Simaroubaceae

Simaroubaceae DC. (1811), nom. cons.
Leitneriaceae Benth. & Hook.f. (1880).

J.W. Clayton

Trees and shrubs, occasionally with thorns; pith conspicuous; triterpenoid compounds of the quassinoid type present throughout vegetative tissues. Leaves alternate, spirally arranged, estipulate (stipules found in *Picrasma*), pinnately compound or unifoliolate (rarely trifoliolate); leaflets entire, coarsely toothed, serrate or basally lobed, sometimes with conspicuous pitted or flattened glands beneath or above; venation pinnate, brochidodromus or occasionally reticulate. Hairs mostly simple, unicellular or multicellular, sometimes glandular-capitate. Inflorescences terminal or axillary determinate thyrses, sometimes appearing raceme-like, pseudo-umbellate, catkin-like or flowers clustered in leaf axils. Flowers perfect, polygamous or unisexual, actinomorphic, bracteate (bracts large and surrounding flowers in *Leitneria*); pedicels bracteolate, occasionally jointed; sepals 4–5 (0 in *Leitneria*), connate below, calyx sometimes splitting unevenly, occasionally bearing glands; petals 4–5(–8) (0 in *Leitneria*), distinct; stamens 4–10(–18), distinct; filaments often with hairy appendage; anthers dorsifixed, basifixed or versatile, dehiscing by 2 longitudinal slits, introrse (occasionally extrorse to latrorse); ovary superior, of (1)2–5 carpels, distinct or connate basally, occasionally connate axially and deeply lobed; placentation axile; ovule one per locule, anatropous; stylodia distinct or connate into a common style, occasionally absent; stigmas on stellately spreading stigmatic branches, or a single slightly lobed or capitate stigma; fruit with 1–5 samaroid or drupaceous mericarps; exocarp thin, fleshy, occasionally dry, nut-like, often carinate; endocarp reticulate or crustaceous; testa membranaceous, cotyledons planoconvex; endosperm mostly lacking.

A family of 22 genera and about 109 species, mainly tropical and subtropical but some temperate species.

Vegetative Morphology. The family is woody, composed of large trees up to 50 m high, shrubs, subshrubs, and occasionally suffructescent plants with all the leaves basal (*Simaba*). The wood is pithy or fistulous (Cronquist 1944d), making it lightweight, and the bark and twigs are often striated. The family is typified by a bitter taste to the bark and twigs, on account of quassinoid compounds in scattered secretory cells throughout the vegetative structures (Cronquist 1981). Thorns are present in *Castela* and in *Holacantha*, where they occur at the tips of all branches (Cronquist 1944d).

Leaves are predominantly once-pinnately compound, arranged spirally around cylindrical stems. Unifoliolate leaves have evolved multiple times (based on studies of character evolution; Clayton, unpubl. data), and are characteristic of *Castela*, *Leitneria*, *Amaroria* and *Samadera*, and are found in six species of *Soulamea* (Jaffré and Fambart 2002) and two species of *Simaba* (*S. monophylla* and *S. obovata*). The leaves of *Holacantha* are reduced to scales or absent entirely, except in the seedlings (Cronquist 1944d). Leaflets are alternate, subopposite or opposite, but always opposite in *Quassia*, which has a distinctive winged and jointed rachis. Leaflet shape is diverse, but strongly asymmetrical leaf bases are common in compound leaves. Leaf margins are predominantly entire, but are serrate or coarsely toothed in temperate species of *Ailanthus*, *Picrasma* and *Brucea*. Stipules are reported from *Picrasma* (Nooteboom 1962) and *Soulamea* (Stevens 2006), but have been shown to be pseudostipules, probably derived from the basal leaflets of a pinnate leaf (Weberling and Leenhouts 1966).

Vegetative Anatomy. Wood anatomy is described in detail by Webber (1936) and Record

and Hess (1943; New World genera). Growth rings are present but indistinct, and diffuse porous or ring-porous (*Ailanthus*, *Leitneria*). Wood is dominated by fibre-tracheids, except in *Holacantha* and *Castela*, in which wood fibres are libriform (Webber 1936). Vessels have spiral thickenings in *Castela*, *Holacantha* and *Leitneria*, but these are rare or absent in the rest of the family. Normal wood parenchyma cells are sparse to moderately abundant, the cells often septate and crystalliferous (Webber 1936; Record and Hess 1943). Vertical secretory canals are common in stems (Spiekerkoetter 1924), and in *Leitneria* resin ducts are described as present in the margin of the pith (Record and Hess 1943). Nodes are tri- or multilacunar, and calcium oxalate crystals are present in parenchymatous tissues (Cronquist 1981). Flattish or concave glands are common on leaf surfaces, typically towards the margin, and often associated with teeth if present. Multicellular secretory glands are found on the abaxial surface of the sepals of *Samadera* (Nair and Joseph 1957). Primarily unicellular, but also multicellular and glandular hairs are common on the inflorescence axes and floral organs (Nair and Joseph 1957; Nair and Joshi 1958; Nair and Sukumaran 1960; Nooteboom 1962).

Inflorescence Structure. Inflorescences can be axillary or terminal, and are determinate thyrses, with the dichasia often appearing fasciculate or reduced to a single flower, giving the appearance of a panicle (sensu Weberling 1989). Thyrses vary between open and spreading (e.g. *Ailanthus*, *Eurycoma*, *Picrolemma*), and narrow, elongate and sparsely branched (e.g. *Brucea*, *Soulamea*, *Amaroria*). In *Simarouba* and *Picrolemma* the staminate thyrses are larger and have more flowers than the carpellate thyrses (Cronquist 1944b). *Picrasma* has a short, broad, rounded thyrse with a long peduncle (often described as a cyme), and in *Samadera* the inflorescence axis is condensed to form a pseudo-umbel (Nair and Joseph 1957). *Quassia amara* has a distinctive long raceme-like thyrse, occasionally branched at the base, and in *Castela* the flowers are occasionally solitary or clustered in the leaf axils (Cronquist 1944d), as in some *Samadera*. In *Leitneria* the inflorescence is an erect or occasionally pendulous catkin-like thyrse: in the staminate inflorescence the flowers cluster in cymules of three in the axils of large, spirally arranged bracts (Fig. 90E, F); in the carpellate inflorescence the flowers are solitary in the bract axils (Fig. 90I, J; Abbe and Earle 1940).

Flower Structure. Flowers in Simaroubaceae are small, actinomorphic, open and 4- or 5-merous (3-merous in *Soulamea*), with an intrastaminal nectary disk. Petals are usually red, pink, yellow, pale green or white. Unlike the majority of the family, *Quassia* has flowers with elongate, glabrous petals (sometimes with hairs at the base) that are coherent, forming a tube, and the stamens and style are exserted. *Leitneria* is unusual in having asepalous and apetalous flowers, although Abbe and Earle (1940) observed vestigial perianth structures in carpellate flowers. *Leitneria* also has a unicarpellate gynoecium, with vascular bundles suggesting reduction from a bicarpellate gynoecium (Abbe and Earle 1940). The androecium in the family is most commonly obdiplostemonous, although it is reduced to haplostemony in *Picrasma*, *Brucea*, *Picrolemma* and *Eurycoma*. In the latter two genera the stamens alternate with staminodes in the staminate flowers. In *Pierreodendron* the outer whorl of stamens is doubled. Adaxial scale-like appendages on the filaments occur in eleven genera, and vary in shape, length, pubescence and bifurcation. In unisexual flowers, vestigial staminodes and pistillodes are common. Filaments are inserted at the base of the nectary disk, which can vary between strongly lobed, cushion-like, tall and cylindrical, conical to inconspicuous. The disk usually enlarges in fruit. The gynoecium of *Soulamea* is reduced to two or three connate carpels (Fig. 91B), and is a single carpel in *Amaroria*.

