Anacardiaceae

Anacardiaceae R. Br. (1818), nom. cons.

S.K. Pell, J.D. Mitchell, A.J. Miller, and T.A. Lobova

Trees, shrubs, rarely subshrubs, lianas, frequently with contact dermatitis-causing exudate; vertical resin canals present in bark and in phloem of petioles and large veins of leaves, also widely present in fruits, flowers, and other tissues. Leaves alternate, rarely opposite or whorled, simple or pinnately compound, very rarely palmate or bipinnately compound, sessile or petiolate; leaflets opposite, subopposite, or alternate, entire, serrate, dentate, or crenate; stipules absent. Inflorescences terminal and/or axillary, thyrsoid, paniculate, racemose, or spicate, rarely cauliflorous, rarely flowers solitary; bracts and prophylls caducous or persistent. Flowers actinomorphic, unisexual or bisexual (plants dioecious, monoecious, andromonoecious, polygamous, or hermaphrodite); pedicels often articulate; hypanthium sometimes present; perianth usually 2-whorled, rarely 1-whorled or absent, imbricate or valvate; sepals (3–)4–5, usually basally fused, rarely bracteate or calyptriform, caducous to persistent, sometimes accrescent in fruit; petals (3)4–5(–8), rarely 0, caducous to persistent, rarely accrescent in fruit; androecium usually actinomorphic, rarely zygomorphic; stamens (1–)5–10(–>100), in 1 or 2 whorls, rarely more whorls, in some genera only 1 or 2 stamens fertile; filaments distinct, rarely basally connate; anthers tetrasporangiate, dorsi- or basifixed, usually longitudinally dehiscent, introrse, rarely extrorse; disk intrastaminal, rarely extrastaminal or 0; gynoecium 1-carpellate or syncarpous and 2–12-carpellate; rarely, the carpels distally distinct and the gynoecium appearing apocarpous; ovary usually superior, rarely inferior, 1–5(–12)-locular; ovule 1 per locule, apotropous, attached basally, apically, or laterally; stylodia 2–5 (–12) or style simple, apical or lateral, erect or recurved, rarely sigmoid; stigmas capitate, discoid, lobate, or spathulate, rarely punctiform. Fruits drupes or samaras (rarely syncarps, utricles, or baccates), fleshy or dry, occasionally subtended by a fleshy hypocarp or an accrescent, chartaceous or fleshy calyx or corolla; mesocarp sometimes with prominent black resin canals. Seeds 1–5(–12); endosperm scant or absent; embryo curved or straight (rarely horseshoe-shaped or pyramidal); cotyledons usually planoconvex or flat and distinct, usually equal in size, rarely fused or ruminate, sometimes bilobed.

Approximately 81 genera and 800 species in dry to moist, mostly lowland habitats in the tropics and subtropics worldwide, but also extending into the temperate zone.

Vegetative Morphology. The family consists primarily of trees and shrubs, with a few subshrubs, scandent trees, and lianas, and rarely herbaceous suffrutexes. Succulent stems occur in dry habitats (e.g., *Cyrtocarpa*, *Spondias purpurea*). Some arid- or cold-adapted genera have thorns (e.g., *Schinopsis*, *Schinus*, *Searsia*). A geoxylic suffrutex habit (massive woody underground trunk usually with annual or short-lived aerial shoots) is found particularly in the Zambezian region of Africa (e.g., *Lannea edulis*, *L. gossweileri*, *L. katangensis*, *L. virgata*, *Ozoroa nitida*, *Searsia kirkii*) (White 1976) and the Cerrado region of central South America (e.g., *Anacardium corymbosum*, *A. humile*, *A. nanum*) (Lopez-Naranjo 1977; Mitchell and Mori 1987). Water storage roots have also been reported for the family (e.g., *Spondias tuberosa*). The nodes are usually trilacunar or occasionally unilacunar. Many representatives of Anacardiaceae have a turpentine-smelling exudate that may turn black with exposure to air. The exudate may be milky, red, orange, yellow, or clear.

The leaves are deciduous or evergreen, estipulate and usually alternate (opposite in *Bouea*,

Blepharocarya). Most taxa have imparipinnate leaves (rarely paripinnate, bipinnate in *Spondias bipinnata*), usually with opposite leaflets (rarely alternate in, e.g., *Pseudospondias*, *Sorindeia*, *Thyrsodium*), while others have trifoliolate leaves (e.g., *Rhus*, *Searsia*, *Smodingium*, *Toxicodendron*) or simple or unifoliolate leaves (e.g., *Anacardium*, *Cotinus*, *Heeria*, *Lithrea*, *Malosma*, *Rhus*); very rarely the simple leaves are palmate (*Campylopetalum*). Leaf margins can be entire, dentate, serrate, or crenate, prominently revolute (e.g., *Abrahamia*, *Anacardium*), or rarely spinose (e.g., *Comocladia*). Various forms of domatia are sometimes present in the secondary vein axils abaxially. Both hairy tuft domatia (e.g., *Choerospondias*, *Dracontomelon*, *Mauria*, *Rhodosphaera*, *Toxicodendron*) and marsupiform domatia (e.g., *Pleiogynium*) are found in the family. See Wilkinson (1979) and O'Dowd and Willson (1991) for reviews of leaf domatia. Cataphylls occur in a few genera (e.g., *Astronium*, *Buchanania*, *Harpephyllum*, *Mangifera*, *Pistacia*).

Leaf architecture within Anacardiaceae is extremely diverse. Primary leaf venation is pinnate, rarely palmate (e.g., *Campylopetalum*). Secondary venation is most commonly eucamptodromous, brochidodromous (usually festooned), craspedodromous, semi-craspedodromous, or cladodromous (which is usually diagnostic of Anacardiaceae when present) and rarely exmedially reticulodromous (e.g., *Rhus thouarsii*). An intramarginal vein is rarely present (e.g., *Spondias*, *Solenocarpus*). Some genera have mixed secondary venation patterns either throughout (e.g., in *Comocladia glabra* lamina, craspedodromous alternates with brochidodromous veins) or directionally (e.g., *Gluta* and *Campnosperma* laminas are apically brochidodromous and basally eucamptodromous). Intercostal tertiary fabric is frequently random reticulate, polygonal-reticulate, mixed alternate-opposite, or opposite-percurrent. Intersecondary veins are frequently present, but the consistency varies in many taxa. Epimedial tertiaries are frequently present: they may be perpendicular to the primary vein, or varying from parallel to variously angled relative to the secondary veins. In several genera (e.g., *Abrahamia*, *Spondias*) the tertiary veins are admedially branched. A diagonally oriented, admedially branched, trunked tertiary is characteristic of several species of *Sorindeia* and *Buchanania*. In *Comocladia*, the tertiary veins are perpendicular to the secondary veins in the intercostal region. In some Anacardioideae (e.g., *Comocladia*, *Rhus*, *Toxicodendron*), the apparently blindly ramifying tertiary veins are interconnected by quaternary veins. Rarely (e.g., *Abrahamia*, *Rhus perrieri* (=*Baronia* or possibly segregate), *Melanococca*), the tertiaries are truly freely ramified (i.e., areoles absent). Marginal veins are rarely of secondary gauge (e.g., *Drimycarpus*, *Lithrea*). A fimbrial vein is typically present, and occasionally the marginal ultimate tertiary venation is looped (e.g., *Spondias bivenomarginalis*). Areoles vary from being clearly defined (e.g., *Anacardium*, *Tapirira*) to being highly variable in shape and pattern (e.g., *Spondias*). Freely ending veinlets (FEVs) are commonly highly branched (either dichotomously or dendritically) or rarely one- to two-branched. Sometimes the FEVs are terminated by highly branched sclereids (e.g., *Sorindeia*, *Spondias radlkoferi*). Some taxa are characterized by having FEVs terminated by prominent tracheoid idioblasts (e.g., *Comocladia*, *Harpephyllum*, *Melanococca*, *Pleiogynium*, *Spondias*). Terminology for leaf architecture is based on the *Manual of Leaf Architecture* (Leaf Architecture Working Group 1999) and subsequent revisions by the Leaf Architecture Working Group (Ellis et al. 2009).

Trichomes are common throughout the family, usually simple, unicellular or multicellular, sessile or stalked, glandular or non-glandular. Two types of trichomes were described in detail for *Rhus* subgenus *Rhus*: acicular and bulbous gland type (Hardin and Phillips 1985). Stellate trichomes are characteristic of *Lannea* and occur rarely in some other taxa (e.g., *Campnosperma*, *Pseudosmodingium*, *Semecarpus*, *Trichoscypha*) (Aguilar-Ortigoza and Sosa 2004a). Lepidote scales are rarely present in the family, but are characteristic of *Campnosperma*.

Vegetative Anatomy. Wood and bark anatomy of Anacardiaceae has been extensively studied by many authors, such as Dadswell and Ingle (1948), Kryn (1952), Roth (1969, 1981), Young (1974), Wannan (1986), Yunus et al. (1990), Gregory (1994), Terrazas (1994, 1995), Giménez and Moglia (1995), and Baas et al. (2000). Resin canals are common in the wood of numerous genera. They develop schizogenously, lysigenously,

or schizolysigenously in the cortex, pith of the stem, phloem, and wood rays (see Venning 1948 for an ontogeny review; therein, resin canals are referred to as laticiferous canals). Resin canals are also found in Anacardiaceae leaves and reproductive structures. Resin canals run parallel to the phloem in leaf petioles and in major lamina veins, and are absent only in the most minor veins. They are also associated with the phloem of every vascular bundle in the reproductive structures of most genera studied (Copeland 1959). Important resin duct and gum duct anatomy studies include examples from *Anacardium* (Nair et al. 1983), *Holigarna* (Nair et al. 1952a), *Lannea* (Venkaiah and Shah 1984; Venkaiah 1992), *Mangifera* (Joel and Fahn 1980), *Rhus* (Fahn 1979), *Semecarpus* (Nair et al. 1952b; Bhatt and Ram 1992), *Toxicodendron* (Vassilyev 2000), *Trichoscypha* (Den Outer and Van Veenedaal 1986), and *Amphipterygium* and *Orthopterygium* (Figueroa 2001).

Leaf anatomy of Anacardiaceae was concisely covered by Metcalfe and Chalk (1950), and selected genera have been investigated by Goris (1910), Silva (1973), Paula and Alves (1973), Arrillaga-Maffei et al. (1973), Gibson (1981), and Muñoz (1990). A detailed survey of the leaf surface anatomy with special emphasis on epidermal features was undertaken by Wilkinson (1971), who later presented a detailed study of *Gluta* (Wilkinson 1983).

Inflorescences. Inflorescence structure is quite diverse in Anacardiaceae, but basically appears axillary and much branched. Inflorescences are often pseudoterminal (e.g., *Spondias*, *Tapirira*), but can be truly terminal (e.g., *Apterokarpos*, *Cotinus*, *Dobinea*, *Heeria*, *Rhus*), or rarely cauliflorous (e.g., *Semecarpus*, *Sorindeia*, *Trichoscypha*). Most are thyrso-paniculate, but racemes and spikes have also been described. Rarely female inflorescences are reduced to solitary flowers (e.g., *Choerospondias*, *Operculicarya*, *Sclerocarya*). Inflorescences of *Schinus* species from the high Andes and Patagonia are often reduced to just a few fascicles.

Members of Anacardioideae tend to have more condensed inflorescences as compared to Spondioideae. These are usually in the form of condensed panicles, thyrses, or thyrsoids, some being extremely condensed (e.g., *Blepharocarya*, *Laurophyllus*). The bracts subtending inflorescences may be very large (e.g., *Trichoscypha*), prominently foliose (e.g., *Anacardium*, *Dobinea*), condensed into a cupule in female flowers (*Blepharocarya*, *Laurophyllus*), or brightly colored (e.g. white to pink foliose bracts in *Anacardium spruceanum*). In some species there is a gradual transition from leaves to bracts subtending the terminal inflorescence (e.g., *Anacardium*, *Dobinea*, *Mauria*).

A detailed review of some South American genera was completed by Barfod (1988), but his claim that thyrsoids evolved from panicles in the family is not supported by the predominant thyrsoid inflorescence type found in the sister family, Burseraceae (Wannan and Quinn 1992). According to Wannan (Wannan et al. 1987; Wannan and Quinn 1992), the cupule of the female inflorescence of *Laurophyllus* is derived from a panicle, whereas the cupule of *Blepharocarya* is derived from a thyrsoid. It is important to note that inflorescence morphology of Anacardiaceae has not been thoroughly studied for a majority of genera, and conflicting reports of inflorescence structure are common. Much research remains to be conducted on whether Anacardiaceae inflorescences are wholly monopodial or are partially sympodial. For a review of Anacardiaceae inflorescence morphology, see Wannan et al. (1987), Barfod (1988), Endress and Stumpf (1991), and Wannan and Quinn (1991, 1992).

Floral Structure. Flowers are sessile or pedicellate, the pedicel frequently articulated and glabrous, or variously pubescent. Hypogyny is the normal state in the family, with some taxa being rarely perigynous (e.g., *Melanochyla*, *Thyrsodium*, Fig. 5E) or epigynous with (*Holigarna*) or without (*Drimycarpus*) a well-developed hypanthium. Very rarely the receptacle partially surrounds the gynoecium, or is apparently hemi-inferior due to the ovary being partially immersed in the receptacle (*Semecarpus*). Most genera have a biseriate perianth; occasionally, the corolla is absent and very rarely the entire perianth is absent. The calyx is usually green, occasionally the same color as the corolla, or becoming colorful in the genera that have an accrescent calyx that facilitates wind dispersal of the fruit (e.g., *Astronium*, *Loxostylis*, *Parishia*). The corolla is usually imbricate or valvate, rarely apert or contorted in bud. The corolla can be greenish, yellow, cream-colored, pink, red,

purple, or rarely brownish. The petals are generally reflexed or patent, sometimes erect at anthesis. Their venation is often inconspicuous, frequently parallel, or sometimes prominently dichotomously branching (e.g., *Pseudosmodingium*). The corolla is usually campanulate, rarely trumpet-shaped (e.g., *Anacardium*); the petal tips are sometimes apiculate. A hypanthium is present in three genera (*Amphipterygium*, *Melanochyla*, *Thyrsodium*, Fig. 5E).

A nectariferous disk is usually present and intrastaminal, rarely extrastaminal (*Mangifera*, *Swintonia*) or lacking (e.g., *Anacardium*, *Gluta*, *Pistacia* male flowers). The disk is variously colored (green, orange, yellow), shaped (e.g., campanulate, saucer-shaped), and lobed (often corresponding to the location of the stamens). It is usually glabrous, but can be variously pubescent, occasionally papillose. In *Mangifera* the disk is often discontinuous (Fig. 3F). In *Thyrsodium* it is adnate to the hypanthium.

