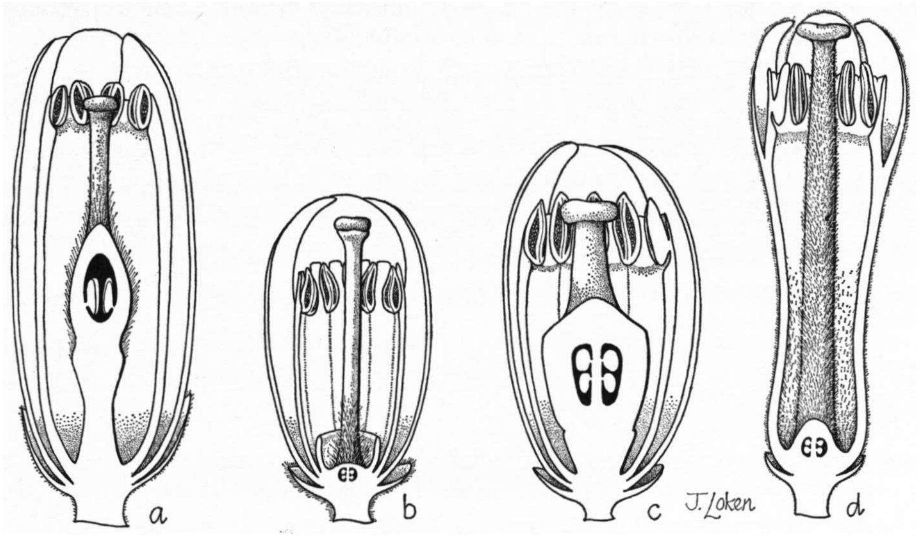

Fig. 11. a. *Heckeldora staudtii* (Harms) Staner, ♂, ×7.5. — b. *Cabralea polytricha* A. Juss., ♂, ×7.5. — c. *Ruagea pubescens* Karst., ⚥, ×7.5. — d. *Turraeanthus zenkeri* Harms, ♂, ×5. (a. *FHI 30772*; b. *Glaziou 20815*; c. *Steyermark 55048*; d. *Zenker 2155*).

80—120 μm; intervascular pits 4.5 μm; gum present. *Ray tissue* heterogeneous Kribs Type 3; rays 1- or 2-seriate, up to 50 cells high, the heterocellular with 1 marginal row; some rays homocellluar with all cells procumbent. *Fibres* septate. *Parenchyma*. Paratracheal: aliform and confluent.

Distribution: One species in Costa Rica, C. America, and about five in western South America from Bolivia and Peru to Venezuela.

Type species: *R. pubescens* Karst.

Relationships: *Ruagea* is separable from *Guarea* by two diagnostic characters. These are the imbricate (not open) calyx-lobes and the peculiar, greatly swollen, basal sarcotesta which is quite unlike that of *Guarea* or *Chisocheton*.

Other characters constant in *Ruagea* but occurring only sporadically in *Guarea* are the 5-merous flowers and the embryo with collateral cotyledons and superior radicle.

Only one slide of the secondary xylem of *Ruagea* has been examined (*R. silviandina* Cuatrec.). This shows the main features of *Guarea*, but the paratracheal parenchyma is rather sparse and only aliform or confluent. This feature, combined with the rather thin-walled fibres, produces an overall pattern which could not be confused with that of *Guarea*.

28. TURRAEANTHUS

Turraeanthus Baill. [Adansonia 11 (1874) 261 *sine descr. gen.*] Hist. Pl. 5 (1874/5) 500; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 147, t. 30 figs. A-D; t. 32. — **Fig. 11d.**
[*Turraeopsis* Baill., Hist. Pl. 5 (1874/5) 483, *nom. nud.*]
Bingeria A. Chev., Vég. Util. Afr. Trop. Franç. 5 (1909) 189.

Trees or treelets with pinnate leaves. *Indumentum* of simple hairs. *Leaflets* without pellucid lines or dots. *Flowers* unisexual (plants dioecious), in axillary panicles or ramiflorous. *Calyx* almost entire or shallowly and irregularly lobed. *Petals* 4 or 5(6), valvate, fused in the upper half to the staminal tube. *Staminal tube* 1—3 cm long, cylindrical, slightly expanded at the mouth, margin crenate or shallowly lobed. Anthers 8—12, glabrous, in a single irregular whorl inserted within the throat of the staminal tube, completely included or partly exserted. *Disk* absent. *Ovary* 4- or 5-locular; loculi with 2 superposed or oblique ovules, placentation axile. Style-head discoid with a slight central depression. *Fruit* a somewhat fleshy, 3—5-valved, loculicidal capsule, the loculi 1-seeded. *Seed* with a fleshy non-vascularized sarcotesta. *Embryo* with thick, plano-convex, superposed cotyledons; radicle included, usually near the abaxial surface.

Germination: cryptocotylar; cataphylls present; eophylls spirally arranged, simple, entire (*T. africanus* (Welw. *ex* C. DC.) Pellegr.).

Chromosome number: 2n= *c.* 280 (*T. africanus* (Welw. *ex.* C. DC.) Pellegr.).

Pollen: Pollen grains 4- or 5-colporate, suboblate, oblate-spheroidal, or spheroidal (55—65 μm; amb rounded). Apocolpium large. Ora lalongate, sometimes crassimarginate. Exine smooth, thickened at the apertures.

Secondary xylem: *Vessels* solitary and in radial groups of 2 or 3; tangential diameter 80—140 μm; intervascular pits 3.75 μm; gum present or absent. *Ray tissue* heterogeneous Kribs Type 3; rays (1)2(3)-seriate, up to 20 cells high, the heterocellular with 1 marginal row. *Fibres* non-septate. *Parenchyma.* Paratracheal: vasicentric, crystals present.

Distribution: Possibly three species in tropical West Africa.

Type species: *T. longipes* Baill. (here chosen as lectotype).

Relationships: *Turraeanthus* is closely related to both *Chisocheton* and *Guarea.* It differs from both in having the corolla fused for the greater part of its length to the staminal tube. Further differences are the lack of the dormant terminal bud on the leaf present in most species of both genera, of the locellate anthers present in most species of *Chisocheton*, and of the stipitate disk characterizing most species of *Guarea.*

In its secondary xylem, *Turraeanthus* is quite distinct from both *Guarea* and *Chisocheton* in having non-septate fibres and very sparse vasicentric paratracheal parenchyma (not confluent or banded). The deposits of silica so characteristic of *Chisocheton* and occasionally found in *Guarea* are absent from the ray tissue of *Turraeanthus.*

29. GUAREA

Guarea ('*Guara*') Allamand *ex* L., Mant. (1771) 150, 228, *nom. cons.*; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 129, t. 31, figs. R-X. — **Fig. 12a, b.**

Samyda L., Sp. Pl. (1753) 443, *nom. rejic.*, *non* Jacq. (1760) *nom. cons.*

Guidonia Mill., Gard. Dict. abridg. ed. 4 (1754).

Elutheria P. Browne, Hist. Jamaica (1756) 369, *non Elutheria* M. J. Roem. (1846) = *Schmardaea* Karst. (1861).

Plumea Lunan., Hort. Jam. 2(2) (1814) 77.

Sycocarpus Britton, Bull. Torrey Bot. Club 14 (1887) 143.

Leplaea Vermoesen, Revue Zoolog. Afric. 9(2) (1921) 37; Harms in Engl. & Prantl., ed. 2, 19 bI (1940) 137.

Urbanoguarea Harms, Notizbl. Bot. Gart. Berl. 13 (1937) 507 *in obs.* 10; in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 136.

Trees or treelets. *Indumentum* of simple hairs. *Leaves* pinnate, with a dormant terminal bud or more rarely a terminal leaflet. *Leaflets* sometimes with pellucid lines or dots. *Inflorescence* axillary or ramiflorous or cauliflorous, usually racemose or spicate, more rarely paniculate. *Flowers* unisexual (plants dioecious). *Calyx* with an almost entire margin, or shallowly or deeply (2)3- or 4(6)-lobed, aestivation open; rarely closed in bud and circumscissile at the base. *Petals* 4(6) in a single whorl, free, imbricate or valvate, rarely fused at the base to the staminal tube. *Staminal tube* 0.4—1.3 cm long, cylindrical, the margin shallowly toothed, crenate, or entire, or with emarginate or truncate appendages. Anthers 8(—12), glabrous, inserted within the throat of the staminal tube, completely included or partly exserted, alternate with the lobes or appendages. Antherodes similar, smaller, without pollen. *Disk* short- or long-stipitate, sometimes expanded to form a collar at the base of the ovary, rarely absent. *Ovary* (2)4—6(10)-locular; loculi with 1 or 2 superposed ovules, placentation axile. Style-head discoid, usually with a small central depression. Pistillode smaller, less swollen, with well-developed ovules. *Fruit* a 2—8-valved loculicidal capsule, sometimes very slow to dehisce; loculi 1- or 2-seeded; pericarp leathery or woody with the endocarp sometimes distinguished as a cartilaginous layer. *Seed* often shaped like the segment of an orange, with a fleshy, sometimes vascularised, or mealy sarcotesta, usually thickened on the adaxial surface. *Embryo* with thick, plano-convex, superposed or more rarely oblique or collateral cotyledons; radicle abaxial, extending to the surface, or rarely central or lateral and then included.

Germination: cryptocotylar, eophylls opposite or spirally arranged, trifoliolate, sometimes becoming simple (*G. cedrata* (A. Chev.) Pellegr., *G. mayombensis* Pellegr.).

Chromosome numbers: 2n= 72 (3 spp.).

Pollen: Pollen grains 3—5-colporate, oblate-spheroidal or spheroidal (30—50 μm; amb rounded). Apocolpium large. Ora circular or rarely lalongate. Exine smooth or rarely scabrous, thickened at the apertures.

Secondary xylem: *Vessels* solitary and in radial rows of 2 or3 (4); tangential diameter 40—240 μm; intervascular pits 2.25—5.25 μm; gum present or absent. *Ray tissue* usually homogeneous Kribs Type 1, rarely heterogeneous Kribs Type 3, or uniseriate-homogeneous; rays 1 or 2(4)-seriate, up to 50 cells high, the heterocellular with 1 marginal row. *Fibres* septate. *Parenchyma.* Paratracheal: confluent and banded, rarely with some aliform as well; with crystals. Diffuse crystalliferous cells very rarely present. Deposits of silica are occasionally present.

Distribution: Five species in tropical Africa and perhaps 30 in tropical America.

Type species: *G. trichilioides* L. = *G. guidonia* (L.) Sleumer.

Relationships: On the basis of this study, we have not been able to agree with Harms' circumscription of *Guarea*, in that he includes one genus that clearly does not belong here, and gives generic rank to two others which in our opinion are congeneric.

The reasons for excluding *Heckeldora* from *Guarea* are given in the commentary following the account of the former genus.

Harms maintains the genus *Urbanoguarea*, based on *Guarea sphenophylla* Urban from Santo Domingo, on account of the distinctive form of the calyx and leaflets. We have not had an opportunity of studying flowering material of this species, but the original description of Urban fits that of *Guarea*. The calyx is deeply divided, but this feature is known elsewhere in *Guarea*, and it appears that the leathery texture of the calyx lobes and leaves is merely an adaptation to a dry habitat. A comparable condition is found in the section *Acanthotrichilia* Urban of *Trichilia* from the same country. Harms also states that the juvenile form has deeply divided leaflets, a condition known to occur sporadically in several other genera, e.g. *Dysoxylum*. On the basis of the available evidence, *Urbanoguarea* does not merit generic rank.

Harms (1940) gives *Leplaea* generic rank on account of the indehiscent fruit. We have examined mature fruit preserved in spirit. These have not dehisced but the inner surface of the pericarp is split along the centre of each loculus and it is clear that this fruit would dehisce into four valves on falling to the ground, if not before. Uncorrelated, dehisced, fallen fruits have been reported by field workers (Hallé, in Herb. Paris). It is often difficult to decide from dried herbarium material whether the fruit of several species of *Guarea*

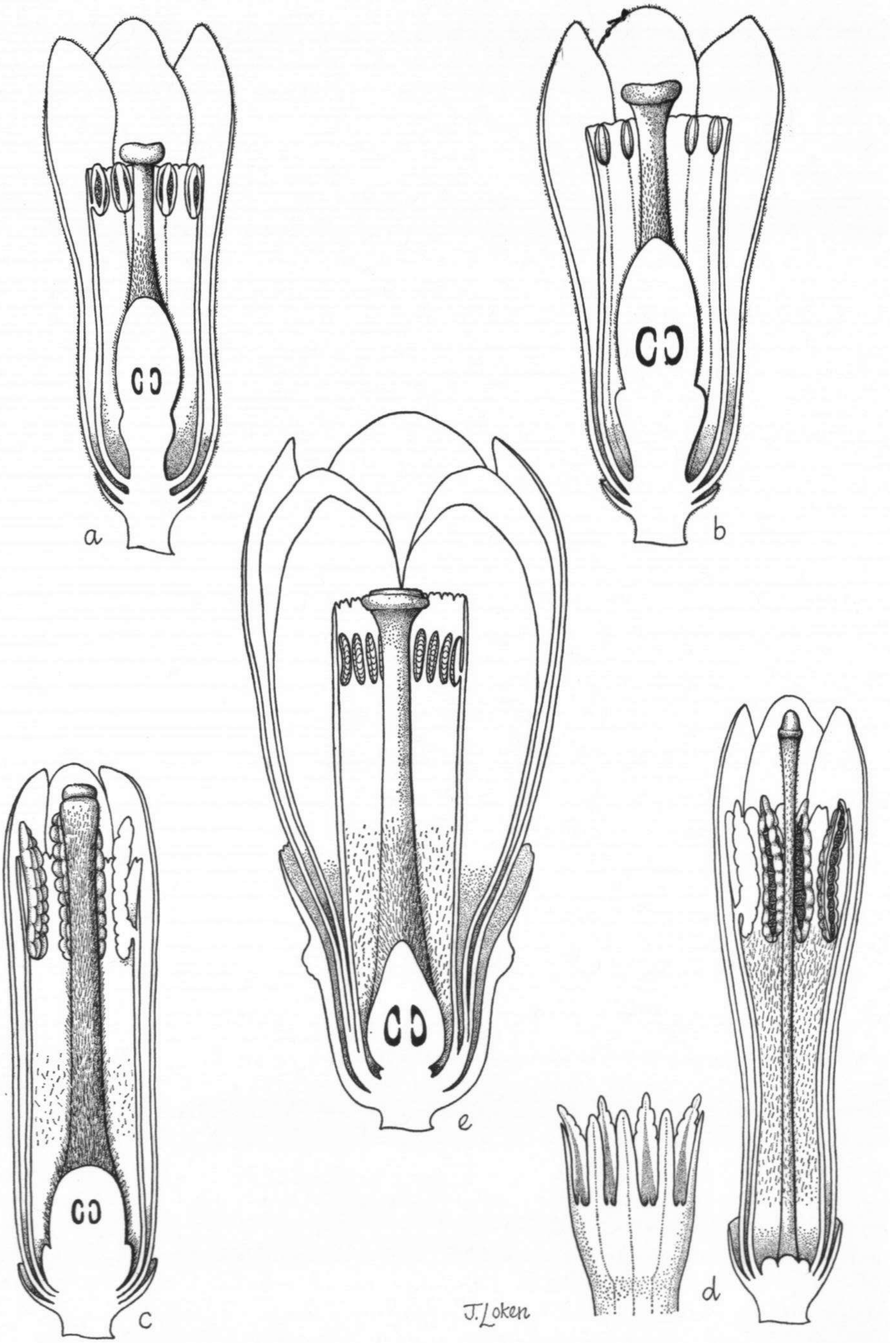

Fig. 12. a. *Guarea guidonia* (L.) Sleumer, ♂, ×10; b. ditto, ♀, ×10. — c. *Chisocheton divergens* Blume, ♀, ×10; d. ditto, ♂, ×10. — e. *Megaphyllaea perakensis* Hemsl., ♀, ×4. (a. *Ekman 9114*; b. *Pennington & Prance 1337A*; c. *Pennington 7995*; d. *Pennington 7830*; e. *Wray s.n.*).

is dehiscent, and field observation of the related genus *Chisocheton* shows that, although there may be no sutures evident on the mature fruit, dehiscence may take place, though sometimes after the fruit has fallen As *Leplaea* resembles *Guarea* in all other characters of gross morphology, wood anatomy, and pollen grain structure, it seems better to reduce it to this genus. Indeed in its vegetative features *L. mayombensis* (Pellegr.) Staner much more closely resembles the African species *Guarea cedrata* (A. Chev.) Pellegr. than the latter resembles the only other tree species in Africa, *G. thompsonii* Sprague & Hutch. Sterile and flowering specimens of *Leplaea* and *G. cedrata* have been confused by herbarium taxonomists.

The relationships of *Guarea* with *Ruagea, Heckeldora, Turraeanthus, Chisocheton, Pseudocarapa, Anthocarapa, Synoum,* and *Dysoxylum* are discussed under the respective genera.

30. CHISOCHETON

Chisocheton Blume, Bijdr. (1825) 168; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 150, t. 30 figs. E-H, t. 33. — **Fig. 12c, d.**

Schizochiton Spreng., Syst. 4(2) *cur. post.* (1827) 251.

Dasycoleum Turcz., Bull. Soc. Nat. Mosc. 31(1) (1858) 414.

Melio-Schinzia K. Schum. in Schum. & Hollrung., Fl. Kaiser Wilh. Land. (1889) 62.

Rhetinosperma Radlk. in Engl. & Prantl, Nat. Pflanzenfam. Nachtrag 3, Ergänzungsheft 2(3) (1907) 204; Harms, tom. cit. 166.

Clemensia Merrill, Philipp. Journ. Sci. 3 (1908) 143; Harms, tom. cit. 155, tab. 34, *non* Schlecht. (1915),

Trees or treelets. *Indumentum* usually of simple, rarely of stellate hairs. *Leaves* pinnate with an intermittently growing terminal bud, very rarely with a terminal leaflet. *Leaflets* without pellucid lines or dots. *Flowers* unisexual (plants dioecious), in axillary or supra-axillary panicles, often long and narrow and thyrsoid or almost racemose, rarely cauliflorous, very rarely epiphyllous. *Calyx* usually with an almost entire margin, rarely 3—6-lobed to the middle, sometimes closed in bud and splitting to produce an irregular margin, and then circumscissile at the base. *Petals* (3) 4 or 5(14) in a single whorl, free, imbricate or valvate, rarely united below or fused at the base to the staminal tube. *Staminal tube* 0.6—3 cm long, cylindrical, sometimes expanded at the mouth, with an entire or crenate margin, or terminated by 4—10(23) emarginate, truncate, narrowly lanceolate, or bilobed appendages. Anthers hairy or glabrous, nearly always locellate, alternate with the lobes or appendages, usually attached within the throat of the staminal tube and then completely included or partly exserted, rarely inserted on the margin. Antherodes very slender, indehiscent, without pollen. *Disk* narrowly or broadly stipitate, annular, patelliform, or absent. *Ovary* 2—7-locular; loculi with 1 or 2 collateral or superposed ovules, placentation axile. Style-head small, capitate, clavate, or discoid. Pistillode very slender, the unexpanded base of the style sunk in the disk; ovules minute or absent. *Fruit* a 2—5(7)-valved loculicidal capsule, often stipitate or rostrate, the loculi 1(2)-seeded; pericarp usually leathery, or almost woody throughout, occasionally with a soft spongy mesocarp. *Seed* scutiform or shaped like the segment of an orange, arillodiate or with a sarcotesta; arillode adaxial or partly surrounding the seed, partly fused to the testa or free; sarcotesta partly or completely thickened and fleshy; hilum often very large, mealy white and strongly vascularised, covering up to ½ or ¾ of the seed. *Embryo* with thick, collateral, oblique or superposed cotyledons; radicle abaxial or included.

