Meliaceae

Meliaceae Juss. (1789, 'Melieae'), nom. cons.

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Trees, treelets, often pachycaul or, more rarely, shrubs or suckering shrublets, monopodial or sympodial, rarely with *Terminalia* branching (*Vavaea*), dioecious (though sometimes, at least, 'male' trees occasionally producing bisexual flowers), polygamous, monoecious or with all flowers bisexual; indumentum of simple, bifid or stellate hairs or stellate or peltate scales or sometimes mixtures of these, sometimes with small glands; buds naked or with scale-leaves. Leaves exstipulate (occasionally pseudostipules present), in spirals, rarely decussate, pinnate, sometimes with a terminal 'bud', i.e. pseudogemmula, trifoliolate, with a single blade (simple or unifoliolate) or rarely bipinnate (*Melia*); rachis very rarely winged; leaflets usually entire, rarely lobed or serrate (or spinous), sometimes with minute black glandular dots. Inflorescences axillary, supra-axillary, ramiflorous, cauliflorous to ground level or rarely epiphyllous (*Chisocheton*), thyrsoid, racemose or spicate, sometimes reduced to fascicles or solitary flowers. Flowers bisexual and/or more usually, unisexual, with well-developed rudiments of opposite sex; calyx usually ± lobed, sometimes with distinct sepals, these occasionally in spirals and transitional to bracts (*Dysoxylum*), sometimes truncate or closed in bud and circumscissile at base at anthesis; petals 3–7(–14) in 1 (rarely in a spiral (*Chisocheton*) to give up to 2 apparent) whorls, green, white, cream, pink to claret and violet or yellow (*Aglaia*); stamens usually partially or completely united by a tube with or without lobes; anthers 3–10(–30) in 1 or, rarely, 2 or more whorls, sometimes locellate, at tips of filaments or at the margin of the tube or within its throat; nectary disk around ovary, cushion-like, tubular or 0; ovary (1)2–6(–20)-locular, each locule with 1–many ovules; ovules pendulous, epitropous, anatropous and bitegmic, less often hemianatropous, campylotropous, or orthotropous, and unitegmic; stylehead discoid to capitate. Fruit a capsule, berry or drupe. Seed with fleshy aril or sarcotesta or a combination of these or winged and these attached to a woody columella, or with corky outer layers, or very rarely without any of these, endosperm usually 0; cotyledons collateral, superposed or, rarely, oblique, emergent or not at germination, when scale-leaves are sometimes produced before first foliage leaves, which can be opposite or in spirals, simple or pinnate with later ones simple to bipinnate. $2n$=16–c. 360.

A family of 50 genera and c. 575 spp., throughout the tropics and subtropics, with weak representation in temperate zones.

Vegetative Morphology[1]. In terms of 'architecture', most Meliaceae correspond to the models of Corner (unbranched, inflorescences lateral) and related structures with this pattern variously reiterated (model of Champagnat) in the scheme of Hallé and Oldeman (1970), from pachycaul to leptocaul, while *Vavaea* has *Terminalia* branching (model of Aubréville) and *Xylocarpus* architecture corresponds to the model of Rauh.

In subfam. Cedreloideae, the buds are surrounded by small subulate scales, which are only sporadically found in subfam. Melioideae. The form of the young emergent leaves is a useful character in the recognition of the sections of *Dysoxylum* (Mabberley in Mabberley et al. 1995: 63). The mature leaves are usually in spirals, though apparently always decussate in *Capuronianthus* and some species of *Turraea* (Mascarenes) and *Dysoxylum*.

[1]General chapters based on Pennington and Styles (1975, 1981) and Mabberley et al. (1995), unless otherwise stated.

Most species have pinnate leaves, those in *Melia* always bipinnate, a feature occurring in juveniles (and very occasionally adults, as in some *Chukraria tabularis*) in other genera. Sometimes the leaflets of pinnate leaves are deeply lobed in mature foliage as well as in juveniles; this is characteristic of some *Dysoxylum* species brought into cultivation because of their 'ferny' foliage, but also in some Mascarene *Turraea*. In most species of *Turraea* besides all of *Calodecaryia*, *Humbertioturraea*, *Nymania* and *Vavaea*, the leaves are simple; unifoliolate leaves are found in some species of *Aglaia*, *Malleastrum*, *Reinwardtiodendron*, *Trichilia* and *Walsura*, exclusively paripinnate ones in *Anthocarapa*, *Khaya*, *Neobeguea*, *Owenia* and *Xylocarpus*. The leaves of most species of *Chisocheton* and *Guarea* have apical 'pseudogemmulae', which are crozier-like buds of undeveloped leaflets, from which leaflets unfold at intervals, such that the leaves develop over several seasons and have annual rings in the ageing petioles. In some species in both of these genera, however, the pseudogemmula is effectively inactive and may fall off before any second 'flush', the leaf appearing paripinnate, whereas some species in these genera have long imparipinnate leaves. In species of *Cabralea*, *Dysoxylum* and *Ruagea*, the development of the apical leaflets may be delayed, but there is a terminal leaflet and no resting meristem in the form of a pseudogemmula.

'Pseudostipules' occur sporadically in the family, notably in South American species of *Trichilia*, but also some species of *Chisocheton*.

Vegetative Anatomy. The wood anatomy of the family is well documented because of the economic significance of the family (see Baas in Mabberley et al. 1995: 5 for a review). The limits of the family, particularly the distinction from Rutaceae in referring *Chloroxylon*, *Flindersia* and *Ptaeroxylon* to the latter, were first realized through a study of wood anatomy (Kribs 1930).

The association of non-septate fibres with terminal parenchyma bands helps to characterize the tribes 'Turraeeae', Melieae, 'Trichilieae' (except *Cipadessa*) and Sandoriceae, while sepate fibres in combination with the absence or only sporadic occurrence of marginal parenchyma characterize the other tribes recognized here. Many individual genera and species overlap in their wood-anatomical range, however, so that only a few genera can be recognized by their wood structure alone: *Aphanamixis*, *Astrotrichilia*, *Azadirachta*, *Cipadessa*, *Ekebergia*, *Melia*, *Nymania*, *Owenia*, *Sandoricum*, *Turraeanthus* and *Vavaea*. It is of interest that several of them have the habitats the most different from the bulk of the family (see below).

An indumentum of stellate hairs or scales is the only type found in *Aglaia*, *Astrotrichilia*, *Lepidotrichilia*, *Melia* and *Pterorhachis* (but occurs sporadically in other genera too).

Inflorescences. Although basically thyrsoid, the inflorescences are sometimes reduced to spikes or solitary flowers. Sometimes, as in some South American *Guarea* species, inflorescences show indeterminate growth (see also under *Melia* below), like the leaves. In *Chisocheton*, inflorescences are borne in axillary, supra-axillary or ramiflorous positions (Fisher and Rutishauser 1990). In each of these places and also on the bole, the inflorescences may be borne on dwarf shoots with reduced leaves. Such shoots are also known in *Melia* (q.v.), where they continue growth after fruit set. There are also species with epiphyllous inflorescences borne on the adaxial surface of the leaf rachis, their vascular supplies being connected directly with that of the adjacent rachis, there being no adnation or other 'fusion'. In *C. tenuis* there are also vegetative buds, their origin like that of the epiphyllous inflorescences in this species, and *C. pohlianus* being considered heterotopic or, indeed, homoeotic.

Floral Morphology. Flowers vary in size from the long tubular ones to 10 cm or more in length in some *Turraea*, to those 0.05 mm across in some species of *Aglaia*. Male flowers are in general smaller than female ones. Flowers are globular in, e.g. *Aphanamixis* and *Aglaia*, tubular in many other genera. Usually the corolla is white or pinkish and often very highly scented. Distinct sepals are found in, e.g. *Ruagea* and *Cabralea*, but also in some *Dysoxylum* in which they grade into bracts. The corolla rarely has more than one whorl (some *Chisocheton*) and sometimes the petals are united by a basal tube, which sometimes also bears the staminal tube.

Generally the stamens are united by a basal tube (e.g. Figs. 34B, 35D), though filaments are

distinct in *Cedrela* and *Toona*, while some species of *Walsura* and *Trichilia* have flattened filaments. There is a gradation from those with a basal tube and otherwise distinct filaments to those with tubes where the anthers are borne along the rim or inserted within it: the genus *Trichilia* shows the complete range. The position of the anthers is often a character of generic value, being inserted at the end of the filaments or, as in *Dysoxylum*, on the margin of the tube with the anthers completely included or partially exserted. However, the positioning does vary within some genera such as *Aglaia* and *Owenia*. The apex of the filaments or margin of the tube often bear appendages, simple or variously lobed. In *Sphaerosacme* and *Reinwardtiodendron*, the anthers are in two distinct whorls.

Nectary disks are common between the ovary base and the androecium, being long cylinders enveloping the ovaries in, for example, *Dysoxylum* but, in some genera like *Aglaia*, *Aphanamixis* and *Lansium*, they are absent. In *Guarea* the ovary is borne on an expanded stipitate disk and, in *Toona* and *Cedrela*, such a structure supports both the gynoecium and androecium. In nearly all Melioideae, each ovary locule has one or two collateral or superposed ovules, in most Cedreloideae they have 3 to many biseriate ones. The styleheads vary from the pinhead-shaped ones in many species of *Aglaia* to the flattened discoid ones of most Cedreloideae and those with large stigmatic lobes in *Azadirachta* and *Melia*; in *Turraea*, the stylehead forms a receptaculum pollinis topped with an apical stigmatic zone, pollen being deposited on the stylehead before the flower opens.

Pollen Morphology. The pollen grains are nearly always isopolar, radially symmetrical, suboblate to subprolate monads (van der Ham in Mabberley et al. 1995: 8). Rarely are they oblate or prolate and only in some *Dysoxylum* are they shed in rhomboidal tetrads. They are tri-, tetra- or penta-colporate, the second being the most frequent condition. In 'Turraeeae' (though not *Munronia*) and in Vavaeeae, they are usually tri-colporate; pollen in most genera has distinctly thickened ecto- and endo-aperture margins. Little is recorded of exine structure. There are no significant pollen differences between the subfamilies.

Karyology. There is a wide range of somatic chromosome number, from $2n = 16$ (*Sandoricum koetjape*) to c. 360 in some African *Trichilia*, with polyploid series in some genera, e.g. *Aphanamixis* and *Aglaia*, and also within species, e.g. *Chisocheton cumingianus*. The base number is probably $x = 6, 7$ (see Khosla and Styles 1975, and Mabberley et al. 1995: 8).

Pollination. Most species appear to be insect-pollinated, the agents possibly being bees, sting-less sweatbees or syrphids in those cases examined (*Aglaia* spp., *Xylocarpus* spp.), while some species are strongly scented particularly in the evening, which, with their white flowers, suggests moth pollination, e.g. *Chisocheton* and *Dysoxylum* spp. of Asia, as recorded in neotropical *Cedrela* and *Guarea* spp. Some species of these two genera have long flagelliform inflorescences suggesting bat pollination, though the Bornean species are known to be visited by spiderhunters; whether these birds are efficacious pollinators is not known.

Reproductive Systems. As it seems that male flowers may fall before females or bisexuals, it is often difficult in the absence of field studies to ascertain the true sexual arrangements of any particular species. Even dioecious species occasionally produce bisexual flowers, as was shown for *Dysoxylum spectabile* in New Zealand (Braggins et al. 1999). Apomixis is recorded in cultivated clones of *Lansium domesticum*.

Fruits and Seeds. There is a wide range of fleshy fruits, from the brightly coloured capsules of *Aphanamixis* and *Dysoxylum* to the dull berries of many *Aglaia* and *Lansium* species. The fruit is most commonly a capsule, loculicidal in Melioideae, septifragal in Cedreloideae (and one species of *Walsura*). Cedreloid capsules are usually woody with a ridged or angled columella (e.g. Fig. 34C), rudimentary in *Schmardaea*, *Carapa* and *Xylocarpus*, and bearing the seeds: dehiscence is basal, apical or both. Capsules of Melioideae have no columella and are fleshy, membranous, leathery or even woody. Indehiscent fruits include berries and drupes, the endocarp of those in *Astrotrichilia* and *Owenia* being very thick and woody.

By contrast with the relative uniformity of the flowers, the seeds of Meliaceae are some of the most diverse and intricate in structure so far investigated (Cheek 1989). The seeds are usually pendulous and epitropous (but apotropous in the Australian *Synoum*) in relation to the placenta. They are usually anatropous (but hemi-anatropous in most 'Turraeeae' and *Cipadessa*), occasionally orthotropous as in all *Chisocheton* and some *Guarea* spp., campylotropous in, e.g. *Nymania*, usually with a distinct funicle and raphe. Integument vascularization occurs in a few bitegmic genera, e.g. *Chisocheton* and *Heynea* (vascularized tegmen), *Dysoxylum* and *Trichilia* (vascularized testa) and is usual in pachychalazal seed-coats. In the 'Guareeae', arillate seeds characterize genera with bitegmic seeds, sarcotestal ones the unitegmic genera, while both conditions are found in *Chisocheton* and *Dysoxylum*, the genus with the greatest variation in seed anatomy investigated by Cheek.

The single most taxonomically useful layer of the seed-coat in the majority of genera is the exotegmen: dimensions of the fibres and their wall characters but also the number of cell layers. However, in *Dysoxylum*, for example, the type of seed appendage and its organization are more helpful in recognizing species groupings because the exotegmen is reduced and poorly developed there. From his survey of the family, Cheek concludes that the ancestral Meliaceous seed was comparatively large and bitegmic, with a small chalaza and a funicular-raphe-aril. From such can be derived the unitegmic sarcotestal state and then unitegmic 'pseudoarillate' seen in many species.

Dispersal. The fruits of species of Cedreloideae are dry dehiscent capsules, the winged seeds of the tall emergent and canopy trees being wind-dispersed, the irregular corky-coated ones of *Xylocarpus* being dispersed by saltwater in which they float just below the surface. The indehiscent fleshy fruits of *Azadirachta indica* are known to be dispersed by bats and baboons in Africa, where it is introduced, those of *Melia azedarach* by birds. Those species of *Aglaia*, *Chisocheton*, *Dysoxylum* and *Aphanamixis* with dehiscent capsules and arillate or otherwise fleshy seeds are also known to be taken by birds, apparently attracted by the contrasting colours of seeds and/or pericarp, while those species with indehiscent fruits, at least in *Aglaia* and *Reinwardtiodendron*, are eaten by primates which pass the seed divested of its fleshy layers. The bird and primate 'syndromes' are associated in a sample of *Aglaia* spp. at least, with characteristic chemistry as might be expected, those taken by birds being high in lipid, those by primates higher in free carbohydrates, but it is clear that few if any tree species are restricted to any one species, or indeed group, of vertebrate dispersers. Moreover, as there are no native primates in some parts of the ranges of certain species—*Aglaia elaeagnoidea* in New Caledonia, for example—it must be concluded that bats or birds are active dispersal agents even for those species which are thought to be dispersed by primates or other terrestrial mammals elsewhere.