Most genera are diplo- or haplostemonous; very rarely, there is a proliferation of stamens (*Gluta*, Fig. 3E), or extreme staminal reduction as seen in *Anacardium* (Fig. 3G) and *Mangifera*, where there are one or more fertile stamens and a series of staminodes, and *Fegimanra* (Fig. 3B), which has a single stamen. Ronse Decraene and Smets (1995) stated that Anacardiaceae are strictly diplostemonous as compared to Burseraceae, which are all obdiplostemonous, but obdiplostemony was recently reported in the cashew family by Bachelier and Endress (2007, 2009). In diplostemonous species the filaments are often prominently unequal. They are usually subulate and can be basally connate, forming a staminal tube of variable height (*Anacardium*). Their insertion is below or outside the disk, except in *Mangifera* and *Swintonia* where they are inside the disk. The anthers are dithecate, usually dorsifixed, less commonly basifixed or versatile, and are usually introrse, rarely extrorse. They are elliptical, sagittate, or orbicular in shape. The anther connective is usually inconspicuous, occasionally prominently apiculate, sometimes glandular, rarely prominently bilobed (*Androtium*). Staminodes are usually present but reduced in female flowers or sometimes absent; rudimentary anthers are frequently sagittate, rarely absent, or without thecae.

The gynoecium is usually superior (rarely, flowers are perigynous as in *Melanochyla* and *Thyrsodium*), or inferior (*Drimycarpus*, *Holigarna*, Fig. 4E), or apparently hemi-inferior due to the ovary being partially immersed in the receptacle (*Semecarpus*). Carpels are fused but nearly apocarpous in *Androtium* and *Buchanania*. The ovary is usually sessile or rarely subtended by a gynophore. The style or the stylodia are usually apical, often subapical or lateral, rarely approaching gynobasic (e.g., *Anacardium*, *Mangifera*), usually erect, rarely patent (e.g., *Searsia*, *Trichoscypha*), sigmoid (e.g., *Anacardium*), apically decurved (e.g., *Fegimanra*), or recurved. The stylodia are basally connate (e.g., *Baronia*, *Heeria*, *Lithrea*) or distinct, rarely apically connate forming a stigmatic head (*Allospondias lakonensis*, *Dracontomelon*), which is more characteristic of Burseraceae (Bachelier and Endress 2009). The stigmas are usually capitate, rarely punctiform (*Anacardium*, *Gluta*), discoid (*Campnosperma*), variously lobed, rarely sessile, often papillose. In male flowers a pistillode is usually present and reduced, sometimes minute or absent (e.g., *Amphipterygium*, *Astronium*, *Campylopetalum*, *Pistacia*, *Sclerocarya*, *Searsia*). See Wannan and Quinn (1991) for a detailed review of Anacardiaceae flower structure, Endress and Stumpf (1991) for androecium structure in Sapindales, Bachelier and Endress (2007) for a detailed study of *Amphipterygium* and *Pistacia* inflorescence and floral structure, and Bachelier and Endress (2009) for a comparative discussion of Anacardiaceae and Burseraceae flowers with emphasis on the gynoecium.

Embryology. Anthers are tetrasporangiate with longitudinal dehiscence. During the maturation of the anther, 1–3 middle layers become obliterated by the end of meiosis (*Pistacia vera*). The tapetum is secretory, the cells becoming binucleate and subsequently being absorbed. The mature anther wall is represented by the epidermis and the endothecium with fibrous bands. Simultaneous cytokinesis follows meiotic divisions in the microspore mother cells. The mature pollen grains are binucleate (Aleksandrovski and Naumova 1985). High levels of pollen sterility are found in cultivated *Mangifera* and *Spondias* (Juliano 1937; Maheshwari et al. 1955).

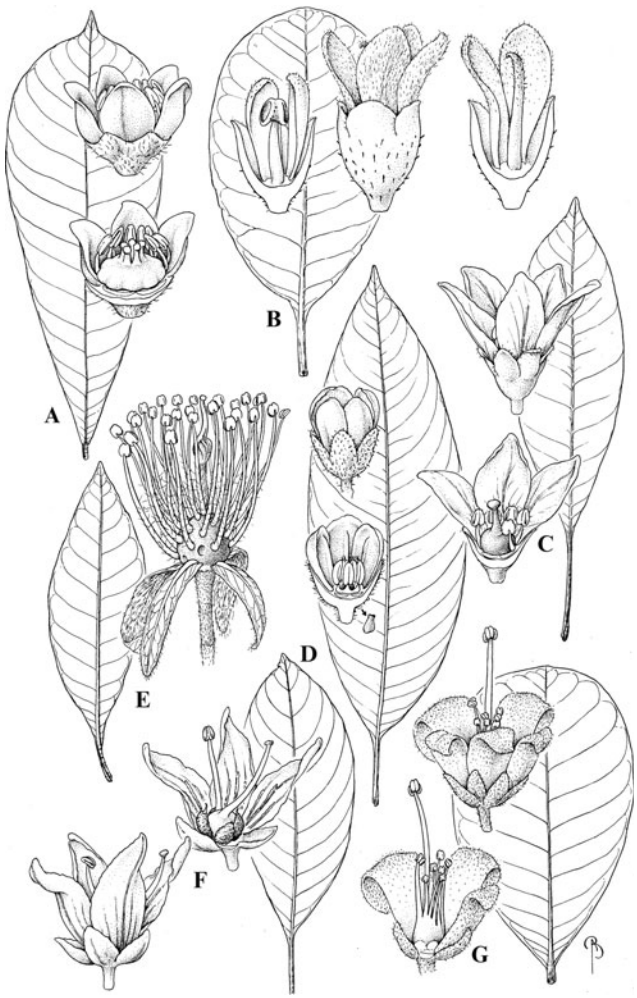

Fig. 3. Anacardiaceae. Flowers and leaves of selected genera. **A** *Buchanania sessifolia*. **B** *Fegimanra afzelii*. **C** *Swintonia acuta*. **D** *Bouea oppositifolia*. **E** *Gluta rugulosa*. **F** *Mangifera monandra*. **G** *Anacardium fruticosum*. (Reproduced with permission of the artist Bobbi Angell)

The ovule is solitary, anatropous or rarely campylotropous (*Semecarpus* in Bachelier and Endress 2009), apotropous ("syntropous" of Bachelier and Endress 2009), apical, lateral or basal, with dorsal or ventral raphe, crassinucellate, with one (e.g., *Anacardium*) or two either entirely or partially developed integuments (e.g., *Lannea*, *Pistacia*, *Rhus*, *Schinus*, *Toxicodendron*) (Geesink et al. 1981). The micropyle is formed by the inner integument, or by both, as in *Schinus molle*. The funicle is long, massive, and bent. A funicular obturator and a cup-like hypostase are present. In addition, a ponticulus (a small bridge between the pollen tube track and the dorsal surface of the ovule) is present in all Anacardiaceae studied by Bachelier and Endress (2009). A nucellar cap of 2–4 cell layers is developed in *Anacardium*, *Lannea*, *Rhus*, *Schinus*, and *Toxicodendron* (Kelkar 1958a, 1958b; Copeland 1961; Grundwag and Fahn 1969; Aleksandrovski and Naumova 1985). The variations and details of ovule structure are summarized by Plisko (1996).

Linear and T-shaped megaspore tetrads are usually formed. Degeneration of megaspore mother cell, megaspore, and embryo sac, and anomalies during meiosis have been observed in *Anacardium*, *Mangifera*, and *Pistacia* (Maheshwari et al. 1955; Copeland 1961; Grundwag and Fahn 1969). An 8-nucleate embryo sac of the Polygonum type develops from a chalazal megaspore (Johri 1963). Cases of development of two embryo sacs occur in *Lannea coromandelica*, *Pistacia chinensis*, *P. vera*, *Searsia mysorensis*, and *Toxicodendron diversilobum*. In *Anacardium*, *Pistacia*, *Rhus*, and *Toxicodendron*, the occurrence of chalazogamy has been observed (Copeland 1961; Grundwag and Fahn 1969; Aleksandrovski and Naumova 1985).

Embryo development is Onagrad-type, with Euphorbia- (e.g., *Lannea*, *Rhus*, and *Semecarpus*), Asterad-, and Penaea-type (*Anacardium*) variations represented in the family. Exact embryogeny is hard to determine in *Pistacia* because of high variations in the orientation of walls during cell divisions in the proembryo (Aleksandrovski and Naumova 1985). During embryo development in *Anacardium* and *Pistacia*, the hypocotyl is turned at a right angle to the cotyledons (Copeland 1961). Chlorophyllous embryos have been reported to occur in *Buchanania latifolia*, *Cotinus coggygria*, *Heeria argentea*, *Pistacia lentiscus*, *P. mutica*, *P. vera*, and *Protorhus longifolia*. Non-chlorophyllous embryos have been reported for *Anacardium occidentale*, *Mangifera indica*, and species of *Ozoroa* (Yakovlev and Zhukova 1973; von Teichman and van Wyk 1996). Endosperm is nuclear, usually absorbed by the growing embryo, or present as a thin layer in *Pistacia* and *Schinus*.

Nucellar polyembryony is well known in *Mangifera* (up to 50 embryos in a seed of *M. indica*; Sachar and Chopra 1957); synergid polyembryony is found in *P. vera* and *Lannea coromandelica* (Grundwag and Fahn 1969). Low seed production frequently occurs in *Anacardium*,

Mangifera, and *Pistacia*. Parthenocarpy is common in *Pistacia* and *Rhus*.

Pollination. Anacardiaceae are primarily entomophilous, but some exceptions are found. *Anacardium* species are pollinated by butterflies and moths (Free and Williams 1976; Mitchell and Mori 1987), and secondarily by bats (Gardner 1977; Dobat and Peikert-Holle 1985). Some *Mangifera* are pollinated by flies, perhaps thrips (Kostermans and Bompard 1993), and secondarily by flying foxes (these bats are feeding on the floral nectar and pollen) (Dobat and Peikert-Holle 1985). A few genera are wind-pollinated (*Amphipterygium*, *Campylopetalum*, *Dobinea*, *Orthopterygium*, *Pistacia*). There is a possibility of heteranthery in *Anacardium* and *Mangifera*, which both have species with emergent large stamens and a set of smaller stamens, both with pollen (Vogel 1978; Mitchell and Mori 1987). Overall, much more research is needed to complete an understanding of pollination biology in the family.

Pollen Morphology. The pollen grains of Anacardiaceae are generally tricolporate, spheroidal; the colpi are long and narrow. The pollen grains vary in size from 17×15 μm in *Schinus polygama* to 46–56×33 μm in *Spondias mombin* and 49×33 μm in *Semecarpus anacardium*. The reticulations are coarse, with high, upstanding ridges enclosing large polygonal lacunae. The sexine can be finely grano-rugulate, striate-reticulate, striate-perforate or reticulate. The germ pore shape varies from spherical to oblong, and its surface can be smooth, ragged, or psilate (for further information, see Heimsch 1940; Erdtman 1952; Marticorena 1968; Anzótegui 1971; Huang 1972; Baksi 1976; Ibe and Leis 1979; Olivera et al. 1998).

The unusual pollen grains of *Campylopetalum* and *Dobinea* were used as a primary argument for the segregation of Podoaceae (Erdtman 1952; Forman 1954). *Pistacia* and the sister genera *Amphipterygium* and *Orthopterygium* (see Jiménez-Reyes and Figueroa 2001) were similarly segregated as distinct families (Pistaciaceae and Julianiaceae, respectively), in part on the basis of their aberrant pollen morphologies. These five genera have pollen with a higher number of smaller, shallower colpi that appear appropriately structured for wind pollination, which may explain their deviating morphology from the rest of the family.

Karyology. Chromosome numbers for the family range from $n = 7$ (*Campylopetalum*, *Dobinea*) to $n = 30$ (*Semecarpus*). Some counts indicate intraspecific variation (e.g., *Anacardium*, *Pistacia*, *Rhus*, *Searsia*), and polyploidy is common in the family (e.g., *Lannea*, *Mangifera*, *Rhus*, *Searsia*). Chromosome numbers reported for the cashew (*Anacardium occidentale*) range from $n = 12$ to $n = 29$. Members of Anacardioideae are usually $n = 15$, but exceptions include *Mangifera* ($n = 20$), *Pistacia* ($n = 12$ or 14), *Searsia dentata* ($n = 16$), and *Schinopsis* and *Schinus* ($n = 14$). Spondioideae vary in chromosome number: $n = 11$ in *Buchanania*, $n = 13$ in *Sclerocarya*, $n = 14$ or 20 in *Lannea*, $n = 16$ in *Spondias* (Goldblatt and Johnson 1979–2008; http://mobot.mobot.org/W3T/Search/ipcn.html).

Fruit and Seed. The fruits are drupes or samaras (rarely syncarps, utricles, or baccates), and all appear to be derived from a fundamentally drupaceous fruit type as elucidated in the family phylogeny (see Taxonomy and Phylogeny section for more detail). They are most often 1-locular, but incompletely 2-, 3-, 4-, and 5-locular fruits are not rare. Those of *Pleiogynium* are 5–12-locular and usually contain 1–5, very rarely up to 12 seeds. The pericarp is multilayered and well differentiated within the family. The exocarp varies in thickness, and can have a lignified outer epidermis (some Anacardioideae) or subepidermal sclereids (*Dracontomelon*, *Pentaspadon*). It is pubescent or glabrous, and is variably colored. In some taxa (e.g., *Lithrea*, *Toxicodendron*), the exocarp is brittle and chartaceous, and separates from the mesocarp at maturity. The mesocarp is usually fleshy and resinous, can be waxy or oily, and is often pulpy and edible (e.g., *Bouea*, *Mangifera*, *Spondias*), dry (e.g., *Amphipterygium*, *Loxopterygium*, *Pachycormus*, *Schinopsis*), or thin (e.g., *Pistacia*, *Solenocarpus*), and sometimes contains dermatitis-causing liquid in usually black resin canals of varying thickness (e.g., *Anacardium*, *Gluta*, *Lithrea*, *Mangifera*, *Toxicodendron*). In *Melanochyla* both the mesocarp and endocarp contain black resin. Anatomically, the mesocarp is rather uniform in structure, and includes scattered vascular bundles and resin

canals, and often fiber bundles or sclerenchyma zones.

The endocarp can be bony, fibrous-woody, or chartaceous. Wannan and Quinn (1990) describe two structurally distinct endocarp types in the family, the Spondias type with a mass of lignified and irregularly oriented sclerenchyma, and the Anacardium type, which is discretely layered and has palisade-like sclereids. The Spondias type is characteristic of the Spondioideae and Anacardioideae members *Campnosperma* and *Pentaspadon*, while the Anacardium type endocarp characterizes the rest of the family (except possibly genera that have not yet been investigated). The presence of Spondias type endocarp in *Canarium* (Burseraceae) suggests that this type may be plesiomorphic and the Anacardium type apomorphic (Wannan and Quinn 1990).