Embryology. Embryology for the family was reviewed by Mauritzon (1935). Detailed studies of embryo anatomy are available for *Ailanthus* (Narayana 1957), *Samadera* (Nair and Joseph 1957), *Brucea* (Nair and Sukumaran 1960) and *Leitneria* (Pfeiffer 1912), and the following characteristics should be considered typical for the family: the anther wall consists of an epidermis, a fibrous endothecium, two to three middle layers and a multinucleate secretory tapetum (binucleate in *Ailanthus excelsa*); microsporogenesis is simultaneous; pollen tetrads are tetrahedral and decussate, shed at the two-celled

stage; ovules are anatrapous or hemi-anatropous, crassinucellate and bitegmic, the inner integument forming the zig-zag micropyle; the nucellus is multinucleate, and the nucellar epidermis divides to form a cap; the archesporium can be multicellular or unicellular (*Ailanthus*), only one archesporial cell developing further; megaspores are arranged linearly (a solitary T-shaped tetrad is reported for *Ailanthus integrifolia*); the chalazal megaspore develops into a Polygonum type embryo sac; fertilisation may be chalazogamous, mesogamous or porogamous (Wiger 1935), but only porogamy is confirmed in *Samadera* and *Brucea*; endosperm development precedes embryo development, and is of the Nuclear type.

Pollen Morphology. Basak (1963, 1967) and Moncada and Machado (1987) used light microscopy to survey pollen morphology in *Quassia*, *Samadera*, *Simarouba*, *Simaba*, *Eurycoma*, *Soulamea*, *Ailanthus*, *Brucea*, *Castela* and *Picrasma*, and Zavada and Dilcher (1986) examined *Leitneria* with SEM and TEM. Pollen grains are 3-zonocolporate, typically 20–35 μm long by 13–30 μm wide, prolate in equatorial view (sometimes subspheroidal in *Castela* and spheroidal in *Samadera* and *Leitneria*) and planaperturate, with distinctly lalongate endoapertures; however, *Quassia* pollen grains are suboblate and angulaperturate, with a square type of endoaperture. Exine is 2–3 μm thick, and the surface pattern finely to coarsely reticulate, sometimes verrucate, in most genera. The exine is striate in *Soulamea* and *Brucea*, and striato-reticulate in *Quassia*.

Karyology. Simaroubaceae have base chromosome numbers of 8–13 (Stevens 2006). Bennett and Leitch (2005) record $2n = 64$ in *Ailanthus integrifolia*, which would suggest the plant is octoploid. Raven (1975) reports $x = 16$ for *Leitneria*, and *Castela coccinea* has $2n = 26$ (Bernardello et al. 1990).

Reproductive Biology. Simaroubaceae can be hermaphroditic, monoecious or dioecious. The extent of self-compatibility is unknown; however, flowers of *Quassia amara* have been shown to self-fertilise (Roubik et al. 1985). Insect-pollination predominates in the family, the flowers typically being small, actinomorphic, open, fragrant and borne in thyrses, attracting generalist small insects such as bees and moths (e.g. Aubréville 1962; Hardesty et al. 2005). *Quassia amara* is hummingbird-pollinated, as suggested by the raceme-like inflorescences bearing deep pink or red tubular flowers. Roubik et al. (1985) observed the role of nectar robbers in reproductive fitness of *Q. amara*, revealing that flowers were visited by nectar-robbing bees (*Trigona*) and hummingbirds, as well as the primary hummingbird pollinator. *Leitneria* shows strong morphological divergence towards wind-pollination in that the flowers lack a perianth and nectary disk, and are borne in catkin-like inflorescences that develop before the leaves emerge.

Fruits and Seeds. Fruits in the family are predominantly schizocarpous with drupaceous mericarps, and typically only 1–3 carpels reach maturity (Figs. 91, 92). The drupes have a thin pericarp, in which the exocarp can be fleshy (e.g. *Hannoa*, *Quassia*, *Simaba*), woody and fibrous (*Samadera*) or thin and dry (*Eurycoma*, *Leitneria*, some *Brucea*). The fleshy fruits can be pale yellow to red to deep purple-black, with a bitter taste, globose, obovoid, ovoid or ellipsoid, and between 0.3 and 10 cm long. The drupes are often carinate or bicarinate and flattened and, in *Samadera indica*, are strongly laterally dorsoventrally compressed with a narrow, unilateral thinner edge in the apical half. In *Ailanthus* each carpel develops into a samaroid mericarp, elliptic in shape and tapering at each end (Fig. 89D). Variation in samara morphology is discussed in some detail by Nooteboom (1962) and Corbett and Manchester (2004). In *Soulamea* the carpels remain connate in fruit, forming a dry, narrowly to broadly winged, obcordate fruit. Fernando and Quinn (1992) discuss variation in pericarp anatomy in the family in detail. The exocarp varies in thickness and lignification and, in *Ailanthus*, is lacking except for the epidermal layer. Fernando and Quinn (1992) describe the endocarp as consisting of "a broad homogeneous zone of irregularly arranged isodiametric sclereids" with a strongly lignified inner epidermis. *Castela* and *Picrasma* lack the typical lightly lignified mesocarp and parenchymatous outer mesocarp. *Nothospondias* has an unusual *Spondias*-type endocarp, similar to that found in Anacardiaceae (Fernando and Quinn 1992).

The embryo is straight or curved, and consists of two large planoconvex cotyledons and a short plumule. Most Simaroubaceae have little or no endosperm, except for *Brucea* (Nair and Sukumaran 1960) and some *Soulamea* (Nooteboom 1962). Fatty oil and aleuron bodies are the most common seed storage products in the family, but starch is also reported from seeds of *Simaba* and *Perriera* (Netolitzki 1926) and *Leitneria* (Pfeiffer 1912), and reserve celluloses also occur (Czaja 1978; Stevens 2006). The seed coat is thin and hard, undistinguished or with scattered lignified cells (Stevens 2006), and is described as membranaceous in some genera.

Dispersal. Fleshy drupaceous fruits of Simaroubaceae are dispersed by fruit-eating birds and mammals, often primates (e.g. Hardesty et al. 2005). The samaroid mericarps of *Ailanthus* disperse over small distances by wind. Fruits of *Samadera indica*, a species that frequents alluvial and swamp forest, and *Soulamea amara*, a littoral species, are dispersed by water (Nooteboom 1962), which may account for their broad geographical distributions. *Leitneria* is also suspected to be water-dispersed, typically growing in freshwater and brackish swamps. In all cases, buoyancy is provided by an air cavity between seed and endocarp.