Germination: cryptocotylar; eophylls spirally arranged, simple, entire.

Chromosome numbers: n= 23, 2n= 46, 92.

Pollen: Pollen grains 3—5-colporate, oblate-spheroidal or spheroidal (35—105 µm;

amb rounded). Apocolpium large. Ora circular or lalongate, sometimes crassimarginate. Exine smooth or scabrous, thickened at the apertures.

Secondary xylem: *Vessels* solitary and in radial rows of 2—4(5); tangential diameter 60—180 μm; intervascular pits 3.5—6 μm; gum present or absent. *Ray tissue* heterogeneous Kribs Type 3, rarely Kribs Type 2; rays 1—3(5)-seriate, up to 60 cells high, the heterocellular with 1 or rarely several marginal rows. *Fibres* septate. *Parenchyma.* Paratracheal: exclusively banded or rarely confluent and banded, crystals usually present. Deposits of silica, often abundant, are found in the great majority of species.

Distribution: About 30 species from the Indo-Malayan region to Australia, New Guinea, and the Solomon Islands.

Type species: *C. divergens* Bl.

Relationships: The only differences which separate *Clemensia* from *Chisocheton sensu stricto* are quantitative. The flowers are larger, with more petals (7—14 compared with 4—6), with more anthers (15—23 compared with 4—15), and the ovary with more loculi (6 or 7 compared with 2—6). In all other important respects, *Clemensia* does not differ from *Chisocheton.* In 1937 Airy-Shaw demoted *Clemensia* to sectional rank within *Chisocheton*, but Harms (1940) retained it as a genus. In our opinion there can be no doubt that Airy-Shaw's view is the more acceptable. The pollen grains of *Clemensia* are larger than those of *Chisocheton sensu stricto* (100—105 μ m compared with 40—80 μ m), but are otherwise similar. The secondary xylem shows no difference. Both species of *Clemensia* were described as having indehiscent fruit, but our own field observation has shown that the fruits of *Chisocheton medusae* Airy-Shaw are tardily dehiscent.

There are no absolutely diagnostic characters that can be used to distinguish *Chisocheton* from *Guarea*, but nevertheless all species of *Chisocheton* differ from *Guarea* at least in two or three differential characters, so that, although the genera are indeed closely related, no practical difficulties arise in their separation.

All except two species of *Chisocheton* studied by us have locellate anthers, a character not seen in any other genus except *Megaphyllaea. Chisocheton* frequently has a capitate style-head and arillodiate seed, whereas in *Guarea* the style-head is always discoid and the seed always has a sarcotesta. Generally the staminal tube of *Chisocheton* is longer and narrower — ratio of length to breadth (2.1)6(21.5) — than that of *Guarea* — ratio (1.4)2 (3.75).

The secondary xylem of these two genera also shows great similarity. They are alike in most features, but *Chisocheton* generally has more heterogeneous ray tissue and exclusively banded paratracheal parenchyma, whereas in *Guarea* there is a mixture of confluent and banded parenchyma. Silica deposits occur in both genera, but much more frequently in *Chisocheton.*

The relationships of *Chisocheton* with *Megaphyllaea* and *Dysoxylum* are discussed under the respective genera.

31. MEGAPHYLLAEA

Megaphyllaea Hemsl. in Hook. Ic. Pl. (1887) 18 t. 1708; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 155. — **Fig. 12e.**

Small trees. *Indumentum* of simple hairs. *Leaves* pinnate, with a dormant terminal bud. *Leaflets* without pellucid lines or dots. *Flowers* (male not seen) unisexual (plants dioecious) in lax axillary or supra-axillary panicles. *Calyx* much thickened in the lower half and with a warty swollen band round the middle; closed in bud and splitting to produce an irregular margin and then circumscissile at the base. *Petals* 8—10, in 2 whorls united below and fused at the base to the staminal tube, imbricate. *Staminal tube c.* 1.2 cm long, cylindrical, with an almost entire, crenate, or shallowly toothed margin. Antherodes 10—16, glabrous, locellate, inserted within the throat of the staminal tube, completely included, slender, not dehiscing, without pollen. *Disk* short, broad, stipitate, obscurely lobed. *Ovary* 7—9-locular; loculi uniovulate, placentation axile. Style-head discoid. *Fruit* (immature studied only) a 7—9-valved loculicidal capsule with a thick leathery pericarp. *Seed* with a fleshy sarcotesta. *Embryo* with thick superposed cotyledons; radicle included.

Pollen: Not seen.

Secondary xylem: *Vessels* solitary and in radial groups of 2 or 3, tangential diameter 140—320 µm; intervascular pits 6µm; gum present. *Ray tissue:* homogeneous Kribs Type 1; rays 2— or 3-seriate, up to 100 cells high. *Fibres*: septate. *Parenchyma.* Paratracheal: banded; crystals present.

Distribution: One or two species in the Malay Peninsula.

Type species: *M. perakensis* Hemsl.

Relationships: This genus can be distinguished from *Chisocheton* by its biseriate corolla. Other characters rarely found in *Chisocheton* are the much thickened calyx and the multilocular ovary (the latter only in section *Clemensia* of *Chisocheton*).

We have seen only one (uncorrelated) slide of the secondary xylem of *Megaphyllaea* which is similar to that of *Chisocheton* but has homogeneous ray tissue (Kribs Type 1) and slightly broader bands of paratracheal parenchyma (7—11 cells wide compared with 6—8 in *C. macrophyllus* King). Silica deposits, present in the majority of species of *Chisocheton*, are absent.

32. SYNOUM

Synoum A. Juss., Mém. Mus. Hist. Nat. Par. 19 (?1830) 226, t. 15; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 138. t. 30 figs. R, S. — Fig. 13a.

Small trees with imparipinnate leaves. *Indumentum* of simple hairs. *Leaflets* without pellucid lines or dots. *Flowers* probably unisexual (plants dioecious), in short axillary panicles. *Calyx* deeply 4(5)-lobed. *Petals* 4(5), free, imbricate. *Staminal tube c.* 0.35 cm long, cyathiform, the margin irregularly and shallowly lobed. Anthers 8(10), glabrous, inserted just inside the throat of the staminal tube and partly exserted. *Disk* represented by the swollen basal portion of the ovary. *Ovary* 2- or 3-locular; loculi with 2 collateral ovules, placentation axile. Style-head discoid, with a slight depression in the centre. *Fruit* a 2- or 3-valved loculicidal capsule, the loculi (1)2-seeded; the 2 collateral *seeds* partly surrounded by a common thick and fleshy arillode which is fused to each seed along the abaxial surface, but is otherwise free. *Embryo* with thick plano-convex, collateral cotyledons; radicle superior, extending to the surface.

Germination: phanerocotylar; eophylls spirally arranged, simple, entire or remotely toothed.

Chromosome number: 2n= 84 (*S. glandulosum* (Smith) A. Juss.)

Pollen: Pollen grains 4-colporate, prolate-spheroidal (40—45 µm; amb rounded). Apocolpium large. Ora lalongate. Exine smooth, thickened at the apertures.

Secondary xylem: *Vessels* in radial rows of (2)3 or 4(6), tangential diameter 60—160 µm; intervascular pits 4.5 µm; gum present. *Ray tissue* heterogeneous Kribs Type 3; rays 1- or 2-seriate, up to 15 cells high, the heterocellular with 1 marginal row. *Fibres* septate. *Parenchyma**. Paratracheal: confluent and banded; crystals absent. Apotracheal: terminal bands present.

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* Note: The parenchyma is very abundant, and it is difficult to distinguish between that associated with the vessels and that which is unassociated.

Distribution: One or two species in eastern Australia.

Type species: *S. glandulosum* (Smith) A. Juss.

Relationships: *Synoum* is closely related to *Guarea* and *Dysoxylum* but may be distinguished from both by the presence of the arillode which unites the two seeds of each locule, a situation unknown elsewhere in the family. *Synoum* has leaves bearing a terminal leaflet and flowers which lack a stipitate disk. These features are rarely encountered in *Guarea*. The staminal tube of *Guarea* is often shortly cylindrical, never cyathiform as in *Synoum*.

Synoum differs from all species of *Guarea* examined by us in having prolate-spheroidal pollen grains (100P/E=108). Those of *Guarea* are oblate-spheroidal or spheroidal (100P/E=93—100). The pollen grains of *Synoum* also differ in having equatorially elongate pores; those of *Guarea* are circular.

The secondary xylem of *Synoum* also shows a number of differences from that of *Guarea*. These are: the absence of crystals in chambered parenchyma cells and the presence of apotracheal banded parenchyma. In addition, heterogeneous ray tissue, characteristic of *Synoum*, is only rarely found in *Guarea*.

Synoum differs from all species of *Dysoxylum* known to us in lacking a cyathiform or tubular disk. The staminal tube of *Dysoxylum* is rarely shortly cylindrical, never cyathiform as in *Synoum*. The pollen grains of these two genera are not significantly different. The secondary xylem of the two genera is similar except that the absence of crystals in the parenchyma of *Synoum* distinguishes the latter from all species of *Dysoxylum* but for *D. acutangulum* Miq., which differs in other respects.

The relationships of *Synoum* with *Pseudocarapa* and *Anthocarapa* are discussed under the respective genera.

33. ANTHOCARAPA

Anthocarapa Pierre, Fl. Forest. Cochinchine 5 (1897) sub t. 343; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 166. — Fig. 13b, c.

Amoora sect. *Pseudo-Guarea* C. DC. in A. & C. DC., Monogr. Phan. 1 (1878) 590 *pro parte quoad A. nitidula* Benth., *A. balanseana* C. DC. *et A. vieillardii* C. DC. *tantum*.

Trees with paripinnate leaves. *Indumentum* of simple hairs. *Leaflets* without pellucid lines or dots. *Flowers* unisexual (plants dioecious), in axillary panicles. *Calyx* 4- or 5-lobed to the middle or below. *Petals* 5, free, imbricate. *Staminal tube* 0.2—0.25 cm long, cyathiform; margin with 10—12 truncate or emarginate appendages. Anthers glabrous, alternate with the appendages, inserted within the throat of the staminal tube and partly exserted; antherodes similar, without pollen, not dehiscing. *Disk* in male flowers thick, fleshy, annular or patelliform, surrounding the pistillode; in female flowers small, annular, and confined to the base of the ovary. *Ovary* (2)3-locular; loculi uniovulate, placentation axile. Style-head discoid. Pistillode slender, immersed in the disk; vestigial ovules present. *Fruit* a tardily dehiscent, 2- or 3-valved, loculicidal capsule; pericarp thick and rather woody. *Seed* with a non-vascularised sarcotesta. *Embryo* with thick collateral cotyledons; radicle superior, included.

Pollen: Pollen grains 4(5)-colporate, prolate-spheroidal (35—40 μm, amb rounded to quadrangular). Apocolpium medium. Ora lalongate. Exine smooth, thickened at the apertures.

Secondary xylem: *Vessels* solitary and in radial groups of 2—4(8); tangential diameter 40—100 μm; intervascular pits 3 μm; gum absent. *Ray tissue* homogeneous Kribs Type 1 or heterogeneous Kribs Type 3; rays 1 or 2(3)-seriate, up to 30 cells high, the

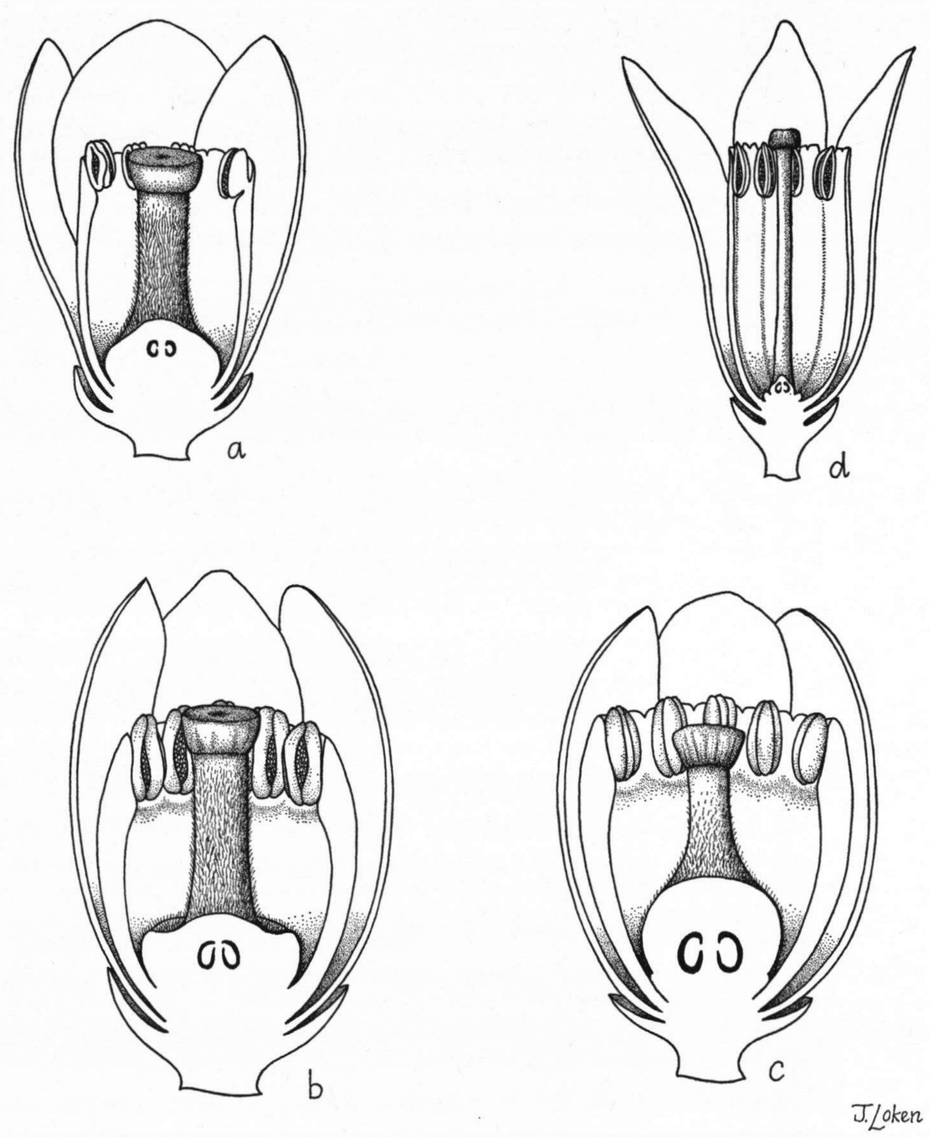

Fig. 13. a. *Synoum glandulosum* (Smith) A. Juss., ?♂, ×9. — b. *Anthocarapa balanseana* (C. DC.) Pierre, ♂, ×15. — c. *A. sp.*, ♀, ×15. — d. *Pseudocarapa championii* (Hook. *f.* & Thoms. *ex.* Thwaites) Hemsl., ☿, ×9. (a. *Constable s.n.*; b. *Pennington 8136*; c. *White 12867*; d. *Walker s.n.*).

heterocellular with 1 marginal row. *Fibres:* septate. *Parenchyma.* Paratracheal: banded, with crystals.

Distribution: Two or three species in Australia, New Guinea, and New Caledonia.

Type species: *A. balanseana* (C. DC.) Pierre (here chosen as lectotype).

Relationships: All three species of this genus were originally placed in *Amoora*, where they remained until 1897 when Pierre transferred the two New Caledonian species (*A. balanseana* C. DC. and *A. vieillardii* C. DC.) to his new genus *Anthocarapa*. The third species, *A. nitidula* Benth. from Australia, was left in *Amoora* by Pierre, but it was removed, in our opinion mistakenly, to *Pseudocarapa* by Merrill and Perry in 1940. In the same year Harms followed Pierre's circumscription of *Anthocarapa*, but also suggested that *Amoora nitidula* Benth. should be placed there, without expressing a firm opinion.

It is clear to us that these three species should belong to the same genus, since they share the following important characters: a corolla with imbricate aestivation, a cyathiform staminal tube, an annular or patelliform disk, uniovulate loculi, and a capsular fruit containing a seed with a sarcotesta.

Anthocarapa differs from *Amoora* in many characters. The indumentum is simple (not stellate); the staminal tube is terminated by appendages; it has an annular or patelliform disk (absent in *Amoora*); it has a long style surmounted by a discoid style-head (style short or absent, style-head never discoid in *Amoora*).

The morphological evidence shows it to be much more closely related to *Guarea*, *Synoum*, *Dysoxylum*, and *Pseudocarapa*. The characters that separate it from *Guarea* are the absence of the dormant terminal bud or terminal leaflet on the leaves and the annular or patelliform disk (not stipitate).

It may be distinguished from *Synoum* by the paripinnate leaves, the staminal tube appendages, the uniovulate loculi, and exarillate seeds. Characters constant in *Anthocarapa* but rarely seen in *Synoum* are: number of petals 5 (nearly always 4 in *Synoum*); number of anthers 10 (nearly always 8 in *Synoum*).

Anthocarapa differs from all species of *Dysoxylum* in having an annular disk (not cyathiform or tubular), and the staminal tube of *Anthocarpa* differs from that of all species of *Dysoxylum* in being cyathiform (not tubular).

The pollen grain characteristics of *Anthocarapa* exclude it from *Amoora*, but the 4-colporate prolate-spheroidal grains are similar to those of many species of *Dysoxylum* and to those of *Synoum*.

The secondary xylem provides additional evidence for discounting *Amoora* as a closely related genus. *Amoora* characteristically has sparse, vasicentric and aliform parenchyma, but in *Anthocarapa* it is abundant and exclusively banded, very similar to that of *Dysoxylum* or *Guarea*.

The differences between *Anthocarapa* and *Pseudocarapa* are discussed in detail under the latter.