Endocarps open by various mechanisms at germination: irregular splitting in the stone wall, regular splitting from one or two sides, or ingenious opening devices such as shutters, stoppers, plugs, caps, or lids (Hill 1933, 1937). The latter opening mechanisms, usually called opercula, are located in the endocarp, and sometimes involve participation of the mesocarp. They are found only in Spondioideae. Opercula are usually visible on the surface of the endocarp, except in fruits of *Spondias* and *Harpephyllum* where they are covered by projections of the endocarp and mesocarp. During germination, the whole operculum becomes detached and is pushed off by the growing radicle (e.g., *Antrocaryon*, *Dracontomelon*, *Pleiogynium*, *Sclerocarya*), or the operculum splits into two equal halves that are pushed apart by the radicle like a pair of shutters (*Haematostaphis*, *Pseudospondias*) (Hill 1933, 1937). *Choerospondias* fruits, although not considered to be operculate, have pits in the endocarp but lack the sealing caps; fibrous coverings occur over the pits instead.

Seeds vary in size from 2 mm to more than 10 cm. They are generally ellipsoid, ovoid, falcate, lenticular, or reniform. Species of *Mangifera* have labyrinth seeds—the extreme form of rumination in which the seed coat deeply encroaches on the endosperm and embryo (Boesewinkel and Bouman 1984). The seed coat s.s. (derived from the integuments) is usually undifferentiated and/or reduced, while the chalaza is well developed and forms the greater part of the seed coat s.l. Pachychalazal seeds with undifferentiated seed coat have been found in *Mangifera* and *Heeria*; partially pachychalazal seeds with some traces of lignification in the seed coat have been found in subfamily Spondioideae, *Campnosperma*, *Ozoroa*, *Pistacia*, and *Rhus*, and both types of seeds, some endotegmic, in subfamily Anacardioideae (von Teichman 1991). von Teichman (1991) suggested that the evolutionary trend of seeds within Anacardiaceae is from pachychalazal, to partially pachychalazal, and ultimately to seeds without extensive chalaza. The embryo of Anacardiaceae is oily, curved or straight, with two expanded cotyledons. Endosperm is scant.

Both epigeal and hypogeal germination are found in the family (sometimes within one genus), with great diversity of seedling features. Epigeal and phanerocotylar seedlings are described in *Anacardium*, *Buchanania*, *Dracontomelon*, *Lannea*, *Parishia*, *Pistacia*, *Rhus*, *Spondias*, and *Toxicodendron*. Hypogeal and cryptocotylar seedlings are described in *Gluta*, *Lannea*, *Mangifera*, *Melanochyla*, *Pistacia*, *Rhus*, and *Semecarpus* (de Vogel 1980; Kamilya and Paria 1995). Epigeal and cryptocotylar seedlings are found in *Astronium graveolens*, *Koordersiodendron*, and *Swintonia* (de Vogel 1980; Carmello-Guerreiro and Paoli 1999). For further information, see von Teichman (1998) and Carmello-Guerreiro and Paoli (1999).

Dispersal. The majority of Anacardiaceae have fleshy drupaceous fruits that are animal-dispersed, but there are also additional fruit modifications adapted for different mechanisms of dispersal. Four genera, *Anacardium*, *Fegimanra*, *Holigarna*, and *Semecarpus*, have an enlarged edible hypocarp subtending or partially enveloping the drupe. One species of *Anacardium*, *A. microsepalum*, which grows in the flooded forests of the Amazon, lacks the hypocarp and may be fish-dispersed (Mitchell and Mori 1987). Water dispersal has been reported or purported for species of three genera, *Mangifera*, *Poupartiopsis*, and *Spondias*. The variety of structural adaptations for wind dispersal seen throughout Anacardioideae include subtending enlarged sepals (*Astronium*, *Loxostylis*, *Myracrodruon*, *Parishia*), subtending enlarged petals (*Gluta*, *Swintonia*), trichome-covered margins on a globose fruit (*Actinocheita*),

trichome-covered margins on a flattened fruit (*Blepharocarya*, *Ochoterenaea*), *Ulmus*-like samaras encircled with a marginal wing (*Campylopetalum*, *Cardenasiodendron*, *Dobinea*, *Laurophyllus*, *Pseudosmodingium*, *Smodingium*), samaras with a single wing (*Faguetia*, *Loxopterygium*, *Schinopsis*), dry samaroid syncarps (multiple fruit, *Amphipterygium*, *Orthopterygium*), dry achene-like drupe without a wing (*Apterokarpos*), and elongated ciliate pedicels of sterile flowers on broken segments of the infructescence that function much like a tumbleweed (*Cotinus*). The dry utricle fruits of *Pachycormus* are most likely wind-dispersed, but there is no report of this in the literature. The major seed dispersers of fleshy-fruited species are birds (e.g., *Metopium*, *Rhus*, *Schinus*, *Searsia*, *Toxicodendron*), bats (e.g., *Anacardium*, *Antrocaryon*, *Campnosperma*, *Mangifera*, *Spondias*, *Thyrsodium*), and primates (e.g., *Anacardium*, *Antrocaryon*, *Mangifera*, *Pseudospondias*, *Sclerocarya*, *Sorindeia*, *Spondias*, *Trichoscypha*). In addition to these, there are also reports in the literature of the following animal dispersers: elephants and ruminants (e.g., *Antrocaryon*, *Pseudospondias*), deer (e.g., *Anacardium*, *Rhus*, *Spondias*), and coyotes, coatis, foxes, peccaries, reptiles, and tapirs (e.g., *Spondias*) (Gautier-Hion et al. 1985; Mitani et al. 1994; Fragoso 1997; Altrichter et al. 1999; Li et al. 1999; Birkinshaw 2001; Poulsen et al. 2001). Squirrels and rodents mostly serve as seed predators, rather than dispersers (Gautier-Hion et al. 1985). A study of local mammal extinction due to the bush meat trade in Cameroon revealed a sharp decline in seed dispersal of *Antrocaryon* (Wang et al. 2007).

Phytochemistry and Toxicity. Toxic compounds and other chemicals within members of Anacardiaceae have been widely investigated (see review in Aguilar-Ortigoza and Sosa 2004b). Several of these studies focused on the medicinal activity of phenolics (Corthout et al. 1994), esters (Corthout et al. 1992, Galvez et al. 1992), and tannins (Corthout et al. 1991; Galvez et al. 1991; Viana et al. 1997). Others have dealt with toxic components such as contact dermatitis-causing compounds (see Mitchell 1990 for a review; Rivero-Cruz et al. 1997; Drewes et al. 1998), and those responsible for causing nut allergies (Jansen et al. 1992; Fernandez et al. 1995). Some of the compounds in Anacardiaceae have been shown to be defensive in function. These include antimicrobials (Saxena et al. 1994), and antifungal and/or insect- and herbivore-repelling compounds (Chen and Wiemer 1984; Cojocaru et al. 1986).

Contact dermatitis-causing compounds are present in approximately 32 genera of Anacardiaceae (Mitchell 1990; Aguilar-Ortigoza and Sosa 2004b). Most of the poisonous substances are phenols, primarily catechols and resorcinols that accumulate in the resin canals. Pentadecylcatechols (often referred to as urushiols) are the dermatitis-inducing component of poison ivy, poison oak, poison sumac, and the Asian lacquer tree (*Toxicodendron* spp.); they are also found in *Gluta*, *Holigarna*, *Lithrea*, *Metopium*, *Semecarpus*, and *Smodingium*. Heptadecylcatechols are found in *Gluta*, *Lithrea*, *Metopium*, *Semecarpus*, and *Toxicodendron*. Salicylic acid derivatives (anacardic acid, etc.) have been identified in *Anacardium occidentale* and *Pentaspadon*. Other poisonous compounds found in the family include bhilawanols (*Semecarpus*), glutarenghol, laccol (*Toxicodendron*), moreakol (*Gluta usitata*) (Behl and Captain 1979), thitsiol (*Gluta*), renghol (*Gluta*, *Semecarpus*), and semecarpol (a monohydroxy phenol found in *Semecarpus*) (Behl and Captain 1979).

The compounds mentioned above are variously structured oleoresins that may cause an immune system reaction upon binding with skin proteins (Mitchell 1990). Humans and other animals allergic to these compounds can have anywhere from a very mild to a deadly reaction depending upon the location of contact, species encountered, and severity of their allergy. The chemistry of the offending compounds has been researched for many taxa (see above and, e.g., Hill et al. 1934; Backer and Haack 1938; Loev 1952; Tyman and Morris 1967; Johnson et al. 1972; Gross et al. 1975; Halim et al. 1980; Stahl et al. 1983; Gambaro et al. 1986), but the cause of the toxicicity in others is unknown.

Taxonomy and Phylogeny. The family Anacardiaceae was first proposed by Lindley in 1830, but its members have been variously placed in other families including Blepharocaryaceae, Comocladiaceae, Julianiaceae, Pistaciaceae,

Podoaceae, Rhoaceae, Schinaceae, Spondiadaceae, and Terebinthaceae. Engler (1892) divided the family into five tribes, Dobineeae (=Dobineae), Mangifereae (=Anacardieae), Rhoideae (=Rhoeae), Semecarpeae, and Spondieae (=Spondiadeae). He circumscribed them using one vegetative and several floral and fruit characters, including number of carpels, insertion of the ovule on the placenta, number of staminal whorls, leaf complexity, number of locules in the ovary and fruit, embryo morphology, and stylar insertion on the ovary. The tribal circumscription was revised by Mitchell and Mori (1987) who updated Ding Hou's (1978) modification of Engler's classification. However, this classification has more recently been questioned. Wannan and Quinn (1990, 1991) used floral and pericarp structure, wood anatomy, and biflavonoid data to investigate the classification of Anacardiaceae. They tentatively identified two groups, A and B, which were each divided into two subgroups, 1 and 2. Engler's tribes Anacardieae, Dobineae, Rhoeae, and Semecarpeae, with the exception of *Androtium*, *Buchanania*, *Campnosperma*, and *Pentaspadon*, were placed in group A, while group B contains all of Spondiadeae plus the four genera named above (two genera each from Anacardieae and Rhoeae). Wannan and Quinn (1991) designated two genera, *Faguetia* and *Pseudoprotorhus* (=Sapindaceae, *Filicium*), as not assignable to any group.

In the first molecular investigation of Anacardiaceae, Terrazas (1994) used sequences of the chloroplast gene *rbc*L, together with data on morphology and wood anatomy to interpret the phylogeny of the family. Her combined *rbc*L-morphology phylogeny elucidated a monophyletic Anacardiaceae comprised of two groups. The first group, clade A2, contains Spondiadeae plus *Pentaspadon*, and is united by the morphological synapomorphy multicellular stalked glands on the leaves. The second group, clade A1, contains the remaining genera in the four other tribes, and is supported by the morphological and wood anatomical synapomorphies, unicellular stalked leaf glands and the presence of both septate and nonseptate fibers. Based on the combined phylogeny, Terrazas (1994) informally proposed splitting the family into two subfamilies, Anacardioideae and Spondioideae. Pell found a similar division of the family based on analysis of three plastid genes, and described and circumscribed the two subfamilies (Pell 2004; Mitchell et al. 2006). This classification is followed herein, with the exception of the subfamilial placement of *Buchanania*: recent molecular data have helped resolve ambiguous morphological data, and suggest that this genus is a member of subfamily Spondioideae. It should be noted that recent, more extensively sampled analyses of cpDNA (*trn*LF and *rps*16) and nrDNA (ETS) data (Pell, unpublished data) indicate that subfamily Spondioideae (formerly recognized as tribe Spondiadeae) is polyphyletic. However, because the two subfamilies as circumscribed by Mitchell et al. (2006) are structurally recognizable, and formal subfamilial rankings have not yet been assigned to the newly resolved clades, the two-subfamily system is used here to divide the genera.

The phylogenies elucidated by Pell (2004, and unpublished data) added support for several relationships within the family. The position within Anacardiaceae of several formerly segregated families including Podoaceae (*Campylopetalum* and *Dobinea*), Julianiaceae (*Amphipterygium* and *Orthopterygium*), and Pistaciaceae (*Pistacia*) has been solidified by molecular data. The core members of former tribe Anacardieae (*Anacardium*, *Bouea*, *Fegimanra*, *Gluta*, *Mangifera*) form a clade. *Rhus* s.l. is polyphyletic, with up to five different origins, and is in urgent need of taxonomic revision (Pell 2004; Pell et al. 2008; see also Miller et al. 2001; Yi et al. 2004, 2007). Moffett (2007) published the new combinations in *Searsia* for the mostly African former *Rhus* species, but much work remains to be done.

Anacardiaceae are most closely allied with Burseraceae. Both families share the synapomorphies vertical intercellular secretory canals in the primary and secondary phloem, and often horizontal ones in the wood rays, and the ability to synthesize biflavonyls (Wannan et al. 1985; Wannan 1986; Wannan and Quinn 1990, 1991; Terrazas 1994). Additionally, in these families the ovules are often attached to a short, broad placental obturator, and the plants are strongly resinous. The close relationship of Anacardiaceae and Burseraceae has been suggested by numerous authors based upon morphological, anatomical, and biochemical data (Gundersen 1950; Cronquist 1981; Wannan 1986; Takhtajan 1987; Thorne 1992), further supported by DNA sequence data (Gadek

et al. 1996; APG 1998, 2003, 2009; Savolainen et al. 2000a, b; Pell 2004). Nevertheless, Anacardiaceae are distinguished from Burseraceae by having a single apotropous ovule per locule versus two epitropous ovules per locule, respectively. Additional features that are not universal, but often effectively separate the two families, include chemical and fruit characteristics. Burseraceae lack chemical compounds that are present in many Anacardiaceae, including 5-deoxyflavonoids and contact dermatitis-causing compounds. All Anacardiaceae fruits are indehiscent, while many Burseraceae fruits are dehiscent; some Burseraceae have stipules or pseudostipules that in Anacardiaceae are lacking; many Burseraceae have a terminal pulvinulus subtending the lamina of the leaflets, which is absent in Anacardiaceae.

Historically the family Anacardiaceae has been placed within the higher taxonomic rankings of Burserales, Rutales, Sapindales, or Terebinthinae. Most modern authors consider it a member of Sapindales, and recent molecular studies at the ordinal level (Gadek et al. 1996) and above (Chase et al. 1993; Bremer et al. 1999; Savolainen et al. 2000a, 2000b; APG 2003, 2009) have supported this classification.