In New Guinea, birds of paradise are the only known dispersal agents for *Chisocheton lasiocarpus* seeds. Those of the Malesian *Dysoxylum angustifolium* and possibly *Sandoricum borneense* are believed to be dispersed by fish, like those of the neotropical *Guarea guidonia* (Pennington and Styles 1981: 11). This 'syndrome' has yet to be analyzed chemically.

The inflated fruits of *Nymania capensis* serve as dispersal units in southern Africa.

Phytochemistry. This is reviewed by Hegnauer in Mabberley et al. (1995: 8). Characteristic of the order Sapindales is the synthesis of nortriterpenoids derived from tetracyclic triterpenes known as protolimonoids. Those of Meliaceae are unique to the family and are of great interest because of their insecticidal qualities.

Meliaceae also differ from the closely allied Rutaceae in both not accumulating large amounts of steam-volatile phenylpropanoids in their essential oils and in the absence of family-specific alkaloids. In Meliaceae true saponins are rare, but saponin-like glycosides are common. Some species, notably of *Azadirachta* and *Dysoxylum*, have characteristic onion- or garlic-like smells due to the presence of sulphur-containing volatiles. More widespread are mono- and sesqui-terpenoids in idioblasts, some of which are insecticidal.

Subdivision and Relationships Within the Family. The family is divisible into two subfamilies (Muellner et al. 2003, 2006, 2008a)—Melioideae and Cedreloideae (monophyletic sister

groups), both pantropical, with the former much larger in terms of numbers of genera and species. Subfam. Melioideae has been divided into eight tribes (Pennington in Pennington and Styles 1975; Leroy 1976) with 36 genera. All those recognized tribes are represented in tropical Asia, but only two ('Guareeae' and 'Trichilieae') are pantropical, while another two are restricted to the Old World ('Turraeeae' and Melieae), the remaining three being restricted to Indomalesia and the western Pacific (Vavaeeae, Aglaieae and Sandoriceae). Trichilieae, Guareeae and Aglaieae have been treated as one tribe by some workers, and molecular work (Muellner and Mabberley 2008; Muellner et al. 2008a) shows that Turraeeae are best combined with Trichilieae, though several genera formerly assigned to the latter are excluded from this pantropical grouping. This modified Trichilieae grouping is sister to one (pantropical) comprising Aglaieae (monophyletic), Guareeae, Vavaeeae (unigeneric) and *Lepidotrichilia* (formerly in Trichilieae). Sandoriceae (unigeneric) are sister to this combined group + *Walsura* (formerly Trichilieae), with *Quivisianthe* (formerly considered to comprise the unigeneric Quivisianthoideae of Madagascar) sister to that. Melieae (monophyletic) are sister to that grouping + *Astrotrichilia* (formerly Trichilieae).

Affinities. These are fully discussed by Pennington and Styles (1975), who argue for the integrity of the family, which is, nevertheless, closely allied to Rutaceae, some of which (*Cneorum* and *Harrisonia*) have very similar limonoids, the oxidised terpenoids which characterize the family, and provide some of the most significant plant products in terms of potential insecticides. DNA work has confirmed that the family is most closely allied to Rutaceae and Simaroubaceae, which with Sapindaceae form the core group of Sapindales (Muellner et al. 2003).

Distribution and Habitats. Muellner et al. (2006) argue that the family is of West Gondwanan origin. At the generic level, the family demonstrates some remarkable transoceanic affinities: Asiatic and Malesian *Toona* with neotropical *Cedrela*; *Dysoxylum* and *Chisocheton* of Indomalesia are apparently close to *Guarea* of the neotropics and Africa; *Xylocarpus* of East Africa to the Pacific is closely allied to *Carapa* of the Neotropics to West Africa, while the species *Carapa procera* is found on both sides of the Atlantic. *Naregamia* has one species in India, one in Africa. No genus is pantropical and Madagascar is remarkable for having no fewer than seven endemic genera (*Astrotrichilia*, *Calodecaryia*, *Capuronianthus*, *Humbertioturraea*, *Malleastrum*, *Neobeguea* and *Quivisianthe*). *Nymania* is found only in southern Africa, *Schmardaea* in Andean cloud forest, *Sphaerosacme* in the Himalaya, but all these are monospecific.

Meliaceae are very common trees of the canopy and understorey of lowland primary forest, notably in Malesia, making up to 17% of all trees over 10 cm bole diameter in the forests of Sumatra, for example, and being absent from only the driest zones, though in Australia they are found even there, as species of *Owenia*. They are represented by species of *Xylocarpus* on rocky shores and in mangrove swamps. They are poorly represented at higher altitudes, although some *Dysoxylum* and *Toona sinensis* are sometimes conspicuous in lower montane forest in Asia, *Ruagea* spp. in America, and *Schmardaea* restricted to the cloud forest of the Andes. The family is represented in freshwater swamp forest in Borneo by *Sandoricum borneense* and *Chisocheton amabilis* and includes some species restricted to limestone, like *C. ruber* of Sarawak, while *Walsura monophylla* is restricted to ultramafics in the Philippines. Along rivers in west Malesia are a number of rheophytic species of *Aglaia* and *Dysoxylum angustifolium*. A few species are tolerant of more open conditions and will colonize large gaps in forest or are frequently encountered in secondary forest, e.g. *Toona* spp., and *Chukrasia tabularis* which colonizes even bare ground along road cuttings in the Malay Peninsula and is a naturalized weedy tree in parts of tropical Australia.

In Africa, the commercially significant cedreloid Meliaceae are emergent trees, some of the biggest in the continent and, in Java, 58-m-tall specimens of the melioid *Dysoxylum mollissimum* were some of the island's tallest trees, but these have long been removed, like the commercial mahoganies, *Swietenia* spp., of South America, now severely depleted, and the red cedar, *Toona ciliata* in north-eastern Australia.

Silviculture and Pests. The most widely grown for timber are Cedreloideae, the neotropical *Swietenia mahagoni*, *S. macrophylla*, and the Asiatic *Toona ciliata* and *Chukrasia tabularis* as well as Old World Melioideae, *Azadirachta indica* and *Melia azedarach*, all of which have also been grown as shade or avenue trees; less often seen are species of *Entandrophragma* and *Khaya*, Cedreloideae from Africa. The major problem besetting plantation forestry of Meliaceae is the attacks of the moths (Lepidoptera, Pyralidae) of the genus *Hypsipyla*, larvae of which burrow into young plants and seedlings, causing their collapse and death, though Melioideae seem to be rarely attacked—a good argument for their promotion as plantation trees.

The shoot-borer is perhaps one of the most economically important insect pests in tropical forestry. In the Neotropics, the moths appear to be attracted by a chemical, possibly an alkaloid or limonoid, allied to substances which, in species from other parts of the world, are toxic to their local moths. Thus, *Toona ciliata* is resistant to attack in Costa Rica and this resistance may be transferred to susceptible *Cedrela odorata* if a scion of this is grafted on to a stock of *Toona*. *Chukrasia tabularis*, on the other hand, is not resistant in Costa Rica. There have been many attempts at biological control of the moths, for externally applied insecticides have little effect and systemic ones are expensive. Mixed and enrichment planting with non-susceptible species has been shown to reduce damage and there are possible advances to be made in breeding resistance to attack (Newton et al. 1993).

Palaeobotany. Fossils with features which, if they were found in a living plant, would place them in the concept of the modern Meliaceae are known from the Upper Cretaceous, some of the earliest ones being referred to the genus *Guarea* (certainly by the Oligocene), while others are referred to *Cedrela* and the closely allied Indomalesian *Toona* from the Eocene of the northern hemisphere (wood of *Cedreloxylon* allied to both of which being known from the Pliocene of China as well as the Eocene and Miocene of central Europe, and possibly the Eocene of North America; Cheng et al. 2006) and, among others, to the African *Entandrophragma* from the Miocene of Kenya, the tropical Old World *Melia* from the Miocene of Poland and Washington State, USA, and *Trichilia* from the Lower Miocene, Cameroon. The volcanic basalt deposits of the Cretaceous/Tertiary boundary, the Deccan Intertrappean beds of Mandla District, have yielded fossils referred to *Aglaioxylon* and *Heyneoxylon*, allied to *Aglaia* and *Heynea* respectively, while '*Carapa* spp.' (i.e. *Xylocarpus* spp.?) are known from the so-called peat bed near Calcutta, 22°08'N (see Mabberley et al. 1995: 2–3 and Muellner et al. 2006 for summaries of the earlier literature; see also Gregory et al. 2009).

Economic Importance and Conservation. The timbers of certain Meliaceae are some of the most sought after in the world, such that natural stands have been much depleted and serious conservation measures have been proposed for wild mahoganies (*Swietenia* spp.) in tropical America. The original 'mahogany' of the furniture-makers Hepplewhite and Chippendale was *S. mahagoni*, allowing the construction of more graceful and woodworm-proof furniture than could the oak and walnut previously used in Europe: this species has suffered severe genetic erosion and most 'mahogany' (if Meliaceous at all!) seen today is derived from *S. macrophylla* introduced to the Old World, probably from Honduras, in 1876 and described as a new species from material cultivated in India.

The other important timbers are also generally Cedreloideae, notably toon, *Toona ciliata*, from India to Australia ('red cedar'), where most of it has been long cut out, having been the most desirable timber on that continent. Others include the neotropical *Cedrela odorata* and species of the African genera *Entandrophragma* (*sapele*, *utile*), *Khaya* (African mahogany) and *Lovoa* (Nigerian golden walnut).

The locally important fruit trees of Malesia, *Lansium domesticum* (langsat) and *Sandoricum koetjape* (sentul) exist in a number of forms, wild, cultivated and naturalized, though they are not grown on a commercial plantation scale, those reaching markets being largely those selected from village trees. Seeds of a number of species of *Chisocheton* and *Aphanamixis* yield an oil which has been used as an illuminant.

The bitterness of the barks of Meliaceae has long been known and they have been used

in medicine, some being eagerly sought by Europeans in the eighteenth century. *Soymida febrifuga* from India was much prized but barks of other genera have been used, while the whole plant of *Munronia pinnata* is an important item of materia medica in southern Asia. The bark and, indeed, the leaves of *Azadirachta indica*, the neem, are powerful insecticides and this tree has a host of uses including planting in the reclamation of derelict land: it is perhaps one of the most all-round useful trees of Asia. Its young shoots are used as a vegetable (sadao) and sold in markets, as in Australia.

The triterpenoids which are responsible for the insecticidal (and molluscicidal, e.g. *Khaya* spp. bark and seeds) properties have aroused considerable commercial interest and have been examined in a number of genera for their use as biological pesticides. The biological activities of these compounds, including insect antifeedant and growth-regulating properties, medicinal effects in humans and other animals, as well as antifungal, bactericidal and antiviral activity, are reviewed by Champagne et al. (1992).

The genera are arranged according to Muellner et al. (2008a) and Muellner and Mabberley (2008), though there is more work to be done, and the tribes recognized by Pennington and Styles (1975) cannot be satisfactorily remodelled as yet (but see above); thus, only those which are clearly monophyletic are dealt with formally below.

Key to the Genera

1. Loculi 1- or 2-ovulate (rarely with 1 or 2 additional vestigial ovules) 2
– Loculi multiovulate 58
2. Leaves decussate, capsule with partial septifragal dehiscence (Madagascar) **12. *Capuronianthus***
– Leaves almost always in spirals, very rarely decussate (in which case capsule with loculicidal dehiscence) 3
3. Fruit dry, seed winged (Madagascar) **18. *Quivisianthe***
– Fruit fleshy or leathery; seed unwinged 4
4. Leaves bipinnate **6. *Melia***
– Leaves pinnate to simple 5
5. Leaves all simple (or unifoliolate) 6
– Leaves pinnate to trifoliolate 18
6. Hairs simple only 7
– Indumentum of at least some stellate hairs and/or stellate or peltate scales 16
7. Fruit a capsule 8
– Fruit a berry or, at least, indehiscent 12
8. Filaments 0 or less than half length of basal tube 9
– Filaments usually united only at base, at most with a tube shorter than them 11
9. Leaves simple (Old World) **34. *Turraea***
– Leaves unifoliolate, with distinct articulation (New World) 10
10. Anthers inserted within the staminal tube **44. *Guarea***
– Anthers on rim of staminal tube or tips of filaments **28. *Trichilia***
11. Capsule inflated (southern Africa) **32. *Nymania***
– Capsule not inflated (Madagascar) **36. *Calodecaryia***
12. Anthers in 2 whorls of 5 (Indomalesia) **48. *Reinwardtiodendron***
– Anthers in 1 whorl 13
13. Flowers conspicuous; trees with *Terminalia* branching (Malesia, Pacific) **23. *Vavaea***
– Flowers small; small trees or shrubs 14
14. Filaments almost distinct (Philippines, Sri Lanka) **20. *Walsura***
– Filaments very short, atop a tube (Madagascar) 15
15. Petals imbricate **35. *Humbertioturraea***
– Petals valvate **30. *Malleastrum***
16. Hairs mixed simple and stellate, suckering shrublets to 1 m **24. *Munronia***
– Indumentum of stellate hairs and/or stellate or peltate scales; suckers 0 17
17. Nectary disk 0 (Indopacific) **50. *Aglaia***
– Nectary disk present (elsewhere) **28. *Trichilia***
18. Leaves all trifoliolate 19
– Leaves pinnate 22
19. Indumentum of stellate hairs and/or stellate or peltate scales **50. *Aglaia***
– Hairs simple 20
20. Fruit a capsule 21
– Fruit a drupe (Malesia) **19. *Sandoricum***
21. Flowers solitary or paired **33. *Naregamia***
– Flowers in thyrses **28. *Trichilia***
22. Leaves with pseudogemmula (apical bud) 23
– Leaves without pseudogemmula 24
23. Disk stipitate, seeds anatropous (Neotropics) **44. *Guarea***
– Disk 0 to patelliform, seeds orthotropous (Indomalesia) **39. *Chisocheton***
24. Leaves with scales and/or stellate hairs 25
– Leaves with simple hairs 32
25. Shrublets with large white flowers and capsular fruits (Indomalesia) **24. *Munronia***
– Trees or treelets 26
26. Nectary disk present 27
– Disk 0; scales often present 30
27. Fruit a drupe (Madagascar) **17. *Astrotrichilia***
– Fruit a capsule 28
28. Rachis winged (west Africa) **29. *Pterorhachis***
– Rachis unwinged 29
29. Nectary disk tubular (Indomalesia, Pacific) **40. *Dysoxylum***
– Nectary disk a fleshy annulus **28. *Trichilia***
30. Petals valvate (Africa, Madagascar) **22. *Lepidotrichilia***
– Petals imbricate (Indomalesia, Pacific) 31