34. PSEUDOCARAPA

Pseudocarapa Hemsl. in Hook. Ic. Pl. (1884) t. 1458; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19 bI (1940) 139. — **Fig. 13d.**

Amoora sect. *Pseudo-Guarea* C. DC. in A. & C. DC., Monogr. Phan. 1 (1878) 591 *pro parte quoad A. championii* (Hook. *f.* et Thoms.) C. DC. *tantum.*

Trees with paripinnate leaves. *Indumentum* of simple hairs. *Leaflets* without pellucid lines or dots. *Flowers* bisexual, in axillary panicles. *Calyx* 4-lobed to the middle. *Petals* 3 or 4, free, valvate at least in the lower half, sometimes imbricate at the apex. *Staminal tube* 0.4—0.6 cm long, cylindrical, the margin with 8 short emarginate appendages. Anthers glabrous, alternate with the appendages, inserted within the throat of the staminal tube and partly exserted. *Disk* annular or patelliform, fused to the base of the ovary. *Ovary* (2)3- or 4-locular; loculi with 2 collateral ovules, placentation axile. Style-head narrowly discoid, with a central depression. *Fruit* a 3- or 4-valved loculicidal capsule, the loculi (1)2-seeded. Pericarp rather hard. *Seed* with a fleshy arillode on the adaxial side. *Embryo* with thick collateral cotyledons; radicle superior, extending to the surface.

Pollen: Pollen grains in rhomboidal tetrads. Individual grains 3-colporate, ? spheroidal (30—35 μm; amb rounded). Apocolpium large. Ora circular. Exine smooth, thickened at the apertures.

Secondary xylem: *Vessels* solitary and in radial groups of 2 or 3(4); tangential diameter 80—140 μm; intervascular pits 4.5 μm; gum absent. *Ray tissue* heterogeneous Kribs Type 3; rays 1—3-seriate, up to 30 cells high, the heterocellular with 1 marginal row. *Fibres:* septate. *Parenchyma.* Paratracheal: vasicentric, aliform and confluent, without crystals.

Distribution: One species in Ceylon, with perhaps one in New Guinea, and one undescribed species in the Philippines.

Type species: *P. championii* (Hook. *f.* & Thoms. *ex* Thwaites) Hemsl.

Relationships: The type species of this genus has been placed in three genera. It was originally described as *Dysoxylum championii* by Hooker *f.* and Thomson (1864), but C. de Candolle (1878) transferred it to section *Pseudo-Guarea* of *Amoora.* Six years later, Hemsley, who was dissatisfied with both these treatments, suggested that it belongs in a distinct genus, *Pseudocarapa.* Harms accepted Hemsley's view, and placed *Pseudocarapa* in the *Guareinae* next to *Synoum.*

This genus is most closely related to *Dysoxylum* from which it differs in having an annular or patelliform disk (not cyathiform or tubular). Its pollen differs from that of *Dysoxylum* in being shed in rhomboidal tetrads. Pollen shed in tetrads is unknown elsewhere in the *Meliaceae.*

It differs from *Amoora* in many features: its simple indumentum (not stellate); its valvate corolla (not imbricate); its cylindrical staminal tube bearing appendages (not cyathiform or globose); its disk (*Amoora* has no disk); its long style and discoid style-head (style short or absent, style-head never discoid in *Amoora*).

Pseudocarapa is also related to *Guarea, Synoum,* and *Anthocarapa.* The following characters distinguish it from *Guarea*: leaves without a terminal bud or leaflet, disk annular or patelliform (not stipitate), ovules collateral (not superposed), seed arillodiate (no sarcotesta as in *Guarea.*)

It may be separated from *Synoum* by the paripinnate leaves, valvate petals, appendages on the staminal tube, and the absence of the common arillode uniting two seeds in each loculus.

Pseudocarapa differs from *Anthocarapa* in a number of characters, which may be referred to in the key.

The wood anatomy of *Pseudocarapa* is of a type rarely found in *Dysoxylum* and allied genera. The rather sparse paratracheal parenchyma has been observed in only two species of *Dysoxylum, D. acutangulum* Miq. and the species represented by *Pennington 7881* from Sabah. It is, however, quite frequently present in species of *Amoora,* but this cannot be regarded as significant as there are so many morphological differences between these two genera.

Notes: (1) The taxonomic position of *P. papuana* Merr. and Perry is uncertain. Harms

(1942) transferred it to *Aglaia* on account of the minute flowers, but it differs from that genus in the simple indumentum, valvate corolla, the presence of a disk, and the discoid style-head. The pollen grains are also larger than those of most species of *Aglaia* and 4-colporate; those of *Aglaia* are almost consistently 3-colporate.

The minute unisexual flowers, densely hairy cyathiform staminal tube, uniovulate loculi, and pollen grains which are shed singly are also quite distinct from *Pseudocarapa*. In the latter character it resembles the genus *Anthocarapa*.

Until fruits of this species are collected it is not possible to place it with any certainty.

(2) We have not been able to examine any material of *P. inopinata* Harms, the third species of this genus..

(3) The species represented by *Loher 255* from the Philippine Islands possibly belongs in *Pseudocarapa*. The specimen, which bears male flowers only, shares the majority of the leaf and flower characters of the genus, but female flowers and fruit are needed to confirm its relationships. The pollen grains of this species are shed singly, not in tetrads as in *P. championii*.

35. DYSOXYLUM

Dysoxylum Blume, Bijdr. (1825) 172; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 1 60 t. 35 figs. F-J. — **Fig. 14a—d.**

? *Ricinocarpodendron* Boehm. in Ludwig, Definit. Gen. Pl., ed. Boehmer (1760) 512.

Alliaria [Rumph., Herb. Amb. 2 (1741) 81, t. 20] O. Kuntze, Rev. Gen. 1 (1891) 108; *non* Fabricius (1759), *nec* Scopoli (1760).

[? *Harpagonia* Noronha, Verh. Batav. Gen. 5(2) (1790) 64, *nom. nud.*]

Epicharis Blume, op. cit. 166; Harms, tom. cit. 167, t. 35 figs. K, N-Q.

Didymocheton Blume, op. cit. 177; Harms, tom. cit. 156, t. 35 figs. L-M.

Hartigshea A. Juss., Mém. Mus. Hist. Nat. Par. 19 (1830) 227.

Cambania Comm. *ex* M. J. Roem., Synops. Monogr. Hesperid. 1 (1846) 83, 102.

Prasoxylon M. J. Roem., tom. cit. 83, 101.

Macrochiton M. J. Roem., tom. cit. 84, 104.

Disyphonia Griff., Not. 4 (1854) 504, in obs., *nomen provisorium.*

[*Meliadelpha* Radlk., Sitzungsber. Bayer. Akad. 20 (1890) 331, in obs., *nom. nud.*]

Trees or treelets. *Indumentum* of simple hairs. *Leaves* pinnate, rarely with limited apical growth. *Leaflets* without pellucid lines or dots. *Flowers* bisexual or unisexual (plants dioecious), in axillary panicles, often narrow and racemose or thyrsoid, more rarely spicate, occasionally ramiflorous or cauliflorous; flowers sometimes subtended by several imbricate bracts. *Calyx* rarely entire, usually shallowly or deeply 3—5(6)-lobed, or sepals free, or calyx closed in bud, splitting to produce an irregular margin and then circumscissile at the base; aestivation open or imbricate. *Petals* 3—6, free or fused to the lower or upper half of the staminal tube, imbricate or valvate. *Staminal tube* 0.2—2.3 cm long, cylindrical, margin entire, crenate, irregularly toothed, or terminated by 6—10(13) short, obtuse, truncate, emarginate, or rarely bilobed appendages. Anthers glabrous or rarely hairy, alternate with the appendages, inserted within the throat of the staminal tube, completely included or partly exserted. *Disk* free, long- or short-tubular, less frequently cyathiform, the margin often crenate or lobed. *Ovary* 2—5-locular; loculi with 1 or 2 collateral or superposed ovules, placentation axile. Style-head discoid, less frequently small and capitate. *Fruit* a 2—5-valved loculicidal capsule, the loculi 1- or 2- seeded. *Seed* arillodiate or with a sarcotesta; arillode fleshy, partly or completely surrounding the seed, partly fused to the testa or free; sarcotesta adaxial or completely surrounding the seed. *Embryo* with thick, collateral, oblique or superposed cotyledons; radicle superior or adaxial, extending to the surface or included.

Germination: cryptocotylar or less frequently phanerocotylar, cotyledons often fugaceous; cataphylls sometimes present; eophylls usually opposite, rarely spirally arranged, simple, trifoliolate, or pinnate, entire or toothed (personal observations and Burger, 1972).

Chromosome numbers: n= 10, 40, 42; 2n= 80, 84.

Pollen: Pollen grains (3)4(5)-colporate, oblate-spheroidal, spheroidal, or prolate-spheroidal (30—60 μm, amb rounded). Apocolpium large or medium. Ora circular or lalongate, rarely crassimarginate. Exine smooth or scabrous, thickened at the apertures.

Secondary xylem: *Vessels* solitary and in radial rows of 2—4(6), with rare pore clusters; tangential diameter 40—240 μm; intervascular pits 3.5—7.5 μm; gum usually present. *Ray tissue* usually heterogeneous Kribs Type 3 or homogeneous Kribs Type 1, rarely heterogeneous Kribs Type 2 or uniseriate-homogeneous or -heterogeneous; rays 1—3(4)-seriate, up to 70 cells high, the heterocellular with 1—6 marginal rows. *Fibres:* septate. *Parenchyma.* Paratracheal: rarely vasicentric, occasionally aliform, usually confluent and banded, in various combinations; crystals usually present. Apotracheal: terminal bands rarely present. Diffuse crystalliferous cells occasionally present. Silica deposits are rarely present.

Distribution: About 60 species from the Indo-Malayan region eastwards to Australia, New Guinea, and Polynesia. One species in New Zealand.

Type species: *D. alliaceum* Bl.

Relationships: The genera *Didymocheton* Bl. and *Epicharis* Bl. have been treated as sections of *Dysoxylum* Bl. by several previous authors, including C. de Candolle (1878) and Harms (1896), but they were raised to generic rank by the latter in the second edition of Die Natürlichen Pflanzenfamilien (1940).

Didymocheton was defined by the free sepals with imbricate aestivation and the flowers frequently subtended by a number of densely overlapping bracts. The calyx characters are not sufficiently clear-cut, as there are a number of borderline cases, e.g. *Dysoxylum pilosum* A. C. Smith and *Dysoxylum spectabile* Hook. *f.* where the calyx may be deeply divided or with free sepals and the aestivation open or imbricate. As these two characters do not appear to be correlated with any of the other variables — for example the fusion of the corolla to the staminal tube, presence or absence of an arillode, valvate or imbricate corolla lobes — there does not seem to be sufficient justification for keeping these species as a separate genus.

Epicharis was distinguished from *Dysoxylum* by Harms because its calyx is closed in bud and circumscissile at the base. However, some species, e.g. *E. hierniana* Harms (*Dysoxylum cauliflorum* Hiern) have been included in *Epicharis* although the calyx is neither closed in bud nor circumscissile at the base. Since other genera, e.g. *Guarea* and *Chisocheton*, may contain a few species which differ from the others in having a closed circumscissile calyx but do not differ in other respects, there seems to be no reason why *Epicharis* should not be united with *Dysoxylum*. If *Epicharis* is given generic rank, it would be logical to separate the circumscissile species of *Chisocheton* and *Guarea* also into segregate genera. In our opinion this would be unwise.

No additional evidence for maintaining *Didymocheton* or *Epicharis* as genera is obtained from the wood anatomy. *Didymocheton* and *Dysoxylum sensu stricto* are indistinguishable. Banded apotracheal parenchyma, which is rarely seen in *Dysoxylum sensu stricto*, occurs in the two species of *Epicharis* which we have examined, but an investigation of several samples of *Epicharis caulostachya* (Miq.) Harms revealed that this type of parenchyma was not always present.

Dysoxylum (including *Didymocheton* and *Epicharis*) differs from *Chisocheton* in one

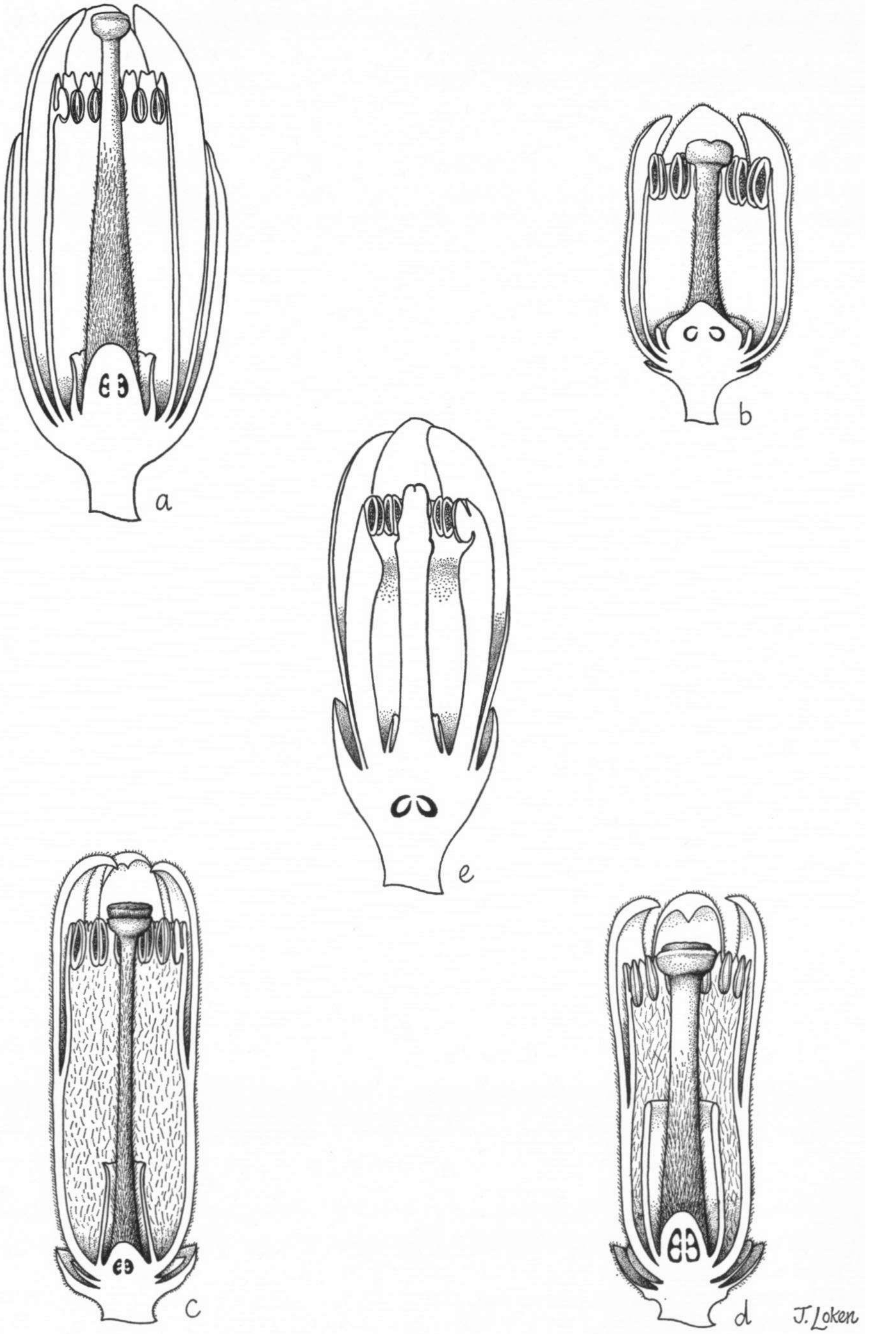

Fig. 14. a. *Dysoxylum caulostachyum* Miq., ♂, ×3. — b. *D. arborescens* (Blume) Miq., ⚥, ×5. — c. *D. amooroides* Miq., ♂, ×5; d. ditto, ♀, ×5. — e. *Sandoricum borneense* Miq., ⚥, ×7.5. (a. *Pennington 8105*; b. *Pennington 7818*; c. *Pennington 8054*; d. *Pennington 8116*; e. *Pennington 7894*).

character: the presence of a cyathiform or tubular disk. The disk of *Chisocheton*, when present, is never more developed than stipitate or patelliform. This difference is supported by a few good differential characters, viz. absence of dormant terminal bud from the leaf and anthers which are not locellate, both of which exclude nearly all species of *Chisocheton*. Some species of *Dysoxylum* have the corolla fused to the staminal tube to half way or beyond, a condition never found in *Chisocheton*, and the seed of *Dysoxylum* is never scutiform with a large mealy-white hilum as it often is in *Chisocheton*.

Dysoxylum is closely related to *Guarea* but may be distinguished from it by one absolutely diagnostic character. In *Guarea* the disk is never cyathiform or tubular. Two additional characters support this distinction. Most species of *Guarea* have a dormant terminal bud on the leaf, a feature never present in *Dysoxylum*. In *Guarea* the corolla is nearly always free from the staminal tube, and only rarely fused to it at the base, whereas in *Dysoxylum* the corolla and staminal tube are often fused to halfway or above.

Silica is rarely found in the wood of *Dysoxylum* whereas it is nearly always present in *Chisocheton* and occasionally in *Guarea*. No other distinguishing features were discovered from the wood structure or pollen morphology.

The differences between *Dysoxylum* and *Anthocarapa*, *Pseudocarapa*, *Cabralea*, *Synoum*, and *Sandoricum* are discussed under the respective genera.

Tribe 7. SANDORICEAE

Tribus **Sandoriceae,** *tribus nova.*

Folia trifoliolata. Tubus stamineus cylindricus, supra costatus. Antherae intra fauces tubi staminei insertae. Discus tubularis. Caput styli stigmate profunde 4-vel 5-lobato praeditum. Fructus drupaceus. Semen sine arillodio, sarcotesta praeditum, sine endospermio.

Typus tribus: *Sandoricum.*

Leaves trifoliolate. Indumentum of simple hairs. Flowers hermaphrodite. Staminal tube cylindrical, ribbed above. Anthers inserted within the throat of the staminal tube. Disk tubular. Style-head bearing a deeply 4- or 5-lobed stigma. Fruit a drupe. Seed exarillodiate, with a sarcotesta, exendospermous. Cotyledons plano-convex, collateral.

Pollen. Subprolate; 3(4)-colporate; exine smooth or scabrous.

Secondary xylem. Vessels solitary and paired; fibres non-septate; apotracheal terminal parenchyma absent; paratracheal parenchyma vasicentric to aliform.