Phytochemistry. Simaroubaceae are characterised by their quassinoid chemistry. Quassinioids are triterpenoid derivatives, biosynthetically related to the limonoids of Rutaceae and Meliaceae (da Silva and Gottlieb 1987), and are considered (Dreyer 1983; Waterman 1983) to be further steps down the oxidative pathway of limonoids. Quassinoid structural and chemical characteristics are summarised in Waterman and Grundon (1983) and da Silva and Gottlieb (1987), who report 35 different structural types in *Picrasma* alone. Pentacyclic triterpenes are also common (Hegnauer 1983). Alkaloids have been reported in nine Simaroubaceae genera (Mester 1983), most commonly tryptophan derived, but also a quinolone alkaloid is reported in *Ailanthus*. Only a single simple coumarin has been detected in the family, in *Picrasma* and *Ailanthus* (Gray 1983). Of the flavonoid groups, flavonol glycosides and glycoflavones are reported in *Ailanthus* (Harborne 1983) and flavonols and flavones in *Leitneria* (Giannasi 1986). Essential oils contained within secretory cells and resin canals contain a low proportion of volatile compounds compared to Rutaceae and Meliaceae, and are in smaller amounts (Hegnauer 1983). Tannin content is low to considerable, and with relatively high levels of gallic and ellagic acid (Hegnauer 1983), although *Leitneria* lacks ellagic acid (Giannisi 1986).

Distribution and Habitats. Simaroubaceae have a primarily pantropical distribution; however, some species of *Brucea*, *Castela*, *Holacantha*, *Ailanthus* and *Picrasma* are subtropical, and *Ailanthus altissima*, *Picrasma quassioides* and *Leitneria floridana* grow in temperate climates. Generic diversity is split evenly among the New World, Africa, and Asia and Australasia; however, half of the species in the family occur in the New World. *Picrasma* is disjunct among Asia, SE Asia and Central and South America, *Brucea* is disjunct between Africa and SE Asia, and *Soulamea* has one species in the Seychelles, one widespread in Malesia and Polynesia, and the remainder endemic to New Caledonia. *Samadera* is primarily Australian and SE Asian, but *S. indica* occurs as far west as India and Madagascar. Several genera in the Simaroubaceae consist of one or two species with restricted geographic ranges, the majority of these genera being in Africa. *Simaba* is the most species-rich genus and is restricted to Central and South America.

Simaroubaceae are found in moist lowland tropical forest (although *Brucea mollis* is recorded as a high as 1,800 m in the Philippines, and *Odyendea gabonensis* at 2,500 m in Gabon), dry deciduous forest, and open sandy or savannah-type vegetation. *Soulamea amara* is a littoral species, *Castela* and *Holacantha* are found in desert and dry scrub environments, and *Leitneria*, *Samadera indica* and occasionally *Pierreodendron* inhabit swamp forest. *Eurycoma* is classified as silicicolous, showing a preference for acidic, leached sandy soils (Nooteboom 1962).

Dating and biogeographic analyses (Clayton et al. 2009) suggest the family originated in North America in the early Tertiary. However, ancient vicariant and dispersal patterns in the family are obscured by a multitude of more recent migration events, within and between the continents, post-Oligocene.

Fossil History. Fossils of the distinctive samaroid fruits of *Ailanthus* are found across the entire Northern Hemisphere, dating from the early Eocene up to the Pleistocene (Corbett and Manchester 2004). Three extinct species have been recognised, with the earliest occurrence a samara of *A. confucii* from the Green River Formation, Wyoming. Leaf fossils are also known with reasonable certainty from the Oligocene of Germany and Miocene of China, exhibiting distinctive basal teeth with enlarged glands on the leaflets, characteristic of extant *A. altissima* (Corbett and Manchester 2004). *Leitneria* has no fossil record from North America, but fossil fruits of it have been found in western Siberia from the Oligocene and in Europe from the Miocene to the Pliocene (Dorofeev 1994; Nikitin 2006); in transverse section, these have identical endocarp anatomy to extant *Leitneria floridana* (Dorofeev 1994). Less well understood are fossil fruits of *Chaneya*, an extinct genus from the Tertiary of North America, Europe and Eastern Asia (Wang and Manchester 2000; Teodoridis and Kvacek 2005). Teodoridis and Kvacek (2005) suggest an affiliation with the extant genus *Picrasma*, based on gynoecial morphology and persistent wing-like petals; however, the fossil has distinctive oil cells typical of Rutaceae. Fossil leaves formerly reported as *Leitneria* from the Eocene of Tennessee (Berry 1916) were subsequently reassigned to Rubiaceae, based on stipule configuration, epidermal anatomy and leaf architecture (Roth and Dilcher 1979). Fossil pollen of Simaroubaceae has been reported for *Ailanthus* (Song et al. 2004) and *Leitneria* (Machen 1971), but given the lack of distinctive morphological characteristics in extant Simaroubaceae pollen (Basa, 1963, 1967; Moncada and Machado 1987), these are considered unreliable.

Affinities. In the traditional circumscription, Simaroubaceae s.l. comprised six subfamilies (Engler 1931). However, molecular work by Fernando et al. (1995; also see Gadek et al. 1996) showed the family to be polyphyletic, with subfamilies originating in several places within eurosids I and II (sensu APG II 2003). Members of subfamily Simarouboideae, however, form a well-supported monophyletic group (excluding *Harrisonia*) within Sapindales. *Leitneria*, a genus traditionally segregated into the monotypic family Leitneriaceae on account of its wind-pollinated flowers (Cronquist 1981; Takhtajan 1997), was also found to be part of the Simarouboideae clade. Hence, the subfamily was recircumscribed as Simaroubaceae s.s., a clade of 20 genera and approximately 95 species by Fernando and Quinn (1995). *Nothospondias*, a monotypic genus sometimes placed in Anacardiaceae (Engler 1905), is a member of the family (Van der Veken 1960; Clayton et al. 2007). Also included is *Laumoniera* (Nooteboom 1987), a monotypic genus from Sumatra that was omitted from the family recircumscription of Fernando and Quinn (1995).

Simaroubaceae are well supported as a member of a Simaroubaceae+Rutaceae+Meliaceae clade in Sapindales (Gadek et al. 1996; Källersjö et al. 1998; Savolainen et al. 2000; Soltis et al. 2000), but the family's sister group is still undetermined, with data supporting three alternative topologies: Rutaceae sister to Simaroubaceae (Gadek et al. 1996); Meliaceae sister to Simaroubaceae (Chase et al. 1999; Muellner et al. 2006); Rutaceae sister to Meliaceae (Fernando et al. 1995; Stevens 2006). Traditional morphological and phytochemical classifications typically suggest an affiliation with Rutaceae and Meliaceae (e.g. Cronquist 1981; Takhtajan 1997).