31. Female inflorescence and infructescence long spicate, scales 0 **46. *Aphanamixis***
– Not this combination of characters **50. *Aglaia***
32. Leaves paripinnate 33
– Leaves imparipinnate 41
33. Stigma with conspicuous lobes; fruit a drupe **15. *Azadirachta***
– Stigma unlobed 34
34. Fruit a capsule 37
– Fruit indehiscent 35
35. Fruit a drupe (Australia) **31. *Owenia***
– Fruit a berry (Indomalesia) 36
36. Anthers in 1 whorl of 10; berries on branches and trunk **49. *Lansium***
– Anthers in 2 whorls of 5; berries on axillary infructescences **48. *Reinwardtiodendron***
37. Anthers on rim of staminal tube or tip of filaments **28. *Trichilia***
– Anthers inserted within throat of staminal tube, at most partially exserted 38
38. Staminal tube cyathiform 39
– Staminal tube cylindrical to patelliform 40
39. Seeds united by joint raphe-arils (Australia) **38. *Synoum***
– Seeds sarcotestal (Malesia to Pacific) **37. *Anthocarapa***
40. Nectary disk present (Indomalesia, Pacific) **40. *Dysoxylum***
– Nectary disk absent (west Africa) **42. *Turraeanthus***
41. Leaf rachis swollen at insertion of leaflets **20. *Walsura***
– Leaf rachis not swollen thus 42
42. Fruit a berry 43
– Fruit a capsule or drupe 44
43. Petals valvate (Madagascar) **30. *Malleastrum***
– Petals imbricate (Malesia) **25. *Pseudoclausena***
44. Stigma with conspicuous lobes; fruit a 1(2)-seeded drupe **15. *Azadirachta***
– Stigma without such lobes; fruit a capsule or drupe with 2–5 (6) pyrenes 45
45. Staminal tube deeply cleft 46
– Staminal tube not deeply cleft 48
46. Corolla valvate; fruit a 5- or 6-pyrened drupe (Indomalesia) **26. *Cipadessa***
– Corolla imbricate 47
47. Fruit a drupe (Africa) **27. *Ekebergia***
– Fruit a 1-seeded capsule 48
48. Abaxial leaf-surface glaucous, rachis contracted at leaflet attachments when dried (Indomalesia) **21. *Heynea***
– Leaves different (not Indomalesia) **28. *Trichilia***
49. Nectary disk 0 50
– Nectary disk present 52
50. Petals 3 (Indomalesia) **46. *Aphanamixis***
– Petals 4 or more 51
51. Staminal tube globose (Himalaya) **47. *Sphaerosacme***
– Staminal tube cylindrical (west Africa) **42. *Turraeanthus***
52. Ovary 1-locular with parietal placentae (west Africa) **41. *Heckeldora***
– Ovary with more than 1 locule 53
53. Nectary disk tubular (to subannular) (Indomalesia, Pacific) **40. *Dysoxylum***
– Nectary disk stipitate to cyathiform 54
54. Leaves with pellucid lines or dots (Neotropics) 55
– Pellucid lines or dots 0 56
55. Stylehead discoid **45. *Cabralea***
– Stylehead capitate **28. *Trichilia***
56. Stylehead capitate **28. *Trichilia***
– Stylehead discoid 57
57. Calyx lobes imbricate, sarcotesta basal, swollen (Neotropics) **43. *Ruagea***
– Calyx lobes open, sarcotesta different **44. *Guarea***
58. Stamens 5 59
– Stamens 8–10 60
59. Seeds winged below, attached to distal end of columella (Neotropics) **2. *Cedrela***
– Seeds winged at both ends or if with one wing attached towards base of columella (Asia) **1. *Toona***
60. Leaves (1)2–4(5)-jugate (maritime Old World) **14. *Xylocarpus***
– Leaves with more leaflets, forest trees 61
61. Seeds unwinged **13. *Carapa***
– Seeds winged 62
62. Capsule globose to trigonous, not or scarcely longer than broad; seeds winged all round 63
– Capsule elongate, at least twice as long as broad; seeds with terminal wing or wings at both ends 64
63. Capsule ± globose with 4–6 valves remaining joined to one another **3. *Khaya***
– Capsule ± trigonous, the valves falling separately (Madagascar) **4. *Neobeguea***
64. Seed with a wing at both ends (India, Sri Lanka) **5. *Soymida***
– Seed with a terminal wing only 65
65. Staminal tube margin entire to crenulate; capsule with 60–100 terminally winged seeds per locule **7. *Chukrasia***
– Staminal tube with appendages or distinct lobes (rarely entire); seeds <20 per locule 66
66. Seeds attached by seed-end towards apex of columella 67
– Seeds attached by the wing-end towards apex of columella 68
67. Leaflets entire; capsule pendent (Africa) **6. *Entandrophragma***
– Leaflets dentate to serrate or undulately lobed; capsule erect 69
68. Capsule claviform or oblong (Africa) **9. *Pseudocedrela***
– Capsule ellipsoid or fusiform (Andes) **8. *Schmardaea***
69. Capsule erect, woody, ovoid or obovoid to oblong; flowers mostly 5-merous (Neotropics) **10. *Swietenia***
– Capsule pendent, subwoody, ellipsoid to tetragonal; flowers 4-merous (Africa) **11. *Lovoa***

Genera of Meliaceae

I. Subfam. Cedreloideae Arn. (1832).

Swietenioideae Kostel. (1836).
Lovooideae Kribs (1930).
Capuronianthoideae T.D. Penn. (1975).

Monoecious or dioecious trees; hairs usually simple; buds nearly always protected by scale-leaves. Leaves pinnate, spirally arranged. Loculi nearly always with 3 or more ovules, these biseriate; stylehead discoid or very rarely capitate. Fruit a septifragal capsule with a central columella. Seeds winged or capsule subwoody or leathery with rudimentary columella and seeds unwinged with a woody or corky outer layer.

1. *Toona* (Endl.) M. Roem.

Toona (Endl.) M. Roem., Fam. Nat. Syn. Monogr.1: 131, 139 (1846); Edmonds, Fl. Males. 12: 358–371 (1995); Peng Hua & Edmonds, Fl. China 11: 112–115 (2008).
Cedrela L. sect. *Toona* Endl. (1840).

Deciduous or semi-evergreen trees to 50 m, monoecious. Leaves usually paripinnate; leaflets entire to serrate, domatia usually present. Inflorescences much-branched thyrses. Flowers unisexual, rarely bisexual; calyx 5(6)-lobed or 5(6) sepals distinct, imbricate to cupulate in bud; petals 5(6), distinct, imbricate (quincuncial), usually adnate to pulvinate androgynophore (disk); stamens 5(6), distinct, arising from androgynophore, sometimes alternating with 1–5 filamentous staminodes; ovary 5-locular, each locule with 6–10 ovules; stylehead discoid, usually 5-rayed. Fruit a woody septifragal capsule; valves opening from apex; columella softly woody, 5-angled, extending to capsule apex. Seeds winged at both ends, when attached distally, or at one end, when attached by seed-end to proximal part of the columella; endosperm residual; cotyledons collateral, flattened, leaf-like; radicle laterally exserted; germination phanerocotylar. $2n = 46, 52, 56$.

Four or five spp. from eastern Pakistan to southern China and eastern Australia. *T. ciliata* M.J. Roem. (toon), almost throughout the range, was the most important cabinet timber (red cedar) in Australia.

2. *Cedrela* P. Br.

Cedrela P. Br., Civ. Hist. Nat. Jamaica: 158, t. 10, Fig. 1 (1756); T.D. Pennington & A.N. Muellner, Monogr. *Cedrela* (2010).

Deciduous trees. Leaves usually paripinnate; leaflets entire. Inflorescence a thyrse. Calyx deeply lobed to cup-shaped; petals 5, distinct, longer than calyx in bud, imbricate and adnate to long columnar andogynophore for up to half their length; stamens 5, distinct, adnate to andogynophore proximally; staminodes 0; ovary 5-locular, each locule with 8–14 ovules; stylehead discoid with glandular stigmatic papillae. Fruit a woody septifragal capsule opening from apex with 5 valves; columella woody, broadly winged, extending to apex of capsule. Seeds with terminal wing attached by seed end to distal part of columella; endosperm residual; cotyledons collateral, leaf-like. Germination phanerocotylar; eophylls opposite, trifoliolate; leaflets sinuate, entire. $2n = 50, 56$.

About 17 spp. in the Neotropics. One of the world's most important timber tree genera, though greatly attacked by *Hypsipela* shoot-borer larvae; *C. odorata* L. (Spanish cedar, invasive in the Galapagos) and lesser quality *C. fissilis* Vell. are often sold mixed together. Timber for all uses, formerly much for cigar-boxes.

3. *Khaya* A. Juss.

Khaya A. Juss., Bull. Sci. Nat. Géol. 23: 238 (1830); White & Styles, Fl. Trop. E. Afr. Meliaceae: 46–49 (1991).

Large trees, monoecious. Leaves paripinnate. Flowers in large thyrses; calyx lobed almost to base, lobes suborbicular, imbricate; petals 4 or 5, distinct, contorted; staminal tube urceolate, margin with 8–10 suborbicular emarginate to irregularly lobed overlapping appendages alternating with included anthers or antherodes; nectary disk in male flowers cushion-shaped, united to base of pistillode but free from base of androecium, smaller in females; ovary 4- or 5-locular, each locule with 12–18 ovules; stylehead discoid with crenulate margin, upper surface with 4 or 5 radiating stigmatic ridges. Fruit an erect subglobose, woody septifragal capsule opening by 4 or 5(6) valves from the apex, the valves remaining joined at the base, often with rough fibrous strands at margins; columella not extending to capsule apex, with 4 or 5(6) sharp tough woody ridges; seed-scars white, conspicuous. Seeds 8–18 per locule, broadly transversely ellipsoid or suborbicular, narrowly winged all round. $2n = 50$.

About 5 spp. in Africa, 1 in Madagascar. Major timber trees (African mahogany) used as a *Swietenia* substitute; some with locally important medicinal bark.

4. *Neobeguea* J.-F. Leroy

Neobeguea J.-F. Leroy, J. Agric. Trop. Bot. Appl. 17: 232 (1970) & Adansonia II, 16: 174, t. 1–3 (1976).

Deciduous trees. Indumentum of simple hairs or dendroid glands. Leaves usually paripinnate, rarely imparipinnate; leaflets entire, crenulated, dentate or denticulate. Inflorescences thyrses, sometimes appearing terminal. Calyx 4-lobed; petals 4(5), distinct, contorted or imbricate, reflexed at anthesis; staminal tube cupular to urceolate, margin with 8–16 ± bifid appendices; anthers 8(10) included to weakly exserted; nectary disk cushion-shaped in male flowers, much reduced in females; ovary (2)3(4)-locular, each locule with 4–6 ovules; stylehead discoid. Fruit a septifragal capsule, ± trigonous, 3-valved, woody, valves falling individually; columella woody, 3-angled, reaching apex of capsule. Seeds 3 or 4 per locule, subcircular, flattened and broadly winged around the margin; endosperm residual; embryo with collateral flattened cotyledons; radicle superior. $2n = 50, 52$.

Three spp., Madagascar.

5. *Soymida* A. Juss.

Soymida A. Juss., Bull. Sci. Nat. Géol. 23: 238 (1830); Mabb., Fl. Ceylon 9: 293–296 (1995).

Deciduous tree. Leaves paripinnate, glabrous; leaflets entire. Thyrses of unisexual flowers, with well-developed vestiges of opposite sex, in the most terminal axils. Sepals 5, ± distinct, imbricate; petals 5, contorted, spreading at anthesis; staminal tube shortly cylindrical to urceolate, margin with 10 bifid spreading lobes; anthers inserted between teeth of the lobes; nectary disk in male flowers shallowly patelliform, united with base of pistillode, in females an obscure swelling at ovary base; ovary 5-locular, each locule with 12–16 ovules; style 0, stylehead discoid, 5-lobed. Capsule ± ovoid, woody, septifragal, erect, opening from apex, the 5 valves separating into two layers: columella woody with 5 distinct ridges and reaching to capsule apex, seed-scars inconspicuous. Seeds unequally winged at both ends, attached by longer wing to distal end of columella; endosperm present; embryo with flattened foliaceous cotyledons; radicle obliquely superior. Germination phanerocotylar, cotyledons becoming green; eophylls opposite or in spirals, simple with minute serrate margin, later trifoliolate. $2n = 56$.

One sp., *S. febrifuga* (Roxb.) A. Juss., C, W and S India, Sri Lanka; locally important medicinal bark, tanbark and timber.

In many respects *Soymida* closely resembles *Khaya*, notably in leaf characters and flowers (petals erect in *Khaya* at anthesis; staminal tube lobes rounded or irregularly lobed) and seeds (winged equally all round in *Khaya*); the capsule in *Khaya* has a perceptibly bilamellate structure but does not separate into two distinct layers.

6. *Entandrophragma* C.DC. Fig. 34

Entandrophragma C.DC., Bull. Herb. Boissier 2: 582, t. 21 (1894); White & Styles, Fl. Trop. E. Afr. Meliaceae: 49–56 (1991).
Heimodendron Sillans (1953).

Large trees, dioecious. Leaves paripinnate, sometimes appearing imparipinnate. Inflorescences large thyrses. Calyx cupuliform, margin entire or with 5 acute lobes with open aestivation; petals 5, distinct, contorted; staminal tube cupular to urceolate, margin entire to lobed with 10 shortly stalked anthers or antherodes on margin or lobes; appendages 0; nectary disk cushion-shaped, united with base of ovary or pistillode but free from androecium and connected to it by 10 or 20 ridges or partitions; ovary 5-locular, each locule with 4–12 ovules; stylehead discoid, with 5 radiating stigmatic lobes. Fruit a pendulous, elongate woody septifragal capsule, opening by 5 valves from the apex or base, or from both simultaneously; columella softly woody, extending to apex of capsule, 5-angled or 5-ridged, deeply indented with the imprints of seeds. Seeds 3–9 per locule, each with a terminal wing, attached by the seed end to distal part of columella and winged towards base of capsule. $2n = 36, 72$.

Eleven spp., tropical Africa. Many important timbers, including sapele (*E. cylindricum* (Sprague) Sprague) with trees to 55 m or more, and utile (*E. utile* (Dawe & Sprague) Sprague).