36. SANDORICUM

Sandoricum Rumph. [Herb. Amb. 1 (1741) 167, t. 64] *ex* Cav., Dissert. 7 (1789) 359, t. 202, 203; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 170, t. 35 figs. A-E. — **Fig. 14e.**

Trees. *Flowers* in axillary panicles, sometimes with cymose branching. *Calyx* almost truncate or shallowly 4- or 5-lobed. *Petals* (4)5, free, imbricate. *Staminal tube* 0.45—0.7 cm long, terminated by 10 short bilobed appendages. Anthers 10, glabrous, inserted opposite the appendages, completely included. *Disk* free, the margin coarsely toothed. *Ovary* slightly sunken in the calyx, 4- or 5-locular; loculi with 2 collateral ovules. Style columnar, expanded above into a narrow annular style-head, bearing a 4- or 5-lobed stigma on a thick cylindrical base. *Fruit* 1—5-locular; the pyrenes 1(2)-seeded; outer mesocarp rather dry-fleshy or rather soft and fibrous, inner mesocarp fleshy or spongy-fibrous; endocarp thin and cartilaginous. *Seeds* bean-shaped, laterally compressed, with a sarcotesta; sarcotesta small and confined to the apex of the seed, or completely surrounding the seed and then thickened on the adaxial surface. *Embryo* with thick cotyledons; radicle superior, extending to the surface or slightly exserted.

Germination: phanerocotylar; eophylls opposite, trifoliolate.

Chromosome numbers: 2n= 28 (*S. radiatum* King: Styles & Khosla, unpublished); 2n= 16, 32 (*S. indicum* Cav.); n= 11, 22 (*S. koetjape* (Burm. *f.*) Merr.).

Pollen: Pollen grains 3(4)-colporate, subprolate (45—60 μm; amb rounded to triangular). Apocolpium large or medium. Ora circular or lalongate, sometimes crassimarginate. Exine smooth or scabrous, thickened at the apertures.

Secondary xylem: *Vessels* solitary and in radial pairs; tangential diameter 40—180 μm; pit size 3—4.5 μm; gum present or absent. *Ray tissue* heterogeneous Kribs Type 2 or 3; rays 1—5-seriate, up to 45 cells high, with 1—4 marginal rows. *Fibres* non-septate. *Parenchyma.* Paratracheal: vasicentric to aliform. Diffuse crystalliferous cells present or absent.

Distribution: Three to five rather variable species from the Indo-Malayan region to New Guinea.

Type species: *S. indicum* Cav.= *S. koetjape* (Burm. *f.*) Merr.

Relationships: *Sandoricum* is a very distinct genus placed after *Dysoxylum* by Harms on account of its free tubular disk. It has little else in common with this genus, and is at once identified by the trifoliolate leaves, the ribbed staminal tube, characteristic style-head with divided stigma, and the indehiscent drupaceous fruit.

The secondary xylem is also unlike that of *Dysoxylum* or of any other genus in the *Guareeae.* The very heterogeneous ray tissue, non-septate fibres, and sparse vasicentric or aliform parenchyma distinguish *Sandoricum* immediately.

The pollen grains are also distinctive by being almost consistently 3-colporate, a feature unknown in *Dysoxylum* and its related genera.

Note: According to Harms, *S. harmandii* Pierre has 1—5-foliolate leaves. This species was described from fruiting material and the flowers are not known. Its position is uncertain.

SUBFAMILY II. QUIVISIANTHOIDEAE

Subfamilia **Quivisianthoideae,** *subfamilia nova.*

Gemmae nudae. Folia spiraliter disposita. Planta dioecia vel flores hermaphrodita. Loculi (1) 2 ovulis praediti. Caput styli capitatum. Fructus capsularis, siccus, loculicide dehiscens; semen alatum.

Typus subfamiliae: *Quivisianthe.*

Buds naked. Leaves spirally arranged. Plants dioecious or flowers hermaphrodite. Loculi (1)2-ovulate, ovules collateral. Style-head capitate. Fruit a dry, loculicidal capsule; seed winged. Endosperm present.

37. QUIVISIANTHE

Quivisianthe Baill. in Grandidier, Hist. phys. natur. Madag. 33, tom. 3 (Atlas 2), fasc. 34 (1893) t. 251; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2., 19 bI (1940) 117. — **Fig. 15a, b.**

Trees with pinnate leaves. *Flowers* in short axillary panicles. *Calyx* 5-lobed to halfway. *Petals* 5, free, valvate. *Staminal tube* 0.3—0.6 cm long, shortly cylindrical or urceolate, with an entire or shallowly lobed margin. Anthers 5, hairy or glabrous, inserted on the margin of the staminal tube; antherodes much smaller, not dehiscing, without pollen. *Disk* annular or patelliform, fused to the base of the ovary and staminal tube, or absent and then the ovary and staminal tube on a short thick stipe. *Ovary* 3(4)-locular. Pistillode similar. Style-head surmounted by a small obscurely 3-lobed stigma. *Fruit* 3(4)-valved, deeply 3(4)-angled; loculi (1)2-seeded, thin but woody. *Seed* with a dry testa, flat, with a large wing at the upper end, attached to the placenta near the base of the wing; thin endosperm present. *Embryo* with flat collateral cotyledons; radicle superior, long, exserted.

Pollen: Pollen grains 4(5)-colporate, spheroidal to prolate-spheroidal (35—45 µm, amb rounded). Apocolpium small to medium. Colpi sometimes shortly bifurcate. Ora circular. Exine medium, smooth, not or only slightly thickened at the apertures.

Secondary xylem: Not seen.

Distribution: One or two species in Madagascar.

Type species: Q. *papinae* Baill.

Relationships: This genus, though occupying a very isolated position in a subfamily of its own, is similar in its floral structure to some genera in the tribe *Trichilieae* of the subfamily *Melioideae*. Harms (1940), who had not examined the fruit, placed it provisionally in the genus *Trichilia*. The complete staminal tube without appendages and with the anthers or antherodes inserted on the margin is also very similar to that of *Ekebergia*. However, the presence of the dry loculicidal capsule containing dry winged seeds immediately distinguishes it from these genera and indeed from all other members of the subfamily *Melioideae*.

SUBFAMILY III. CAPURONIANTHOIDEAE

Subfamilia **Capuronianthoideae**, *subfamilia nova*.

Gemmae nudae. Folia decussata. Planta monoecia. Loculi duobus ovulis evolutis et 1 vel 2 ovulis vestigialibus praediti. Caput styli capitatum. Fructus siccus pro parte septifrage dehiscens; semen sarcotesta corticosa.

Typus subfamiliae: *Capuronianthus*.

Buds naked. Leaves decussate. Plants monoecious. Loculi with 2 fully developed and 1 or 2 vestigial ± superposed ovules. Style-head capitate. Fruit dry, with partial septifragal dehiscence; seed with a corky sarcotesta. No endosperm.

Secondary xylem. Rays 2- or 3-seriate, partly heterogeneous. Crystals present in marginal ray cells. Paratracheal parenchyma sparse (vasicentric).

38. CAPURONIANTHUS

Capuronianthus J. F. Leroy, Compt. Rend. Acad. Sci. Par. 247 (1958) 1374; Journ. Agric. Trop. Bot. Appl. 5 (1958) 762. — Fig. 15c, d.

Trees with pinnate leaves. *Flowers* unisexual in short axillary racemes or panicles. *Calyx* deeply 4-lobed or of 4 free imbricate sepals. *Petals* 4(5), free, usually contorted, less frequently imbricate. *Staminal tube* 0.3—0.35 cm long, urceolate or shortly cylindrical, the margin with 8 deltate, ovate, or sometimes shortly bifid appendages alternating with the anthers. Anthers 8, glabrous, inserted on the margin of the staminal tube between the appendages, the base inside the throat, the apex exserted slightly beyond the appendages; antherodes much smaller, very slender, not dehiscing, and without pollen. *Disk* in male flowers a conspicuous swollen annulus fused to the base of the ovary; in female flowers reduced to an indistinct swelling round the base of the enlarged ovary, or absent; both sexes with a thin, patelliform, extra-staminal swelling fused to the base of the staminal tube. *Ovary* 2—4-locular; pistillode slender, with 3 or 4 ovules, either all vestigial or with 2 somewhat larger and better developed. Style very short or absent; style-head small. *Fruit* a 3- or 4-valved, shortly rostrate capsule with a short stipe; each valve 1- or

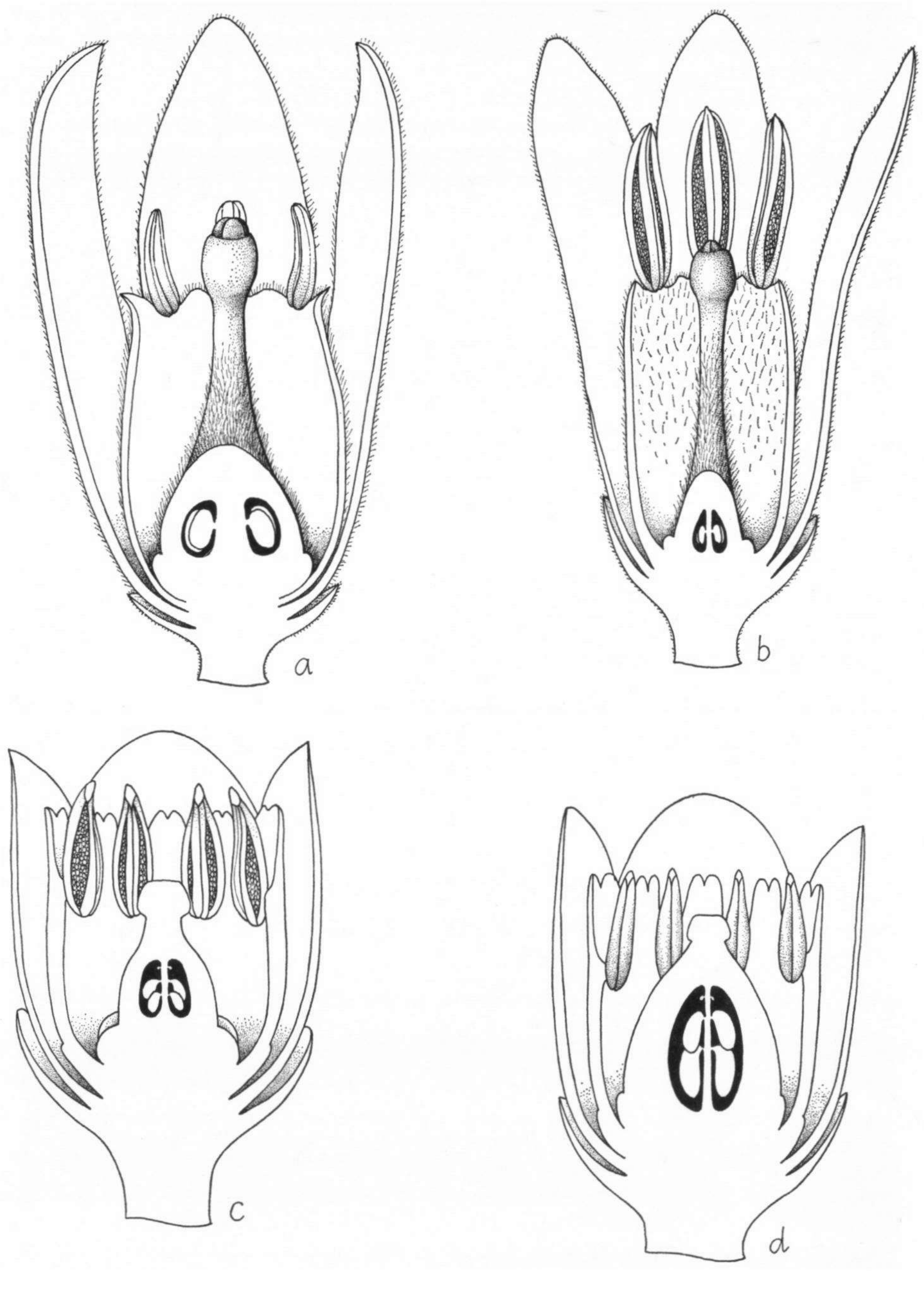

Fig. 15. a. *Quivisianthe sp.*, ♀, × 12.5,— b. Q. *sp.*, ♂, × 12.5. — c. *Capuronianthus mahafalensis* J. F. Leroy, ♂, × 12.5; d. ditto, ♀, × 12.5. (a. *McWhirter 169*; b. *Capuron 9214*; c, d. *Capuron 27258*).

2-seeded; epicarp and mesocarp dry-fleshy and fibrous, dehiscing irregularly or indehiscent; endocarp cartilaginous, regularly dehiscent along the septa. *Seed* with a thick testa. *Embryo* with plano-convex collateral or oblique cotyledons; radicle superior or adaxial, extending to the surface or slightly projecting.

Chromosome number: 2n= 58.

Pollen: Pollen grains 4-colporate; subprolate (27—35 μm; amb rounded). Apocolpium medium. Ora circular. Exine medium, smooth, unthickened or occasionally slightly thickened at the apertures.

Secondary xylem: *Vessels* solitary and in radial rows of 2—4, with some clusters. Tangential diameter 20—80 μm; intervascular pits 3—4.5 μm: gum present. *Ray tissue* heterogeneous Kribs Type 3; rays 2- or 3-seriate, up to 25 cells high, the heterocellular with 1 marginal row. The marginal ray cells contain conspicuous crystals. *Fibres* non-septate. *Parenchyma*. Paratracheal: vasicentric. Diffuse crystalliferous cells abundant.

Distribution: One species in Madagascar.

Type species: *C. mahafalensis* J. F. Leroy.

Relationships: Although *Capuronianthus* is an isolated genus in the *Meliaceae* it appears to be distantly related to *Carapa* and *Xylocarpus* in the *Swietenioideae*. It shares with them both the partial septifragal dehiscence of the fruit, and the seed has the corky sarcotesta of *Xylocarpus*. Its chromosome number is the same as that of *Carapa* (2n=58). However, in all other characters of subfamily importance it differs from these genera; moreover, in some floral characters it resembles very closely genera in the tribe *Trichilieae* of the subfamily *Melioideae*. The xeromorphic habit of the plant and the floral structure are similar to those of the endemic Australian genus *Owenia*. The loculi containing only 2 fully developed ovules and the capitate style-head are characteristic of many members of the *Melioideae*, although it must be pointed out that the presence of an additional vestigial ovule in the loculus rarely occurs in the latter subfamily.

In its secondary xylem *Capuronianthus* is intermediate between the *Swietenioideae* and the *Melioideae*. It possesses the crystals in the marginal ray cells of the former and the abundant crystals in chambered parenchyma cells and narrower rays of the latter. It is thus intermediate between the two subfamilies, but nevertheless quite distinct from both.

SUBFAMILY IV. SWIETENIOIDEAE

Buds nearly always protected by a cluster of scale-leaves. Leaves spirally arranged. Monoecious. Loculi nearly always with 3 or more ovules, these biseriate. Style-head discoid or very rarely capitate. Fruit a woody septifragal capsule, with a central columella; seed winged; capsule less frequently subwoody or leathery and then with a rudimentary columella and seed unwinged with a woody or corky sarcotesta.

Pollen: subprolate or prolate-spheroidal; 4-colporate; exine smooth.

Secondary xylem: Rays nearly always broad, (2)3—6(7)-seriate, and heterogeneous. Crystals usually present in marginal ray cells, often absent in wood parenchyma. Paratracheal parenchyma rather sparse (vasicentric or aliform).

Tribe 1. CEDRELEAE

Flowers with an androgynophore (? disk) (very short in *Toona*); base of petals adnate to the androgynophore by a carina. Stamens 5, free, sometimes together with a whorl of staminodes *(Toona)*; appendages absent. Capsule woody or rarely membranaceous, with a soft columella; seeds winged at one or both ends; cotyledons flat, leaflike; residual endosperm present.

Pollen and Secondary xylem as for the subfamily.

1. Seeds winged below, attached by the seed towards the apex (distal end) of the central columella; androgynophore column-shaped, longer than the ovary; first leaflets of seedlings entire . . . . 39. *Cedrela*

1a. Seeds winged at both ends, or if with one wing only then attached by the seed-end towards the base of the central columella (proximal end) and winged above; androgynophore cushion-shaped, shorter than or equalling the ovary; first leaflets of seedlings lobed or toothed . . . . 40. *Toona*

39. CEDRELA

Cedrela P. Browne, Hist. Jamaica (1756) 158, t. 10 fig. 1; L., Syst. Nat. ed. 10 (1759) 940; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 40, t. 2 A–C, K.; Earle Smith, Fieldiana, Botany 29 (1960) 295—341. — **Fig. 16a, b.**

Cedrus Mill., Gard. Dict. ed. 7 (1759) (without pagination); *non* Trew (1757) *nom. cons.*, nec Duham. (1755) *nom. rejic.*

Johnsonia Adans., Fam. Pl. 2 (1763) 343. 564; *non* Mill. (1754) (=*Callicarpa* L.) *nom. rejic.*, *nec* R. Br. (1810) *nom. cons.*

Pterosiphon Turcz., Bull. Soc. Nat. Mosc. 36 (1863) 589.

Deciduous trees. *Leaves* paripinnate (very rarely imparipinnate), leaflets entire, glabrous or with simple hairs. *Flowers* 5-merous, unisexual, but with well-developed vestiges of the opposite sex present, borne in much-branched thyrses. *Calyx* lobed ± to the base, shallowly dentate, or cup-shaped and split down one side. *Petals* 5, free, longer than the calyx in bud, imbricate and adnate for ¼ of length to a long columnar androgynophore (? disk) by a median carina (thereby preventing their spreading in open flowers). *Stamens* 5, free, adnate to the androgynophore below; anthers in ♂ flowers yellow and dehiscing, antherodes in ♀ flowers shrivelled, brownish, and not producing pollen. No staminodes. *Ovary* 5-locular, borne at the apex of the gynophore, each loculus with 6—12 ovules; style short, style-head discoid with glandular stigmatic papillae. Pistillode in ♂ flowers more slender, with well-developed loculi and a longer style, vestigial ovules very small. *Fruit* a pendulous (erect in one species, fide Earle Smith), thinly or thickly woody, obovoid or claviform, septifragal capsule, opening from the apex by 5 valves. Columella woody, sharply 5-angled, extending to the apex of the capsule, seed scars conspicuous. *Seeds* with a terminal wing attached by the seed-end to the distal part (apex) of the columella and winged towards the base of the capsule; with residual endosperm. Cotyledons collateral, flattened and leaf-like; radicle laterally exserted.

Germination: phanerocotylar; eophylls opposite, trifoliolate, the leaflets sinuate, entire.

Chromosome numbers: $2n = 50,56$.

Distribution: About 5 poorly-defined species in the New World tropics, from Mexico to Argentina and in the Caribbean.

Type species: *C. odorata* L.

Relationships: The relationships of this genus with *Toona* are discussed after the latter.

40. TOONA

Toona (Endl.) M. J. Roem., Synops. Monog. Hesper. 1 (1846) 131, 139; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 44, t. 2 D–H, L. — **Fig. 16c, d.**

Cedrela sect. *Toona* Endl., Gen. Pl. 2 (1840) 1055.

Cuveraca Jones, Asiat. Res. 4 (1790) 281.

Surenus Rumph. [Herb. Amb. 3 (1743) 66, t. 39] *ex* O. Kuntze., Rev. Gen. 1 (1891) 110.