Relationships Within the Family. Engler's (1931) classification of Simaroubaceae s.l. divided subfamily Simarouboideae (Simaroubaceae s.str.) into three tribes: Simaroubeae, Picrasmeae and Soulameae. Tribes were delimited by the presence or absence of filament appendages and the degree of connation of carpels. Of Engler's tribes, molecular data (Clayton et al. 2007) show only Soulameae, composed of *Soulamea* and *Amaroria*, to be monophyletic. Relationships based on DNA sequence data from the chloroplast genome (*rbc*L, *atp*B, *mat*K) and nuclear genome (1 kb of *phy*C) produced a well-resolved and well-supported phylogeny, excluding *Laumoniera* and *Iridosma* (Fig. 87; Clayton et al. 2007). Simaroubaceae consist of three major clades: the *Picrasma* clade (22 spp.), comprising *Picrasma*, *Castela* and *Holacantha*, sister to the rest of the family; the *Soulamea* clade (22–23 spp.), comprising *Leitneria*, *Brucea*, *Laumoniera* and *Soulamea* (with *Amaroria* nested within *Soulamea*); the *Simarouba* clade (45–48 spp.), composed of *Simarouba*, *Simaba*, *Pierreodendron*,

Hannoa, *Perriera*, *Gymnostemon*, *Odyendea*, *Iridosma* and *Eurycoma*. *Ailanthus* (5 spp.) diverges after the *Picrasma* clade, and a grade of *Nothospondias*, *Picrolemma*, *Quassia* and *Samadera* (10–11 spp.) follows the *Soulamea* clade (see Fig. 87). The relationship of *Laumoniera* to *Brucea* is unknown. The position of *Iridosma* is also unknown but likely to be within the *Simarouba* clade. Relationships among the four subclades of the *Simarouba* clade (*Hannoa* +*Perriera*+*Gymnostemon*, *Eurycoma*, *Odyendea* and *Pierreodendron*+*Simarouba*+*Simaba*) are poorly resolved; this lack of resolution is attributed to a rapid radiation that occurred in the Miocene (Clayton et al. 2009).

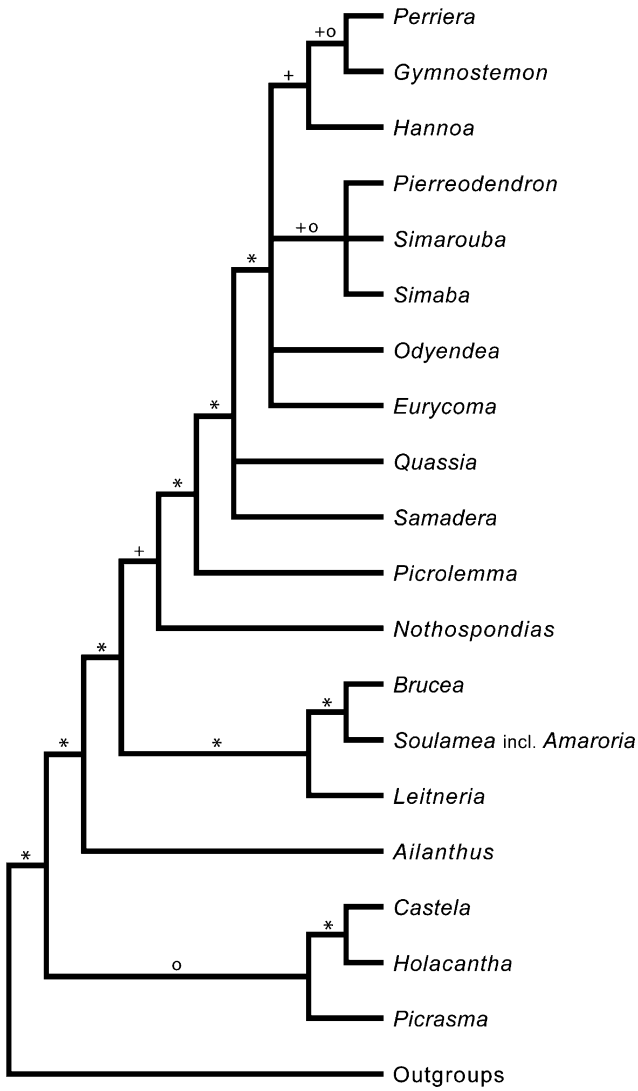

Fig. 87. Simaroubaceae. Phylogenetic hypothesis of relationships of Simaroubaceae based on three chloroplast genes and one nuclear gene, modified from Clayton et al. (2007). All genera except for *Simaba* have posterior probability (PP) = 1.0 and bootstrap support (BS) = 100%. *Laumoniera* and *Iridosma* were not sampled for this study. (orig.). *: PP = 1.0 and BS = 100%; +: PP > 0.95; o: BS > 70%

Economic Importance. A range of biological properties has been demonstrated by the quassinoids of Simaroubaceae, including antimalarial, antileukemic, antiviral, insecticidal and amoebicidal properties (Polonsky 1983; Klocke et al. 1985), and correspondingly, many genera are used locally as medicinal plants. *Quassia amara* and *Picrasma quassioides* have been used to aid digestion, and treat chronic dyspepsia. Fruits of *Brucea javanica* were imported into Europe as a drug (Nooteboom 1962), and the plant is used locally in Malaysia to treat malaria and dysentry. *Eurycoma* is used to treat malaria, diabetes, hypertension and stomach ache, typically by boiling the roots for drinking. *Ailanthus* is known in traditional Chinese and Korean medicine as a treatment for digestive complaints, haemorrhoids and mastitis. Simaroubaceae are not commercially harvested for timber but are used locally in building in some areas of both the Old and New World. *Leitneria* (corkwood) is one of the lightest known woods, and has been used traditionally by fisherman for net floats. *Ailanthus* (Tree of Heaven), *Simarouba* (paradise tree) and *Quassia amara* are cultivated and planted as ornamentals.

Key to the New World Genera

1. Perianth vestigial or absent; flowers surrounded by large, hirsute bracts **5. *Leitneria***
– Petals +, sepals +; bracts not large, not surrounding flowers 2
2. Stamens with appendaged filaments 3
– Filaments lacking appendage 5
3. Leaf rachis distinctly winged and jointed **12. *Quassia***
– Leaf rachis not winged, not jointed 4
4. Flowers unisexual; stigmas as long as style or longer, stellately spreading; leaflets alternate **21. *Simarouba***
– Flowers bisexual; stigmas capitate or lobed; leaflets typically opposite or subopposite **22. *Simaba***
5. Leaves unifoliolate or absent; plant often armed with thorns; stamens twice as many as petals 6
– Leaves pinnately compound; plant without thorns; stamens equal in number to petals 7
6. Plant with leaves; petals 4–5; stamens 8–10 **2. *Castela***

– Plant leafless, or leaves reduced to scales; petals 6–8; stamens 12–16 **3. *Holacantha***
7. Staminodes present in staminate flowers; inflorescence elongate, narrowing above; fruit ellipsoid, elongate, 20–30 mm long **11. *Picrolemma***
– Staminodes absent or in carpellate flowers only; inflorescence short, broad and rounded; fruit globose, less than 15 mm long **1. *Picrasma***