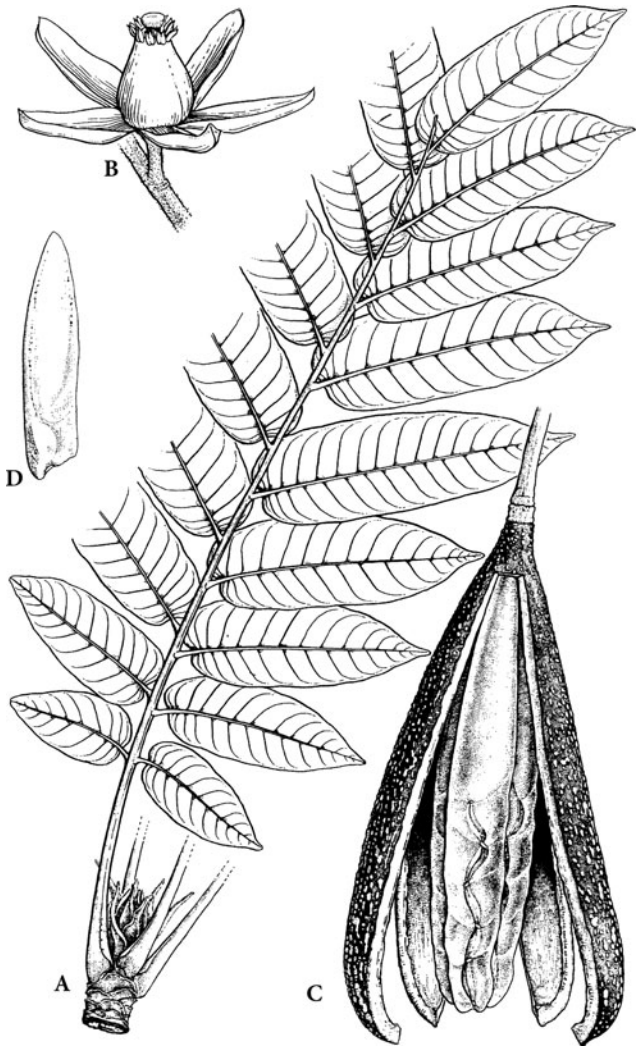

Fig. 34. Meliaceae. *Entandrophragma utile*. **A** Leaf and apical bud. **B** Flower. **C** Capsule, one valve removed. **D** Seed. (White and Styles 1991; drawn by Janet Dyer)

7. *Chukrasia* A. Juss.

Chukrasia A. Juss., Bull. Sci. Nat. Géol. 23: 239 (1830); Kalangire et al., Austr. J. Bot. 50: 319–330 (2002).

Deciduous trees. Leaves paripinnate with terminal leaflet represented by a spike, imparipinnate and bipinnate with incised or lobed leaflets in juveniles, rarely retained at maturity. Thyrses axillary, often subterminal appearing terminal. Calyx 4- or 5-lobed; petals 4 or 5, distinct, contorted and much longer than calyx in bud; staminal tube cylindrical, somewhat narrowing distally, margin entire to crenulate; anthers attached to margin; nectary disk obscure to narrowly cushion-shaped; ovary flask shaped, 3–5-locular, each loculus with numerous ovules; stylehead capitate with 3–5 stigmatic ridges. Capsule ovoid or ellipsoid, woody, opening by 3–5 values from the apex, the valves splitting into an outer and inner bifid layer; columella with 3–5 sharply angled ridges, extending to apex of capsule; seed-scars conspicuous. Seeds 60–100 per locule, wings terminal, arranged laterally in tiers in two ranks; endosperm present; cotyledons subcircular; radicle obliquely exserted. $2n = 26$.

One somewhat variable sp., *C. tabularis* A. Juss., from India and Sri Lanka, eastwards through tropical Asia to western Malesia, perhaps divisible into ecological races or even ecospecies (Kalangire et al. 2002). Valuable timber (*chickrassy*, *yinma* or Chittagong wood).

8. *Schmardaea* H. Karst.

Schmardaea H. Karst., Fl. Columb. 1: 187, t. 93 (1861); Styles, Fl. Neotrop. 28: 387–389 (1981).

Tree or shrub, deciduous. Leaves usually imparipinnate; leaflets with crenate to coarsely dentate margins. Flowers unisexual, in axillary thyrses. Calyx lobed almost to base, lobes 4, imbricate; petals 4, linear, contorted; staminal tube with 8 appendages; anthers included or shortly exserted, connective extended into long thread-like appendage; nectary disk ridged, short-stipitate; ovary 4-locular, each locule with up to 25 ovules; stylehead narrowly discoid with 4 stigmatic lobes. Capsule septifragal, erect, opening from apex with 4 valves; inner layers of valves linked by fibrous network; columella 0. Seeds up to 20 per locule with terminal wing, attached to dissepiments; endosperm in thick layer, embryo with thin collateral cotyledons; radicle laterally exserted.

One sp., *S. microphylla* (Hook.) C. Muell., Andes from Venezuela to Peru, up to 2,700 m in cloud forest.

9. *Pseudocedrela* Harms

Pseudocedrela Harms in Engl., Bot. Jahrb. Syst. 22: 153 (1895); White & Styles, Fl. Trop. E. Afr. Meliaceae: 56–58 (1991).

Tree, monoecious. Leaves paripinnate. Calyx (4)5-lobed almost to base, lobes ovate to suborbicular; petals (4) 5 distinct, slightly contorted, boat-shaped; staminal tube urceolate, margin with (8) 10 bifid reflexed lobes with anthers between them; nectary disk annular surrounding ovary base; ovary 4- or 5-locular, each locule with 4–6 ovules; stylehead discoid, upper surface with 4 or 5 radiating stigmatic ridges. Fruit an erect elongate woody septifragal capsule, opening from the apex by 5 divergent valves remaining attached at the base, connected by a fibrous network; columella woody extending to capsule apex, sharply 4- or 5-angled, indented with imprints of the seeds. Seeds 4 or 5 per locule, winged, attached by the seed-end to distal part of columella. $2n = 56$.

One sp., *P. kotschyi* (Schweinf.) Harms, tropical Africa. Timber valuable.

10. *Swietenia* Jacq.

Swietenia Jacq., Enum. Syst. Pl.: 4, 20 (1760); Lamb, Mahogany of trop. America (1966); Styles, Fl. Neotrop. 28: 389–406 (1981).

Deciduous trees. Leaves almost always paripinnate; leaflets entire. Flowers unisexual in axillary thyrses; calyx 5-lobed to half way, lobes rounded to obtuse, imbricate; petals (4)5, contorted; staminal tube cup-shaped to urceolate, with 8–10 partially exserted anthers (antherodes) and 8–10 acuminate appendages; nectary disk annular; ovary (4)5(6)-locular, each locule with 9–16 ovules; stylehead discoid with (4)5 stigmatic lobes. Capsule septifragal, oblong to ovoid, erect, the 5 valves opening from base or from base and apex simultaneously, separating into two layers, the outer thick and woody; columella the length of the capsule, 5-angled. Seeds 9–16 per locule, hanging by wing-end from distal part of columella; endosperm present; embryo with thin cotyledons. $2n = 48, 54, 56$.

Three spp., the true mahoganies (see Lamb 1966), tropical America extending to southern Florida. *S. mahagoni* (L.) Jacq. (Caribbean) and *S. macrophylla* King are widely planted for timber (Spanish mahogany), the latter perhaps now the most valuable timber in South America, because the former has been so reduced in quantity and quality through over-exploitation and genetic erosion.

11. *Lovoa* Harms

Lovoa Harms in Engl. & Prantl, Nat. Pflanzenfam. III, 4: 307 (1896); White & Styles, Fl. Trop. E. Afr., Meliaceae: 58–60 (1991).

Large trees, monoecious. Leaves paripinnate. Flowers in large thyrses; calyx lobed almost to base, lobes 2 + 2, imbricate; petals 4, distinct, imbricate; staminal tube cupular or shortly cylindrical, margin entire or with paired deltate-acuminate appendages alternating with 8 anthers; nectary disk broadly cushion-shaped, enveloping base of ovary or pistillode but free from androecium; ovary 4-locular, each locule with 4–6(–8) locules; stylehead discoid or capitate, obscurely 4-lobed. Fruit a pendulous, elongate, tetragonal or ellipsoid, thinly woody septifragal capsule, dehiscing from the apex or from the apex and base simultaneously; columella softly woody, extending to apex of capsule, 4-ridged, each ridge shallowly indented with imprints of seeds. Seeds c. 2 per locule, winged, attached to distal part of columella by wing-end, the body of the seed hanging towards the apex of the capsule. $2n = 50, 52, 56$.

Two spp., tropical Africa. Important timbers, especially *L. trichilioides* Harms (Nigerian golden walnut).

12. *Capuronianthus* J.-F. Leroy Fig. 35

Capuronianthus J.-F. Leroy, Compt. Rend. Hebd. Séances Acad. Sci. 247: 1374 (1958) & Adansonia II, 16: 176–181 (1976).

Trees, monoecious. Buds naked. Leaves pinnate, decussate. Flowers in thyrses or short racemes; calyx deeply lobed or of 4 distinct sepals, lobes imbricate; petals 4(5), distinct, generally contorted, more rarely imbricate; staminal tube urceolate or shortly cylindrical, margin with 8 appendices alternating with anthers inserted on margin; nectary disk present; ovary locules with 2 superposed ovules plus 1 or 2 vestigial ones; style very short or 0, stylehead capitate, minute. Fruit a 3- or 4-valved capsule dehiscing irregularly or not at all; epicarp and mesocarp fibrous, indehiscent or with partial irregularly septifragal dehiscence; endocarp cartilaginous. Seeds 1 or 2 per valve, unwinged; testa thick; endosperm 0; cotyledons plano-convex, collateral to oblique; radicle superior or adaxial. $2n = 58$.

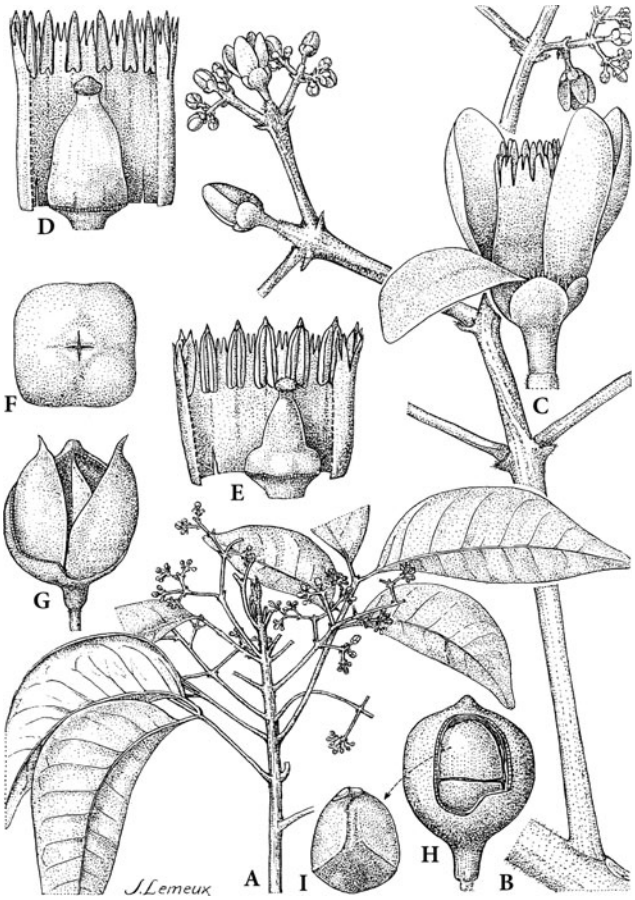

Fig. 35. Meliaceae. *Capuronianthus vohemarensis*. **A** Flowering branch. **B** Inflorescence. **C** Flower. **D** Flower, probably functionally male, with perianth removed. **E** Same, probably functionally male. **F** Fruit, seen from above. **G** Fruit with part of pericarp removed, the dehiscing endocarp visible. **H** Fruit with two superposed seeds in one locule. **I** Seed. (Leroy 1976; drawn by J. Lemeux)

Two spp., Madagascar (one far north, one far south).

Although the genus has recently been afforded subfamilial rank, Muellner et al. (2003) argue for its inclusion in Cedreloideae, supporting earlier anatomical work, for the seed-coat is like that of *Carapa* (Cheek 1989).

Genera 13 and 14 make up:

Tribe Xylocarpeae Blume (1825).

Carapeae Harms (1896).

Trees. Flowers without a gynophore; petals distinct; staminal tube urceolate or cupular, margin lobed; anthers 8–10. Capsule ± woody or leathery with a rudimentary columella. Seeds unwinged, with a corky or woody outer layer; cotyledons large, united; endosperm 0.

13. *Carapa* Aubl.

Carapa Aubl., Hist. Pl. Guian. Franç. 2, suppl.: 32, t. 387 (1775); Styles, Fl. Neotrop. 28: 406–418 (1981).

Deciduous or semi-evergreen trees, monoecious. Leaves almost always paripinnate. Flowers in large, erect, axillary thyrses, sometimes subterminal and appearing terminal; calyx 4- or 5-lobed almost to base, the lobes rounded or ovate, imbricate; petals 4 or 5(6), imbricate; staminal tube cupular to cylindrical or urceolate with 8–10 entire to lobed appendages alternating with sessile included anthers (antherodes); nectary disk cushion-shaped, free of staminal tube; ovary 4- or 5(6)-locular, partly sunk in disk, each locule with (2)3–8 ovules; stylehead discoid. Capsule septifragal, subglobose to cylindrical, pendulous, opening from apex and base simultaneously by 4 or 5 leathery valves, columella disintegrating. Seeds 8–35, angular, with outer surface rounded; sarcotesta woody, thick; endosperm 0; embryo with large united cotyledons. $2n = 58$.

Two variable spp. (possibly divisible into more) in tropical America and Africa, *C. procera* DC. in both. Timber valuable; seed oil (andiroba) locally medicinal.

14. *Xylocarpus* Koenig Fig. 36

Xylocarpus Koenig, Naturforscher 20: 2 (1784); Mabb., Malays. For. 45: 448–450 (1982), rev., Fl. Ceylon 9: 296–300 (1995) & Fl. Males. 12: 371–380 (1995).

Semi-evergreen maritime trees. Twigs lenticellate, cicatrose. Leaves paripinnate with (1)2–4(5) pairs leaflets, entire, glabrous. Flowers unisexual in short axillary thyrses; calyx 4-lobed to about the middle, valvate; petals 4, contorted and much longer than the calyx in bud; staminal tube margin with 8 suborbicular, retuse or shallowly and irregularly divided lobes; anthers 8, included; nectary disk cushion-shaped, beneath or surrounding and united with ovary, red; ovary 4(5)-locular, each locule with 3 or 4 (–6) ovules; style short, stylehead discoid, its margin crenellate and its upper surface with four radiating

stigmatic grooves. Fruit a large pendulous subspherical capsule, tardily dehiscing by 4(5) leathery valves from apex. Seeds 5–20, large, irregularly tetrahedral or pyramidal, outermost surface convex, attached to central columella, with aerenchymatous (?sarcotestal) coat; embryo with the radicle lying above the hilum; germination cryptocotylar, the numerous subulate cataphylls verticillate or in spirals; true leaves simple, entire, later ones trifoliolate (rarely first ones thus). $2n = 52$.