Distribution. The family is native to the Western Hemisphere (from southern Canada to Patagonia); Africa; southern Europe; temperate, subtropical and tropical Asia; tropical and subtropical Australia; and most of the Pacific Islands. Anacardiaceae are noticeably absent from the floras of northern Eurasia, southwestern Australia, New Zealand, the Galapagos Islands, northern North America, and extreme desert and high-elevation habitats. The primary centers of diversity are in Mexico, South America, southern and equatorial Africa, Madagascar, Indochina, and Malesia. The Paleotropics are richer in species number than are the Neotropics.

Paleobotany. Anacardiaceae have rich fossil records because of their woody growth form, and past and current wide distribution. Anacardiaceae pollen and wood first appear in the Paleocene, 65 to 55 million years ago (Hsu 1983; Muller 1984), and are found throughout the world. Fossils occur mostly in the western Unites States south to Panama from the Eocene and Oligocene (Taylor 1990; Ramírez and Cevallos-Ferriz 2002). Leaf fossil material of four species of *Rhus* and one putative species of *Cotinus* with its distinctive cladodromous secondary venation have been identified from the Eocene in the Florissant fossil beds of Colorado (Meyer 2003). Silicified wood fragments from the lower Miocene formations of central west Sardinia have been allied with *Sclerocarya birrea* (Biondi 1981). Many purported Anacardiaceae leaf and wood fossils have been determined to belong to taxa outside of the family, and many others are of dubious affinity.

Fossil fruits assigned to *Antrocaryon* have been found in the 3 million year-old deposits of the Lower Omo Valley (Bonnefille and Letouzey 1976), and the early-middle Miocene (>16 Ma) Bakate Formation (Tiffney et al. 1994) in Ethiopia. Fruits with possible affinities to *Pistacia* (see Taylor 1990) and *Dracontomelon* have also been found (Collinson 1983). Fossils with affinities to *Tapirira* include fruits (Reid 1933), flowers preserved in amber, and fossil wood (see Taylor 1990 for a review). Six genera from the London Clay flora have been provisionally assigned to Anacardiaceae, and appear to be related to the Spondioideae due to the presence of opercula-like structures on the fossilized endocarps (Collinson 1983). Miocene fruit fossils of *Loxopterygium* have recently been identified in Andean Ecuador (Burnham and Carranco 2004). Numerous *Anacardium* fossils were reported by Berry (1924, 1929) from North and South America, and recently, Manchester et al. (2007) reported *Anacardium* fossils from the Eocene of Europe, greatly expanding the range of this genus. Some endocarp fossils originally assigned to *Dracontomelon* have subsequently been transferred to extinct genera (Manchester 1994).

Economic Importance. The major agricultural food products of Anacardiaceae are cashews (*Anacardium*), mangos (*Mangifera*), pink peppercorns (*Schinus*), and pistachios (*Pistacia*). However, numerous taxa have other edible parts of high regional value (e.g., *Antrocaryon*, *Buchanania*, *Choerospondias*, *Cyrtocarpa*, *Harpephyllum*, *Lannea*, *Ozoroa*, *Rhus*, *Searsia*, *Spondias*, *Tapirira*, and *Trichoscypha*). *Sclerocarya birrea* has recently become economically important outside of its native range of sub-Saharan Africa and Madagascar, due to the export of a liquor, Amarula Cream, made from its fruit,

marula (Hall et al. 2002). The cashew (*Anacardium occidentale*) yields three major economic products: seed ("cashew"), hypocarp ("cashew apple"), and mesocarp resin ("cashew nutshell liquid"). The cashew seed is eaten raw and roasted, powdered to make a beverage, and is used in confections. Cashew apples are more important locally than globally, and are eaten fresh, juiced, and fermented to make alcoholic beverages. The cashew nutshell liquid is used industrially in the manufacturing of various polymers such as plastics, adhesives, lubricants, and resins. Examples of specific products are wallboard and break linings. Of these products, the seed is by far the most economically important. Major countries of production are Brazil, India, Indonesia, Guinea, Mozambique, Nigeria, Tanzania, and Vietnam (Behrens 1996). Cashew is native to lowland South America, and was brought to India by the Portuguese; other early colonialists introduced the cashew of commerce into cultivation throughout the lowland tropics of the New and Old Worlds.

No species of Anacardiaceae ranks as a major, internationally important timber tree but many have an important role in smaller timber markets, and are valued for their quality wood and rot resistance (Record 1939; Hess 1949). One of the most prized rot-resistant Anacardiaceous timber trees comes from species of the South American genus *Schinopsis* (quebracho), which has been used extensively in Argentina for railroad ties (Kerr 1935). *Astronium* (gonçalo alvez) and *Myracrodruon* are also of significant importance for exported lumber. Other timber genera are locally important and used for making matchsticks, cabinetry, bows, charcoal, housing, axe-handles, furniture, firewood, and kitchenware.

Many Anacardiaceae species are also valued for their horticultural appeal. Specimens of *Cotinus*, *Harpephyllum*, *Lannea*, *Pistacia*, *Rhodosphaera*, *Rhus*, *Schinus*, *Searsia*, *Smodingium*, and *Toxicodendron* are planted for their beautiful inflorescences, infructescences, evergreen foliage, and/or fall foliage. A few agricultural and horticultural species have escaped cultivation and become invasive in their non-native areas. Japanese wax tree, *Toxicodendron succedaneum*, is an Asian species that was originally cultivated in Brazil but escaped after introduction, and is now invasive. Brazilian pepper tree or pink peppercorn, *Schinus terebinthifolia*, is another notoriously problematic species where it occurs in the Everglades of central and southern Florida, in the Hawaiian Islands, and various other parts of the subtropics and tropics (Gilman 1999; Mitchell 2004). More recently, *Pistacia chinensis* has become naturalized and invasive in Texas (McWilliams 1991).

Anacardiaceae have long been known for their medicinal properties. *Spondias* and *Rhus* are used extensively by native populations for everything from healing broken bones to treating colds. Other taxa are used to treat fever (e.g., *Buchanania*, *Comocladia*), hepatitis (*Haematostaphis*), gastrointestinal illness (e.g., *Anacardium*, *Antrocaryon*, *Heeria*, *Lannea*, *Ozoroa*, *Pseudospondias*, *Schinus*, *Sorindeia*), respiratory disease (e.g., *Astronium*), skin disease and/or wounds (e.g., *Buchanania*, *Lannea*, *Metopium*, *Ozoroa*, *Schinus*, *Sclerocarya*, *Searsia*, *Sorindeia*, *Trichoscypha*), venereal disease (e.g., *Buchanania*, *Lannea*), various pregnancy-related conditions (e.g., *Metopium*, *Ozoroa*, *Trichoscypha*), and as an astringent (e.g., *Anacardium*, *Astronium*, *Mangifera*) (Morton 1981; Burkill 1985; Mitchell 2004).

Modern medicine has investigated many of these ethnobotanical uses and isolated several active compounds from various plant structures. Cardol, a compound extracted from the pericarp of the cashew, has been shown to exhibit antifilarial activity useful against filariasis, a major tropical disease caused by filarial parasites that has affected more than 400 million people worldwide (Suresh and Raj 1990). Three anacardic acids isolated from the juice of the "apple" (swollen hypocarp) of the cashew have been shown to have significant in vitro cytotoxicity against BT-20 breast carcinoma cells (Kubo et al. 1993). Three anacardic acids isolated from the cashew nut shell oil provide potent antibacterial activity against *Streptococcus mutans* (a component of plaque), the bacterium that adheres to the smooth surface of the tooth and facilitates the accumulation of other oral microorganisms that produce organic acids that destroy enamel, leading to the formation of cavities (Muroi and Kubo 1993).

Anacardiaceae contact dermatitis is responsible for a great deal of lost work worldwide. In the US state of California, *Toxicodendron diversilobum* (poison oak) dermatitis costs the state

ca. 1% of its workers' compensation budget, and nearly one third of US forest fire fighters are disabled by this dermatitis when responding to fires on the US west coast (Epstein 1994). Several of the Asian contact dermatitis-causing taxa are used for their tannins and in the lacquerware industry. The resins of *Toxicodendron vernicifluum* and *Gluta* species are used in Burma, China, Japan, Thailand, and Vietnam to create decorative, long-lasting wooden art pieces such as trays, jewelry boxes, vases, picture frames, and furniture. Resin collected from the trees is refined and applied to fine wood, increasing the woods' chemical, heat, and humidity resistance. Unfortunately, the oleoresins' activity is not completely suppressed upon drying, and lacquerware can continue to cause much discomfort in unsuspecting admirers for years (Kullavanijaya and Ophaswongse 1997; Prendergast et al. 2001; Rodriguez et al. 2003). Other industrial uses of Anacardiaceae species include the production of dyes for marking laundry (e.g., *Lannea*, *Semecarpus*) and automobile break linings (*Anacardium*) (Mitchell and Mori 1987).

Key to the Subfamilies

1. Trees, shrubs, rarely vines or perennial herbs; exudate often present and sometimes causing contact dermatitis; leaves simple, unifoliolate, or multifoliolate; 1 or more whorls of perianth sometimes absent; androecium haplo-, diplo-, or greater than diplostemonous; carpels 1–3 (5 in *Androtium*) and fused; ovary 1-locular (often by abortion; 2-locular in *Campnosperma*); ovule apical, basal, or lateral; exocarp usually thin; opercula 0; fruit sometimes wind-dispersed **I. Subfam. Anacardioideae**
– Trees or shrubs; exudate often present and not causing contact dermatitis (very rarely causing dermatitis in *Spondias*); leaves multifoliolate (rarely simple/unifoliolate in *Buchanania*, *Haplospondias*, *Lannea*, and *Sclerocarya*); perianth always present; androecium diplostemonous; carpels 4–5 (1 in *Solenocarpus*, more than 5 in *Buchanania* and *Pleiogynium*); ovary (1)4–5(+)-locular; ovule apical to subapical (basal or sublateral in *Buchanania*); exocarp thick; opercula often present; fruit never wind-dispersed **II. Subfam. Spondioideae** (Key p. 21)

Key to the Genera of Anacardioideae

1. Leaves simple or unifoliolate 2
– Leaves compound 41
2. Leaves opposite 3
– Leaves alternate or subopposite 8
3. Leaves always opposite; style 1, stigma 1 4
– Leaves opposite, subopposite, alternate, or verticillate, more than one position usually present on plant; stylodia 1–3; stigmas 3 5
4. Trees; evergreen; bud scales present; leaves coriaceous, margins always entire; flowers bisexual, perianth always biseriate **11. *Bouea***
– Subshrubs to shrubs; deciduous; bud scales absent; leaves not coriaceous (chartaceous to membranaceous), margins serrate (at least at base); flowers unisexual, perianth biseriate in male flowers and 0 in female flowers 7
5. Style 1; drupe ellipsoidal and symmetrical; cotyledons usually fused and ruminate **1. *Abrahamia*** p. p.
– Stylodia 3; drupe reniform and oblique; cotyledons not fused or ruminate 6
6. Leaves often pubescent abaxially, young leaves green; pedicel articulate; ovule lateral or basal; widespread sub-Saharan Africa and Arabian Peninsula **42. *Ozoroa*** p. p.
– Leaves glabrous abaxially, young leaves orange-red; pedicel non-articulate; ovule subapical; endemic to southeast South Africa **47. *Protorhus***
7. Leaves palmately lobed and veined; pistillode absent; disk present in male flowers **13. *Campylopetalum***
– Leaves not palmately lobed and veined; pistillode present; disk absent in male flowers **17. *Dobinea*** p. p.
8. Ovary inferior 9
– Ovary superior 10
9. Prominent marginal secondary vein absent; petiole with spur-like, caducous or persistent appendages; corolla valvate; ovule apical **25. *Holigarna***
– Prominent marginal secondary vein present; petiole appendages 0; corolla imbricate; ovule basal **18. *Drimycarpus***
10. Stilt roots frequently present; hypanthium present **33. *Melanochyla***
– Stilt roots usually absent (very rarely present in *Gluta* and *Campnosperma*); hypanthium absent 11
11. Unicarpellate; style 1; stigma 1, undivided 12
– Tricarpellate or >3 carpels; stylodia 1 or more; stigma >1 16
12. Stamen one; staminodes absent; perianth always 4-merous **21. *Fegimanra***
– Stamens one or more, if only one, then stamen fertile; staminodes present; perianth usually more than 4-merous 13
13. Domatia often present in secondary vein axils abaxially; staminal tube present; drupe usually subtended by fleshy hypocarp; mesocarp woody **4. *Anacardium***
– Domatia absent; staminal tube absent; hypocarp 0; mesocarp fleshy or resinous 14
14. Plants hermaphrodite; calyx calyptriform, circumscissile or bursting irregularly at anthesis, caducous; disk absent; gynophore present **22. *Gluta***
– Plants andromonoecious; calyx imbricate, persistent; disk present, extrastaminal (very rarely intrastaminal in *Mangifera*); gynophore absent 15
15. Glandular ridges on petals; androecium usually zygomorphic, stamens 5(–10), only 1–2 (3–5 or all) fertile,