Key to the Old World Genera

1. Stamens with appendaged filaments 2
– Filaments lacking appendage 8
2. Leaves unifoliolate; inflorescence a pseudo-umbel **13. *Samadera***
– Leaves pinnately compound; inflorescence not umbellate 3
3. Leaf rachis jointed and often narrowly winged **12. *Quassia***
– Leaf rachis not jointed, not winged 4
4. Stamens alternating with outer whorl of staminodes or staminodial scales in staminate flowers; induplicate– valvate aestivation; Indomalesia **14. *Eurycoma***
– Staminodes absent in staminate flowers; contorted, imbricate, occasionally valvate aestivation; tropical Africa 5
5. Petals 7–8, valvate in bud; stamens 12–13 **19. *Iridosma***
– Petals 4–5, imbricate or contorted in bud; stamens 8–10(–15) 6
6. Stamens (10–)15(–18); leaves with 11–31 leaflets, up to 1 m long; leaflets apex with hard, pointed gland **20. *Pierreodendron***
– Stamens 8–10; leaves with 3–15 leaflets, less than 60 cm long; leaflets without hard pointed gland at apex 7
7. Calyx in bud irregularly rupturing into 2–3 lobes; 5 petals; 10 stamens; 5 carpels; fruits 15–35 mm long **17. *Hannoa***
– Calyx connate with 4(–5) very short obtuse lobes; 4(5) petals; 8(–10) stamens; 4 carpels; fruits 50–70 mm long **18. *Odyendea***
8. Gynoecium of 1 or 2(3) connate carpels 9
– Gynoecium of (2)3–5 carpels (if 2 then carpels distinct) 10
9. Gynoecium a single carpel; fruit ovoid, not winged; flowers 4- or 5-merous **7. *Amaroria***
– Gynoecium of two or three carpels; fruit obcordate, winged; flowers predominantly 3-merous **6. *Soulamea***
10. Fruit samaroid **4. *Ailanthus***
– Fruit drupaceous, fleshy or dry and nut-like 11
11. Stamens equal in number to petals 12
– Stamens twice as many as petals 14
12. Inflorescence short, broad and rounded; sepals and petals persistent in fruit, accrescent; fruit globose **1. *Picrasma***
– Inflorescence mostly unbranched, elongate; petals caducous in fruit; fruit ovoid or ellipsoid, or nut-like with 2 ribs when mature 13
13. Leaves imparipinnate; stigmas distinct, recurving; fruit 7–18 mm long **8. *Brucea***
– Leaves paripinnate; stigmas connate, discoid; fruit 45–60 mm long **9. *Laumoniera***
14. Carpels 2; inflorescence axillary; Madagascar **16. *Perriera***
– Carpels 4–5; inflorescence typically terminal; tropical Africa 15
15. Leaves with 19–43 leaflets; flowers 4-merous; fruits up to 45 mm in length; tropical west Africa **10. *Nothospondias***
– Leaves with 13–25 leaflets; flowers 5-merous; fruits about 100 mm in length; Côte d'Ivoire endemic **15. *Gymnostemon***

Genera of Simaroubaceae

1. *Picrasma* Blume Fig. 88

Picrasma Blume, Bijdr. Fl. Ned. Ind.: 247 (1825); Cronquist, Brittonia 5: 128–147 (1944), rev.
Aeschrion Vell. (1827).

Small trees, sometimes to 20 m, or shrubs, monoecious or dioecious. Leaves imparipinnate, pseudostipules present, early caducous; leaflets opposite to subopposite, petiolulate, entire or serrate-crenate, glabrous or nearly so, without glands. Flowers in axillary, short and broad, rounded determinate thyrses with puberulent axes; sepals 4(5), distinct or basally connate; petals 4(5), valvate, mostly glabrous; stamens 4(5), filaments lacking appendage; anthers dorsifixed; staminodes absent in staminate flowers; disk fleshy, sometimes conical, glabrous or hairy; carpels (2–)4(5), distinct; stylodia connate above, sometimes distinct; stigmatic branches filiform, recurved. Fruit 1–3(–5) drupaceous mericarps, globose, not carinate, 5–12 mm long, exocarp red to blue-black at maturity, pericarp fleshy.

Eight species, two in Asia and SE Asia, six in Mexico to Argentina, and Caribbean islands.

2. *Castela* Turpin

Castela Turpin, Ann. Mus. Natl. Hist. Nat. 7: 78 (1806), nom. cons.; Cronquist, J. Arnold Arb. 25: 122–128 (1944), rev.

Shrubs, erect or trailing, or small trees to 5 m, dioecious, armed with (occasionally branching) thorns. Leaves unifoliolate, petiolate, entire, glabrous to tomentose-pubescent, without glands. Flowers solitary, clustered in leaf axils, or in axillary, sparsely flowered determinate thyrses, with typically a single, sparsely to densely hairy axis; sepals

Fig. 88. Simaroubaceae. *Picrasma javanica*. **A** Flowering twig. **B** Full-grown pseudostipules. **C** Male flower. **D** Female flower. **E** Fruits. (Nooteboom 1962; artwork: C. van Crevel)

4(5), basally connate; petals 4(5), imbricate, glabrous to occasionally pubescent; stamens 8 or 10; filaments lacking appendage; anthers dorsifixed; staminodes absent in staminate flowers; disk fleshy, ring-like, glabrous; carpels 4(5), weakly united or distinct, stylodia connate at base, stigmatic branches linear, divergent or recurved, occasionally circinately rolled. Fruit 1–2(–4) drupaceous mericarps, lenticular, bicarinate, 6–12 mm long, exocarp red at maturity, pericarp fleshy.

Twelve species from southern United States to Argentina, the Caribbean islands and the Galápagos.

3. *Holacantha* A.Gray

Holacantha A.Gray, Mem. Am. Acad. Arts II, 5 (Pl. Nov. Thurb.): 310, t. 8 (post May 1855); Cronquist, Brittonia 5: 128–147 (1944), rev.

Depressed, ascending or erect shrubs or small trees to 5 m, dioecious, armed with thorns at branch tips, essentially leafless or leaves scale-like. Flowers in axillary, short, densely flowered determinate thyrses with one or two strongly hirsute axes, or appearing fasciculate in leaf axils; sepals 5–8, basally connate; petals 6–8, imbricate, strigose on abaxial surface; stamens 12–16, filaments lacking appendage, anthers dorsifixed, staminodes absent in staminate flowers; disk narrow and ring-like, densely hairy to glabrous; carpels 6–8, weakly united; style short and broad, stellately spreading into 5 stigmatic branches. Fruit 1–4 drupaceous mericarps, ovoid and slightly compressed, sometimes carinate on abaxial side, 5–9 mm long; exocarp red or greenish at maturity; pericarp fleshy.

Two species from southern California, southern and western Arizona to Mexico.

4. *Ailanthus* Desf. Fig. 89

Ailanthus Desf., Mém. Acad. Sci. Paris 1786: 270, t. 8 (1789), nom. cons.; Nooteboom, Fl. Males. I, 6: 215–220 (1962).

Large trees to 60 m, dioecious or monoecious. Leaves imparipinnate or paripinnate; leaflets opposite, subopposite or alternate below, petiolulate, entire to coarsely toothed, glabrous to densely pubescent, with sometimes large abaxial glands, occasionally domatia present as hair tufts at leaf base. Flowers in axillary or terminal determinate thyrses with glabrous to sparsely hairy axes; sepals 5(6), connate basally or calyx cupular with very short lobes; petals 5(6), induplicate-valvate, glabrous to pubescent; stamens 10, filaments lacking appendage; anthers ± ventrifixed; staminodes absent in staminate flowers; disk fleshy, glabrous; carpels 2–5; stylodia distinct to connate; stigmatic branches peltate, stellately spreading, sometimes recurved. Fruit 1–5 samaroid mericarps with elongate, membranous wings tapering towards the ends, 25–220 mm long; exocarp brown at maturity; pericarp dry.