Three spp. throughout the coastal regions of the Old World tropics from E Africa to the W Pacific in mangrove swamps and coastal woodlands on rock and other substrates. The wood and bark are locally important for construction, and both tanning and medicine.

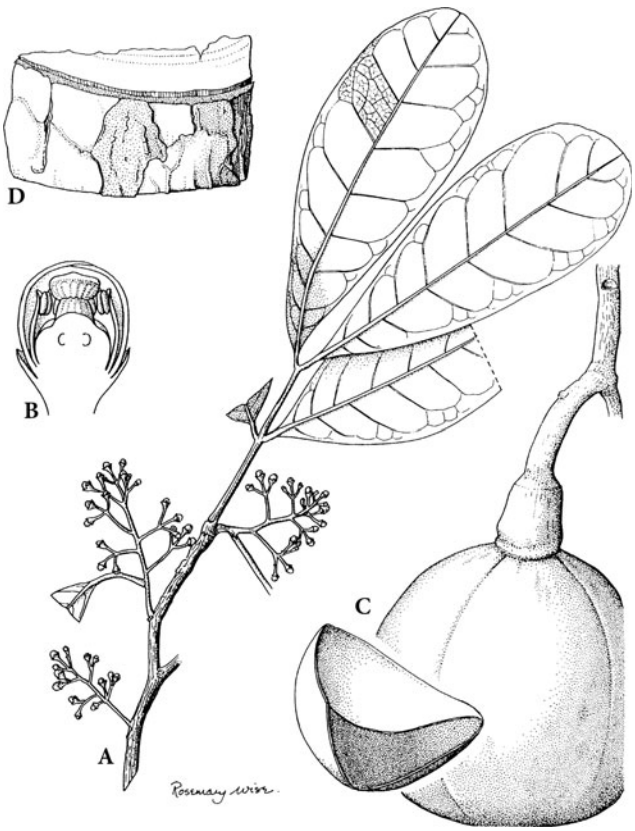

Fig. 36. Meliaceae. *Xylocarpus granatum*. **A** Flowering branch. **B** Flower in longisection. **C** Unripe fruit and seed. **D** Bark. (Mabberley et al. 1995; drawn by Rosemary Wise)

II. Subfam. Melioideae Arn. (1832).

Trichilioideae Kostel. (1836).
Quivisianthoideae T.D. Penn. & Styles (1975).

Buds usually naked; plants dioecious, polygamous or with bisexual flowers entirely; loculi 1-, 2- or 3-ovular with vestigial third ovule, very rarely multiovulate; ovules collateral or superposed. Fruit a columella-less fleshy or leathery capsule, berry or drupe. Seed usually with a fleshy testa or aril or combination of these, very rarely (*Quivisianthe*) winged; endosperm present or absent. Pantropical.

Genera 15 and 16 make up:

Tribe Melieae DC. (1824).

Trees, polygamous; hairs stellate and/or simple. Leaves pinnate or bipinnate. Flowers bisexual or male; staminal tube cylindrical, lobed; nectary disk annular; stylehead 3–8-lobed. Fruit a drupe. Seed exarillate; endosperm thin; cotyledons collateral; radicle superior, exserted.

15. *Azadirachta* A. Juss.

Azadirachta A. Juss., Bull. Sci. Nat. Géol. 23: 236 (1830); Mabb., Fl. Ceylon 9: 280–284 (1995) & Fl. Males. 12: 337–343 (1995).

Trees; hairs simple; buds thinly encrusted with resin. Leaves pinnate with 2 pairs of glands at base of petiole. Flowers bisexual and male on same individual (polygamous); calyx 5-lobed to proximal half, the lobes imbricate; petals 5, distinct, imbricate; staminal tube cylindrical, slightly expanded at mouth, margin (8–)10-lobed, the lobes rounded, truncate, emarginate or bifid; anthers (8–)10, glabrous, inserted at base of and opposite lobes; nectary disk annular, united with base of ovary; ovary 3-locular, each locule with 2 collateral ovules; stylehead with apical swollen torus with 3 acute, partially united papillose stigmatic lobes. Fruit a 1(2)-seeded drupe; endocarp thin, cartilaginous. Seed ovoid, distally pointed; testa thin, membranous with small adaxial sarcotesta; cotyledons plano-convex, collateral; radicle superior, short projecting from cotyledons. Germination phanerocotylar; eophylls opposite, trifoliolate, leaflets deeply incised or pinnatifid. $2n = 28, 30$.

Two spp. native to Indomalesia, though one, *A. indica* A. Juss., the neem, is widely cultivated

in warm countries throughout the world and is naturalized in some of them, colonizing deforested land.

Formerly confused with *Melia*, *Azadirachta* differs in its simple indumentum, pinnate leaves, collateral ovules, 3-lobed stylehead and 1(2)-seeded drupes. The wood is readily distinguished in that that of *Melia* is ring porous.

In West Africa, where the tree has come to dominate large areas of the savanna, the seeds are dispersed by fruit bats and baboons, after passage through which their germination is enhanced. Held sacred by the Hindus, the neem is potentially one of the most important of all tropical seasonal forest trees, having proved to be very adaptable and able to withstand arid conditions. It can be grown in impoverished soil and is a fast-growing source of fuelwood. In Central America, it is now being planted as a substitute for *Swietenia* mahogany. It is also widely planted as a windbreak, shade and avenue tree, the world's biggest plantation being of 50,000 trees in the plains of Saudi Arabia, planted to shade the two million or so Muslim pilgrims camping there annually for 'Haj' rites. It is a soil ameliorant and is potentially a source of many valuable by-products: it has been an ingredient of soaps, toothpaste and lotions in commerce for decades. The seeds contain some 40% oil by weight and this bitter material has been used in lamps and as a lubricant and has potential as a fuel-source, the mesocarp being a promising substrate for the production of methane gas. Neem cake is an excellent fertilizer and the leaves and twigs are used as a mulch in Asia. The bark produces a valuable gum and tannin worth exploiting. The pressed leaves have long been put in books to ward off insects, the repellent being the limonoid azadirachtin, which is in the seeds as well as the leaves; house-sparrows in India incorporate leaves into their nests, perhaps reducing parasite loads. Azadirachtin is absorbed by plants and acts as a systemic insecticide so efficient that Japanese beetles and other insects, even including the desert locust, will starve rather than eat plants treated with it. Of the five limonoids known from the tree, deacetylaxadirachnol (salannin) is as potent as azadirachtin in inhibiting ecdysis in tobacco budworm. Neem seed powder with carbofuran greatly reduces leaf-hoppers and rice tungro virus in rice. The leaves, bark and seed oil have been used in the treatment of a wide range of ailments, including malaria, eczema, dysentery and ulcers, but particularly effective as a parasiticide for skin diseases such as scabies. Neem oil also has significant post-coital contraceptive action (see Mabberley et al. 1995: 342–343).

16. *Melia* L.

Melia L., Sp. Pl.: 384 (1753); Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19b1: 99–102, t. 26, 27 (1940); Mabb., Gdns' Bull. Sing. 37: 49–62 (1984) & Fl. Ceylon 9: 274–279 (1995) & Fl. Males. 12: 329–336 (1995).
Antelaea Gaertn. (1788).

Trees, occasionally flowering precociously as shrublets; hairs simple and stellate-tufted. Leaves 2(3)-pinnate. Inflorescence thyrsoid, axillary. Calyx 5(6)-lobed to near base, lobes somewhat imbricate; petals 5(6), distinct, imbricate; staminal tube narrowly cylindrical, slightly expanded at mouth, 10(12)-ribbed, with 10 or 12 truncate, bifid or 4-fid filiform lobes; anthers 10(12), inserted at margin of or just within tube, alternating with or opposite lobes; nectary disk small, surrounding base of ovary; ovary 4–8-locular, each locule with 2 superposed ovules; stylehead capitate to coroniform with 4–8 short, erect or incurved stigmatic lobes. Drupe 3–8-locular; endocarp thick, bony, deeply dimpled at base and apex; loculi 1(2)-seeded. Seed oblong, laterally compressed; testa leathery sometimes slightly swollen and fleshy around hilum; embryo embedded in oily endosperm; cotyledons flat. Germination phanerocotylar; eophylls opposite, pinnatisect or trifoliolate. $2n = 28$.

Two or three spp., one, *M. azedarach* L. (white cedar, Persian lilac), in Indomalesia and one or possibly two in S tropical Africa. Forms of *M. azedarach* are widely cultivated and naturalized throughout the warm parts of the world.

The 'inflorescences' of *M. azedarach* are often short shoots with terminal buds. The true inflorescences are borne in the axils of rudimentary leaves and, after fruit abscission, the terminal bud may grow out into a leafy shoot. The fruits, which have been long used for beads, are toxic to man, some 6–8 considered a fatal dose, and also to pigs but apparently not to birds, sheep or goats: the toxic principles are the limonoids, meliatoxins A1, A2, B1, B2. The wood of different forms of the species has been used for furniture and light construction and for the production of fibreboard. It has been used as a fast-growing coffee-shade and it has been alleged that fruit trees grown under it remain relatively free from aphids. Indeed, a decoction of the fruits has long been used as an insecticide for plants in India and fruits or leaves have been placed with dry fruit, clothing and in books to keep insects away. A glycopeptide, meliacin, isolated from the leaves and roots is responsible for inhibition of in-vitro replication of various DNA and RNA viruses, e.g. poliovirus, herpes simplex Type I (see Mabberley 1995: 336).

17. *Astrotrichilia* (Harms) T.D. Penn.

Astrotrichilia (Harms) J.-F. Leroy ex T.D. Penn., Blumea 22: 477–478 (1975); J.-F. Leroy & Lescot, Bull. Mus. Natl. Hist. Nat. IV, 18: 20–34 (1996).
Trichilia P. Br. sect. *Astrotrichilia* Harms (1896).

Trees or shrubs. Indumentum of stellate hairs, rarely bifid, mixed with simple hairs and small glandular hairs. Leaves pinnate to trifoliolate. Flowers unisexual in axillary thyrses; calyx with 5 distinct lobes, imbricate or open in bud; petals 5, distinct, imbricate; staminal tube cyathiform or shortly cylindrical, margin entire or with 10(11) dentiform appendages bearing anthers; nectary disk patelliform or 0; ovary 2–5-locular, each locule with 2–5 superposed, rarely collateral, ? orthotropous ovules; stylehead discoid. Fruits drupes with ± persistent calyx, 1–3-locular; pericarp thick, resinous; endocarp chartaceous. Seeds one per locule, exarillate; endosperm thick; embryo with thin flat collateral cotyledons, radicle small, abaxial.

Twelve spp., Madagascar.

18. *Quivisianthe* Baill.

Quivisianthe Baill. in Grandidier, Hist. Phys. Madagascar 33, 3 [fasc. 34], Atlas 2: ad t. 251 (1894); T.D. Penn., Blumea 22: 508–509 (1975).

Trees; hairs simple; buds naked. Leaves pinnate, in spirals. Flowers usually unisexual (trees dioecious), in thyrses; calyx 5-lobed; petals distinct, valvate; staminal tube urceolate to shortly cylindrical, margin entire or subentire; anthers 5 inserted on the margin; nectary disk annular to patelliform or 0 or a short stipe; ovary 3- or 4-locular, each locule with (1)2 ovules; stylehead obscurely 3-lobed. Fruit a loculicidal capsule, 3(4)-angled, 3(4)-valved. Seeds (1)2 per locule; testa dry with apical wing attached to placenta; endosperm present; embryo with lateral flat cotyledons; radicle superior, exserted.

Two spp., Madagascar.

Although recently assigned to a subfamily of its own, on DNA grounds (Muellner et al. 2003) the genus appears close to *Ekebergia* ('Trichilieae'). The bitegmic seeds are like those of Cedreloideae.

19. *Sandoricum* Cav.

Sandoricum Cav., Diss. 7: 359 (1789); Mabb., Blumea 31: 146–151 (1985), rev. & Fl. Males. 12: 344–353 (1995).

Trees; hairs simple. Leaves trifoliolate. Flowers in axillary thyrses; calyx ± truncate to shallowly 4- or 5-lobed; petals (4)5, distinct, imbricate; staminal tube cylindrical, ribbed distally; margin with 5 or 10 short lobes; anthers 10, glabrous, included; nectary disk tubular, free, margin coarsely toothed; ovary slightly sunk in receptacle, 4- or 5-locular, each locule with 2 collateral ovules; stylehead with 4- or 5-lobed stigma. Fruit a drupe, 1–5-locular, pyrenes 1(or 2)-seeded; outer mesocarp rather dry-fleshy or soft and fibrous, inner mesocarp fleshy or spongy-fibrous; endocarp thin, cartilaginous. Seeds exarillate, pachychalazal, kidney-shaped, laterally compressed with thin sarcotesta; endosperm 0; cotyledons thick, plano-convex, collateral, radicle apical, extending to surface or slightly exserted. Germination phanerocotylar; eophylls trifoliolate, opposite. $2n$ =16, 22, 44, 64.

Five spp., all but one, *S. koetjape* (Burm.f.) Merr., restricted to W Malesia, where the cultivated forms of *S. koetjape* (santol) may have arisen, though wild relations appear to be native as far east as New Guinea. All five are wild in Borneo, to which three are restricted.

The fruit (where known as mature) of all species is edible and the timber of some value, the bark used for tannin and medicine locally, some of the triterpenoids extracted from the stems having been shown to have significant cytotoxic activity against cultured cancer cells and to be insect antifeedants.

20. *Walsura* Roxb.

Walsura Roxb., Fl. Ind. 2: 386 (1832); T. Clark, Blumea 38: 247–291 (1994), rev.; Mabb., Gdns' Bull. Sing. 55: 195–199 (2003).
Napeodendron Ridl. (1920).

Pachycaul to leptocaul trees; hairs simple and/or bifid. Leaves imparipinnate or unifoliolate, leaflets opposite. Inflorescences axillary thyrses of hemaphrodite and male flowers. Calyx 5-lobed; petals 5, distinct, imbricate to valvate; androecium of distinct filaments or a 10-lobed tube with truncate to weakly bifid lobes; nectary disk annular; ovary 2 (or incompletely 4?)-locular, each locule with 2 collateral ovules; stylehead capitate to cylindrical, sometimes with 2 apical lobes. Fruit a 1- or 2(?4)-seeded berry or 1- or 2-seeded weakly dehiscent capsule; pericarp with thin layer of sclerenchyma, the locules separated by a thin septum. Seeds pre-raphe-funicular-arillate. $2n$ = 28.