Deciduous or semi-evergreen trees. *Leaves* paripinnate, sometimes imparipinnate, leaflets entire, serrate, or dentate; glabrous or with simple hairs. *Flowers* 5-merous, unisexual, but with well-developed vestiges of the opposite sex present, borne in much-branched thyrses. *Calyx* free or (4)5-lobed. *Petals* 5, free, longer than the calyx in bud, imbricate, adnate at the base by a carina to a short cushion-shaped androgynophore (? disk). *Stamens* 5, free, arising from the androgynophore; anthers in ♂ flowers yellow and dehiscing, antherodes in ♀ flowers brown and shrivelled, not producing pollen; 1—5 thread-like staminodes sometimes present. *Ovary* 5-locular, at the apex of the androgynophore, each loculus with 6—10 ovules; style short, style-head discoid with glandular stigmatic papillae. Pistillode in ♂ flowers more slender, with well-developed loculi and a longer style; vestigial ovules very small. *Fruit* a pendulous, membranaceous or thinly woody, ellipsoid or obovoid, septifragal capsule, opening from the apex by 5 valves. Columella softly woody, 5-angled, extending to the apex of the capsule. *Seeds* either winged at both ends and attached towards the apex (distal end) of the columella or, if with a single wing, then attached by the seed-end to the base (proximal part) of the columella and winged above; with residual endosperm. Cotyledons collateral, flattened, and leaf-like; radicle laterally exserted.

Germination: phanerocotylar; eophylls opposite, trifoliolate, the leaflets deeply lobed or dentate.

Chromosome numbers: n= 26, 28, 39; 2n= 46, 52, 56.

Distribution: Approximately 6 poorly-defined species in the Old World eastwards from India to Australia.

Type species: *T. ciliata* M. J. Roem.

Relationships: *Cedrela* and *Toona* are clearly distinct from all other genera in the *Swietenioideae* and from almost all others in the family in possessing 5 free stamens and an androgynophore (? disk) to which they and the petals are attached. We believe that Roemer was justified in raising Endlicher's section *Toona* of *Cedrela*, containing the Old World species to generic rank, and most monographers have followed him. Although the two are closely related, they can be separated easily by a number of sound morphological characters. The androgynophore (? disk) is considerably longer (columnar) in *Cedrela* than in *Toona* and both stamens and petals are adnate to it for up to ⅓rd their length. In *Toona* it is patelliform and strongly resembles the disk in some other genera in *Meliaceae*, although the stamens appear to arise directly from it. A whorl of staminodes, which are never present in *Cedrela*, also occurs in some species. The capsules of *Cedrela* are always more strongly woody than in *Toona*, in which they tend to be delicate and membraneous. One species of *Toona*, *T. microcarpa* C. DC. does, however, have capsules with fairly thick woody valves with warty excrescences on the surface, reminiscent of *C. odorata* L. Germination is identical in both genera, although the leaflets of the first leaves in *Cedrela* spp. are always entire; those of *Toona* are dentate, lobed, or variously divided. Chromosomal evidence suggests different evolutionary histories for the two genera.

Tribe 2. SWIETENIEAE

Flowers with or without a gynophore; petals free; stamens 8—10, filaments partly or completely united into a cylindrical, urceolate, or bowl-shaped tube with or without appendages. Capsule woody, nearly always with a well-developed columella; the valves sometimes separating into an outer woody and an inner membranous layer. Seeds variously winged; cotyledons collateral, flattened; (residual) endosperm present.

Pollen and Secondary xylem as for the subfamily.

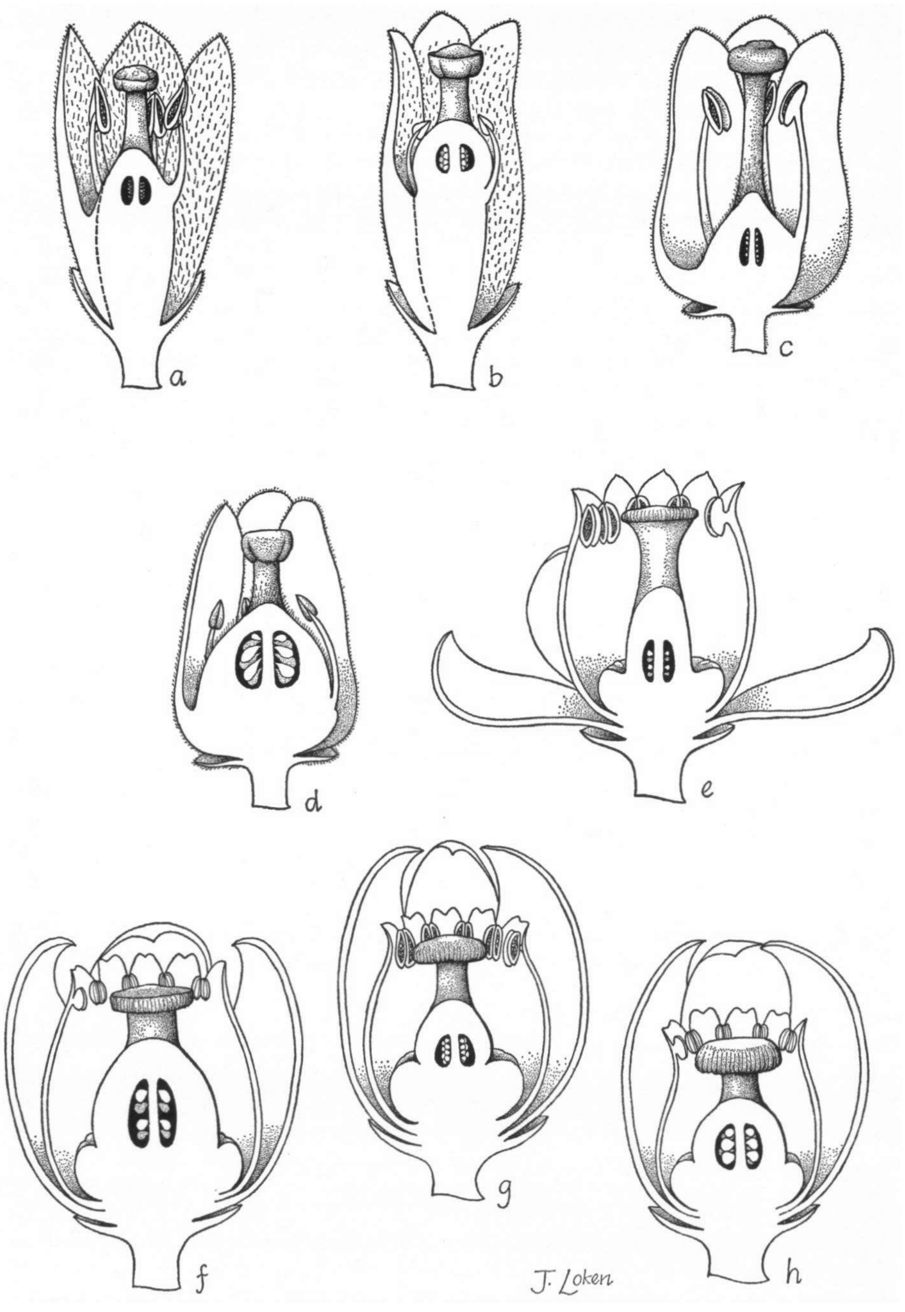

Fig. 16. a. *Cedrela odorata* L., ♂; b. ditto, ♀. — c. *Toona ciliata* M. J. Roem., ♂; d. ditto, ♀. — e. *Carapa grandiflora* Sprague, ♂; f. ditto, ♀. — g. *Xylocarpus granatum* Koen., ♂; h. ditto, ♀. All × 5. (a, b. *Pennington & Sarukhán 9650*; c, d. *Styles 266*; e, f. *Styles 177*; g. *Faulkner 1512*; h. *Hoogland 4302*).

1. Capsule globose, subglobose, or trigonous, not or scarcely longer than broad; seeds orbicular to suborbicular, winged all the way round.
  2. Capsule globose or subglobose, dehiscing by 4—6 valves which remain joined together at the base; wing of seed narrow, opaque . . . . 41. *Khaya*
  2a. Capsule ± trigonous, the valves falling separately at dehiscence; wing of seed broad and transparent . . . . 42. *Neobeguea*

1a. Capsule elongate, at least twice as long as broad, ovoid, obovoid, ellipsoid, claviform, or fusiform; seeds with a single terminal wing or with a wing at both ends.
  3. Seed with a wing at both ends, the upper (distal) wing the longer; anthers or antherodes inserted between the deltate teeth of the lobes of the staminal tube . . . . 43. *Soymida*
  3a. Seed with a single terminal wing.
    4. Seeds very numerous, arranged laterally in tiers in each locule; margin of staminal tube entire or crenulate . . . . 45. *Chukrasia*
    4a. Seeds up to 20 per locule, attached by the seed-or wing-end towards the proximal (base) or distal (apex) part of the columella; staminal tube with appendages or variously divided, very rarely entire.
      5. Seeds attached by the seed-end towards the distal end (apex) of the columella (i.e. seed winged below).
        6. Leaflets entire; capsule pendulous; valves lacking a fibrous network; staminal tube lacking appendages 44. *Entandrophragma*
        6a. Leaflets undulately-lobed, crenate, serrate, or dentate; capsule erect, valves held together at dehiscence by a fibrous network.
          7. Capsule claviform or oblong; anthers or antherodes inserted between the bifid teeth of the lobes of the staminal tube; connective not produced . . . . . . 46. *Pseudocedrela*
          7a. Capsule ellipsoid or fusiform; anthers or antherodes inserted between the lobes of the staminal tube; connective produced, much elongated and threadlike . . . 47. *Schmardaea*
      5a. Seeds attached by the wing-end towards the distal end (apex) of the columella (i.e. seed winged above).
          8. Capsule large, erect, very woody, ovoid, oblong, or obovoid; flowers mostly 5-merous . . . 48. *Swietenia*
          8a. Capsule pendulous, small, thinly-woody, ellipsoid or tetragonal; flowers 4-merous . . . . . . 49. *Lovoa*

41. KHAYA

Khaya A. Juss., Mém. Mus. Hist. Nat. Par. 19 (?1830) 249. — Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 49, t. 4 A-I, t. 5. — **Fig. 17a, b.**
Garretia Welw., Apont. Phytog. (1859) 587; *non Garrettia* Fletcher (1937).

Deciduous trees. *Leaves* paripinnate, leaflets entire, glabrous. *Flowers* 4- or 5-merous, unisexual, but with very well-developed vestiges of the opposite sex present, borne in large, much-branched, axillary thyrses. *Calyx* 4- or 5-lobed almost to the base, the lobes subcircular, imbricate. *Petals* 4 or 5, free, much longer than the calyx in bud, contorted, erect in open flowers, somewhat hooded. *Staminal tube* urceolate or cup-shaped, bearing 8—10 included anthers or antherodes towards the apex and terminated by 8—10 subcircular, emarginate or irregularly lobed, overlapping appendages alternating with the anthers or antherodes. *Disk* in ♂ flowers cushion-shaped, fused to the base of the pistillode, but free from the staminal tube; in ♀ flowers ± reduced to an indistinct swelling at the base of the ovary. *Ovary* 4- or 5-locular, each loculus with 12—16(—18) ovules. Style-head thick, discoid with crenulate margin, almost completely blocking the entrance of the staminal tube, upper surface with minute receptive papillae and 4 or 5 radiating stigmatic ridges. Pistillode similar to the pistil but more slender and with a longer style; loculi well-developed, but vestigial ovules very small. *Fruit* an erect, (sub)globose woody, septifragal capsule, opening by 4 or 5(6) valves from the apex; valves remaining joined at the base; margins of valves often with rough fibrous strands. Columella not extending to the apex of the capsule, with 4 or 5(6) sharp, hard, woody ridges; seed scars white, conspicuous. *Seeds* 8—18 per loculus, broadly transversely ellipsoid to suborbicular, narrowly winged all round the margin, residual endosperm present. *Embryo* with flattened collateral cotyledons; radicle lateral, slightly exserted.

Germination: cryptocotylar; eophylls opposite, simple and entire, apex often long acuminate; later ones spirally arranged, trifoliolate or imparipinnate, often red.

Chromosome numbers: 2n= 50 (6 species).

Distribution: About 7 species, 5 in tropical Africa and two in Madagascar and the Comores.

Type species: *K. senegalensis* (Desr.) A. Juss.

Relationships: The relationships of this genus with *Neobeguea* are discussed under that genus.

42. NEOBEGUEA

Neobeguea J. F. Leroy, Compt. Rend. Acad. Sci. Paris (1958) 2641; Journ. Agr. Trop. Bot. Appl. 5 (1958) 594 [*nom. illegit., gallice tantum descripta*]; Journ. Agr. Trop. Bot. Appl. 17 (1970) 232. — **Fig. 17c, d.**

Deciduous trees. *Leaves* paripinnate, leaflets entire, crenate, or serrate, glabrous or with simple or dendroid glandular hairs. *Flowers* 4(5)-merous, unisexual, but with well developed vestiges of the opposite sex present, borne in clustered thyrses either terminally or on short, lateral shoots. *Calyx* 4-lobed to about the middle or less. *Petals* 4(5), free, contorted-imbricate, much longer than the calyx in bud, reflexed in open flowers. *Staminal tube* urceolate or cup-shaped, bearing 8(10) included or slightly exserted anthers or antherodes on the inner surface towards the apex and terminated by 8—10 bifid appendages. *Disk* in ♂ flowers cushion-shaped, fused to the base of the pistillode, but free from the staminal tube; in ♀ flowers reduced to an indistinct swelling at the base of the ovaray. *Ovary* 3-locular, each loculus with 4—6 ovules. Style-head thick, discoid with a swollen receptive surface. Pistillode similar to the pistil but more slender and with a longer style; receptive surface not differentiated; loculi well-developed but vestigial ovules very small. *Fruit* an erect (fide Leroy), ± trigonous, 3-valved, woody, septifragal capsule, opening from the apex, valves falling singly. Columella woody, with 3 sharp ridges, extending to the apex of the capsule; seed scars inconspicuous. *Seeds* 3 or 4 per loculus, subcircular, flattened and broadly winged round the margin; residual endosperm present. *Embryo* with flattened somewhat collateral cotyledons; radicle obliquely superior or slightly laterally exserted.

Germination: phanerocotylar, the cotyledons cordate, becoming green; eophylls simple, opposite, with a serrate margin; hypocotyl somewhat swollen.

Chromosome numbers: 2n= 50, 52 (*N. mahafalensis* J. F. Leroy).

Distribution: 3 species in Madagascar.

Type species: *N. ankaranensis* J. F. Leroy.

Relationships: *Neobeguea* is clearly closely related to *Khaya*. It demonstrates an interesting reduction from the latter in the number of its floral parts (flowers 4- or 5-

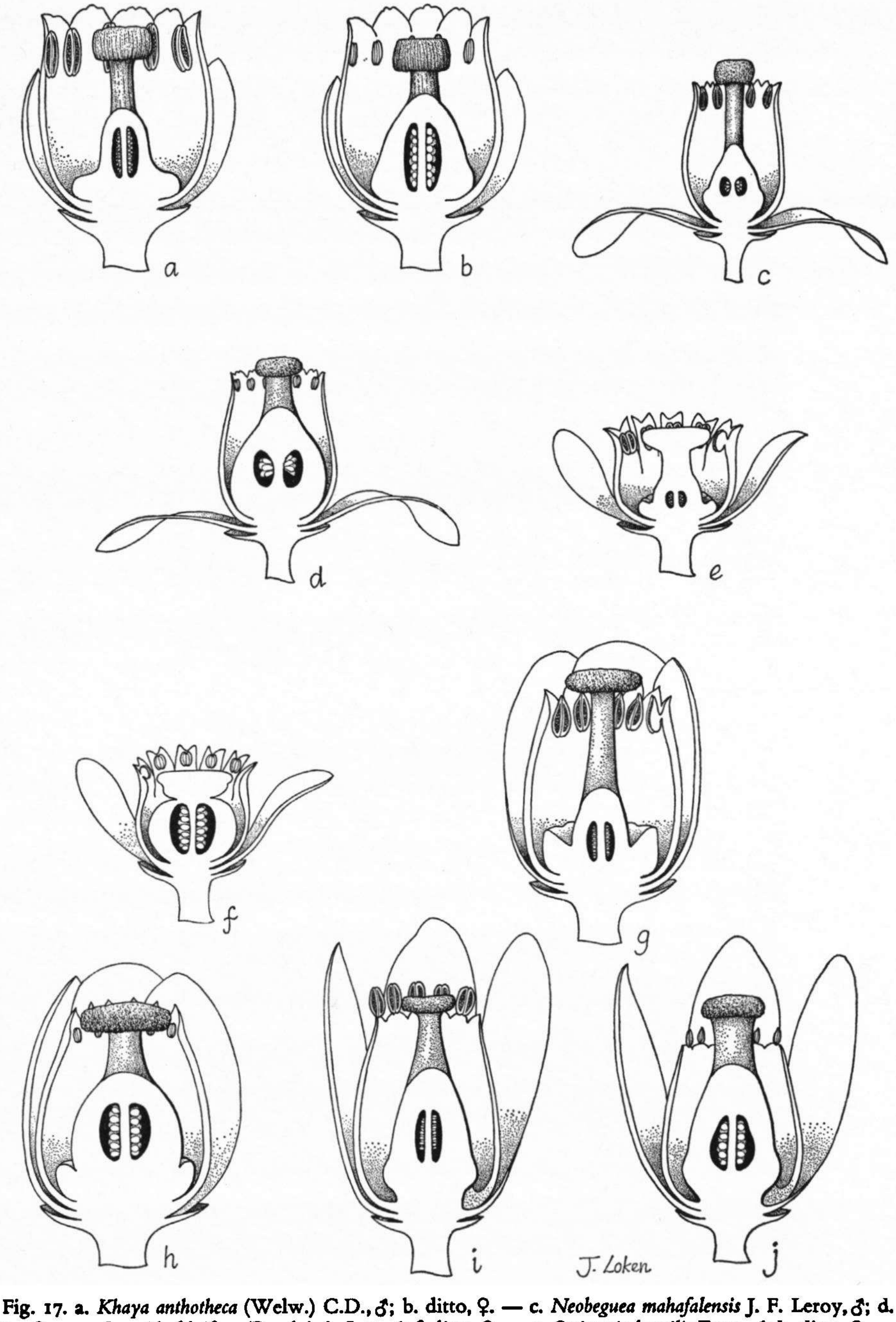

Fig. 17. a. *Khaya anthotheca* (Welw.) C.D., ♂; b. ditto, ♀. — c. *Neobeguea mahafalensis* J. F. Leroy, ♂; d. ditto, ♀. — e. *Soymida febrifuga* (Roxb.) A. Juss., ♂; f. ditto, ♀. — g. *Swietenia humilis* Zucc., ♂; h. ditto, ♀. — i. *Entandrophragma excelsum* (Dawe & Sprague) Sprague, ♂; j. ditto, ♀. All × 5. (a, b. *Styles 399*; c. d, *McWhirter 244*; e, f. *Beddome s.n.*; g. h, *Styles 91*; i, j. *Styles 252*).

merous in *Khaya*, 4-merous in *Neobeguea*); in the number of locules and ovules in the ovary (4—6 locules with up to 18 ovules per loculus in *Khaya*, 3 locules each with up to 6 ovules in *Neobeguea*); and in the greater degree of fusion of the sepals (free in *Khaya*, fused ± to the middle in *Neobeguea*). Seed structure is more specialized than in *Khaya*, the seed of *Neobeguea* having a broader, diaphanous wing and smaller embryo.