Five species from Turkestan, India, China, SE Asia and northern Australia.

5. *Leitneria* Chapm. Fig. 90

Leitneria Chapm., Fl. S. U. St.: 427 (1860).

Small tree to 6 m; typically dioecious. Leaves unifoliolate, petiolate, entire, villous, without

Fig. 89. Simaroubaceae. *Ailanthus altissima*. **A** Flowering twig. **B** Male flower. **C** Female flower. **D** Fruit. (Takhtajan 1981; artwork: A. Schilitschkin)

Fig. 90. Simaroubaceae. *Leitneria floridana*. **A** Branch. **B** Young female catkins. **C** Young male catkins. **D** Elongating male catkins. **E** Male catkin with anthetic flowers. **F** Partial inflorescence thereof. **G** Stamen. **H** Twig with anthetic female catkins. **I** Female catkin with exposed stylodia. **J** Female flower. **K** Gynoecium in vertical section. **L** Seed. **M** Fruit. (Takhtajan 1980)

glands. Staminate flowers in axillary, catkin-like, highly reduced thyrses with 1–3-flowered cymules; carpellate flowers solitary in carpellate inflorescences, surrounded by densely hirsute bracts and arranged on an single glabrous axis; perianth 0 in male flowers, vestigial in carpellate flowers; stamens (1–)4 per flower in bract axil; filaments lacking appendage; anthers basifixed to dorsifixed; staminodes absent in staminate flowers; disk absent or rudimentary; carpel 1, stigmatic branch distally expanded, recurved. Fruit a drupe, narrowly ellipsoid, conspicuously flattened, bicarinate, 12–30 mm long; exocarp brown at maturity; pericarp dry to occasionally fleshy.

One species, *L. floridana* Chapm., in SE United States.

6. *Soulamea* Lam. Fig. 91

Soulamea Lam., Encyc. 1: 449 (1783); Jaffré & Fambart, Adansonia III, 24: 159–168 (2002).

Shrubs or small trees to 5(–15) m, dioecious or flowers bisexual (*S. amara*). Leaves unifoliolate or imparipinnate; leaflets opposite, petiolulate, leaves petiolate, entire and often revolute, densely pubescent or glabrous on adaxial surface, sometimes with glands. Flowers in axillary, elongate determinate thyrses, typically with a single, often ferruginous-tomentose major axis; sepals 3(–5), basally connate; petals 3(–5), glabrous to pubescent towards the base; stamens 6(–10); filaments lacking appendage; anthers basifixed to dorsifixed; staminodes absent in staminate flowers; disk fleshy, glabrous; carpels 2(3), connate; stylodia distinct, flattened, horizontally appressed to carpel, stigma fleshy, rarely reniform. Fruit samaroid, 2-celled, obcordate, flattened, with a distinct wing, 10–20 mm long, exocarp brown at maturity, pericarp dry.

Thirteen species, one widespread in SE Asia and Polynesia (*S. amara* Lam.), one endemic to the Seychelles (*S. terminalioides* Baker), and eleven species endemic to New Caledonia.

Fig. 91. Simaroubaceae. *Soulamea amara*. **A** Fruiting twig. **B** Flower. **C** Flower sectioned, pistil removed. **D** Fruit. (Nooteboom 1962; artwork: C. van Crevel)

7. *Amaroria* A.Gray

Amaroria A.Gray, Bot. U. St. Expl. Exped. 1: 356, t. 40 (1854); Smith, Fl. Vit. Nova 3: 479–487 (1985).

Small tree to 15(–20) m, dioecious. Leaves unifoliolate, petiolate, entire; glands unknown. Flowers in axillary, elongate determinate thyrses with a single major axis; sepals 4–5, basally connate; petals 4–5, glabrous or sometimes short strigillose along adaxial midline; stamens 8 or 10; filaments lacking appendage; anthers dorsifixed; staminodes absent in staminate flowers; disk fleshy, globose; carpel 1; stigma sessile. Fruit a drupe, ovoid to subglobose, slightly flattened, sometimes inconspicuously carinate, 17–30 mm long; exocarp greenish yellow, becoming white at maturity; pericarp fleshy.

One species, *A. soulameoides* A. Gray, endemic to Fiji.

8. *Brucea* J.F. Mill.

Brucea J.F. Mill., Icon.: t. 25 (1779), nom. cons.

Shrubs or small trees to 12 m, dioecious or polygamous. Leaves imparipinnate; leaflets opposite, petiolulate to subsessile, entire or crenate-serrate, ferruginous-pubescent to glabrous, with dotted glands associated with peripheral secondary venation underneath. Flowers in axillary, elongate determinate thyrses, typically with a single glabrous to densely pubescent major axis; sepals (3)4(5), basally connate; petals (3)4(5), imbricate, glabrous to densely pubescent; stamens (3)4(5), protruding between disk lobes, filaments lacking appendage; anthers basifixed to dorsifixed, staminodes absent in staminate flowers; disk fleshy, glabrous; carpels (3)4(5), distinct or united at the base; stylodia connate at base, stigmatic branches linear, recurved or bending inwards. Fruit 1–2(–4) drupaceous mericarps, ovoid, bicarinate, 4–18 mm long, exocarp red to black at maturity, pericarp dry to thinly fleshy.

Six to seven species, tropical Africa to tropical and subtropical Asia and northern Australia.

9. *Laumoniera* Noot.

Laumoniera Noot., Blumea 32: 383 (1987).

Small tree to 16 m, dioecious. Leaves paripinnate; leaflets petiolulate, entire, glands unknown. Flowers in axillary determinate thyrses, typically with a single pubescent axis; sepals 4, basally connate; petals 4, sparsely pubescent; stamens 4, filaments lacking appendage; staminodes absent in staminate flowers; disk fleshy, slightly hairy; carpels 4, distinct; stigmas sessile, connate, discoid, covering top of ovaries. Fruit 1–4 drupaceous mericarps, ellipsoid, 45–60 mm long; exocarp yellow at maturity, pericarp fleshy.

One species, *L. bruceadelpha* Noot., Indonesia.

10. *Nothospondias* Engl.

Nothospondias Engl., Bot. Jahrb. Syst. 36: 216 (1905); Van der Veken, Bull. Jard. Bot. Etat Brux. 30: 105–109 (1960).

Tree to 25 m, dioecious. Leaves imparipinnate; leaflets opposite to alternate, petiolulate, entire, glabrous, without glands. Flowers in axillary or terminal determinate thyrses, with multiple densely pubescent axes; sepals 4, basally connate; petals 4, slightly imbricate, glabrous to puberulent; stamens 8; filaments lacking appendage; anthers basifixed; staminodes absent in staminate flowers; disk fleshy, glabrous; carpels 4, distinct, style simple. Fruit 1–4 drupaceous mericarps, ovoid-ellipsoid, 20–45 mm long; exocarp yellow to orange at maturity; pericarp fleshy.

One species, *N. staudtii* Engl., in tropical west Africa.

11. *Picrolemma* Hook.f.

Picrolemma Hook.f. in Benth. & Hook., Gen. Pl. 1: 312 (1862); Cronquist, Brittonia 5: 128–147 (1944).