the staminodes much reduced; enlarged petals absent in fruit **31. *Mangifera***
– Glandular ridges absent from petals; androecium always actinomorphic, stamens 5, staminodes 0; enlarged petals subtending fruit **57. *Swintonia***
16. Connective apically bilobed, prolonged and dilated; carpels 5 **5. *Androtium***
– Connective not apically bilobed, prolonged or dilated; carpels 3 17
17. Perianth absent in female flowers; disk absent in male flowers, present in female flowers; drupe peltate on an accrescent, obovate, or rounded bract that aids in wind dispersal **17. *Dobinea*** p. p.
– Perianth present in female flowers; disk present in all flowers; drupe not as above 18
18. Fleshy hypocarp subtending drupe **54. *Semecarpus***
– Fleshy hypocarp absent 19
19. Fruits with fleshy mesocarp 20
– Fruits with waxy, dry, or resinous (not fleshy) mesocarp 25
20. Leaves linear to lanceolate; perianth of tepals in male flowers, biseriate in female flowers **23. *Haplorhus***
– Leaves various; perianth biseriate in all flowers 21
21. Leaves with peltate or lobed scales; drupes often incompletely bilocular with only one locule fertile **12. *Campnosperma***
– Leaves without peltate or lobed scales; drupes 1-locular 22
22. Perianth usually 4-merous 23
– Perianth usually 5-merous 24
23. Style 1; stigma 1, capitate to trilobed; India and Sri Lanka **39. *Nothopegia***
– Stylodia 3–4 (very rarely 6); stigmas 3, capitate to shallowly bilobed; sub-Saharan Africa **60. *Trichoscypha*** p. p.
24. Androecium haplostemonous or less 31
– Androecium diplostemonous or greater 39
25. Fruit with elongated wing-like structure 26
– Fruits without elongated wing-like structure 27
26. Leaves entire; fruit a laterally winged samara; South America **51. *Schinopsis*** p. p.
– Leaves serrate; fruit a syncarp subtended by a winged peduncle; Mexico to Costa Rica **3. *Amphipterygium*** p. p.
27. Some flowers in inflorescence aborting, and their pedicels elongating and becoming villous; infructescence wind-dispersed like a tumbleweed **16. *Cotinus***
– Flowers, inflorescence, and infructescence not as above 28
28. Inflorescence highly condensed, characterized by fusion of higher-order branches into flattened broad segments; style 1; ovule apical **26. *Laurophyllus***
– Inflorescence branches not fused; stylodia 3 or style branches 3; ovule basal 29
29. Leaves simple; exocarp readily separating from mesocarp; mesocarp waxy and white with black resin canals 30
– Leaves dissected and simple, both on same plant; exocarp and mesocarp not as above **10. *Bonetiella***
30. Marginal secondary vein absent from leaflets; hairy tuft domatia sometimes in secondary vein axils abaxially; androecium haplostemonous; eastern Asia **59. *Toxicodendron*** p. p.
– Leaflets with marginal secondary vein; hairy tuft domatia 0; androecium diplostemonous; Brazil, Paraguay, Argentina, Uruguay, and Chile **27. *Lithrea*** p. p.
31. New World 32
– Old World 33
32. Leaves evergreen or deciduous; exocarp red with glandular trichomes **50. *Rhus*** subg. ***Lobadium*** p. p. and ***R. chiangii***
– Leaves always evergreen; exocarp white, glandular trichomes 0 **30. *Malosma***
33. Madagascar 34
– Africa, Asia, Europe 36
34. Fruit ellipsoidal, symmetrical; cotyledons usually fused and ruminate; endocarp bony **1. *Abrahamia*** p. p.
– Fruit sigmoid or reniform, asymmetrical; cotyledons not as above; endocarp thin (chartaceous or cartilaginous) 35
35. Inflorescence pendent; corolla pink to red; style 3-branched **36. *Micronychia***
– Inflorescence erect; corolla white, yellow, or green; stylodia 3 **8. *Baronia***
36. Leaves trisect, inflorescence cauliflorous, thorns present **53. *Searsia*** p. p. (=*S. problematodes*)
– Leaves entire, inflorescence terminal and/or axillary, thorns absent 37
37. Exudate watery; leaves strongly discolorous with fine silvery pubescence abaxially; fruits 25–30 mm at longest axis **24. *Heeria***
– Exudate milky or brown; leaves not as above; fruits 4–14 mm at longest axis 38
38. Leaves often pubescent abaxially, young leaves green; pedicel articulate; ovule lateral or basal; widespread sub-Saharan Africa and Arabian Peninsula **42. *Ozoroa*** p. p.
– Leaves glabrous abaxially, young leaves orange-red; pedicel non-articulate; ovule subapical; endemic to southeast South Africa **47. *Protorhus***
39. Calyx deeply lobed; stylodia usually 3; exocarp generally separating from mesocarp at maturity **52. *Schinus*** p. p.
– Calyx shallowly lobed; style always 1; exocarp not separating from mesocarp at maturity 40
40. Plants dioecious (very rarely monoecious); stamens 10–20; Africa **56. *Sorindeia*** p. p.
– Plants hermaphrodite; stamens 10; Central to South America **32. *Mauria*** p. p.
41. Leaves opposite **9. *Blepharocarya***
– Leaves alternate 42
42. Leaves trifoliolate 43
– Leaves greater than trifoliolate (multifoliolate) 48
43. Fruit winged 44
– Fruit not winged 45

44. Inflorescence terminal and/or axillary thyrses; perianth 5-parted, biseriate; fruit a samara with a marginal wing; South Africa **55. *Smodingium***
– Inflorescence axillary, male flowers arranged in pendent thyrses, female flowers tightly arranged and subtended by an involucre; calyx 6–8-parted in male flowers, 0 in female flowers, corolla 0; fruit a syncarp subtended by a winged peduncle; Mexico to Costa Rica **3. *Amphipterygium*** p. p.
45. Exudate turning black with exposure to air; exocarp readily separating from mesocarp; mesocarp waxy and white or gray with black resin canals 46
– Exudate not turning black with exposure to air; exocarp and mesocarp not as above 47
46. Marginal secondary vein present; hairy tuft domatia 0; androecium diplostemonous; Brazil, Bolivia, Paraguay, Argentina, Uruguay, and Chile **27. *Lithrea*** p. p.
– Marginal secondary vein absent; hairy tuft domatia sometimes in secondary vein axils abaxially; androecium haplostemonous; southern Canada to Guatemala, and eastern Asia **59. *Toxicodendron*** p. p.
47. Terminal inflorescence branches spicate; exocarp reddish with glandular trichomes; southern Canada to Panama **50. *Rhus*** subg. ***Lobadium*** p. p.
– Terminal inflorescence branches not spicate; exocarp not as above, if reddish, not with glandular trichomes; Africa, Sicily, Middle East to China **53. *Searsia*** p. p.
48. Fruit likely wind-dispersed (samaras, dry drupes with enlarged trichomes, dry achene-like drupes, utricles) 49
– Fruit likely animal-dispersed (fleshy drupes or dry but not winged) 63
49. Plants caudiciform; fruit a utricle **43. *Pachycormus***
– Plants not caudiciform; fruit not a utricle (various) 50
50. Fruit subtended by stiffened enlarged sepals 51
– Fruit not as above 54
51. Perianth 4-merous **44. *Parishia***
– Perianth 5-merous 52
52. Pistillodes present and reduced; fruit globose to subglobose **38. *Myracrodruon***
– Pistillodes absent; fruit not as above 53
53. Rachis alate; flowers large with showy petals; stylodia lateral; South Africa **29. *Loxostylis***
– Rachis not alate; flowers inconspicuous; stylodia apical; Mexico to South America **7. *Astronium***
54. Perianth absent in female flowers; flowers wind-pollinated; fruit a syncarp subtended by a winged peduncle 55
– Perianth present in female flowers; flowers insect-pollinated; fruit not as above 56
55. Male inflorescence pendant and large; sepals 5–8, longer than stamens; Mexico to Costa Rica **3. *Amphipterygium*** p. p.
– Male inflorescence erect and small; sepals 3–8, shorter than stamens; Peru **41. *Orthopterygium***
56. Gynoecium and fruits with long trichomes on surface and/or margins 57
– Gynoecium and fruits glabrous, or trichomes inconspicuous if present 58
57. Leaflets entire; fruit a samara, laterally compressed with trichomes occurring prominently on the margins; inflorescence corymbose; Venezuela, Panama, and Colombia south to Bolivia **40. *Ochoterenaea***
– Leaflets broadly pinnately lobed (leaf fern-like); fruit a globose drupe covered with trichomes; inflorescence not corymbose; Mexico **2. *Actinocheita***
58. Fruit not winged **6. *Apterokarpos***
– Fruit winged 59
59. Fruit with an elongated wing 60
– Fruit compressed and encircled by a winged margin 62
60. Samara wing terminal and ending in style remnants; Madagascar **20. *Faguetia***
– Samara wing lateral and not ending in style remnants; South America 61
61. Plants polygamodioecious; leaves usually deciduous; wing chartaceous with conspicuous venation, consisting of exocarp tissue **28. *Loxopterygium***
– Plants dioecious or monoecious; leaves usually evergreen; wing stiffened and thick, lacking conspicuous venation, consisting of exocarp and mesocarp **51. *Schinopsis*** p. p.
62. Flowers sessile; stylodia 3; ovule basal; drupe with two unequal, narrow lateral wings; Bolivia **14. *Cardenasiodendron***
– Flowers pedicellate; style 3-branched; ovule apical; drupe with two equal, broad lateral wings; Mexico **48. *Pseudosmodingium***
63. Flowers apetalous, wind-pollinated; stylodia plumose **46. *Pistacia***
– Flowers with petals, insect-pollinated; stylodia not plumose 64
64. Perianth 3–4-merous 65
– Perianth 5-merous 66
65. Leaflets usually spinose; perianth 3(–4)-merous; West Indies, Mexico, Belize, and Guatemala **15. *Comocladia***
– Leaflets entire; perianth always 4-merous; sub-Saharan Africa **60. *Trichoscypha*** p. p.
66. Hypanthium present **58. *Thyrsodium***
– Hypanthium absent 67
67. Domatia in axils of secondary veins abaxially; androecium usually consisting of one whorl of fertile stamens and one whorl of staminodes **45. *Pentaspadon***
– Domatia usually 0 (sometimes present in *Toxicodendron* and *Mauria*); androecium of uniform stamens 68
68. Androecium haplostemonous 69
– Androecium diplostemonous or greater 75
69. Exudate usually turning black with exposure to air; leaves often with black spots where injured; exudate toxic 70
– Exudate not turning black with exposure to air; leaves without conspicuous black spots; exudate not toxic (possibly toxic in *Apterokarpos*) 71
70. Plants polygamodioecious; leaves usually deciduous (rarely evergreen); stylodia 3; exocarp white to gray or yellow, easily separating from mesocarp; mesocarp white or gray with black resin canals **59. *Toxicodendron*** p. p.

– Plants dioecious; leaves evergreen; style 1; exocarp orange to brown, not easily separating from mesocarp; mesocarp resin canals not conspicuous **35. *Metopium***

71. Drupe dry, with longitudinal grooves; northeastern Brazil **6. *Apterokarpos***
– Drupe fleshy, lacking longitudinal grooves; not in Brazil 72

72. Leaves palmately compound (usually pentafoliolate) **53. *Searsia*** p. p.
– Leaves pinnately compound 73

73. Leaflet venation lacking areolation; exocarp black **34. *Melanococca***
– Leaflet venation with areolation; exocarp red to reddish brown 74

74. Erect or scandent shrubs or small trees (up to 7 m); fruit covered with glandular trichomes; seed fills most of the locule **50. *Rhus*** p. p.
– Medium to large trees (up to 20 m); fruit glabrous; seed fills only a small portion of the locule **37. *Mosquitoxylum***

75. Neotropics 76
– Paleotropics 78

76. Leaflets with a prominent marginal secondary vein; fruits pale gray to whitish **27. *Lithrea*** p. p.
– Leaflets lacking marginal secondary vein; fruit color variable but not as above 77

77. Leaflets petiolulate; corolla valvate or subvalvate; exocarp not easily separating from mesocarp at maturity **32. *Mauria*** p. p.
– Leaflets sessile to subsessile; corolla imbricate; exocarp easily separating from mesocarp at maturity **52. *Schinus*** p. p.

78. Prominent diagonally oriented admedial tertiary veins in leaflets often present; androecium often greater than diplostemonous; Africa and Madagascar **56. *Sorindeia*** p. p.
– Admedial tertiary veins in leaflets, if present, not prominent and not diagonally oriented; androecium diplostemonous; Australia, New Caledonia, and New Guinea 79

79. Leaves paripinnate or imparipinnate often with very reduced terminal leaflet, leaflets usually alternate; anther connective glandular; style 1; mesocarp fleshy **19. *Euroschinus***
– Leaves usually imparipinnate, terminal leaflet not reduced, leaflets opposite or subopposite; anther connective not glandular; stylodia 3; mesocarp woody **49. *Rhodosphaera***

Key to the Genera of Spondioideae

1. Leaves simple or unifoliolate 2
– Leaves compound 5

2. Stellate trichomes present; perianth 4-merous, stylodia 4 **71. *Lannea*** p. p.
– Stellate trichomes absent; perianth 4–5-merous; style 1 or stylodia 3 3

3. Leaves always simple; outside of Africa 4
– Leaves 1(–9)-foliolate; E Africa **78. *Sclerocarya*** p. p. (=*S. gillettii*)

4. Carpels 1, possibly pseudomonomerous; restricted to Yunnan, China **68. *Haplospondias***
– Carpels 4–6, distinct or basally distinct and syncarpous at mid ovary; widespread in tropical Asia, Malesia, Australia, Micronesia, Melanesia, and Samoa **63. *Buchanania***

5. Leaves bipinnately compound **80. *Spondias*** p. p. (=*S. bipinnata*)
– Leaves once compound 6

6. Stellate trichomes present **71. *Lannea*** p. p.
– Stellate trichomes absent 7

7. Hairy tuft domatia in secondary vein axils abaxially 8
– Hairy tuft domatia 0 14

8. Domatia hairy and marsupiform; stylodia and locules 5–12 9
– Domatia hairy and not marsupiform; stylodia and locules 1–5 10

9. Leaves evergreen; calyx valvate; stylodia and locules 5–12 **74. *Pleiogynium***
– Leaves deciduous; calyx slightly imbricate; stylodia and locules 5 **80. *Spondias*** p. p. (=*S. petelotii*)

10. Endocarp with opercula; fruits maturing dark red, (blue-)black, or dark brown 11
– Endocarp sometimes with 5 pores but lacking external opercula; fruits maturing yellowish or red to purplish 13

11. Leaflet apex usually emarginate or rounded, often with a pubescent mucro; fruits maturing dark red; endocarp not lobed, one apical operculum **67. *Haematostaphis***
– Leaflet apex usually acuminate, not mucronate; fruits maturing dark brown or (blue-)black; endocarp slightly 5-lobed, 3–5 subapical opercula 12

12. Plants hermaphrodite, carpels connate at apex and base only; perianth 5-merous; fruit depressed-globose or depressed-obovoid, 1–5 locules fertile; endocarp with 5 simple opercula or lids **66. *Dracontomelon*** p. p.
– Plants dioecious; carpels connate at base only; perianth 3–4-merous; fruit oblong-obovoid to ellipsoid, 1(–2) locule fertile; endocarp with 3–4 (–5) bipartite opercula (split into 2 equal halves by the radicle emergence) **77. *Pseudospondias*** p. p.

13. Scandent shrubs or climbers; leaflets always toothed; stylodia connivent, stigma discoid; fruits maturing red to purplish, endocarp crustaceous, 1-locular, lacking pores **73. *Pegia***
– Trees; leaflets usually entire but sometimes toothed; stylodia separate; stigmas capitate; fruits maturing green to yellow, the endocarp bony, 5-locular, with 4–5 pores toward the apex **64. *Choerospondias***

14. Leaf rachis alate 15
– Leaf rachis not alate 17

15. Leaf rachis broadly alate, leaflets microphyllous; fruits solitary, globose, endocarp relatively smooth, interrupted only by the opercula **72. *Operculicarya*** p. p.