The pollen of *Neobeguea* is similar to that of other members of the *Swietenioideae* and the characters of its secondary xylem are shared by related genera.

43. SOYMIDA

Soymida A. Juss., Mém. Mus. Hist. Nat. Paris 19 (?1830) 251 t. 22; Harms in Engl. & Prantl, Nat.Pflanzenfam. ed. 2, 19 bI (1940) 54, t. 4 K-M. — **Fig. 17e, f.**

Deciduous trees. *Leaves* paripinnate; leaflets entire, glabrous. *Flowers* 5-merous, unisexual, but with well-developed vestiges of the opposite sex present, borne in much-branched terminal or axillary thyrses. *Calyx* 5, the sepals ± free to the base, imbricate. *Petals* 5, with a short claw, contorted, spreading in open flowers. *Staminal tube* urceolate or cup-shaped, somewhat thickened towards the apex, and terminated by 10 bifid spreading lobes; the anthers or antherodes inserted between the deltate teeth of the lobes. *Disk* in ♂ flowers shallowly patelliform, fused to the base of the pistillode; in ♀ flowers reduced to an indistinct swelling below the ovary. *Ovary* 5-locular, each loculus with 12—16 ovules; style absent; style-head discoid, much expanded, ± completely blocking the entrance to the staminal tube; receptive surface differentiated into 5 lobes. Pistillode similar to the pistil but with a slender style and less glandular style-head; loculi well-developed, vestigial ovules very small. *Fruit* an erect, woody, ovoid, oblong, or obovoid, 5-valved, septifragal capsule, opening from the apex, the valves separating into two layers. Columella woody, with 5 sharp ridges, extending to the apex of the capsule; seed scars inconspicuous. *Seeds* up to 12 per loculus, oblong or slightly curved, unequally winged at both ends and attached to the apex (distal end) of the columella by the longer wing; endosperm present as a residual layer. *Embryo* with flattened foliaceous cotyledons; the radicle obliquely superior.

Germination: phanerocotylar; the cotyledons cordate at the base, becoming green; eophylls simple, opposite or spirally arranged; the margin minutely serrate; later ones trifoliolate.

Chromosome number: 2n = 56.

Distribution: One species in India and Ceylon.

Type species: *S. febrifuga* (Roxb.) A. Juss.

Relationships: *Soymida* is extremely similar to some species of *Khaya* in its leaf morphology. The flowers also appear similar except that the petals are spreading (erect in *Khaya*) and the appendages of the staminal tube are regularly bifid (subcircular or irregularly lobed in *Khaya*). The seed is also very similar. In *Soymida* the wing is unequally elongated at each end, whereas in *Khaya* the seed is winged ± equally all the way round the circumference. The bilamellate structure of the capsule is perceptible in *Khaya* although the valves do not separate into two distinct layers as in *Soymida*.

44. ENTANDROPHRAGMA

Entandrophragma C. DC., Bull. Herb. Boiss. 2 (1894) 582, fig. 21, 55, t. 6-10; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 55, fig. 6. — **Fig. 17i, j.**
Wulfhorstia C. DC., Mém. Herb. Boiss. 10 (1900) 77.
Leioptyx Pierre *ex* De Wild., Ann. Mus. Congo Belge, Bot. 5 (2) (1908) 258.
Heimodendron Sillans, Bull. Soc. Bot. France 100 (1953) 263.

Deciduous trees. *Leaves* paripinnate, leaflets entire, glabrous or with simple hairs. *Flowers* 5-merous, unisexual, but with well-developed vestiges of the opposite sex present, borne in much-branched thyrses. *Calyx* ± entire and cupular or 5-lobed to half-way or almost to the base, the lobes acute; aestivation open. *Petals* 5, free, contorted, much longer than the calyx in bud, reflexed or patent in open flowers. *Staminal tube* urceolate or bowl- or goblet-shaped, the margin entire, shallowly or deeply lobed, with 10 anthers or antherodes borne on short filaments on the margin of the tube or its lobes; appendages absent. *Disk* in ♂ flowers cushion-shaped, fused to the base of the ovary or pistillode but free from the staminal tube and connected to it by 10 or 20 short ridges or partitions (sometimes obscure in ♀ flowers). Disk in ♀ flowers ± reduced to an indistinct swelling at the base of the ovary. *Ovary* 5-locular, each loculus with 4—12 ovules. Style-head discoid with 5 radiating stigmatic lobes, ± completely blocking the entrance to the staminal tube. Pistillode similar to the pistil but more slender and with a longer style, style-head often projecting from the apex of the tube; loculi well-developed, but vestigial ovules very small. *Fruit* a pendulous, elongate, woody, cigar-shaped, fusiform, cylindrical or claviform, septifragal capsule opening by 5 valves from the apex or base or from the apex and base simultaneously. Columella softly woody, extending to the apex of the capsule, 5-angled or 5-ridged, deeply indented with the imprints of the seeds; seed-scars conspicuous or inconspicuous. *Seeds* with a terminal wing, 3—9 per loculus, attached by the seed-end to the distal part of the columella and winged towards the base of the capsule; residual endosperm present as a thin layer. *Embryo* with thin cotyledons; radicle laterally exserted.

Germination: phanerocotylar, the cotyledons becoming green; eophylls opposite, simple, entire; later ones becoming trifoliolate and imparipinnate. In *E. bussei* Harms and *E. caudatum* (Sprague) Sprague the hypocotyl becomes much enlarged and swollen.

Chromosome numbers: 2n= 36, 72 (7 species).

Distribution: 11 species in tropical Africa.

Type species: *E. angolense* (Welw.) C. DC.

Relationships: A very distinct genus. The long-pendulous fruits and the ridges which connect the staminal tube to the disk in the flower are features not seen in any other genus in the family. The capsules of some species of *Cedrela* are strikingly similar to those of *Entandrophragma* but those of the former genus are shortly stipitate at the base.

45. CHUKRASIA

Chukrasia A. Juss., Mém. Mus. Hist. Nat. Paris 19 (?1830) 251, fig. 22.; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 65, fig. 4 S, T. — **Fig. 18c, d.**

Plagiotaxis Wall. [Catal. No. 1269, 1270 (1829) *nom. nud.*] *ex* O. Kuntze, Rev. Gen. Pl. 1 (1891) 110.

Chickassia Wight & Arn., Prodr. Fl. Penins. Ind. Or. 1 (1834) 122.

Deciduous trees. *Leaves* imparipinnate; leaflets entire, unequally-sided; leaves of young trees mostly bipinnate with incised or lobed leaflets; glabrous or with simple hairs. *Flowers* large, 4 or 5-merous; unisexual, but with well-developed vestiges of the opposite sex present; thyrses axillary, usually shorter than the leaves. *Calyx* shallowly and irregularly divided or 4- or 5-lobed. *Petals* 4 or 5, free, contorted, much longer than the calyx in bud, reflexed in open flowers. *Staminal tube* broadly cylindrical, narrowing towards the apex, or globet-shaped, entire or with a crenulate margin; anthers or antherodes attached to the margin. *Disk* in ♂ flowers stipitate, scarcely distinguishable from the base of the pistillode; in ♀ flowers narrowly cushion-shape. *Ovary* flask-shaped, 3—5-locular, each loculus with numerous ovules; style slender, style-head capitate with 3—5 stigmatic ridges. Pistillode scarcely distinguishable from the pistil, loculi and rudimentary ovules well-developed; style-head thinner and less glandular. *Fruit* an erect, woody, ovoid or ellipsoid, septifragal capsule, opening by 3—5 valves from the apex; the valves separating into an outer and an inner layer, the margin of the outer layer with coarse fibrous strands, the apex of the inner ones deeply bifid. Columella with 3—5 sharply-angled ridges, extending to the apex of the capsule; seed scars conspicuous. *Seeds* with a terminal wing, 80—100 per loculus, arranged laterally in tiers in the valve; endosperm present. *Embryo* with flattened subcircular cotyledons; radicle obliquely exserted.

Germination: phanerocotylar; cotyledons unequally-sided; eophylls opposite, irregularly imparipinnate, the leaflets lobed or irregularly-toothed; later leaves bipinnate.

Chromosome numbers: n=13; 2n= 26.

Distribution: One or two species in India eastwards to Malesia and southern China.

Type species: *C. tabularis* A. Juss.

Relationships: A very distinct genus easily distinguishable from other members of the *Swietenioideae* by its large flowers with a ± entire staminal tube. The type of arrangement and number of seeds in each valve of the fruit are unique features in the subfamily.

46. PSEUDOCEDRELA

Pseudocedrela Harms, Bot. Jahrb. 22 (1895) 153; in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 67, t. 11. — **Fig. 18a, b.**

Deciduous trees. *Leaves* pari- or imparipinnate, leaflets opposite or subopposite, sometimes ± alternate, undulately lobed or dentate; indumentum of simple hairs. *Flowers* unisexual, but with well-developed vestiges of the opposite sex present, borne in short axillary thyrses. *Calyx* (4) 5-lobed almost to the base; lobes ovate or subcircular. *Petals* (4) 5 free, slightly contorted, much longer than the calyx in bud, boat-shaped and spreading in open flowers. *Staminal tube* urceolate, terminated by 8(10) bifid reflexed lobes, the anthers or antherodes inserted between the deltate teeth of the lobes. *Disk* in ♂ flowers patelliform, fused to the base of the pistillode, but free from the base of the staminal tube; in ♀ flowers reduced to a ridge round the base of the ovary. *Ovary* 4- or 5-locular, each loculus with 4—6 ovules. Style-head large, discoid, almost completely blocking the entrance of the staminal tube, upper surface with 4 or 5 stigmatic lobes or ridges. Pistillode similar to the pistil but more slender and with a longer style; loculi well-developed, vestigial ovules minute. *Fruit* an erect, elongate, narrowly claviform, woody, septifragal capsule opening from the apex by 4 or 5 reflexing valves, the valves remaining firmly attached at the base connected by a fibrous network. Columella woody, sharply 4- or 5-angled and extending to the apex of the capsule, indented with the imprints of the seeds; seed-scars inconspicuous. *Seeds* 4 or 5 per loculus, with a terminal wing, attached by the seed-end to the distal part of the columella; endosperm present as a very thin layer. *Embryo* with thickened collateral cotyledons; radicle slightly exserted.

Germination: cryptocotylar; eophylls simple, opposite or spirally arranged, entire or with a sinuate margin.

Chromosome number: 2n= 56.

Distribution: A single species in the Sudan zone of tropical Africa.

Type species: *P. kotschyi* (Schweinf.) Harms.

Relationships: A very distinct genus and one of the few in the family with lobed leaflets. When first described it was placed by Schweinfurth (1868) in *Cedrela*, the fruit of which it resembles when unopened. Another specimen of the type species was placed by the same author in *Soymida*.

The curious fibrous network which holds the valves of the fruit together at dehiscence is seen again in the Andean genus *Schmardaea*.

47. SCHMARDAEA

Schmardaea Karsten, Fl. Columb. 1 (1861) 187, t. 93; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 69 t. 12, 13. — **Fig. 18e, f.**

Elutheria M. J. Roem., Synops. Monog. Hesperid. 1 (1846) 87, 122; *non* P. Browne (1756) *nom. rejic.* (= *Guarea*), *nec* Steud. (1821) *nom. nud.* (=*Croton*).

Small, much-branched, deciduous trees or shrubs. *Leaves* pari- or imparipinnate; leaflets with crenate, serrate, or coarsely dentate margins; indumentum of simple hairs. *Flowers* large, 4-merous, unisexual, but with well-developed vestiges of the opposite present; borne in very short, few-flowered, axillary thyrses. *Calyx* lobed ± to the base, imbricate. *Petals* linear, contorted and much longer than the calyx in bud. *Staminal tube* broadly cylindrical, terminated by 8 shortly bifid or ± entire appendages; the anthers or antherodes ± included and alternating with the appendages; anthers large, the connective produced into a long thread-like appendage. *Disk* ridged, shortly stipitate, resembling a gynophore. *Ovary* 4-locular, each loculus with up to 25 ovules; style long and slender. Style-head narrowly discoid with 4 stigmatic lobes. Pistillode similar to the pistil but with a longer style and less differentiated style-head; loculi well-developed but vestigial ovules very small. *Fruit* an erect, thin-woody, fragile, ellipsoid or fusiform, septifragal capsule opening from the apex by 4 valves, the valves separating into two layers, the inner one membraneous, and remaining held together by a fibrous network. *Seeds* up to 20 per loculus with a terminal wing attached by the seed-end to the distal part of the central axis (? rudimentary columella); endosperm present as a thick layer. *Embryo* with thin, collateral cotyledons; radicle laterally exserted.

Distribution: Probably one species only in northern South America from Venezuela to Peru (Andean region).

Type species: *S. microphylla* (Hook. *f.*) Karsten.

Relationships: When the type of this little-known genus was first described by Hooker he placed it provisionally in *Guarea* as he had not then seen the distinctive fruit. Even now complete material in the form of undamaged capsules is not available for study. For this reason the nature and structure of the central columella is not known with certainty. Published drawings by Karsten and Harms also do not illustrate this satisfactorily. The woody, ridged columella so typical of the *Swietenieae* seems to be poorly developed in *Schmardaea* and the seeds are apparently attached to the dissepiments which become woody. In all other respects *Schmardaea* is typical of the tribe, although the large flowers and much-elongated thread-like connectives of the anthers are striking features rarely seen elsewhere in the family.

48. SWIETENIA

Swietenia Jacq., Enum. Pl. Carib. (1760) 4; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 70, t. 14. — **Fig. 17g, h.**

Mahagoni Adans., Fam. Pl. 2 (1763) 343.

Roia Scopoli, Introd. (1777) 226.

Suitenia Stokes, Bot. Mat. Med. 2 (1812) 479.

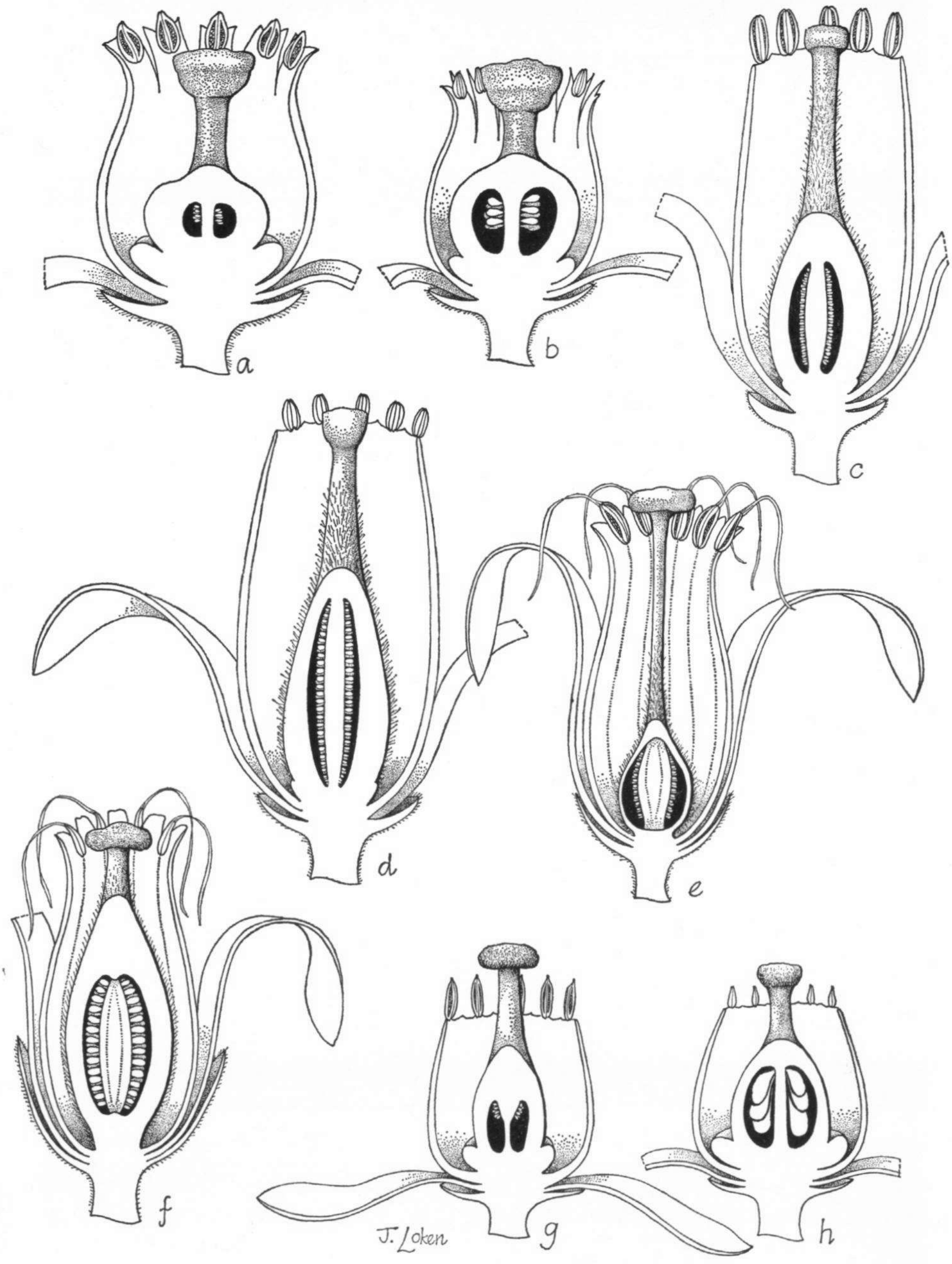

Fig. 18. a *Pseudocedrela kotschyi* (Schweinf.) Harms, ♂, ×10; b. ditto, ♀, ×10. — c. *Chukrasia tabulais* A. Juss., ♂, ×5; d. ditto, ♀, ×5. — e. *Schmardaea microphylla* (Hook.) Karst., ♂, ×5; f. ditto, ♀, ×5. —g. *Lovoa trichilioides* Harms, ♂, ×5; h. ditto, ♀, ×5. (a, b. *Styles 278*; c. *K. N. Bahadur* s.n.; d. *Kerr 19,631*; e. *Hooker s.n.*; f. *Sandeman s.n.*; g, h. *Styles 15*).