Sixteen spp., from Sri Lanka to the Himalaya and Indochina through Malesia to New Guinea.

21. *Heynea* Roxb.

Heynea Roxb. in Curt., Bot Mag. 41: t. 1738 (1815); Mabb., Fl. Males. 12: 41–44 (1995); Peng Hua & Mabb., Fl. China 11: 120–121 (2008).
Walsura Roxb. sect. *Heynea* (Roxb.) Harms (1896), nom. illeg.
Ailantopsis Gagnep. (1944).
Picroderma Gagnep. (1944).

Trees; twig pith vessel-less; hairs simple. Leaves imparipinnate; rachis compressed, not swollen at points of attachment of leaflets; abaxial surface of leaflets papillate, glandular. Inflorescences corymbose cymes with long peduncles. Calyx 4- or 5-lobed, the lobes imbricate; petals 4 or 5, ± imbricate; androecium with cylindrical staminal tube to 1/3 length with 8 or 10 filaments with bifid apices; nectary disk annular; ovary 2- or 3-locular, each locule 2-ovulate; stylehead 2- or 3-lobed. Fruit a capsule; pericarp with sclereids. Seeds 1 or 2, pre-raphe-funicular-arillate. $2n = 28$.

Two spp., E and SE Asia.

22. *Lepidotrichilia* (Harms) T.D. Penn.

Lepidotrichilia (Harms) J.-F. Leroy ex T.D. Penn., Blumea 22: 473–475 (1975); J.-F. Leroy & Lescot, Bull. Mus. Natl. Hist. Nat. Paris IV, 18, B Adansonia: 7–13 (1996).
Trichilia sect. *Lepidotrichilia* Harms (1896).

Trees; hairs simple and stellate. Leaves imparipinnate. Flowers unisexual, rarely bisexual, in axillary thyrses; calyx 5(6)-lobed; petals 5, distinct, valvate; staminal tube entire or with distinct filaments, cylindrical; appendages filiform to lanceolate; anthers 10, inserted between appendices; nectary disk 0; ovary 2–5-locular, each locule with 1 ovule; stylehead capitate with 3–5 stigmatic lobules. Fruit a 2–5-locular drupe; endocarp membranous or cartilaginous. Seeds 1–5, oblong to globose, exarillate, testa (?pachychalaza) membranous or cartilaginous; endosperm 0; embryo with collateral or oblique plano-convex cotyledons; radicle superior or abaxial, included to slightly exserted. $2n = 38$.

Four spp., 1 in tropical E Africa, 3 in Madagascar.

23. *Vavaea* Benth.

Vavaea Benth. in Hook., Lond. J. Bot. 2: 212 (1843); T.D. Penn., Blumea 17: 351–366 (1969), rev. & 22: 464–466 (1975).
Lamiofrutex Lauterb. (1924).

Trees or treelets with sympodial *Terminalia* branching. Hairs simple. Leaves simple. Flowers mostly bisexual; calyx 4 or 5(7)-lobed, with open rarely imbricate aestivation; petals (3)4–6, distinct, imbricate, rarely contorted; staminal tube cylindrical or cyathiform; anthers 9–23, attached at ends of filaments, filaments partly distinct; nectary disk patelliform or cyathiform, united to base of tube, or forming androecial ribbing, or 0; ovary 2–6-locular, locules with 1 or with 2(3) collateral ovules or with 4–10 in 2 rows. Fruit a berry with fleshy to woody pericarp. Seeds 1–3 (7) ovoid or plano-convex, with thin sarcotesta; thin endosperm sometimes present; cotyledons plano-convex, collateral; radicle superior, small, included or extending to the surface. Germination cryptocotylar, eophylls opposite, simple.

Four spp. from Sumatra eastwards to tropical Australia, Micronesia, Melanesia and Polynesia, with one restricted to Fiji and two to New Guinea.

24. *Munronia* Wight Fig. 37

Munronia Wight, Ic. Pl. Ind. Orient. 1, 5: [1] (1838); Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19b1: 91–93 (1940); Mabb., Fl. Males. I, 12: 30–34 (1995); Peng Hua & Mabb., Fl. China 11: 118–119 (2008).

Unbranched or sparsely branched shrublets, sometimes suckering with apparently short-lived shoots, sometimes possibly dioecious; hairs simple and bifid or stellate. Leaves imparipinnate to simple, margins often crenate to serrate. Flowers bisexual, solitary or in few-flowered thyrses, pseudopedicellate, usually white; calyx 5-lobed to near base, lobes often somewhat foliaceous; petals 5, valvate to imbricate, adnate to staminal tube basally, rarely becoming free later; staminal tube narrowly cylindrical or weakly obconical, the margin with 10 entire or bilobed appendages or, rarely, with 10 reflexed filiform appendages recurved some distance below margin; anthers 10, pubescent, inserted on tube rim, alternating with appendages, connective often produced

apically forming an appendage, which is rarely filiform; nectary disk 0 or tubular, free or united with base of staminal tube; ovary (3) 5-locular, each loculus with 1 or 2 superposed ovules; stylehead capitate, sometimes with 5 stigmatic lobes. Fruit a 5-valved loculicidal capsule, each locule with 1 or 2 seeds. Seed plano-convex with a bony tegmen with an outgrowth enveloping a thick sarcotesta (Cheek 1989). $2n = 50$.

About four spp., tropical Asia and subtropical China, two extending eastwards to Timor.

25. *Pseudoclausena* T. Clark

Pseudoclausena T. Clark, Blumea 38: 291–295 (1994) & Fl. Males. 12: 55–57 (1995).

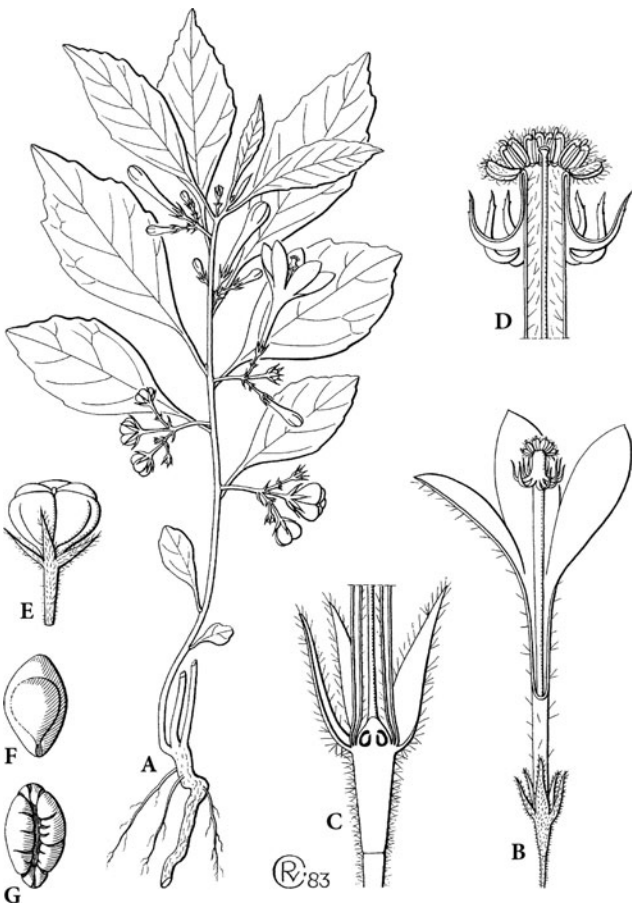

Fig. 37. Meliaceae. *Munronia humilis*. **A** Habit. **B** Flower, half corolla removed. **C** Ovary, vertical section. **D** Androecium, vertical section. **E** Fruit. **F, G** Seeds. (Mabberley et al. 1995; drawn by R. van Crevel)

Tree; hairs simple. Leaves imparipinnate. Inflorescences thyrses of bisexual or male flowers. Calyx 5-lobed; petals distinct, imbricate; androecium ± cylindrical, each filament linear with bifid apex; nectary disk 0; ovary 4- or 5-locular, each locule with 1 ovule. Fruit a 1- or 2-seeded berry, asymmetric, shortly beaked. Seed ellipsoid, exarillate, possibly pachychalazal.

One variable sp., *P. chrysogyne* (Miq.) T. Clark, Indochina to west New Guinea, in wet evergreen forest.

26. *Cipadessa* Blume

Cipadessa Blume, Bijdr.: 162 (1825); Mabb., Fl. Ceylon 9: 270–274 (1995) & Fl. Males. 12: 57–60 (1995).

Small tree; hairs simple. Leaves imparipinnate. Inflorescences polygamous, axillary thyrses. Calyx 5-lobed in apical half; petals 5(6), distinct, valvate; filaments alternatively long and short, connate near base, terminated by a pair of narrowly lanceolate to filiform or erose appendages; anthers 10, acute, inserted between the appendages, pubescent; nectary disk patelliform; ovary 5(6)-locular; each locule with 1(2) collateral ovules; style short, stout, columnar, swollen stylehead with 5(6) stigmatic lobes. Fruit a globular drupe with 5(6) pyrenes, each 1 (2)-seeded; endocarp bony. Seed orange-segment-shaped, exarillate; testa thin, membranous; embryo embedded in endosperm; cotyledons thin, flat, collateral; radicle superior, long exserted. $2n = 28, 56$.

One sp., *C. baccifera* (Roth) Miq., tropical and subtropical Asia from Nepal, India and Sri Lanka to S China, Indochina and C Malesia.

The rest of the genera (see introductory remarks) make up the remodelled:

Tribe Trichilieae DC. (1824), including a modified Turraeeae Harms (1896, including Nymanieae F. White (1986)), Guareeae T.D. Penn. (1975) and Aglaieae Blume (1825).

Trees, shrubs or suffrutices; hairs simple or stellate, rarely peltate scales. Leaves usually pinnate, rarely trifoliolate, unifoliolate or simple. Indumentum of simple or stellate hairs. Plants dioecious or flowers bisexual; staminal tube usually complete or filaments partially connate, rarely distinct; anthers nearly always inserted

apically on margin of staminal tube or on filaments; disk small, usually annular or patelliform, rarely 0. Fruit a capsule, berry or drupe. Seed usually arillate or with sarcotesta, mostly without endosperm; cotyledons usually collateral.

27. *Ekebergia* Sparrm.

Ekebergia Sparrm., Kongl. Vetensk. Akad. Handl. 40: 282, t. 9 (1779); White & Styles, Fl. Trop. East Africa, Meliaceae: 37–39 (1991).

Trees or shrubs, dioecious; hairs simple. Leaves imparipinnate. Inflorescences of contracted thyrses. Calyx (4)5(6)-lobed in distal half; petals (4)5 distinct, imbricate; staminal tube cup-shaped, with very short distinct filaments, appendages 0; anthers usually 10, inserted on rim; nectary disk in male flowers annular or patelliform, partly united with base of staminal tube and ovary, in females a small swelling at ovary base; ovary 2–5(6)-locular, each locule with 2 superposed ovules; style short and stout; stylehead capitate with 2–5 indistinct lobes. Fruit a drupe with 2–4(–6), 1(2)-seeded pyrenes. $2n = 46, 50$.

Four spp., tropical Africa.

28. *Trichilia* P. Br.

Trichilia P. Br., Civ. Hist. Nat. Jamaica: 278 (1756), nom. cons.; de Wilde, Meded. Landbouw. Wageningen 68-2(1968), reg. rev.; T.D. Penn., Fl. Neotrop. 28: 25–233 (1981), reg. rev.
Pseudobersama Verdc. (1956).
Burseranthe Rizz. (1974).

Trees and treelets, usually dioecious, rarely polygamous. Buds usually naked, rarely subtended by a cluster of small scale-leaves; hairs simple, less often malpighiaceous, forked or stellate hairs, or with peltate scales. Leaves pinnate, less often unifoliolate, trifoliolate or rarely digitate; leaflets sometimes glandular-punctate and -striate. Infloresences thyrses, rarely fasciculate or corymbose or few-flowered racemes. Calyx usually (3)4–6-lobed, rarely sepals distinct, aestivation usually open; petals (3)4 or 5(6), distinct or partially united, imbricate, rarely quincuncial; staminal tube cyathiform, urceolate or shortly cylindrical, margin usually toothed or lobed, rarely stamens distinct; anthers (4)5–10 (–12) inserted between teeth or lobes or apical on distinct filaments; nectary disk usually a fleshy annulus around ovary base; ovary 2- or 3(–5)-locular, locules with 1 or 2 collateral or less often superposed ovules; stylehead usually capitate, with or without lobes. Fruit a 2- or 3(4 or 5 [*Pseudobersama*])-valved loculicidal capsule with leathery or woody valves and 1 or 2 seeds per locule. Seed ± plano-convex, with partial to complete raphe-funicular aril or sarcotesta (pachychalaza), usually without endosperm; embryo usually with plano-convex collateral cotyledons; radicle superior, usually included. $2n = 24, 28, 46, 50, 92$, c. 360.

About 70 spp. in mainly lowland tropical America, 18 in Africa, 6 in Madagascar. Frequent understorey trees in Amazonia.

Pseudobersama is included here with a little hesitation: it has five-lobed fruits but otherwise seems indistinct (cf. Cheek 1992). Asiatic species recently included are now referred back to *Heynea*.

29. *Pterorhachis* Harms

Pterorhachis Harms in Engl., Bot. Jahrb. Syst. 22: 155 (1895); T.D. Penn., Blumea 22: 471–472 (1975).

Small tree, dioecious; hairs stellate. Leaves imparipinnate or trifoliolate, rachis winged. Flowers in axillary thyrses. Calyx 5-lobed to near base, aestivation ± imbricate; petals 5, distinct, imbricate; staminal tube urceolate to cylindrical, with distinct filaments as long as it, each terminated by (3)4–6(10) unequal filiform appendages (fewest in females), the outer pair longer than the rest; anthers (9)10 inserted just below appendages, connective aciculate; nectary disk a swollen annulus; ovary 3(4)-locular, each locule with 1 or 2 superposed ± orthotropous ovules; stylehead capitate with 3(4) minute obtuse lobes. Capsule loculicidal, 3(4)-valved, each locule with 1 or 2 seeds. Seed plano-convex with flattened base; testa leathery with aril surrounding basal part; endosperm 0; embryo with plano-convex collateral cotyledons, radicle superior. $n = 14$.

One (*P. zenkeri* Harms) or possibly two spp., Cameroon and Gabon.

30. *Malleastrum* (Baill.) J.-F. Leroy

Malleastrum (Baill.) J.-F. Leroy, J. Agric. Trop. Bot. Appl. 11: 128–149 (1964); Leroy & Lescot, Bull. Mus. Natl. Hist. Nat., Paris IV, 18: 13–20 (1996).
Cipadessa Bl. sect. *Malleastrum* Baill. (1874).