– Leaf rachis narrowly alate, leaflets medium sized to large; fruits in racemes or panicles, (oblique-)oblong, endocarp surrounded by a fibrous matrix or interrupted by several irregular cavities 16
16. Leaflets falcate; stylodia 4–5; endocarp interrupted by several irregular cavities, opercula internal; South Africa **69. *Harpephyllum***
– Leaflets not falcate; stylodia 3; endocarp surrounded by a thick fibrous matrix, opercula not apparent; Madagascar **76. *Poupartiopsis***
17. Leaflets with an intramarginal vein (rarely a marginal secondary) 18
– Leaflets without an intramarginal or marginal secondary vein 19
18. Trees; stylodia (4–)5; drupe 4–5-locular, endocarp surrounded by a fibrous matrix **80. *Spondias*** p. p.
– Scandent trees; style 1; drupe 1-locular, endocarp woody and smooth (fibrous matrix lacking) **79. *Solenocarpus*** p. p. (=*S. indica*)
19. Drupe depressed-globose 20
– Drupe oblong, (ob)ovoid, or globose but not depressed 21
20. Plants polygamodioecious; leaves deciduous; drupe radially symmetric (pedicel scar on stone usually centered); fruit maturing yellow or light orange, endocarp surface pitted **62. *Antrocaryon***
– Plants hermaphrodite; leaves evergreen; drupe oblique (pedicel scar on stone markedly excentric); fruit maturing black or brown, endocarp surface relatively smooth **66. *Dracontomelon*** p. p.
21. Female flowers usually solitary; stamens 10–16(23); pistillode absent **78. *Sclerocarya*** p. p.
– Female flowers, if present, not solitary; stamens usually 10; pistillode present, or absent and flowers hermaphroditic 22
22. Scandent trees or hemi-epiphytes; style 1; fruit with single persistent style **79. *Solenocarpus*** p. p. (=*S. philippinensis*)
– Trees; stylodia 3–5; fruit with more than one persistent stylodia or style 0 23
23. Perianth usually 3–4-merous; continental Africa **77. *Pseudospondias*** p. p.
– Perianth usually 5-merous; outside of continental Africa 24
24. Pistil(ode) sparsely to densely pubescent; endocarp cartilaginous to crustaceous (rarely bony, e.g., *Tapirira mexicana*) 25
– Pistil(ode) usually glabrous; endocarp bony 26
25. Flowers usually unisexual; ovary not lobed; fruits maturing dark purple to black; cotyledons with purple striations; Neotropics **81. *Tapirira***
– Flowers bisexual; ovary 5-lobed; fruits maturing yellow; cotyledons without purple striations; Malesia **70. *Koordersiodendron***
26. Corolla valvate; external opercula absent; tropical Asia **62. *Allospondias***
– Corolla imbricate; external opercula present; Neotropics and Indian Ocean islands 27
27. Anther connective usually glandular; Neotropics **65. *Cyrtocarpa***
– Anther connective eglandular; Indian Ocean islands 28
28. Opercula 1; embryo horseshoe-shaped **72. *Operculicarya*** p. p.
– Opercula 2–5; embryo curved **75. *Poupartia***

I. Subfam. Anacardioideae Link (1831)

1. *Abrahamia* Randrianasolo & P.P. Lowry II

Abrahamia Randrianasolo & P.P. Lowry II (ined.).
Protorhus Engl. (1881), p. p.

Dioecious shrubs or trees with clear to milky white to red resinous exudate. Leaves alternate, opposite, or subopposite, simple, petiolate, entire; secondary veins parallel, usually evenly spaced. Inflorescences terminal and/or axillary panicles. Flowers pedicellate, articulate; perianth (4–)5(–6)-parted; sepals minute, connate; petals imbricate; androecium haplostemonous; filaments subulate; anthers dorsifixed; pistillode present or 0 in male flowers; staminodes reduced; disk glabrous, annular to cup-shaped with crenulate margin; carpels 3; style short, 3-branched; stigmas capitate; ovules 3, subapical, only 1 fertile. Drupe ellipsoid to oblong, 3-locular or unilocular; exocarp often beige, longitudinally striated; mesocarp fleshy; endocarp chartaceous to cartilaginous. Seed cotyledons ruminate, usually connate.

Nineteen species endemic to Madagascar.

2. *Actinocheita* F.A. Barkley

Actinocheita F.A. Barkley, Ann. Missouri Bot. Gard. 24: 2 (1937).
Rhus L. (1753), p. p.

Polygamodioecious shrubs or trees. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets sessile, densely pubescent. Inflorescences axillary panicles. Perianth 5-parted, densely pubescent; petals imbricate; androecium haplostemonous; anthers ovoid; filaments thickened and longer than anthers, pilose; pistillode reduced; staminodes reduced; disk modified into a gynophore; carpels 3, densely pubescent, trichomes often surpassing stylodia; stylodia 3, short; stigmas capitate; ovule basal. Drupe probably wind-dispersed, globose, 1-locular; exocarp reddish

brown, covered with very long-villous, violet-reddish trichomes.

A single species, *A. filicina*, endemic to south central Mexico.

3. *Amphipterygium* Schiede ex Standl.

Amphipterygium Schiede ex Standl., Contr. U.S. Natl. Herb. 23: 672 (1923); X.M.C. Figueroa, Ibugana Bol. IBUG 13(1): 27–47 (2005), rev.
Hypopterygium Schltdl. (1843).
Juliania Schltdl. (1843).

Dioecious shrubs or trees with milky exudate. Leaves deciduous, alternate, imparipinnate, trifoliolate, or rarely unifoliolate; leaflets opposite. Inflorescences axillary; male flowers arranged in pendent thyrses, female flowers tightly arranged and subtended by an involucre. Flowers perigynous; calyx 6–8-parted in male flowers, 0 in female flowers; corolla 0; androecium haplostemonous; filaments short; pistillode and staminodes 0; disk 0; carpels 3; stylodia 3; stigmatic lobes 3–4 per stylodium, revolute; ovule basal. Fruit a samaroid syncarp, 1-locular; exocarp brown; endocarp bony; peduncle much-dilated with tapering margins.

Four to five species in western Mexico south to northwestern Costa Rica.

Together with *Orthopterygium*, this genus is often segregated into the family Julianiaceae, but morphological and molecular data place it well within Anacardiaceae.

4. *Anacardium* L. Fig. 3G

Anacardium L., Sp. Pl. 383 (1753); Mitchell, Brittonia 44: 331–338 (1992), rev.; Mitchell & Mori, Mem. N. Y. Bot. Gard. 42: 1–76 (1987), rev.
Acajou (Tournefort) Adans. (1763).
Rhinocarpus Bert. & Balb. ex Humb., Bonpl. & Kunth (1824).

Andromonoecious subshrubs or trees with contact dermatitis-causing exudate. Leaves generally evergreen, alternate, simple, sessile to petiolate, entire, chartaceous to coriaceous; domatia usually present in secondary vein axils abaxially. Inflorescences terminal and/or axillary thyrsoids. Flowers pedicellate, articulate; perianth 5-parted; calyx imbricate; corolla of reflexed petals; stamens (6–)8–10(–12), fertile stamens 1(–4), much larger and exserted; filaments basally connate into a staminal tube; pistillode very reduced; staminodes 0 or in bisexual and male flowers reduced; disk 0; gynoecium pseudomonomerous; style straight to sigmoid (sometimes approaching gynobasic), apical or lateral; stigma punctiform, obscure; ovule basal. Drupe reniform, 1-locular, subtended by hypocarp, sigmoid to pyriform (rarely 0), white, green, yellow, or red; pericarp woody with large rectangular cavities containing caustic oils; exocarp greenish to brown to black. Seed with reniform embryo. $n = 12, 29$.

Eleven or more species, Honduras south to Paraguay, Brazil and Bolivia. *Anacardium occidentale* is cultivated pantropically.

5. *Androtium* Stapf

Androtium Stapf in Hook., Icon. Pl., t. 2763 (1903).

Hermaphrodite trees. Leaves evergreen, alternate, spiral, simple, petiolate, entire and recurved; primary and secondary veins prominent on ad- and abaxial surfaces. Inflorescences axillary panicles, pubescent. Flowers pedicellate, articulate, perianth (4–)5-parted, imbricate; petals pink with white tips; androecium diplostemonous; filaments subulate; anthers basifixed; connective apically bilobed, prolonged and dilated; disk glabrous, cupular and crenulate; carpels 5, connate at the base, pilose, only 1 (larger) fertile; style obscure; stigma oblique, slightly lateral; ovules 5, basal, only 1 fertile. Drupe lentiform, apex depressed, 5-locular.

A single species, *A. astylum* in peninsular Malaysia and Borneo.

Androtium is very similar in its gynoecium morphology to *Buchanania*, which has recently been shown to be a member of Spondioideae. Future studies may reveal that *Androtium* should also be recognized in this subfamily.

6. *Apterokarpos* C.T. Rizzini

Apterokarpos C.T. Rizzini, Leandra 5(6): 40 (1975).
Loxopterygium Hook.f. (1862), p. p.

Dioecious shrubs or trees. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite to subopposite. Inflorescences terminal panicles. Flowers subsessile to pedicellate; perianth

5-parted, imbricate; androecium haplostemonous; anthers dorsifixed; pistillode 0; staminodes reduced; disk glabrous; carpels 3; style simple; stigma 3-lobed; ovule 1. Drupe dry, oblique, laterally compressed, obovoid to discoid with persistent calyx; 1-locular.

A single species, *A. gardneri*, endemic to the Caatinga of northeastern Brazil.

7. *Astronium* Jacq.

Astronium Jacq., Enum. Syst. Pl. 10 (1760); F.A. Barkley, Phytologia 16: 107–152 (1969), rev.

Dioecious trees with clear contact dermatitis-causing exudate; bark sometimes with exfoliating patches. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite (alternate), petiolulate; cataphylls sometimes present. Inflorescences terminal and/or axillary thyrsoids. Flowers pedicellate, articulate; perianth 5-parted, imbricate; calyx larger in female flowers; corolla greenish white or yellowish and turning pink with age; androecium haplostemonous; stamens alternating with petals and lobes of disk; pistillode 0; staminodes reduced; disk glabrous, 5-lobed, very thin; carpels 3; stylodia 3, recurved; stigmas capitate; ovule apical or basal. Fruit fusiform, glabrous baccate or nutlet-like, wind-dispersed by accrescent, chartaceous sepals, often with persistent stylodia, 1-locular; mesocarp resinous; endocarp thin, brittle when dry. Seed with straight or pyramidal embryo. $n = 15$.

Seven or more species in Mexico south to Paraguay and northern Argentina.

8. *Baronia* Baker

Baronia Baker, J. Bot. 20: 67 (1882).
Rhus sect. *Baronia* (Baker) H. Perrier (1944).

Dioecious or hermaphrodite trees, rarely shrubs, with clear to milky or red exudate. Leaves evergreen or deciduous, alternate to subopposite, simple, petiolate, entire. Inflorescences terminal and/or axillary panicles. Flowers articulate; perianth 5-parted, imbricate; corolla white, yellow, or green; stamens 5(–4); anthers dorsifixed; pistillode rudimentary; staminodes reduced; disk glabrous, cup-shaped, crenulate; ovary glabrous; carpels 3; stylodia 3, short, basally connate, apical to lateral; stigmas capitate; ovule lateral. Drupe widely depressed, ovoid or sigmoid, with persistent calyx; exocarp with longitudinal striations; endocarp chartaceous.

One to three species endemic to Madagascar.

This genus is often treated as a subgeneric taxon of *Searsia* (*Rhus* s.l.), but molecular phylogenetic data (Pell et al. 2008) show that the three species (*B. taratana*, *Rhus perrieri*, and *R. thouarsii*) are far removed from *Searsia* (and *Rhus* s.s.), and indicate that two of the species (*R. perrieri* and *R. thouarsii*), recognized by some in *Protorhus*, should perhaps be placed in a new segregate genus.

9. *Blepharocarya* F. Muell.

Blepharocarya F. Muell., Fragm. 11: 15 (1878); Jessup, Fl. Australia 25: 170–187 (1985); B.S. Wannan, J.T. Waterhouse & C.J. Quinn, Bot. J. Linn. Soc. 95: 61–72 (1987), rev.

Dioecious trees with contact dermatitis-causing exudate. Leaves opposite, paripinnate or imparipinnate; leaflets opposite or subopposite. Inflorescences terminal and/or axillary highly condensed thyrsoids. Male inflorescences bracteate glomerules usually consisting of three 7-flowered dichasial cymes; female flowers inside a cupule of partly coherent and connate, bracteate, cymose branches; perianth 4-parted, more or less sepaloid; calyx basally connate; corolla imbricate in male flowers; androecium diplostemonous; anthers dorsifixed, introrse; pistillode columnar, apically pilose; staminodes 0; disk pilose, raised-annular in female flowers, flat-annular in male; carpels 1; style lateral, excentric filiform, dilated at stigma; ovule pendulous, lateral. Infructescence a cupule opening by numerous branched valves; drupe dry, indehiscent, laterally compressed, subreniform, ciliate; 1-locular.

Two species, Australia, one in monsoon forests of the Northern Territory, and one in dry and rain forests on the east coast of northern Queensland.

10. *Bonetiella* Rzed.

Bonetiella Rzed., Ciencia (Mexico) 16: 139 (1957).

Polygamodioecious shrubs with contact dermatitis-causing exudate. Leaves deciduous, alternate, simple, petiolate, entire, linear to trifid or pinnatifid. Inflorescences axillary panicles. Flowers subsessile to shortly pedicellate; perianth 5-parted,

imbricate; corolla greenish white; androecium haplostemonous; pistillode reduced; staminodes reduced; disk glabrous, 5-lobed; carpels 3; stylodia 3, short, subapical and unequal; stigmas 3; ovule basal. Drupe laterally compressed and subreniform, 1-locular; exocarp with numerous glands near remnant stylodia, yellowish; mesocarp thin, resinous; endocarp fibrous.

A single species, *B. anomala*, endemic to northern to central Mexico.

Morphological and molecular evidence suggests that *Bonetiella* is closely allied with *Pseudosmodingium*.

11. *Bouea* Meisn. Fig. 3D

Bouea Meisn., Pl. Vasc. Gen. 1: 75; 2: 55 (1837).

Andromonoecious trees with prominent terminal and axillary buds with bud scales. Leaves evergreen, opposite-decussate, simple, petiolate. Inflorescences axillary (rarely also terminal) panicles. Flowers pedicellate, non-articulate; perianth 3–5-parted; calyx valvate; corolla imbricate, white, greenish, or yellow, petals keeled along midrib; androecium haplostemonous; filaments subulate, glabrous; anthers basifixed with an apiculate connective; pistillode very reduced; staminodes 0; disk glabrous, small, flat or concave; gynoecium pseudomonomerous; style short; stigma rounded and flat, sometimes 2–3-grooved; ovule basal. Drupe subglobose to ellipsoid, 1-locular; exocarp yellow, orange, or red; mesocarp fleshy, edible; endocarp fibrous. Seed with straight embryo.