Deciduous trees. *Leaves* paripinnate, very rarely imparipinnate, leaflets entire, glabrous. *Flowers* unisexual, but with well-developed vestiges of the opposite sex present; borne in short, little-branched, axillary thyrses. *Calyx* 5-lobed to about the middle, the lobes obtuse, imbricate. *Petals* (4)5, much longer than the calyx in bud, contorted, reflexed in open flowers. *Staminal tube* cup-shaped or urceolate, bearing on the inside 8—10 partially exserted apiculate anthers or antherodes and terminated by 8—10 deltate-acuminate or bluntly acuminate, non-overlapping appendages, alternating with the anthers or antherodes. *Disk* in ♂ flowers patelliform, fused to the base of the staminal tube, forming an annulus around the pistillode; in ♀ flowers reduced to a swelling at the base of the ovary. *Ovary* 5-locular, each loculus with 12—16 ovules. Style-head discoid, ± completely blocking the entrance to the staminal tube, the upper surface with 5-stigmatic lobes. Pistillode similar to the pistil, but more slender, with a longer style and thinner style-head; the loculi well-developed but rudimentary ovules minute. *Fruit* an erect, strongly woody, oblong, ovoid, or obovoid, septifragal capsule, opening by 5 valves from the base or base and apex simultaneously, the valves separating into an outer thickly woody and an inner thinner layer. Columella woody, 5-angled, extending to the apex of the capsule; seed scars conspicuous. *Seeds* 9—16 per loculus, attached by the wing-end to the apex (distal part) of the columella; the seed-body hanging towards the base of the capsule; endosperm present as a thin layer. *Embryo* with thin cotyledons; radicle slightly exserted.

Germination: cryptocotylar, cataphylls present; eophylls opposite, simple, entire; later ones trifoliolate or imparipinnate.

Chromosome numbers: 2n= 48, 54, 56 (3 species).

Distribution: 3 poorly defined species in tropical America (from Mexico to Brazil) and the Caribbean.

Type species: *S. mahagoni* (L.) Jacq. (see Styles, 1968).

Relationships: Most of the genera of the *Swietenioideae* when first described were placed in *Swietenia*, possibly because of the great similarity in overall structure of their fruits. The woody septifragal capsule with a central columella and winged seeds is characteristic of almost all genera in the *Swietenieae*. The secondary xylem of *Swietenia* is very similar to that of *Khaya* but there is no justification for uniting these genera as proposed by Lamb (1966).

49. LOVOA

Lovoa Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(4) (1896) 307; Bot. Jahrb. 23 (1896) 165.; in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 74, fig. 15. — **Fig. 18g, h.**

Litosiphon Pierre *ex* Harms in Dalla Torre & Harms, Gen. Siphonog. (1901) 262; A. Chev., Vég. util. Afr. Trop. Franç. 9 (1917) 124.

Deciduous trees. *Leaves* paripinnate, leaflets entire, glabrous or with simple hairs. *Flowers* 4-merous, unisexual, but with well-developed vestiges of the opposite sex present, borne in large, showy, much-branched thyrses. *Calyx* lobed almost to the base, the lobes in an inner and outer whorl of 2+2, imbricate. *Petals* 4, free, imbricate, much longer than the calyx in bud; reflexed or spreading in open flowers. *Staminal tube* cup-shaped or shortly cylindrical, the margin entire or with very short teeth with 8 anthers or antherodes on the margin, or with paired deltate-acuminate appendages alternating with the anthers or antherodes. *Disk* short, broadly cushion-shaped, enveloping the base of the ovary or pistillode, but free from the staminal tube. *Ovary* 4-locular, each loculus with 4—6(—8) ovules. Style-head narrowly discoid or capitate, obscurely 4-lobed, ± blocking the entrance of the staminal tube. Pistillode similar to the pistil but more slender, with a longer style and thinner style-head, the loculi well-developed, but vestigial ovules very small. *Fruit* a pendulous, elongate, tetragonal or ellipsoid, thinly woody, septifragal capsule, dehiscing from the apex or from base and apex simultaneously, the valves thinly woody. Columella softly woody, extending to the apex of the capsule, 4-ridged, each face shallowly indented with the imprints of 1 or 2 seeds. *Seeds c.* 2 per loculus, attached to the apex (distal part) of the columella by the wing-end, leaving inconspicuous scars on falling, the body of the seed hanging towards the base of the capsule; endosperm present as a very thin layer. *Embryo* with flat thin cotyledons; radicle slightly exserted.

Germination: phanerocotylar; cataphylls present; eophylls opposite, pari- or imparipinnate, sometimes bipinnate; leaflets entire with a sinuous margin, reddish; rhachis broadly winged.

Chromosome number: 2n= 50, 52, 56 (Styles & Khosla, unpublished).

Distribution: 2 species in tropical Africa.

Type species: *L. trichilioides* Harms.

Relationships: The position of *Lovoa* in the *Swietenioideae* has already been discussed (Chapt. 3). Although it differs from the majority of the genera in its wood structure it shares with these all the morphological (floral and fruit) characters found in this subfamily.

Tribe 3. XYLOCARPEAE*

Flowers without a gynophore. Petals free. Stamens 8—10, filaments completely united to form an urceolate or cup-shaped tube with appendages on the margin. Capsule subwoody or leathery with a rudimentary columella; seeds unwinged with a corky or woody sarcotesta; cotyledons large, fused together; endosperm absent.

Pollen and Secondary xylem as for the subfamily.

1. Inflorescence much-branched, many-flowered, > 25 cm long; sepals imbricate, ± free to the base; leaflets 6—12(—18) pairs; seed with a woody sarcotesta 50. *Carapa*
1a. Inflorescence little-branched, few-flowered, < 25 cm long (often very short); sepals valvate, united in the lower half; leaflets (1—)2—3(—4) pairs; seed with a corky sarcotesta . . . . 51. *Xylocarpus*

50. CARAPA

Carapa Aublet, Hist. Pl. Guian. Franç. 2 (1775) Suppl. 32, t. 387; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 77, t. 16, 17, 18; Noamesi, A revision of the *Xylocarpeae*, unpublished thesis Univ. of Wisconsin (1958) 155 pp. — **Fig. 16e, f.**

Persoonia Willd., Sp. Pl. 2 (1799) 331; *non* Smith (1798) (*Proteaceae*), *nec* Michx. (1803) (=*Marshallia* Schreb. *Compositae*).

[*Amapa* Steud., Nom. ed. 1 (1821) 69, *nom. nud.*]

Zurloa Tenore in Atti 3a Riun. Sc. Ital. (1841) 504.

Touloucouna M. J. Roem., Synops. Monog. Hesper. 1 (1846) 123.

Racapa M. J. Roem. *loc. cit.*

Granatum Rumph. [Herb. Amb. 3 (1743) 92, tab. 61, 62] *ex* O. Kuntze, Rev. Gen. Pl. 1 (1891) 110, *p.p.* (not. including the type).

Deciduous or ? evergreen trees or treelets. *Leaves* paripinnate with a dormant glandular leaflet at the apex, or exceptionally imparipinnate, leaflets 6—12(—18) pairs, entire, glabrous or with simple hairs. *Flowers* 4- or 5-(6-)merous; unisexual, but with well-devel-

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* In the present work we are following Noamesi (1958) in using the name *Xylocarpeae* (M. J. Roem., 1846) as the tribal name rather than the more usually accepted *Carapeae* (Harms, 1896). This is in accordance with Article 11 of the current edition of the International Code of Botanical Nomenclature (1972).

oped vestiges of the opposite sex present, borne in large, much-branched, many-flowered, axillary thyrses. *Calyx* 4- or 5-lobed ± to the base, the lobes rounded or broadly ovate, imbricate. *Petals* 4- or 5-(6), slightly contorted, longer than the calyx in bud, spreading in open flowers. *Staminal tube* cup-shaped, cylindrical, or urceolate, divided at the apex into 8—10 entire, shortly bifid, or crenellately lobed appendages, and bearing on the inside alternately with the appendages 8—10(—12) ± sessile anthers or antherodes. *Disk* well-developed, cushion-shaped, surrounding the ovary and free from the staminal tube. *Ovary* 4 or 5(6)-locular, partially sunk in the disk, with (2)3—8 ovules in each loculus; style short, style-head discoid, ± blocking the entrance to the staminal tube, the receptive surface thickened and glandular. Pistillode similar to the pistil, but with a longer more slender style and thinner style-head; loculi well-developed, but rudimentary ovules small. *Fruit* a large, pendulous, sub-woody, sub-globose or oblong-cylindrical, septifragal capsule, opening by 4 or 5 valves from the base and apex simultaneously, the valves becoming leathery on drying; columella reduced, ultimately breaking down. *Seeds* large, 8—35, angular due to mutual compression, with the outer surface opposite the hilum rounded; sarcotesta woody, thick, smooth; endosperm absent. *Embryo* with the large cotyledons fused together; the radicle lying above the hilum.

Germination: cryptocotylar; cataphylls spirally arranged; eophylls simple, entire; later ones trifoliolate, bright red.

Chromosome number: 2n= 58 (2 species).

Distribution: A small genus of *c.* 3 or 4 species in the Neotropics and west and central Africa.

Type species: *C. guianensis* Aubl.

Relationships: These are discussed under *Xylocarpus.*

51. XYLOCARPUS

Xylocarpus Koen., Naturforscher 20 (1784) 2; Harms in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19 bI (1940) 81, t. 19; Noamesi, A revision of the *Xylocarpeae*, unpublished thesis Univ. of Wisconsin (1958) 155 pp.. — **Fig. 16 g, h.**

Carapa sensu Lam., Encycl. 1 (1785) 621.

Monosoma Griff., Notul. 4 (1854) 502.

Granatum Rumph. [Herb. Amb. 3 (1743) 92, tab. 61, 62] *ex* O. Kuntze, Rev. Gen. 1 (1891) 110 *p.p.*; *non* St. Lag. (1880).

Semi-evergreen trees or shrubs. *Leaves* paripinnate, leaflets (1) 2 or 3(4) pairs, entire, glabrous. *Flowers* unisexual, but with well-developed vestiges of the opposite sex present, borne in short, little-branched, axillary thyrses. *Calyx* 4-lobed to about the middle, valvate. *Petals* 4, free, much longer than the calyx in bud, spreading or reflexed in open flowers; contorted in bud. *Staminal tube* urceolate or bowl-shaped, bearing 8 included anthers or antherodes towards the apex and terminated by 8 subcircular, retuse or shallowly and irregularly-lobed appendages alternating with the anthers or antherodes. *Disk* large, red, cushion-shaped, situated beneath, or surrounding and fused to, the ovary and free from the staminal tube. *Ovary* 4-locular, each loculus with 3 or 4(—6) ovules; style short, style-head discoid almost blocking the entrance to the staminal tube, margin crenellate, upper surface with 4 radiating stigmatic grooves. Pistillode similar to the pistil but with longer more slender style and thinner style-head; loculi well-developed, but rudimentary ovules small. *Fruit* a large, pendulous, almost spherical, leathery, septifragal capsule, tardily dehiscing by 4 valves from base and apex simultaneously; columella rudimentary, septa thin, ultimately breaking down. *Seeds* 8—20, large, pyramidal or tetrahedral, with angular margins due to mutual compression, outer side somewhat rounded, attached by the apex to the columella forming a spherical mass; testa corky, inlaid with fibres, smooth; endosperm absent. *Embryo* with the large cotyledons fused together; the radicle lying above the hilum.

Germination: cryptocotylar, the numerous subulate cataphylls in whorls or spirally arranged; eophylls simple, entire, becoming trifoliolate later.

Chromosome number: 2n= 52 (2 species).

Distribution: An Old-World genus of two or three species in mangrove swamps or coastal scrub.

Type species: *X. granatum* Koen.

Relationships: *Carapa* and *Xylocarpus* are very closely related and have been combined by Lamarck (1785). They are, however, easily separable on a number of differential characters, the most important being the aestivation of the calyx and the nature of the sarcotesta. Biologically they represent a clear case of ecological specialization and generic allopatry in that *Carapa* occurs in forests of the Neotropics and in west and central Africa, whereas the more specialized *Xylocarpus* occurs in mangrove swamps and coastal scrub in the Old World. The corky testa of the seed in *Xylocarpus* represents an adaptation to dispersal by water.

The morphology of the seedlings of both is similar and specialized. There is an interesting difference in diploid chromosome numbers.

ANALYTICAL KEY TO THE IDENTIFICATION OF GENERA OF THE MELIACEAE

1a. Loculi 1- or 2-ovulate (rarely with 1 or 2 additional vestigial ovules) 2
b. Loculi multiovulate. 52
2a. Leaves decussate; capsule with partial septifragal dehiscence **38. Capuronianthus**
b. Leaves nearly always spirally arranged or fasciculate, very rarely decussate but then the capsule with loculicidal dehiscence 3
3a. Fruit dry; seed winged . . . . **37. Quivisianthe**
b. Fruit fleshy or leathery, rarely woody; seed never winged 4
4a. Fruit dehiscent. 5
b. Fruit indehiscent 36
5a. Disk free, cyathiform or tubular 6
b. Disk annular, patelliform, stipitate, or absent, rarely cyathiform but then fused to the base of the staminal tube. 9
6a. Anthers inserted apically on the filaments or on the margin of the staminal tube 7
b. Anthers inserted within the throat of the staminal tube 8
7a. Staminal tube 1.5—3.0(—4.0) cm long; ovary 5-locular; petals partly fused to the staminal tube; sarcotesta membraneous . . . . **1. Munronia**
b. Staminal tube 0.25—0.5(—1.2) cm long; ovary 2- or 3-locular; petals free from staminal tube; sarcotesta, if present, not membraneous . . . . . **10. Trichilia**
8a. Leaves with transparent gland dots and/or lines . . . . **26. Cabralea**
b. Leaves without gland dots or lines . . . . **35. Dysoxylum**
9a. Anthers inserted apically on the filaments or on the margin of the staminal tube 10
b. Anthers inserted within the throat of the staminal tube 22
10a. Anthers locellate; leaves showing limited apical growth or with a dormant apical bud . . . . **30. Chisocheton**
b. Anthers not locellate; leaves not showing limited apical growth; dormant apical bud absent 11
11a. Indumentum of stellate hairs or peltate scales, or a mixture of simple with bifid and/or stellate hairs 12
b. Indumentum of simple hairs 15
12a. Filaments completely united 13
b. Filaments partly or completely free 14
13a. Staminal tube long tubular . . . . **1. Munronia**
b. Staminal tube short, globular or cyathiform . . . . **20. Aglaia**
14a. Staminal tube appendages 3—10 times as many as filaments . **12. Pterorhachis**
b. Staminal tube appendages not more than twice as many as filaments or absent **10. Trichilia**
15a. Leaves simple 16
b. Leaves trifoliolate or pinnate, rarely unifoliolate (with a pulvinus) 18
16a. Filaments fused for two-thirds of their length or completely united **3. Turraea**
b. Filaments usually fused only at the base, always free for more than half their length 17
17a. Capsule not inflated; filaments 0.6—1.1 cm long, anthers basifixed **5. Calodecaryia**
b. Capsule inflated; filaments 1.6—2.3 cm long, anthers dorsifixed **6. Nymania**
18a. Leaves trifoliolate, rarely unifoliolate 19
b. Leaves pinnate 20

19a. Staminal tube 2—3.5 cm long; filaments completely united, without appendages **2. Naregamia**

b. Staminal tube not more than 0.6 cm long; filaments often free in the upper half and terminated by short appendages . . . . **10. Trichilia**

20a. Leaflets deeply lobed to partite . . . . **3. Turraea**

b. Leaflets entire 21

21a. Capsule (4) 5-valved, valves thick, woody, rugulose, bearing branched antler-like appendages . . . . **11. Pseudobersama**

b. Capsule 2 or 3(4)-valved, valves usually thinner, less woody, sometimes warty but never with antler-like appendages . . . . **10. Trichilia**

22a. Style-head modified to form a *receptaculum pollinis* . . . . **3. Turraea**

b. Style-head not modified to form a *receptaculum pollinis* 23

23a. Anthers in 2 alternating whorls within the staminal tube. . **24. Sphaerosacme**

b. Anthers in a single whorl 24

24a. Indumentum of stellate hairs or lepidote scales 25

b. Indumentum of simple hairs 28

25a. Filaments free in the upper half and terminated by (3)4—6(—10) unequal filiform appendages . . . . **12. Pterorhachis**

b. Filaments completely united; appendages, if present fewer 26

26a. Leaves with a dormant apical bud; staminal tube cylindrical **30. Chisocheton**

b. Leaves without a dormant apical bud; staminal tube cyathiform or globular . 27

27a. Inflorescence a long spike or panicle with spicate branches; cotyledons fused, collateral . . . . **22. Aphanamixis**

b. Inflorescence paniculate, branches thyrsoid or indeterminate, rarely some female inflorescences reduced to a short spike; cotyledons free, nearly always superposed **20. Aglaia**

28a. Sarcotesta greatly swollen, surrounding the base of seed . . . . . . **27. Ruagea**

b. Sarcotesta absent, or if present then not basal and swollen 29

29a. The 2 seeds of a valve united by a common arillode. . . . . . . **32. Synoum**

b. Seeds not united by a common arillode 30

30a. Petals fused to the staminal tube for the greater part of its length **28. Turraeanthus**

b. Petals free from the staminal tube or fused only at the base. 31

31a. Petals 3, imbricate; staminal tube globose or deeply cyathiform; style-head usually with large, conical, 3-angled stigma; cotyledons fused . . . **22. Aphanamixis**

b. Petals (3)4—6(10), imbricate or valvate; staminal tube usually cylindrical; style-head discoid or capitate; cotyledons free 32

32a. Leaves paripinnate 33

b. Leaves with a dormant terminal bud, or more rarely a terminal leaflet . . . 34

33a. Petals 3 or 4, valvate at least in the lower half; staminal tube cylindrical; loculi with 2 collateral ovules . . . . **34. Pseudocarapa**

b. Petals 5, imbricate; staminal tube cyathiform; loculi uniovulate **33. Anthocarapa**

34a. Petals in 2 whorls, united below . . . . **31. Megaphyllaea**

b. Petals in a single whorl 35

35a. Anthers nearly always locellate; style-head often capitate; seed often scutiform (ovule orthotropous), arillodiate or with a sarcotesta . . . . **39. Chisocheton**

b. Anthers never locellate; style-head discoid; seed never scutiform (ovule anatropous), exarillodiate, with a fleshy, mealy, or vascularised sarcotesta . . . **29. Guarea**