Trees, shrubs or shrublets; hairs simple. Leaves imparipinnate to trifoliolate or unifoliolate; rachis sometimes winged. Flowers bisexual or unisexual, in small axillary thyrses; calyx 4- or 5-lobed or -dentate; petals (3) 5 or 6, distinct, valvate; staminal tube entire, cyathiform to shortly cylindrical, to filaments almost distinct; appendices (8–)10, narrowly lanceolate or filiform, ± bifid; anthers (8–)10, alternating with appendices; nectary disk annular or 0; ovary of 1–3(–5)-locular, each locule with 2 superposed or slightly oblique ovules; stylehead capitate with small stigma with apical depression. Fruit a berry, often asymmetric with 1–3 (5) locules and thin pericarp. Seeds 1 per locule, oblong or spheroid, exarillate, pachychalaza thin, membranous, sometimes thicker and hard; endosperm 0; embryo with plano-convex cotyledons, collateral to oblique; radicle superior, usually not exserted.

Twenty-three spp., Madagasacar. Some locally medicinal.

31. *Owenia* F. Muell.

Owenia F. Muell. in Hook., Kew J. Bot. 9: 303 (1857); T.D. Penn., Blumea 22: 478–479 (1975); Mabb., Telopea 8: 47–48 (1998).

Deciduous trees with resinous buds and often milky sap, dioecious; hairs simple. Leaves paripinnate. Flowers in axillary thyrses; calyx of 5 distinct imbricate sepals; petals 5, distinct, imbricate; staminal tube irregularly lobed or with distally distinct filaments, each with 2 apical appendages; anthers 10, glabrous; nectary disk obscure, annular; ovary 2–4-locular, each locule 1-ovulate; stylehead conical. Drupe 2–4-locular; mesocarp fleshy to leathery; endocarp woody, hard. Seed ovoid to orange-segment-shaped, with thin sarcotesta. $2n = 28$.

Five spp., Australia, particularly drier regions.

32. *Nymania* Lindb.

Nymania Lindb., Not. Sällsk. Fauna Fl. Fenn. Förh. 9: 290 (1868, 'Trans. Nov. Scand.'); White, Bothalia 16: 146–148 (1986).
Aitonia Thunb. (1781), non *Aytonia* Forst. & Forst.f. (1776).

Shrub; hairs simple. Leaves simple, in fascicles on short lateral shoots. Flowers bisexual, axillary, solitary; calyx 4-lobed to near base; petals 4, distinct, imbricate; filaments 8 or 9, curved, with basal tube, anthers glabrous, versatile; nectary disk thin, partly united with staminal tube; ovary 4(5)-locular, each locule with 2 collateral campylotropous ovules; style long with minute capitate stylehead. Capsule loculicidal, thinly membranous, each locule with 1 (or 2) seeds. Seed reniform, with fleshy sarcotesta around hilum. $2n = 40$.

One sp., *N. capensis* (Thunb.) Lindb., Namibia and South Africa.

The inflated pink to purple capsular fruits are blown about and break up, thereby scattering the seeds. The placement in 'Turraeeae' is confirmed by the presence of the limonoid nymania-1, typical of *N. capensis*, in *Turraea obtusifolia* Hochst. (Fraser et al. 1995).

33. *Naregamia* Wight & Arn.

Naregamia Wight & Arn., Prodr. Fl. Pen. Ind. Or. 1: 116 (1834), nom. cons.; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19bI: 90–91 (1940); T.D. Penn., Blumea 22: 454–455 (1975).
Nelanaregam Adans. (1763), nom. rejic.

Small shrublets, sometimes geoxylic; hairs simple. Leaves trifoliolate, leaflets entire to weakly lobed, rachis broadly winged. Flowers bisexual, axillary, solitary or paired; calyx 4- or 5-lobed to middle; petals 4 or 5, distinct, imbricate; staminal tube narrowly cylindrical, margin entire to weakly crenulated; anthers 8 or 10 with connective produced apically to form an appendage up to as long as anther; nectary disk absent; ovary 3- or 4-locular, each locule with 2 collateral ovules; style slender; stylehead discoid to obconical. Fruit a 3- or 4-valved loculicidal capsule, each locule with 1 or 2 seeds. Seed curved, truncate at both ends; testa bony, thick; aril small. $2n = 46$.

Two spp., one on west coast of India, one in Angola.

Cheek (1996) combined this with *Turraea*, but molecular analyses (Muellner et al. 2003, 2006) support earlier authors' view as to its distinctness.

34. *Turraea* L.

Turraea L., Mant. Alt.: 150 (1771); Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19b1: 85–90 (1940); Mabb., Fl. Males. I, 12: 24–27 (1995), reg. rev.; Mabb. & Cheek, Taxon 41: 541–545 (1992), typification.

Small trees or shrubs; hairs simple. Leaves simple entire, sometimes sinuate or crenate (*T. pulchella* (Harms) T.D. Penn. (South Africa) with imparipinnate or trifoliolate leaves). Flowers bisexual, in axillary or apparently terminal, fascicles or thyrses, or solitary; calyx cupuliform, (3) 4 or 5 (6)-lobed or -toothed; petals (3) 4 or 5, distinct, imbricate or contorted; staminal tube cylindrical or rarely cyathiform, complete or filaments less than half as long as basal tube; margin shallowly lobed or entire or terminated by simple or bilobed appendages, as many as or twice as many as the anthers; anthers (7–)10(20); nectary disk small or 0; ovary (3)4–10(20)-locular; loculi biovulate; style usually expanded near apex forming a *receptaculum pollinis* surmounted by a discoid stigmatic area. Fruit a (3)4–10(–20)-valved, loculicidal capsule; loculi 1- or 2-seeded. Seed plano-convex, raphe-funicular-arillate. $2n = 36, 46, 50$.

About 60 spp., in Africa, Madagascar (31), the Mascarenes (8) and one in Indomalesia, extending from India, through Malesia to tropical Australia. The African species are found in a variety of forest types and bush vegetation, often markedly seasonal.

The formerly enigmatic *Turraea breviflora* Ridl., found in a few localities in the Malay Peninsula, is now referred to *Munronia* (Muellner and Mabberley 2008).

35. *Humbertioturraea* J.-F. Leroy

Humbertioturraea J.-F. Leroy, Compt. Rend. Hebd. Séances Acad. Sci. D, 269: 2311, figs D, H, P, S & 2322 (1969).

Small trees, shrubs or shrublets; hairs simple. Leaves simple, entire. Flowers bisexual in small axillary fascicles, sometimes 1- or 2-flowered. Calyx cupuliform, (4)5-lobed; petals (4)5, distinct, imbricate; staminal tube cylindrical, margin subentire, appendices alternating with anthers, emarginate to bifid; anthers 10–12, sessile or shortly stalked, connective developed into apical mucro; nectary disk small, ± united with base of tube, margin often lobed; ovary 10–14-locular, each locule with 2 superposed ovules; stylehead enlarged into a *recaptaculum pollinis*, with apical stigmatic surface. Fruits indehiscent, 10–14-locular. Seeds plano-convex, with thick woody, glabrous testa; sarcotesta adaxial, hilum large.

Ten spp., Madagascar.

36. *Calodecaryia* J.-F. Leroy

Calodecaryia J.-F. Leroy, J. Agric. Trop. Bot. Appl. 7: 379–382, Fig. 1–4 (1960).

Small trees or shrubs; hairs simple. Leaves simple, entire. Flowers bisexual, in small axillary thyrses or fascicles; calyx 4- or 5-lobed to middle; petals 4 or 5, distinct, contorted; stamens 8–10, united only at base or almost distinct; anthers basifixed; nectary disk annular to patelliform; ovary 4- or 5-locular, each locule with 2 collateral campylotropous ovules; style straight; stylehead capitate to discoid, usually with 4 or 5 small stigmatic lobes. Fruit a 2–5-valved loculicidal capsule, each locule with 1 or 2 plano-convex to reniform seeds; testa thick, tough, sarcotesta surrounding hilum. $2n = 36$.

Two spp., Madagascar.

37. *Anthocarapa* Pierre

Anthocarapa Pierre, Fl. For. Cochinch. 5: ad t. 343 (1897); Mabb., Fl. Nouv.-Caléd. 15: 70–74 (1988) & Fl. Males. 12: 133–136 (1995), reg. revs.

Trees; hairs simple. Leaves paripinnate. Flowers unisexual (trees dioecious or monoecious), in axillary or supra-axillary thyrses. Calyx 4- or 5-lobed; petals (4)5, distinct, imbricate at least at apices; staminal tube ± urceolate, margin crenulate; anthers 10, inserted within tube; nectary disk obscure, thick, fleshy, annular or patelliform in male flowers, small, annular at the base of ovary in females; ovary (2)3(4)-locular, locules uniovulate, placentation axile; stylehead discoid. Fruit a 2- or 3(4)-valved capsule, (tardily) dehiscent. Seed with non-vascularized sarcotesta; embryo with thick collateral cotyledons; radicle superior, included.

One (*A. nitidula* (Benth.) Mabb.) or possibly two spp., from Philippines to New Caledonia.

38. *Synoum* A. Juss.

Synoum A. Juss., Bull. Sci. Nat. Géol. 23: 237 (1830); T.D. Penn., Blumea 22: 499–500 (1975); Mabb., Telopea 8: 48 (1998).

Tree; hairs simple. Leaves imparipinnate. Flowers unisexual, in axillary thyrses. Calyx deeply 4- or 5-lobed, extended into pseudopedicel; petals 4 or 5, distinct, imbricate; staminal tube cyathiform, margin irregularly and shallowly lobed; anthers

8 or 10, partly exserted; nectary disk obscure. Capsule loculicidal, 2- or 3-valved, locules usually 2-seeded. Seeds collateral, pendulous, epitropous, united by joint raphe-arils partly enveloping them; embryo with thick plano-convex, collateral cotyledons, radicle superior. $2n = 84$.

One sp., *S. glandulosum* (Sm.) A. Juss., NE Australian rain forests.

39. *Chisocheton* Blume Fig. 38

Chisocheton Blume, Bijdr.: 168 (1825); Mabb., Bull. Br. Mus. Nat. Hist. Bot. 6: 301–386 (1979) & Gdns' Bull. Sing. 55: 189–195 (2003).

Megaphyllaea Hemsl. (1887).

Trees pachycaul to leptocaul, sometimes unbranched, sometimes laticiferous or myrmecophilous, very rarely foetid, dioecious or polygamous; indumentum usually of simple, rarely of 4-stellate, hairs, sometimes irritant, with small glandular hairs. Leaves pinnate and pseudogemmulate or imparipinnate, very rarely paripinnate. Inflorescence paniculate to thyrsoid or with long peduncle and congested racemose, axillary to supra-axillary, ramiflorous or rarely borne on congested cauliflorous branches, or epiphyllous (New Guinea). Flowers sometimes with elongated receptacle (pseudopedicel); calyx ± cupuliform, usually obscurely 3–6-lobed; petals (3)4–6(–14) in 1(2) whorls, distinct, imbricate, quincuncial or alternative, often merely at apices, or valvate, rarely weakly united below or with base of staminal tube; staminal tube cylindrical, margin entire, crenate or with 4–10(–30) emarginate, truncate or narrowly lanceolate 2- or 3-fid lobes; anthers (3)4–10(–30), usually attached within the tube, alternating with lobes, usually locellate; nectary disk usually 0, less often stipitate, annulate or patelliform, occasionally lobed; ovary 2–8-locular, each locule with 1 or 2 collateral or superposed orthotropus ovules; stylehead clavate or discoid. Fruit a 2–5(–8)-valved capsule, the valves 1(2)-seeded. Seeds obovoid-spheroid to scutelliform or orange-segment-shaped, variously arillate or sarcotestal, orthotropous, with large chalaza; cotyledons collateral, oblique or superposed. $2n = 46, 92$.

Fifty-three spp., from Assam and tropical China throughout Malesia SE to N New South Wales and Vanuatu.

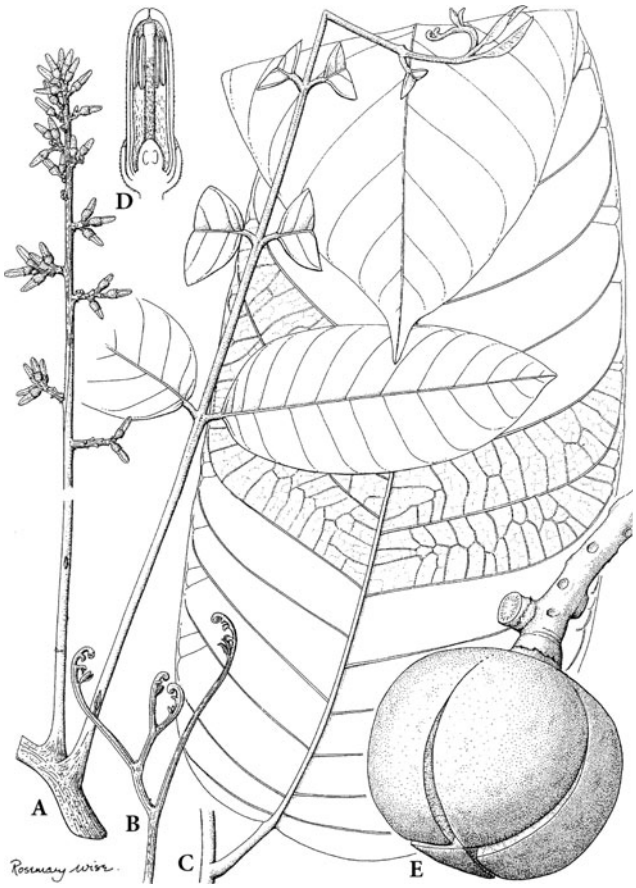

Fig. 38. Meliaceae. *Chisocheton macrophyllus*. **A** Leaf and inflorescence. **B** Young leaves. **C** Leaflet. **D** Flower, vertical section. **E** Fruit. (Mabberley et al. 1995; drawn by Rosemary Wise)

40. *Dysoxylum* Blume

Dysoxylum Blume, Bidjr.: 172 (1825); Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 19b1: 160–166 (1940); Mabb., Fl. Nouv.-Caléd. 15: 23–70 (1988), Fl. Ceylon 9: 241–248 (1995), Fl. Males. 12: 61–133 (1995), Telopea 10: 725–729 (2004), Tree Fl. Sabah & Sarawak 6: 146–176 (2007) & Fl. China 11: 125–129 (2008).
Piptosaccos Turcz. (1858).
Pseudocarapa Hemsl. (1884).
Meliadelpha Radlk. (1890).