Three or more species in SE Asia south to western Malesia.

12. *Campnosperma* Thwaites

Campnosperma Thwaites in Hook., J. Bot. Kew Gard. Misc. 6: 65, t. 1 (1854), nom. cons.

Polygamodioecious trees with *Terminalia*-branching, often trunk buttressed or with stilt roots, and with contact dermatitis-causing exudate. Leaves evergreen, alternate, simple, sessile to petiolate (petioles sometimes with auriculate appendages), entire, coriaceous, peltate or lobed scales present ad- and abaxially; stellate trichomes sometimes present ad- and abaxially. Inflorescences axillary panicles. Perianth (3)4(5)-parted; corolla imbricate, white, greenish, yellow; stamens in two whorls of unequal length; anthers dorso-basifixed; pistillode very reduced; staminodes reduced; disk glabrous; round and flat in male flowers, cupular in female flowers; carpels 2; style short or obscure; stigma flattened, discoid, irregularly lobed; ovule pendulous, apical. Drupe subglobose or ovoid, incompletely 2-locular; exocarp generally red to black; endocarp woody. Seed cotyledons faintly plano-convex or flat; embryo curved.

Thirteen or more species: two from Honduras to northwest Ecuador and Amazonia; eleven or more in Madagascar (4+), the Seychelles (1), Sri Lanka (1), southeast Asia, Malesia, Micronesia, and Melanesia.

13. *Campylopetalum* Forman

Campylopetalum Forman, Kew Bull. 4: 555 (1954).

Dioecious herbaceous suffrutex. Leaves deciduous, opposite, decussate, simple, petiolate, palmately trilobed; domatia in secondary vein axils abaxially. Inflorescences terminal panicles, subtended by a pair of pinnately veined entire margined bracts in male plants and by palmately lobed bracts in female plants. Flowers pedicellate; perianth present in male flowers, 0 in female flowers, but female flowers subtended by a single bract; calyx apert, cup-shaped, with teeth-like lobes; corolla valvate, 4-parted; androecium diplostemonous; anthers with extrorse dehiscence, slightly pubescent; pistillode and staminodes 0; disk glabrous in male flowers, extremely reduced to 0 in female flowers; carpels 1; style filiform; stigma not differentiated; ovule pendulous, basal. Drupe subtended by an accrescent bract that aids in wind dispersal, 1-locular; exocarp brown; $n = 7$.

A single species, *C. siamense*, is endemic to northern Thailand.

Together with *Dobinea*, this genus is often placed in a separate family, Podoaceae, but molecular and morphological data suggest that it belongs in Anacardiaceae.

14. *Cardenasiodendron* F.A. Barkley

Cardenasiodendron F.A. Barkley, Lloydia 17: 242 (1954). *Loxopterygium* Hook.f. (1862), p. p.

Dioecious trees with contact dermatitis-causing exudate. Leaves deciduous, alternate,

imparipinnate, petiolate; leaflets opposite or subopposite, petiolulate; venation craspedodromous. Inflorescences terminal and/or axillary, compound panicles with ultimate branches spicate. Flowers sessile, subtended by three triangular bracts; perianth 5-parted, imbricate; androecium haplostemonous; stamens alternating with lobes of disk; pistillode minute; disk glabrous, 5-lobed; carpels 3; stylodia 3; stigmas 3; ovule basal. Samara obovate to subreniform with two unequal wings and persistent calyx, 1-locular. Seed obliquely curved.

A single species, *C. brachypterum*, endemic to Bolivia.

15. *Comocladia* P. Br.

Comocladia P. Br., Civ. Nat. Hist. Jamaica 124 (1756).

Polygamodioecious shrubs or trees, usually not branching, with contact dermatitis-causing exudate turning black with exposure to air. Leaves alternate, imparipinnate, petiolate; leaflets opposite, petiolulate, entire or toothed to spinose. Inflorescences axillary panicles; perianth 3–4-parted, imbricate; calyx light red; corolla red to purple; androecium haplostemonous; filaments subulate to filiform, inserted at notches in disk; anthers basifixed; pistillode very reduced; staminodes very reduced; disk glabrous, cup-shaped, slightly lobed; carpels 3; stylodia 0 or 3, short; stigmas 3; ovule pendulous, basal. Drupe oblong-ellipsoidal with persistent calyx, 1-locular; exocarp yellow, red, or black; mesocarp fleshy. Seed oblong; cotyledons fleshy.

Sixteen or more species widespread in central Mexico south to Guatemala, Belize, and the Greater and Lesser Antilles.

16. *Cotinus* Miller

Cotinus Miller, Gard. Dict. Abr. Ed., 4 (1754).
Rhus L. (1753), p. p.

Dioecious or gynodioecious (polygamodioecious or monoecious), shrubs or trees with contact dermatitis-causing exudate. Leaves deciduous, alternate, simple, petiolate, entire, oblong, secondary venation cladodromous. Inflorescences terminal panicles. Flowers pedicellate; perianth 5-parted, imbricate; corolla greenish or yellowish white; androecium haplostemonous (diplostemonous); filaments subulate; pistillode present; staminodes present or 0; disk glabrous; carpels 3; stylodia 3, lateral; stigmas 3; ovule pendulous, basal. Drupe obliquely ovoid, 1-locular, with persistent calyx; fruiting panicles wind-dispersed like a tumbleweed, aided by elongated plumose pedicels of numerous aborted flowers. Seed reniform. $n = 15$.

Four or more species: one in temperate, southern United States and northern Mexico; one in central to southern Europe, east to China; and two species in south-central China.

Two Mexican species, *C. chiangii* and *C. carranzae*, are problematic and need further taxonomic investigation. We recognize the former species in *Rhus* here, but it may represent a distinct evolutionary lineage apart from other former tribe Rhoeae members. An additional species, *C. kanaka*, was transferred from *Rhus* in *Flora of India*, but this affinity is somewhat uncertain.

17. *Dobinea* Buch.-Ham. ex D. Don

Dobinea Buch.-Ham. ex D. Don, Prod. Fl. Nep. 249 (1825).
Podoön Baill. (1887).

Dioecious shrubs. Leaves opposite or alternate, simple, petiolate, serrate. Inflorescences terminal, pyramidal panicles. Flowers pedicellate (female pedicels very short), non-articulate; perianth 4-parted in male flowers, 0 in female flowers but these flowers each subtended by a leafy bract; calyx cupular with tiny dentate lobes; corolla yellowish; androecium diplostemonous, glabrous; pistillode very reduced, style pilose; staminodes 0; disk 0 in male flowers, glabrous and annular in female flowers; carpels 1; style filiform, curved; stigma not differentiated; ovule pendulous, basal or sublateral. Drupe orbicular and compressed, peltate on an accrescent, obovate or rounded bract that aids in wind dispersal, 1-locular; bract and fruit with prominent venation; style persistent and curled; exocarp whitish to brown. n=7.

Two species in northern India, Nepal, Bhutan, and China.

Together with *Campylopetalum siamense*, this genus is often placed in a separate family, Podoaceae, but molecular and morphological data suggest that it belongs in Anacardiaceae.

18. *Drimycarpus* Hook. f.

Drimycarpus Hook.f. in Benth. & Hook.f., Gen. Pl. 1: 424 (1862).
Semecarpus L. f. (1781), p. p.
Holigarna Buch.-Ham. ex Roxb. (1820), p. p.

Polygamodioecious trees. Leaves evergreen, alternate, simple, petiolate, entire. Inflorescences terminal and/or axillary panicles or racemes. Flowers articulate, epigynous; perianth (4–) 5-parted, imbricate; corolla white, greenish, or yellow; androecium haplostemonous; anthers dorsifixed; pistillode reduced; staminodes reduced; disk glabrous; ovary inferior; carpels 3; style short; stigmas 3, capitate; ovule pendulous, basal to sublateral. Drupe transverse oblong, 1-locular; mesocarp resinous; endocarp coriaceous. Seed with straight embryo.

Three or more species in India to Myanmar, Indo-China to Borneo.

19. *Euroschinus* Hook. f.

Euroschinus Hook.f. in Benth. & Hook., Gen. Pl. 1: 422 (1862).

Polygamodioecious trees. Leaves evergreen, alternate, paripinnate (imparipinnate with terminal leaflet very reduced), petiolate; leaflets alternate, often falcate, with hairy tuft domatia sometimes in vein axils abaxially; cataphylls sometimes present. Inflorescences terminal and/or axillary thyrsiform panicles. Flowers sessile or short pedicellate, articulate; calyx apert, fused at base; corolla imbricate; androecium diplostemonous; connective glandular; pistillode reduced; staminodes reduced; disk glabrous, 5-lobed; carpels 3; style short; stigmas 3; ovule pendulous, subapical. Drupe obliquely ovoid, 1-locular; exocarp green, gray, blue, purple or blue-black; mesocarp fleshy.

Nine or more species: one in New Guinea, one in Australia, seven in New Caledonia.

20. *Faguetia* Marchand

Faguetia Marchand, Rév. Anacard.: 174 (1869).

Dioecious, or possibly monoecious, trees. Leaves evergreen, alternate, imparipinnate, petiolate; leaflets opposite, petiolulate, falcate. Inflorescences axillary, branched cymes. Flowers pedicellate; perianth 4(–5)-parted in male flowers, 4-parted in female flowers; calyx subvalvate; corolla imbricate, venation prominent; androecium haplostemonous; filaments distinct, alternating with petals; pistillode very reduced; staminodes reduced; disk glabrous, annular, 4–6-lobed; carpels (2)3; style 0; stigma 2–3-lobed, capitate; ovule lateral to subbasal. Samara large, dry, flattened with a terminal wing; exocarp (and possibly mesocarp) with copious oleoresins.

A single species, *F. falcata* Marchand, endemic to eastern Madagascar.

21. *Fegimanra* Pierre ex Engl. Fig. 3B

Fegimanra Pierre ex Engl. in Engl. & Prantl, Natürl. Pflanzenfam. III, 5: 458 (1896).

Andromonoecious or monoecious trees with contact dermatitis-causing exudate. Leaves evergreen, alternate, simple, petiolate, entire, subcoriaceous to coriaceous. Inflorescences terminal and/or axillary thyrsoids. Flowers short pedicellate; perianth 4-parted; calyx apert; corolla imbricate, forming a tube basally, apically spreading; stamen 1; filament subulate, villous; anther basi- or dorsifixed; pistillode very reduced; staminode may be present but only slightly reduced (fertility of stamen in female/bisexual flower is in doubt); disk 0: gynoecium pseudomonomerous or possibly truly monomerous; style apically decurved, lateral; stigma minutely bilobed or punctiform; ovule lateral. Drupe asymmetrically reniform and subtended by a small hypocarp.

Three species in Upper Guinean West Africa and Cameroon south to Gabon.

22. *Gluta* L. Fig. 3E

Gluta L., Mant. Pl. 2: 293 (1771).
Melanorrhoea Wall. (1829).

Hermaphrodite trees, rarely large shrubs with contact dermatitis-causing exudate. Leaves evergreen or deciduous, alternate, simple, sessile to petiolate, entire. Inflorescences axillary panicles. Flowers pedicellate, articulate or non-articulate; calyx calyptriform, circumscissile or bursting irregularly at anthesis, caducous; corolla imbricate and/or contorted, rarely valvate; petals (4)5 (8), white, often red or yellow at base and/or changing to pink; stamens 4, 5, 10 to 100+, sometimes inserted on conical torus; filaments glabrous or pubescent; anthers dorsifixed; disk

0; gynoecium sessile or supported by a gynophore atop the torus, obovoid, ellipsoid or subglobose, glabrous or pubescent, pseudomonomerous; style filiform, lateral to sublateral; stigma punctiform; ovule basal. Drupe smooth to wrinkled, sessile or stalked, globose to reniform, 1-locular; some species wind-dispersed by persistent, accrescent, wing-like petals; exocarp brown to purplish red to black. Seed cotyledons sometimes incompletely fused; embryo straight (rarely slightly curved).

Thirty or more species in Madagascar (1), India, Myanmar to Indo-China and Malesia.

23. *Haplorhus* Engl.

Haplorhus Engl., Bot. Jahrb. 1: 419 (1881).

Dioecious trees. Leaves evergreen, alternate, simple, sessile to very short petiolate, linear to lanceolate. Inflorescences axillary panicles. Flowers sessile; perianth 5-parted; epicalyx and red to purple tepals of female flowers imbricate; male flowers subtended by bracts, tepals pink, imbricate; androecium haplostemonous; anthers basifixed; pistillode 0; staminodes 0; disk glabrous; carpels 3; stylodia 3, short; stigmas capitate; ovule pendulous, basal. Drupe obliquely ovoid, 1-locular; exocarp red; mesocarp thin, fleshy; endocarp cartilaginous.

A single species, *H. peruviana*, endemic to dry inter-Andean valleys of central Peru south to northern Chile.

24. *Heeria* Meisn.

Heeria Meisn., Gen. Comm.: 55 (1837).
Anaphrenium E. Mey. ex Endl. (1841), p. p.

Dioecious shrubs or small trees with watery exudate. Leaves evergreen, alternate, simple, petiolate, entire, coriaceous, strongly discolorous with fine silvery trichomes and parallel venation prominent abaxially. Inflorescences terminal or axillary, spiciform panicles, with lignified, unicellular trichomes on subtending bracts, pedicels, and abaxial surface of calyx. Flowers pedicellate, articulate; perianth 5-parted; corolla imbricate, recurved at anthesis, cream-colored; androecium haplostemonous; pistillode reduced; staminodes reduced; disk glabrous, orange; lobed in male flowers, annular in female flowers; carpels 3; stylodia 3, excentric, distinct or basally connate; stigmas capitate; ovule basal to sublateral. Drupe globose, depressed, 1-locular; pericarp coriaceous and slightly shriveled; exocarp yellowish green, longitudinally rugose-striate. Seed large, recalcitrant.

A single species, *H. argentea*, endemic to South Africa.

25. *Holigarna* Buch.-Ham. ex Roxb. Fig. 4

Holigarna Buch.-Ham. ex Roxb., Hort. Beng.: 22 (1814).