36a. Disk tubular . . . . **36. Sandoricum**

b. Disk annular, patelliform, stipitate, or absent 37

37a. Placentation parietal; berry rostrate . . . . **25. Heckeldora**
b. Placentation axile; fruit not rostrate 38
38a. Anthers in 2 alternating whorls of 5 . . . . **23. Reinwardtiodendron**
b. Anthers in a single whorl 39
39a. Leaves simple 40
b. Leaves 2- or 3-pinnate, pinnate, trifoliolate, or rarely unifoliolate 42
40a. Style-head expanded to form a *receptaculum pollinis*; flowers long tubular **4. Humbertioturraea**
b. Style-head small; flowers small, cyathiform 41
41a. Petals valvate; filaments or staminal tube bearing terminal appendages; loculi with 2 superposed ovules . . . . **15. Malleastrum**
b. Petals imbricate; filaments without appendages; loculi uniovulate or with 2 (3) collateral ovules . . . . **9. Vavaea**
42a. Leaves 2- or 3-pinnate . . . . **7. Melia**
b. Leaves not 2- or 3-pinnate 43
43a. Indumentum of stellate hairs or peltate scales 44
b. Indumentum of simple hairs 46
44a. Corolla with valvate aestivation . . . . **14. Lepidotrichilia**
b. Corolla with imbricate aestivation 45
45a. Style-head thick discoid; fruit a drupe with thin fleshy mesocarp and thick woody endocarp; seed with thick endosperm . . . . **17. Astrotrichilia**
b. Style-head small, not discoid; fruit a berry or nut; seed without endosperm **20. Aglaia**
46a. Fruit a berry 47
b. Fruit a drupe 49
47a. Anthers inserted within the throat of the staminal tube; margin of staminal tube without appendages . . . . **21. Lansium**
b. Anthers inserted apically on filaments or on margin of staminal tube, these mostly with appendages 48
48a. Style-head minute, capitate; petals valvate; loculi with 2 superposed ovules **15. Malleastrum**
b. Style-head well-developed, capitate, truncate, or pileate; corolla usually imbricate; loculi uniovulate or with 2 collateral ovules . . . . **13. Walsura**
49a. Corolla with valvate aestivation . . . . **19. Cipadessa**
b. Corolla with imbricate aestivation 50
50a. Loculi uniovulate . . . . **18. Owenia**
b. Loculi biovulate 51
51a. Style-head capitate or thick discoid; ovules superposed . . . . **16. Ekebergia**
b. Style-head 3-lobed; ovules collateral . . . . **8. Azadirachta**
52a. Fruit indehiscent . . . . **9. Vavaea**
b. Fruit a septifragal capsule with a central columella (sometimes rudimentary) . 53
53a. Stamens free 54
b. Stamens partly or completely united into a staminal tube 55
54a. Seeds winged below, attached by the seed towards the apex (distal end) of the central columella; androgynophore column-shaped, longer than the ovary; first leaflets of seedlings entire . . . . **39. Cedrela**
b. Seeds winged at both ends, or if with one wing only then attached by the seed-end towards the base of the central columella (proximal end) and winged above; androgynophore cushion-shaped, shorter than or equalling the ovary; first leaflets of seedlings lobed or toothed . . . . **40. Toona**

55a. Seeds without a wing 56
b. Seeds winged 57
56a. Inflorescence much-branched, many-flowered, > 25 cm long; sepals imbricate, ± free to the base; leaflets 6—12(—18) pairs; seed with a woody sarcotesta **50. Carapa**
b. Inflorescence little-branched, few-flowered, < 25 cm long (often very short); sepals valvate, united in the lower half; leaflets (1) 2 or 3(4) pairs; seed with a corky sarcotesta **51. Xylocarpus**
57a. Capsule globose, subglobose, or trigonous, not or scarcely longer than broad; seed orbicular to suborbicular, winged all the way round 58
b. Capsule elongate, at least twice as long as broad, ovoid, obovoid, ellipsoid, claviform, or fusiform; seed with a single terminal wing or with a wing at both ends 59
58a. Capsule globose or subglobose, dehiscing by 4—6 valves which remain joined together at the base; wing of seed narrow, opaque . . . . **41. Khaya**
b. Capsule ± trigonous, the valves falling separately at dehiscence; wing of seed broad and transparent . . . . **42. Neobeguea**
59a. Seeds with a wing at both ends, the upper (distal) wing the longer **43. Soymida**
b. Seeds with a single terminal wing 60
60a. Seeds very numerous, arranged laterally in tiers in each valve; margin of staminal tube entire or crenulate . . . . **45. Chukrasia**
b. Seeds up to 20 per locule, attached by the seed- or wing-end towards the proximal (base) or distal (apex) part of the columella; staminal tube with appendages or variously divided, rarely entire 61
61a. Seeds attached by the seed-end towards the distal end (apex) of the columella (i.e. seed winged below) 62
b. Seeds attached by the wing towards the distal end (apex) of the columella (i.e. seed winged above) 64
62a. Leaflets undulately-lobed, crenate, or dentate; capsule erect, valves held together at dehiscence by a fibrous network 63
b. Leaflets entire; capsule pendulous, valves lacking a fibrous network; staminal tube lacking appendages . . . . **44. Entandrophragma**
63a. Capsule claviform or oblong; anthers or antherodes inserted between the bifid teeth of the lobes of the staminal tube; connective not produced **46. Pseudocedrela**
b. Capsule ellipsoid or fusiform; anthers or antherodes inserted between the lobes of the staminal tube; connective produced, much elongated and threadlike **47. Schmardaea**
64a. Capsule erect, large, very woody, ovoid or oblong; flowers mostly 5-merous **48. Swietenia**
b. Capsule pendulous, small, thin-woody, ellipsoid or tetragonal; flowers 4-merous **49. Lovoa**

SYNOPTIC KEY TO THE GENERA IN MELIACEAE

The numbers correspond to those allocated in the codification list at the end of this key. Genera, cited under one lead only, are printed in **bold type**.

1. Bud scales
   a. present: **39.40.41.42.43.44.45.46.47.48.49.50.51.**
   b. absent: **1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27. 28.29.30.31.32.33.34.35.36.37.38.**

2. Leaf arrangement
   a. spiral: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.37.39.40.41.42.43.44.45.46.47.48.49.50.51.
   b. decussate: 38.
3. Leaf type
   a. simple: 1.3.4.5.6.9.15.
   b. unifoliolate: 10.13.15.20.23.
   c. trifoliolate: 1.2.10.12.13.15.17.20.23.36.
   d. imparipinnate: 1.3.8.10.11.12.13.14.15.16.17.19.20.21.22.23.24.25.26.27.28.29.30.31.32.35.37.38.39.40.45.46.47.48.50.
   e. paripinnate: 8.10.11.17.18.20.21.22.23.26.28.29.30.31.33.34.35.37.38.39.40.41.42.43.44.46.47.48.49.50.51.
   f. terminal bud present: 29.30.31.
   g. bipinnate: 7.
4. Indumentum type
   a. simple: 2.3.4.5.6.8.9.10.11.13.15.16.18.19.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.51.
   b. stellate hairs or peltate scales: 1.7.10.12.14.17.20.22.30.
   c. mixture of simple and bifid hairs: 1.
5. Leaflets with gland dots or lines
   a. present: 10. 26. 27. 29.
   b. absent: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.27.28.29.30.31.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.51.
6. Sex distribution
   a. monoecious: ?27.38.39.40.41.42.43.44.45.46.47.48.49.50.51.
   b. dioecious: ?9.10.11.12.13.?14.?15.16.?17.18.20.21.22.24.25.26.?27.28.29.30.31.32.33.35.37.
   c. polygamous: 7.8.?9.13.19.
   d. bisexual: 1.2.3.4.5.6.9.14.15.17.21.22.23.?27.34.35.36.37.
7. Fusion of sepals
   a. free: 4.10.13.18.21.22.23.24.26.27.35.38.39.40.41.43.44.46.47.49.50.
   b. partially united: 1.2.3.5.6.7.8.9.10.11.12.13.14.15.16.17.19.20.21.22.23.24.25.26.27,28.29.30.31.32.33.34.35.36.37.38.39.40.41.42.44.45.46.47.48.49.50.51.
   c. completely united: 3.9.10.15.28.29.30.31.35.36.
8. Sepals foliaceous or not
   a. foliaceous: 1.3.
   b. not foliaceous: 2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.51.
9. Calyx
   a. circumscissile at base: 29.30.31.35.
   b. not circumscissile at base: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.51.
10. Aestivation of calyx
    a. valvate: 51.
    b. not valvate (either imbricate, contorted, open or closed in bud): 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.

11. Aestivation of corolla
    a. imbricate: 1.2.3.4.6.7.8.9.10.11.12.13.16.17.18.20.21.22.23.24.25.26.27.29.30.31.32.33.34.35.36.38.39.40.42.49.
    b. valvate: 3.10.13.14.15.19.28.29.30.34.35.37.
    c. contorted: 3.5.9.13.38.41.42.43.44.45.46.47.48.50.51.
12. Corolla whorls
    a. petals in a single whorl: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.51.
    b. petals in 2 whorls: 31.
13. Petal number
    a. 3: 3.9.15.20.22.30.34.35.
    b. 4: 2.3.4.5.6.9.10.13.16.20.25.28.29.30.32.34.35.36.38.41.42.45.46.47.48.49.50.51.
    c. more than 4: 1.2.3.4.5.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.23.24.26.27.28.29.30.31.32.33.35.36.37.38.39.40.41.42.43.44.45.46.48.50.
14. Fusion of petals
    a. petals fused to staminal tube or androgynophore: 1.20.21.22.23.28.29.30.31.35.39.40.
    b. petals free from staminal tube but gamopetalous (fused to halfway or more): 10.20.30.31.
    c. petals free from staminal tube, polypetalous or fused only at base: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.24.25.26.27.29.30.32.33.34.35.36.37.38.41.42.43.44.45.46.47.48.49.50.51.
15. Union of filaments
    a. filaments completely free from each other: 10.13.39.40.
    b. filaments partially united: 3.5.6.9.10.11.12.13.14.15.16.18.19.44.
    c. filaments completely united: 1.2.3.4.7.8.10.14.15.16.17.18.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.37.38.41.42.43.44.45.46.47.48.49.50.51.
16. Shape of androecium if filaments united
    a. globose: 10.20.21.22.23.24.
    b. cyathiform: 3.5.6.9.10.11.13.14.15.16.17.18.19.20.21.22.23.24.32.33.38.41.42.43.44.45.48.49.50.51.
    c. urceolate: 10.12.13.14.15.16.18.19.20.21.22.23.37.38.41.42.43.44.45.46.48.50.51.
    d. cylindrical: 1.2.3.4.5.6.7.8.9.10.12.14.15.16.20.25.26.27.28.29.30.31.34.35.36.37.38.45.47.49.50.
17. Filament appendages
    a. apex of filaments or staminal tube bearing appendages, equalling the anthers in number or twice as many: 1.3.4.7.8.10.13.14.15.18.19.26.29.30.33.34.35.36.38.41.42.43.46.47.48.49.50.51.
    b. apex of filaments or staminal tube bearing appendages 3—10 times as many as anthers: 12.
    c. apex of filaments or staminal tube without appendages: 2.3.5.6.9.10.11.13.16.17.20.21.22.23.24.25.27.28.29.30.31.32.35.37.39.40.44.45.49.
18. Ratio of anther number to petal number
    a. anthers equalling petals in number: 10.20.22.30.31.35.37.39.40.
    b. anthers more than petals: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.38.41.42.43.44.45.46.47.48.49.50.51.

19. Anthers inserted
    a. on ends of filaments or margin of staminal tube: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.30.37.38.39.40.43.44.45.46.47.49.
    b. within throat of staminal tube: 3.7.8.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.41.42.48.50.51.
20. Number of whorls of anthers
    a. a single whorl: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.25.26.27.28.29.30.31.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.51.
    b. two alternating whorls: 23.24.
21. Anther connective
    a. produced to form appendage: 1.2.3.4.12.13.19.22.23.47.48.
    b. not produced: 1.3.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19,20.21.22.24.25.26.27.28.29.30.31.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.48.49.50.51.
22. Anthers
    a. locellate: 30.31.
    b. not locellate: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.51.
23. Disk
    a. absent: 1.2.9.10.14.15.17.20.21.22.23.24.28.29.37.38.
    b. patelliform, free from staminal tube: 7.10.13.30.33.
    c. patelliform, fused to base of staminal tube or ovary: 3.4.5.6.9.10.11.16.17.19.34.37.43.46.48.
    d. stipitate: 10.25.27.29.30.31.45.47.
    e. androgynophore: 39.40.
    f. cyathiform, fused to base of staminal tube or ovary: 3.4.9.10.35.
    g. cyathiform, free: 10.26.
    h. tubular: 1.35.36.
    i. annular or cushion shaped: 3.5.7.8.10.12.13.15.16.18.30.32.33.34.37.38.41.42.43.44.45.46.48.49.50.51.
24. Number of locules
    a. 1: 15.20.25.
    b. 2 or 3: 2.3.8.9.10.12.13.14.15.16.17.18.20.22.23.27.29.30.32.33.34.35.37.38.42.45.
    c. 4 or 5: 1.2.3.4.5.6.7.9.10.11.13.14.15.16.17.18.19.20.21.22.23.24.26.27.28.29.30.34.35.36.37.38.39.40.41.43.44.45.46.47.48.49.50.51.
    d. more than 5: 3.4.7.9.10.16.19.29.30.31.35.50.
25. Number of ovules per locule
    a. locules all uniovulate: 9.13.14.18.19.20.21.23.24.30.31.33.
    b. at least some locules with 2 collateral ovules: 2.3.5.6.8.9.10.11.13.17.19.20.22.23.25.30.32.34.35.36.37.
    c. at least some locules with 2 superposed ovules: 1.3.4.7.10.12.15.16.17.20.22.26.27.28.29.30.35.
    d. 2 and a vestigial one: 9.38.
    e. 3 to many ovules, ovules biseriate: 9.39.40.41.42.43.44.45.46.47.48.49.50.51.
26. Style-head type
    a. capitate, without conspicuous lobes: 1.3.5.6.9.10.11.12.13.14.15.16.19.20.23.30.35.37.38.45.49.
    b. conical: 10.18.20.22.
    c. discoid: 2.3.5.9.16.17.25.26.27.28.29.30.31.32.33.34.35.39.40.41.42.43.44.45.46.47.48.49.50.51.

d. pileate: 13.23.24.
e. bearing large stigmatic lobes: 7.8.10.36.
f. receptaculum pollinis: 2.3.4.
g. truncate: 21.22.

27. Fruit
   a. loculicidal capsule: 1.2.3.5.6.10.11.12.20.22.24.25.26.27.28.29.30.31.32.33.34.35.37.
   b. septifragal capsule: 38.39.40.41.42.43.44.45.46.47.48.49.50.51.
   c. berry: 4.9.13.15.20.21.23.25.
   d. drupe: 7.8.14.16.17.18.19.36.
   e. nut: 20.
28. Dehiscence of capsule, sometimes tardily
   a. from apex: 1.2.3.5.6.10.11.12.20.22.24.26.27.28.29.30.31.32.33.34.35.37.38.39.40.41.42.43.44.45.46.47.49.
   b. from base: 44.48.
   c. from base and apex simultaneously: 44.48.49.50.51.
29. Fruit
   a. inflated: 6.
   b. not inflated: 1.2.3.4.5.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.51.
30. Columella
   a. present: 39.40.41.42.43.44.45.46.?47.48.49.?50.?51.
   b. absent: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.37.38.?47.?50.?51.
31. Fruit
   a. with warts or appendages: 10.11.29.35.
   b. without appendages: 1.2.3.4.5.6.7.8.9.10.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.51.
32. Seed
   a. unwinged: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.38.50.51.
   b. winged: 37.39.40.41.42.43.44.45.46.47.48.49.
33. Arillode and sarcotesta
   a. arillode present: 2.3.10.11.12.13.20.21.22.24.26.30.32.34.35.
   b. fleshy sarcotesta present: 4.5.6.8.9.10.17.18.20.23.25.27.28.29.30.31.33.35.36.
   c. corky or woody sarcotesta present: 38.50.51.
   d. sarcotesta membraneous: 1.
   e. arillode and sarcotesta absent: 7.13.14.15.16.19.23.37.38.39.40.41.42.43.44.45.46.47.48.49.
34. Union of arillodes
   a. two collateral seeds united by common arillode: 32.
   b. seeds not united by common arillode: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.27.28.29.30.31.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.51.
35. Presence of swollen basal sarcotesta
   a. seed with swollen basal sarcotesta (chalaza): 27.
   b. seed without swollen basal sarcotesta: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.21.22.23.24.25.26.28.29.30.31.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.50.51.

36. Endosperm
    - a. present: 1.2.3.4.5.6.7.8.9.10.11.16.17.18.19.37.39.40.41.42.43.44.45.46.47.48.49.
    - b. absent: 9.10.12.13.14.15.16.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.38.50.51.
37. Cotyledons
    - a. flat: 1.2.3.4.5.6.7.10.17.19.37.39.40.41.42.43.44.45.47.48.49.
    - b. planoconvex: 8.9.10.11.12.13.14.15.16.18.20.21.22.23.24.25.26.27.28.29.30.31.32.33.34.35.36.38.46.50.51.
38. Cotyledons, position
    - a. free, superposed: 20.21.23.28.29.30.31.35.
    - b. free, oblique: 14.15.20.29.30.35.38.
    - c. free, collateral: 1.2.3.4.5.6.7.8.9.10.11.12.13.14.15.16.17.18.19.20.25.26.27.29.30.32.33.34.35.36.37.38.39.40.41.42.43.44.45.46.47.48.49.
    - d. completely fused together: 22.24.50.51.
39. Radicle, position
    - a. superior, exserted: 1.2.3.4.5.6.7.8.10.11.12.13.14.15.16.18.19.26.27.36.37.38.39.40.41.42.43.44.45.46.47.48.49.?50.?51.
    - b. superior, included: 9.10.11.12.13.14.15.18.22.24.25.26.27.32.33.34.35.36.38.?50.?51.
    - c. abaxial, exserted: 14.17.
    - d. abaxial, included: 28.29.30.
    - e. central, included: 20.21.23.29.30.31.
    - f. adaxial, included: 35.38.

Codification of the genera:

1 = Munronia; 2 = Naregamia; 3 = Turraea; 4 = Humbertioturraea; 5 = Calodecaryia; 6 = Nymania; 7 = Melia; 8 = Azadirachta; 9 = Vavaea; 10 = Trichilia; 11 = Pseudobersama; 12 = Pterorhachis; 13 = Walsura; 14 = Lepidotrichilia; 15 = Malleastrum; 16 = Ekebergia; 17 = Astrotrichilia; 18 = Owenia; 19 = Cipadessa; 20 = Aglaia; 21 = Lansium; 22 = Aphanamixis; 23 = Reinwardtiodendron; 24 = Sphaerosacme; 25 = Heckeldora; 26 = Cabralea; 27 = Ruagea; 28 = Turraeanthus; 29 = Guarea; 30 = Chisocheton; 31 = Megaphyllaea; 32 = Synoum; 33 = Anthocarapa; 34 = Pseudocarapa; 35 = Dysoxylum; 36 = Sandoricum; 37 = Quivisianthe; 38 = Capuronianthus; 39 = Cedrela; 40 = Toona; 41 = Khaya; 42 = Neobeguea; 43 = Soymida; 44 = Entandrophragma; 45 = Chukrasia; 46 = Pseudocedrela; 47 = Schmardaea; 48 = Swietenia; 49 = Lovoa; 50 = Carapa; 51 = Xylocarpus.

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