Small shrubs, up to 6 m, dioecious. Leaves imparipinnate; leaflets opposite to sometimes alternate below, petiolulate, entire, glabrous, punctate glands associated with secondary venation underneath. Flowers in terminal determinate thyrses, with multiple glabrous axes; sepals (4)5, basally connate; petals (4)5, imbricate, glabrous; stamens 5, filaments lacking appendage; anthers dorsifixed; staminodes alternating with petals in staminate flowers; disk fleshy, glabrous; carpels (4)5, distinct; stylodia distinct but cohering, stigmatic branches fleshy, club-like. Fruit 1–2 drupaceous mericarps, ellipsoid and slightly elongate, not carinate, 20–30 mm long; exocarp brown to red at maturity; pericarp fleshy.

Two species from Peru and Brazil.

12. *Quassia* L.

Quassia L., Sp. Pl. ed. 2: 553 (1762); Engl. in Engl. & Prantl, Nat. Pflanzenfam., 2nd edn, 19a: 377–379 (1931).

Shrub or small tree to 8 m. Leaves imparipinnate, rachis and petiole conspicuously winged in *Q. amara* L., narrowly winged or wingless in *Q. africana* Baill., articulated; leaflets opposite, sessile, entire, glabrous, with punctate glands towards leaf apex adaxially. Flowers bisexual, in axillary or terminal determinate thyrses, appearing raceme-like in *Q. amara*, with puberulent axes; sepals 5, distinct, overlapping at base; petals 5, contorted, glabrous or basally pubescent inside, cohering into a tube in *Q. amara*; stamens 10; filaments with basal appendage; anthers dorsifixed, staminodes absent in staminate flowers; disk fleshy, narrowing towards base, glabrous; carpels 5, distinct; style simple; stigma capitate or slightly lobed. Fruit 1–2 drupaceous mericarps, obovoid to ellipsoid, bicarinate, 10–25 mm long; exocarp dark red at maturity; pericarp fleshy.

Two species, 1 neotropical, 1 in tropical west Africa.

13. *Samadera* Gaertn.

Samadera Gaertn., Fruct. 2: 352, t. 156, 'f. 3' (1791), nom. cons. *Hyptiandra* Hook.f. (1862).

Small tree, occasionally up to 20 m. Leaves unifoliolate, entire, glabrous, with scattered punctate glands. Flowers bisexual, in axillary or terminal pseudo-umbels, axes glabrous to puberulent, or clustered in leaf axils; sepals (3)4(5), distinct or mostly connate with short lobes, occasionally with a concave gland; petals (3)4(5), imbricate or contorted, glabrous to pubescent abaxially; stamens 8 or 10; filaments with basal appendage; anthers dorsifixed; staminodes absent in staminate flowers; disk fleshy, conical or cylindrical, glabrous; carpels 4–5; stylodia conglutinate into a common style; stigma capitate or slightly lobed. Fruit 1(–5) drupaceous mericarps, ovoid, ellipsoid or semicircular and flattened, slightly to strongly carinate, 5–50 mm long; exocarp orange to red or brown at maturity; pericarp fleshy or dry and woody.

Five to six species from Madagascar, Indo-China, SE Asia and Australia.

14. *Eurycoma* Jack Fig. 92

Eurycoma Jack, Malay. Misc. 2, 7: 44 (1822); Nooteboom, Fl. Males. I, 6: 193–226 (1962).

Small trees to 10 m, or rarely shrubs, monoecious or dioecious. Leaves imparipinnate; leaflets opposite to subopposite, sessile or nearly so, sometimes appearing articulated, entire, glabrous, without glands. Flowers in axillary determinate thyrses, multiple axes with thick, capitate-glandular hairs; sepals 5(6), basally connate, with capitate-glandular hairs; petals 5(6), induplicate-valvate, pubescent, with capitate-glandular hairs; stamens 5(6); filaments with very small appendage near base; anthers dorsifixed; staminodes 5(6), alternating with stamens in

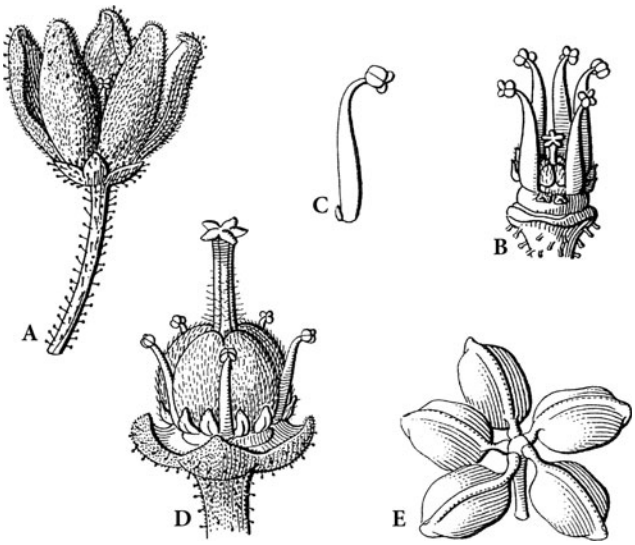

Fig. 92. Simaroubaceae. *Eurycoma longifolia*. **A** Male flower. **B** Same, perianth removed. **C** Stamen. **D** Female flower, petals removed. **E** Fruit. (Nooteboom 1962; artwork: C. van Crevel)

staminate flowers; disk inconspicuous; carpels 5 (6), distinct, stylodia connate or cohering; stigma lobed, peltate. Fruits 1–5 nut-like mericarps, ovoid, bicarinate, 10–20 mm long; exocarp brown at maturity; pericarp dry.

Three species, tropical SE Asia, Sumatra, Malay peninsula, Borneo, S. Philippines.

15. *Gymnostemon* Aubrév. & Pellegr.

Gymnostemon Aubrév. & Pellegr., Bull. Soc. Bot. France 84: 183 (1937).

Large tree, with bisexual flowers or polygamous. Leaves imparipinnate; leaflets opposite to subopposite, subsessile, entire, glabrous, with punctate glands regularly spaced towards apex adaxially. Flowers in axillary or terminal determinate thyrses, with multiple densely short-hairy axes; sepals 5, connate, with short lobes; petals 5, slightly imbricate, villous; stamens 10; filaments lacking appendage; anthers dorsifixed; staminodes absent in staminate flowers; disk fleshy, pubescent; carpels 5, distinct, style simple; stigma simple or slightly lobed. Fruit a single drupaceous mericarp, ovoid, up to 100 mm long; pericarp fleshy, fibrous.

One species, *G. zaizou* Aubrév. & Pellegr., endemic to Côte d'Ivoire.

16. *Perriera* Courchet

Perriera Courchet, Bull. Soc. Bot. France 52: 284 (1905); Capuron, Adansonia II, 1: 87 (1961).

Tree to 30 m. Leaves imparipinnate; leaflets opposite to subopposite, subsessile, entire, pubescent when young, becoming glabrous, with punctate glands regularly spaced towards apex adaxially. Flowers typically bisexual, in axillary determinate thyrses, with multiple pubescent axes; sepals 5, basally connate; petals 5, induplicate-valvate, slightly villous; stamens 10; filaments lacking appendage; anthers dorsifixed; staminodes absent in staminate flowers; disk fleshy; carpels 2, slightly united at base, style simple; stigmatic branches divergent. Fruit typically a single drupaceous mericarp, ovoid, up to 50 mm long; exocarp pale yellow at maturity; pericarp fleshy.