Trees or shrubs, often very pachycaul, dioecious, more rarely with bisexual flowers; hairs simple, very rarely stellate. Leaves in spirals, rarely opposite, pinnate, occasionally with tardily developed apical leaflets, very rarely with winged rachis. Inflorescences thyrses to racemose or spicate, sometimes reduced to fascicles or solitary flowers, axillary, ramiflorous or cauliflorous, sometimes with conspicuous bracteoles and these

sometimes transitional to distinct sepals. Calyx of distinct sepals or, more usually, a 3–5(6)-lobed tube; petals 3–6, distinct or adnate to base of staminal tube; staminal tube cylindrical to urceolate, margin entire, lobed or tipped with 6–10(–13) appendages; anthers 6–16, within throat of tube, pollen very rarely shed in tetrads; nectary disk free, tubular though sometimes short or even subannular, margin sometimes lobed; ovary 2–6-locular, each locule with 1 or 2 seeds; stylehead capitate to discoid. Fruit a 2–6-valved capsule, each valve with 1 or 2 seeds. Seeds anatropous, very variable, usually with aril or sarcotesta.

About 80 spp., from India and Sri Lanka (3) to S China (11), Indochina, throughout Malesia (including Christmas Island, 1) to the Pacific S to Australia (14), New Caledonia (9), Norfolk Is. (1), Lord Howe Is. (1, endemic), New Zealand (1, endemic) and E to Niue (1), the greatest distribution of any Indopacific genus in the family with high levels of endemism in New Guinea (16 of 28; cf. Borneo with 2 of 22, Malay Peninsula with 2 of 17), Fiji (7 of 9) and New Caledonia (8 of 9), demonstrating a distinctly austral richness by comparison with its ally *Chisocheton* and the other large genus in Malesia, *Aglaia*.

41. *Heckeldora* Pierre.

Heckeldora Pierre, Bull. Mens. Soc. Linn. Paris 2: 1286 (1897); de Wilde, Blumea 52: 179–199 (2007), rev.
Guarea F. Allam. sect. *Heckeldora* (Pierre) Harms (1940).

Small trees, dioecious; hairs simple. Leaves imparipinate. Flowers in narrow axillary thyrses or racemes; calyx shallowly 3–5-lobed; petals 4, distinct, imbricate; staminal tube cylindrical, margin with shallow rounded lobes; anthers 8, inserted within tube and sometimes partly exserted; nectary disk long, slender, at apex forming collar beneath constricted ovary base; ovary 1-locular with 2(3) parietal placentas, each with 2 collateral orthotropous ovules; stylehead discoid, flat or with slight central depression. Fruit a narrow rostrate 2–4-seeded berry, with constrictions between seeds. Seed with unitegmic vascular sarcotesta (pachychalazal); embryo with thick plano-convex collateral cotyledons, radicle superior, extending to surface.

Six closely allied spp., tropical W Africa.

42. *Turraeanthus* Baill.

Turraeanthus Baill., Adansonia 11: 261 (1874); T.D. Penn., Blumea 22: 493–494 (1975).

Trees or treelets, dioecious; hairs simple. Leaves impari- or paripinnate. Calyx almost entire; petals 4 or 5(6), valvate, united to half way or more with the staminal tube; staminal tube cylindrical, margin crenate or shallowly lobed; anthers 8–12 in a single whorl within the throat; nectary disk 0; ovary 4- or 5-locular, each locule with 2 superposed or oblique ovules; stylehead discoid with a central depression. Fruit a leathery 3–5-valved loculicidal capsule. Seeds with sarcotestal seed-coat (pachychalazal?); embryo with thick plano-convex, superposed cotyledons, radicle included. $2n$ = c. 280.

Three spp., tropical W Africa. Wood used in cabinet-making.

43. *Ruagea* H. Karst.

Ruagea H. Karst., Fl. Columb. 2: 51, t. 126 (1863); T.D. Penn., Fl. Neotrop. 28: 242–255 (1981), rev.
Guarea sect. *Ruagea* (H. Karst.) C. DC. (1878).

Trees and treelets, dioecious; bud-scales rare. Leaves pinnate, sometimes with limited apical growth; leaflets not glandular-punctate or -striate. Inflorescences paniculate, axillary or in axils of fallen bud-scales. Sepals 5, distinct, quincuncial; petals 5, distinct, quincuncial; staminal tube cylindrical, cyathiform or urceolate, margin shallowly lobed; anthers (7–)10(11), inserted within throat; nectary disk usually short, rarely 0; ovary (2)3(4)-locular, each locule with (1)2 superposed ovules; stylehead discoid. Fruit a 2- or 3-valved loculicidal capsule, each locule with 1(2) superposed seeds; endocarp thin, cartilaginous. Seed with fleshy raphe-chalazal aril; embryo with thick plan-convex, collateral cotyledons; radicle apical.

Five poorly defined spp. of montane rain forest and cloud forest from Guatemala, Costa Rica, Panama and south to Peru.

44. *Guarea* F. Allam.

Guarea F. Allam. in L., Mant. Pl.: 150 (1771), nom. cons.; Pennington, Fl. Neotrop. 28: 255–359 (1981).
Samyda L. (1753), nom. rejic.
Leplaea Vermoesen (1921).
Urbanoguarea Harms (1937).

Trees and treelets, dioecious. Bud-scales 0; hairs simple. Leaves usually pinnate with terminal pseudogemmula, very rarely unifoliolate. Leaflets sometimes glandular-punctate and -striate. Inflorescence an axillary to cauliflorous panicle, raceme or spike. Calyx with almost entire margin to 3–7-lobed, aestivation open; petals (3)4–6(7), distinct, usually valvate; staminal tube cylindrical, sometimes contracted at throat, margin entire to lobed; anthers (7)8–12(–14) inserted within throat, alternate with lobes; nectary disk short to long-stipitate usually forming a collar around ovary base; ovary 2–10(–14)-locular, each locule with 1 or 2 superposed anatropous to orthotropous ovules; stylehead discoid. Fruit a 2–10(–14)-valved loculicidal capsule, each locule with 1 or 2 seeds; pericarp leathery or woody, endocarp thin, cartilaginous. Seed often orange-segment-shaped with thin fleshy sarcotesta; endosperm 0; embryo with thick plano-convex usually superposed cotyledons, radicle abaxial. $2n = 72$.

About 40 spp., tropical America and five in tropical Africa. Some promising timbers.

45. *Cabralea* A. Juss.

Cabralea A. Juss., Bull. Sci. Nat. Géol. 23: 237 (1830); T.D. Penn., Fl. Neotrop. 28: 234–242 (1981).

Tree or treelet; hairs simple. Leaves usually pinnate; leaflets glandular-punctate and -striate. Inflorescences of panicles, axillary, rarely borne on branches or trunk. Flowers usually bisexual; calyx of 5 ± distinct usually imbricate or quincuncial sepals; petals 5, distinct; staminal tube cylindrical, margin with (9)10(–12) appendages; anthers alternating with appendages, within throat; nectary disk cyathiform; ovary (4)5-locular, semi-inferior, each locule with 2 superposed ovules; stylehead discoid. Fruit a 4- or 5-valved loculicidal capsule, each locule with 1 or 2 seeds, held together by entwined funicular-raphe arils; embryo with thick plano-convex cotyledons; radicle apical.

One variable sp., *C. canjerana* (Vell.) Mart., from Costa Rica through tropical South America to northern Argentina.

46. *Aphanamixis* Blume

Aphanamixis Blume, Bijdr.: 165 (1825); Mabb., Blumea 31: 136–140 (1985), rev. & Fl. Males. 12: 187–194 (1995).
? *Ricinocarpodendron* Boehm. (1760).

Trees or pachycaul treelets with cicatrose twigs; hairs simple, rarely basally bifid and stellate. Leaves imparipinnate, leaflets opposite. Inflorescences axillary to supra-axillary, male flowers (smallest) in panicles, female and bisexual in long spikes or racemes, rarely panicles. Calyx deeply 5-lobed, lobes imbricate; petals 3, imbricate, united with staminal tube basally; staminal tube globose to deeply cyathiform; anthers 3–8, glabrous, inserted within tube; ovary 3(4)-locular, each locule with (1)2 collateral to superposed ovules; style stout; stylehead conical to truncate, 3-angled or with impressions of anthers. Fruit a 2- or 3(4)-valved, loculicidal capsule, loculi 1- or 2-seeded. Seeds arillate, cotyledons plano-convex, collateral (?) united; radicle small, superior, included. $2n = 36, 76$, c. 150.

Three very closely related spp. in Indomalesia from Ceylon and India to Bhutan, tropical China and Indochina, throughout Malesia, to the Solomon Is. Local timber, oil for soap-making and medicaments; leaf extracts are effective anti-feedants.

Except for the apparent unity of the cotyledons (a feature not investigated in all *Aglaia* spp. so far), there is no other macroscopic character which separates *Aphanamixis* from *Aglaia* absolutely. At the microscopic level, only one *Aglaia* sp. has the 4-colporate pollen grains found in *Aphanamixis* and the wood of the latter differs from that of the *Aglaia* species formerly included in *Amoora* in having confluent and banded paratracheal parenchyma (Pennington in Pennington and Styles 1975).

47. *Sphaerosacme* Royle

Sphaerosacme Wall. ex Royle, Ill. Bot. Himal. Mts: 142 (1835); Pennington, Blumea 22: 488–489 (1975); Grierson [& Mabb.], Fl. Bhutan 2: 35–36 (1991).

Tree, dioecious; hairs simple. Leaves imparipinnate. Flowers in axillary to supra-axillary panicles with racemose branches. Calyx 4- or 5-lobed, lobes imbricate to open; petals 5, distinct, imbricate; staminal tube almost globose, margin undulate; anthers 10, in 2 alternate whorls of 5, the upper partly exserted; ovary 5-locular, each locule with 1 ovule; style 0, stylehead pileate, 5-lobed. Fruit a 2–5-lobed loculicidal capsule. Seed partly or completely enclosed in aril;

embryo with plano-convex, collateral, united cotyledons; radicle small, superior, included.

One sp., *S. decandra* (Wall.) T.D. Penn., Himalaya.

48. *Reinwardtiodendron* Koord.

Reinwardtiodendron Koord., Meded. s'Lands Plantentuin 19: 389 (1898); Mabb., Blumea 31: 144–146 (1985), rev. & Fl. Males. 12: 322–328 (1995); Peng Hua & Mabb., Fl. China 11: 124–125 (2008).
Aglaia Lour. sect. *Lansium* (Corrêa) Kosterm. (1966), p.p.

Trees; hairs simple. Leaves pinnate or unifoliolate, the leaflets alternate, the most apical on one side appearing terminal; petiolules often swollen; domatia frequently present. Inflorescences spikes or basally branched panicles of spikes. Flowers bisexual, yellow; calyx deeply 5-lobed, the lobes orbicular, imbricate; petals 5, distinct from each other but united with staminal tube at base; staminal tube globose to ovoid, with an undulate to toothed margin; anthers 10 in 2 whorls of five, glabrous, the upper ones partly exserted, the lower alternating with the upper and completely included, their connectives extended to form a short acute appendage; ovary 5-locular, each locule with one ovule; style very short, with a small capitate or pileate, obscurely lobed apex. Fruit a 1–5-seeded berry. Seed apparently sarcotestal; embryo with thick plano-convex, superposed, free cotyledons, radicle included.

Probably seven spp., restricted to Indomalesia, one, *R. anaimalaiense* (Bedd.) Mabb., in the western Ghats of India, the rest occurring in Malesia, with one extending to southern China.

Reinwardtiodendron closely resembles *Aglaia* in pollen and secondary xylem as well as overall facies but it differs in its simple indumentum, the two whorls of anthers with appendages and the 5-locular ovary. It is closest to *Lansium* which shares the indumentum and the leaflet form and has similar venation but differs in its single whorl of 10 stamens without appendages, the ramiflorous to cauliflorous inflorescences and the seeds which are arillate and pachychalazal.

49. *Lansium* Corrêa

Lansium Corrêa, Ann. Mus. Hist. Nat. Paris 10: 157 (1807); Mabb., Blumea 31: 140–143 (1985), rev. & Fl. Males. 12: 314–322 (1995).
Aglaia Lour. sect. *Lansium* (Corrêa) Kosterm. (1966).

Trees; hairs simple. Leaves pinnate, the leaflets subopposite to alternate, to most apical on one side appearing terminal; petiolules pulvinate at base. Inflorescences spikes, racemes or more rarely basally branched panicles with spicate or racemose branches, borne on twigs, branches or bole. Flowers unisexual (tree dioecious) and bisexual, these larger than male ones; calyx deeply 5-lobed, the lobes imbricate; petals 5, free from each other but united with staminal tube in proximal third to half, imbricate; staminal tube globose to cyathiform, margin ± undulate; anthers (8)10 in one whorl inside the throat of the tube, their tips not or slightly exserted, without appendages; ovary 3–5-locular, each locule with one ovule; style long and broad-columnar, its flanks ribbed with the impressions of the surrounding anthers. Fruit a 1–5-seeded berry. Seed usually arillate, aril completely enveloping seed; embryo with thick plano-convex, superposed free cotyledons, radicle included. $2n = 144$.

Three spp., the genus possibly being the only one restricted to Malesia, but planting of the important local fruit tree *L. domesticum* Corrêa (langsat) elsewhere, which may be native in southern Thailand in any case, has obscured this.

50. *Aglaia* Lour. Fig. 39

Aglaia Lour., Fl. Cochinch.: 173 (1790), nom. cons.; Pannell, Kew Bull. Add Ser. 16 (1992), rev.
Amoora Roxb. (1820).

Trees, dioecious. Indumentum of stellate hairs or scales or of peltate scales. Leaves imparipinnate. Flowers (males smaller than females) in axillary thyrses, male thyrses larger than female. Calyx (2)3–5-lobed, aestivation open or imbricate; petals usually 3 or 5; anthers sessile, inserted within staminal tube; ovary with (1)2 or 3 locules; stigma sessile, either ovoid with 2 or 3 apical lobes or depressed-globose. Fruits dehiscent with 3 locules or indehiscent with with 1 or 2 locules. Seeds 0 or 1 per locule; aril completely surrounding rest of seed to vestigial. $2n$=40, 92.

About 120 spp., Indomalesia to Australia and E to Samoa. As currently understood (with *Amoora*, etc. included), paraphyletic with regard to *Lansium* and *Reinwardtiodendron* (Muellner et al. 2008b). Some locally important fruit trees and timbers.

Fig. 39. Meliaceae. *Aglaia silvestris*. **A** Leaf and male inflorescence. **B** Infructescence with young fruits. **C** Male flower longitudinally sectioned. **D** Mature fruits. **E** Peltate scale. (Mabberley et al. 1995; drawn by Rosemary Wise)

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