One or two species endemic to Madagascar.

17. *Hannoa* Planch.

Hannoa Planch., London J. Bot. 5: 566 (1846).

Trees to 50 m or shrubs, sometimes suffructescent. Leaves imparipinnate; leaflets opposite to alternate, subsessile to petiolulate, entire, glabrous, with punctate glands on upper surface, more so towards margins. Flowers typically bisexual, in terminal or occasionally axillary determinate thyrses, with multiple glabrous to sparsely pubescent axes; sepals 5, or often calyx rupturing into 2–3 irregular lobes; petals 5, imbricate, puberulent to densely tomentose; stamens 10; filaments with appendage; anthers dorsifixed; staminodes absent in staminate flowers; disk fleshy, sometimes with gynoecium sunken within, glabrous; carpels 5, distinct; style simple; stigmatic branches short, spindly lobes. Fruit 1–3 drupaceous mericarps, ellipsoid or ovoid, slightly bicarinate, 15–35 mm long; exocarp red to purplish brown at maturity; pericarp fleshy.

Five to seven species in tropical Africa.

18. *Odyendea* (Pierre) Engl.

Odyendea (Pierre) Engl. in Engl. & Prantl, Nat. Pflanzenfam. III, 4: 215 (1896); Aubrév. & Pellegr., Fl. Gabon 3: 33–52 (1962).

Tree to 30 m. Leaves imparipinnate; leaflets opposite to subopposite, petiolulate, entire,

glabrous, with punctate glands on upper surface, more so towards margins. Flowers bisexual, in terminal or axillary determinate thyrses, with multiple glabrous axes; sepals 4(5), calyx cupular with short or absent lobes; petals 4(5), imbricate, puberulent adaxially; stamens 8(–10); filaments with densely hairy appendage; anthers dorsifixed; staminodes absent in staminate flowers; disk fleshy, subcylindrical, with gynoecium slightly immersed within, glabrous; carpels 4, distinct or united at base; style simple, with very short, divergent stigmatic branches. Fruit a single drupaceous mericarp, obovoid to ellipsoid, strongly carinate, up to 70 mm long; exocarp red at maturity; pericarp fleshy.

One species, *O. gabonensis* (Pierre) Engl., endemic to Gabon and Cameroon.

19. *Iridosma* Aubrév. & Pellegr.

Iridosma Aubrév. & Pellegr., Fl. Gabon 3: 47 (1962).

Trees. Leaves imparipinnate; leaflets opposite to subopposite, subsessile, entire, glabrous, glands unknown. Flowers bisexual, in determinate thyrses, with multiple pubescent axes; calyx cupular, irregularly undulating; petals (7)8, valvate, villous; stamens 12–13; filaments with appendage; anthers dorsifixed; staminodes absent in staminate flowers; disk fleshy, pubescent; carpels 4, distinct; stylodia spirally twisted to form single column; stigma peltate, stellate. Fruit unknown.

One species, *I. le-testui* (Pellegr.) Aubrév. & Pellegr., endemic to Gabon and Cameroon.

20. *Pierreodendron* Engl. (1906) non A. Chev. (1917).

Mannia Hook.f. (1862) non Opiz (1829) non Trevis (1857).

Tree to 15 m. Leaves imparipinnate; leaflets subopposite to alternate, petiolulate, entire, glabrous to sparsely pubescent below, without glands. Flowers bisexual, in axillary or terminal determinate thyrses, with one or two major axes; sepals 5; calyx cupular with short lobes; petals 5, imbricate or contorted; stamens (10–)15(–18); filament appendage short with small free tip; anthers basifixed; staminodes absent in staminate flowers; disk fleshy, sometimes with gynoecium sunken within, glabrous; carpels 5, distinct, style simple, with short, divergent stigmatic branches, or stigma discoid. Fruits 1–5 drupaceous mericarps, oblong-ellipsoid, laterally compressed, 70–80 mm long; exocarp yellow at maturity; pericarp fleshy, fibrous.

Two species, tropical Africa (Côte d'Ivoire, Nigeria to Angola and Congo).

21. *Simarouba* Aubl. Fig. 93

Simarouba Aubl., Hist. Pl. Guiane: 859 (1775), nom. cons.; Cronquist, Bull. Torrey Bot. Club 71: 226–234 (1944), rev.

Shrubs and trees to 35 m, dioecious. Leaves paripinnate or imparipinnate; leaflets alternate to occasionally subopposite, petiolulate, entire, glabrous or densely tomentose below, with punctate glands scattered on upper surface, more so towards apex. Flowers in terminal determinate thyrses, with multiple glabrous axes; sepals 5, basally connate; petals 5, imbricate or contorted, glabrous; stamens 10; filaments with glabrous to pubescent appendage; anthers dorsifixed; staminodes absent in staminate flowers; disk

Fig. 93. Simaroubaceae. *Simarouba glauca*. **A** Flowering twig. **B** Male flower. **C** Female flower, perianth removed. **D** Longisection of ovary. **E** Staminode. **F** Fruits. (Takhtajan 1981; artwork: A. Schilitschkin)

fleshy, short, glabrous to pubescent; carpels 5, distinct or weakly united, stylodia connate below, stigmatic branches stellately spreading, recurved. Fruit 1–3 drupaceous mericarps, ovoid or ellipsoid, slightly flattened, bicarinate, 10–25 mm long; exocarp orange-red to black at maturity; pericarp fleshy.

Six species in Central and South America, the Caribbean islands and south Florida.

22. *Simaba* Aubl.

Simaba Aubl., Pl. Gui.: 409, t. 153 (1775); Cronquist, Lloydia 7: 81–92 (1944); Cavalcante, Rev. tax. Gen. *Simaba*. Publ. Avuls. Mus. Goeldi 37, 87 pp. (1983), rev.

Trees to 30 m, shrubs, rarely suffructescent with all leaves basal. Leaves paripinnate or imparipinnate, trifoliolate or rarely unifoliolate; leaflets usually opposite, petiolulate to sessile, entire, glabrous to occasionally pubescent, with punctate glands on upper surface, and occasionally with conspicuous apical gland. Flowers bisexual, in terminal or axillary determinate thyrses, with multiple glabrous to densely pubescent axes, or occasionally reduced to axillary clusters; sepals (4)5, basally connate; petals (4)5, imbricate, puberulent to densely pubescent; stamens (8–) 10; filaments with appendage; degree of fusion between filament and appendage variable; anthers dorsifixed; staminodes absent in staminate flowers; disk fleshy, cylindrical, glabrous to densely pubescent; carpels (4)5, distinct or weakly connate; style simple, stigma capitate or slightly lobed. Fruit 1(–5) drupaceous mericarps, ellipsoid to obovoid, lenticular, slightly carinate or occasionally strongly winged, 10–80(–100) mm long; exocarp orange, red, brown, black or yellow at maturity; pericarp fleshy.

Twenty five species in tropical South America, *S. cedron* Planch. extending into Central America.

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