Polygamodioecious or dioecious trees with contact dermatitis-causing exudate turning black with exposure to air. Leaves alternate, spiral, simple, petiolate (4 spur-like caducous or persistent appendages along petiole margins), entire. Inflorescences terminal and/or axillary panicles. Flowers pedicellate, epigynous, with a well-developed hypanthium; perianth 5-parted; calyx imbricate, cupular; corolla valvate; androecium

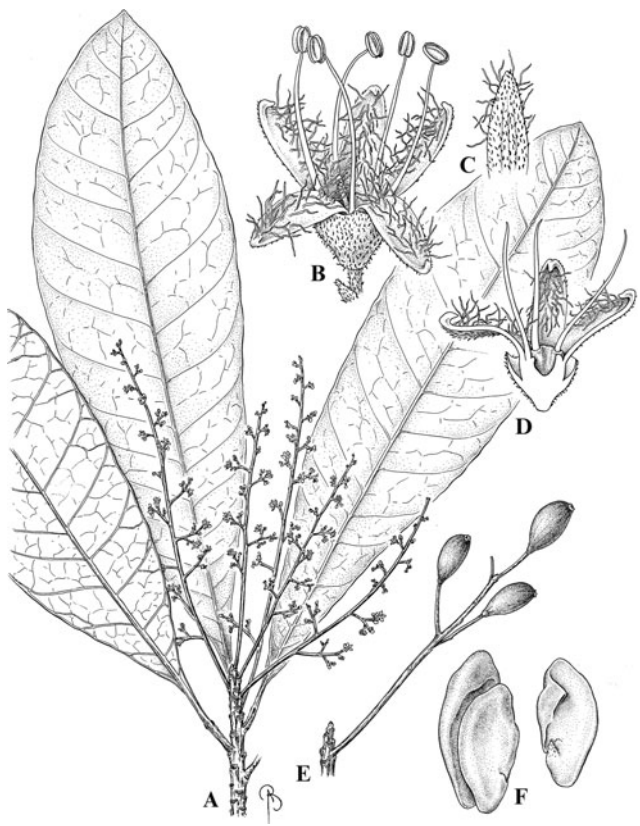

Fig. 4. Anacardiaceae. *Holigarna ferruginea*. **A** Branchlet of male plant. **B** Male flower. **C** Abaxial surface of petal. **D** Male flowers with anthers missing, vertical section. **E** Infructescence showing fruit derived from inferior ovary. **F** Embryo with large cotyledons. (Reproduced with permission of the artist Bobbi Angell)

haplostemonous; disk glabrous, obscure in bisexual flowers; carpels 3–5; ovary inferior; stylodia 3–5, apical; stigmas clavate; ovule pendulous, apical or lateral. Drupe sometimes enclosed within obconic and turbinate hypocarp, 1-locular; mesocarp contains an abundance of black resin.

Seven or more species in India, Bangladesh, Myanmar, and Indochina.

26. *Laurophyllus* Thunb.

Laurophyllus Thunb., Nov. Gen. Pl. 6: 104 (1792).
Botryceras Willd. (1860).

Dioecious shrubs. Leaves evergreen, alternate, simple, petiolate, elliptic-oblong, serrate. Inflorescences terminal and/or axillary, highly condensed panicles characterized by fusion of higher order branches into flattened broad segments. Flowers pedicellate; perianth 4–5-lobed almost to the base, imbricate; petals white, lanceolate in female flowers; androecium haplostemonous; filaments filiform; pistillode and staminodes 0; disk glabrous, fleshy and broad; carpels 1; style lateral or excentric; stigma bilobed or trilobed, capitate; ovule pendulous, apical or subapical. Samara hard, ovoid, laterally compressed with a marginal wing, 1-locular; pericarp with prominent venation.

A single species, *L. capensis*, endemic to wooded hillsides and stream banks of the eastern Cape of South Africa.

27. *Lithrea* Hook.

Lithrea Hook., Bot. Misc. 3: 175 (1833), sphalm., nom. cons.
Lithraea Miers ex Hook. & Arn. (1826), partim.; F.A. Barkley, Phytologia 8(7): 329–365 (1962), rev.
Schinus L. (1753, 1754), p. p.

Dioecious shrubs or trees with contact dermatitis-causing exudate. Leaves evergreen, alternate, imparipinnate or unifoliolate, petiolate; rachis often alate; leaflets sessile, entire; marginal secondary vein prominent. Inflorescences terminal and/or axillary panicles. Flowers pedicellate, articulate; perianth 5-parted; calyx apert to slightly imbricate, lobes minutely deltate; corolla valvate in bud, greenish-white to greenish-yellow; androecium diplostemonous; pistillode reduced; staminodes reduced; disk glabrous, 10-lobed; carpels 3; stylodia 3, basally connate, apical; stigmas capitate; ovule basal. Drupe globose, 1-locular; exocarp pale gray to whitish, smooth, brittle and easily separating from mesocarp at maturity; mesocarp resinous, attached to endocarp; endocarp bony. $n = 15$.

Three species in Brazil, Bolivia, Paraguay, Argentina, Uruguay, and Chile.

28. *Loxopterygium* Hook. f.

Loxopterygium Hook.f. in Benth. & Hook., Gen. Pl. 1: 419 (1862); F.A Barkley, Lloydia 25: 109–122 (1962), rev.

Polygamodioecious trees with contact dermatitis-causing exudate, clear or white and turning black with exposure to air. Leaves usually deciduous (*L. sagotii* may be evergreen), alternate, imparipinnate, petiolate; leaflets opposite or alternate, petiolulate, entire to crenate or serrate. Inflorescences axillary or rarely terminal thyrsoids. Flowers pedicellate; perianth 5-parted, imbricate; corolla yellowish green; androecium haplostemonous; pistillode reduced; staminodes reduced; disk glabrous, annular and 5-lobed; carpels 3; stylodia 3, unequal, lateral; stigmas capitate or discoid; ovule pendulous or short-funiculate, basal to lateral. Samara falcate, 1-locular; lateral wing chartaceous with prominent venation, stigmas persistent in fruit; endocarp bony. Seed with curved embryo. $n = 15$.

Three species with disjunct distributions from Venezuela south to Argentina, absent from Amazonia; *L. sagotii* in Venezuela and the Guianas; *L. huasango* in southwestern Ecuador to northwestern Peru; *L. grisebachii* in Bolivia south to northwestern Argentina.

29. *Loxostylis* Spreng. f. ex Rchb.

Loxostylis Spreng. f. ex Rchb., Ic. Exot. Cent. 3: 3, t. 205 (1827).

Dioecious trees with contact dermatitis-causing exudate. Leaves evergreen, alternate, imparipinnate, petiolate; rachis alate; leaflets opposite, sessile, entire. Inflorescences terminal panicles. Flowers pedicellate, non-articulate; perianth 4–5-parted, imbricate; calyx fused at base, initially green, turning pink to dark red in flower and fruit; corolla white to cream-colored, caducous; androecium haplostemonous; stamens unequal in length; pistillode 0; staminodes reduced; disk glabrous, with five 2-lobed projections;

ovary papillose; carpels 1–4; stylodia 1–4, lateral; stigmas capitate; ovule basal. Drupe ellipsoidal, resinous and flattened, subtended by enlarged, dark red calyx, 1-locular; exocarp brown, brittle and easily separating from mesocarp at maturity, rippled.

A single species, *L. alata* Spreng. f. ex Rchb., endemic to rocky outcroppings of eastern South Africa.

30. *Malosma* Nutt. ex Abrams

Malosma Nutt. ex Abrams, Fl. Los Angeles 3: 220 (1917). *Rhus* subg. *Malosma* Nutt. ex Torr. & A. Gray (1838). *Rhus* sect. *Venenatae* Engl. (1881), p. p.

Polygamodioecious shrubs or trees. Leaves evergreen, alternate, simple, petiolate, entire, longitudinally plicate. Inflorescences terminal thyrsoids. Flowers pedicellate; perianth 5-parted, imbricate; corolla whitish; androecium haplostemonous; pistillode reduced; staminodes reduced; disk glabrous; carpels 3; stylodia 3, short; stigmas 3; ovule basal. Drupe laterally compressed, glabrous, 1-locular; exocarp white; mesocarp thick, waxy; endocarp bony.

A single species, *M. laurina*, in chaparral of southern California south to central Baja California, Mexico.

Malosma is segregated from *Rhus* on the basis of having a white exocarp and lacking glandular trichomes.

31. *Mangifera* L. Fig. 3F

Mangifera L., Sp. Pl.: 200 (1753); A.J.G.H. Kostermans & J.M. Bompard, The mangoes: their botany, nomenclature, horticulture and utilization. Academic Press, San Diego, CA, (1993), rev.

Andromonoecious trees with contact dermatitis-causing exudate. Leaves evergreen, alternate, simple, petiolate, entire, lanceolate; apex acute to acuminate; cataphylls sometimes present. Inflorescences terminal and/or axillary thyrsoids. Flowers pedicellate, articulate; perianth 5-parted, imbricate; corolla white to pink, often with yellow or pink glandular ridges on adaxial surface; stamens 5(–10), only 1–2 (3–5 or all) fertile, the others much reduced; filaments distinct or connate at base; anthers dorsifixed; pistillode reduced; disk glabrous, extrastaminal (intrastaminal), papillose or glabrous, 4–5-lobed; gynoecium pseudomonomerous; style lateral, sometimes approaching gynobasic; stigma punctiform; ovule basal. Drupe subglobose, sigmoid, subreniform or ovoid, 1-locular; exocarp green, yellow, orange, red to brown or black; mesocarp fleshy; endocarp woody-fibrous. Seed oblong-ovoid, compressed; cotyledons usually plano-convex (sometimes lobed and the radicle ascendant), rarely the cotyledons and inner seed coat form a labyrinth; testa chartaceous; embryo curved. n=20 or 30, polyploidy common.

Sixty-nine species in tropical Asia and India east to Malesia and the Solomon Islands; greatest diversity in western Malesia. *Mangifera indica* is cultivated pantropically.

32. *Mauria* Kunth

Mauria Kunth, Ann. Sci. Nat. I, 2: 338 (1824).

Hermaphrodite, sometimes cleistogamous, or less frequently polygamodioecious shrubs or trees with contact dermatitis-causing exudate. Leaves evergreen or deciduous, alternate, simple, trifoliolate, or imparipinnate, petiolate; leaflets opposite, petiolulate, entire or weakly toothed; hairy tuft domatia sometimes present in secondary vein axils abaxially. Inflorescences terminal and/or axillary panicles or pleiothyrsoids; flowers pedicellate; perianth 5-parted; calyx short-cupulate; corolla valvate or subvalvate; androecium diplostemonous; stamens sometimes of unequal lengths; filaments subulate; anthers dorsifixed, connective extended slightly above anthers; disk glabrous, 10-crenulate; carpels 3; style short; stigma 3-lobed; ovule pendulous, lateral or subapical. Drupe laterally compressed, oblique, crowned by vestigial style, 1-locular; exocarp orange, red, to brown; mesocarp thin, fleshy; endocarp chartaceous. Seed with flattened embryo.

Ten to fifteen Andean and Central American species: El Salvador south to eastern Venezuela and extreme northern Argentina.

33. *Melanochyla* Hook. f.

Melanochyla Hook.f., Fl. Brit. Ind. 2: 38 (1876); Ding Hou, Fl. Males. I, 8: 490–499 (1978).

Dioecious trees with short buttresses or stilt roots and contact dermatitis-causing exudates turning

black with exposure to air. Leaves alternate, simple, petiolate, entire, papillose abaxially. Inflorescences terminal and/or axillary panicles, rarely fascicles. Flowers pedicellate, articulate, perigynous; perianth 5-parted; corolla imbricate, campanulate, white, yellow, or dark brown; petals pubescent ad- and abaxially; androecium haplostemonous; filaments distinct or lower part adnate to petals, densely pubescent; anthers dorsifixed; pistillode present or 0 in male flowers, very reduced; staminodes reduced; disk glabrous, rim-like, 4–5-lobed; carpels 3; style short; stigmas 3; ovule pendulous, apical to subapical. Drupe ellipsoid, ovoid, subglobose, depressed globose, oblong; adnate to base of hypanthium, subtended by an accrescent calyx; 1-locular; exocarp yellow, covered with rusty-brownish trichomes; mesocarp and endocarp with black resin. Seed cotyledons distinct; embryo straight.

Thirty species in Thailand, Sumatra, Peninsular Malaysia, and Borneo.

34. *Melanococca* Blume

Melanococca Blume, Mus. Bot. Lugd. Bat. 1: 236 (1850).
Duckera F.A. Barkley (1942).
Rhus sect. *Melanocarpae* Engl. (1881).
Rhus subg. *Melanococca* (Blume) Brizicky (1963).

Dioecious trees with white exudate turning black with exposure to air. Leaves alternate, imparipinnate, petiolate; leaflets petiolulate, entire; tertiary and quaternary veins freely ramified (i.e., no areolation). Inflorescences terminal and/or axillary panicles, branches tomentose. Flowers short pedicellate; perianth 5-parted, imbricate; sepal margins pubescent; corolla cream-white, rarely pink; petals basally hairy adaxially; androecium haplostemonous; anthers dorsifixed; pistillode reduced; staminodes reduced; disk glabrous, 10-lobed; carpels 3; style obscure; stigmas 3, more or less united; ovule basal. Drupe subglobose, 1-locular; exocarp black, not separating from mesocarp when ripe; stigmas persistent in fruit.

A single species, *M. tomentosa* (=*Rhus taitensis*), in Australia (Queensland), Philippines, and Java east to Tahiti.

Melanococca is segregated from *Rhus* on the basis of having a black exocarp that does not separate from the mesocarp at maturity.

35. *Metopium* P. Br.

Metopium P. Br., Civ. Nat. Hist. Jamaica: 177 (1756); F.A. Barkley, Ann. Missouri Bot. Gard. 24: 265–499 (1937), rev.
Rhus L. (1753), p. p.

Dioecious trees or shrubs with prominent resin ducts and contact dermatitis-causing exudate turning black with exposure to air. Leaves evergreen, imparipinnate, petiolate; leaflets petiolulate, entire; mature leaflets often speckled with black spots. Inflorescences axillary panicles, lax. Flowers pedicellate, non-articulate; perianth 5-parted, imbricate; calyx fused; corolla yellow-green with dark veins; androecium haplostemonous; anthers basi- or dorsifixed; pistillode reduced; staminodes reduced; disk glabrous, 5-lobed; carpels 3; style short; stigma 3-lobed; ovule pendulous, basal. Drupe ellipsoidal to obovoid, 1-locular; exocarp orange to brown, glabrous. Seed compressed, somewhat quadrangular; funicle expanded, covering one margin; embryo oriented vertically but with a curved radicle.

Three species in West Indies, southern Florida (US), Mexico, and northern Central America.

36. *Micronychia* Oliv.

Micronychia Oliv. in Hook., Icon. Pl. 14: 27, t. 1337 (1881); Randrianasolo, Adansonia III, 22: 145–155 (2000), rev.; Randrianasolo & Lowry II, Adansonia III, 31: 157–168 (2009), key.

Dioecious trees with clear to milky exudate. Leaves evergreen, alternate to subopposite, simple, sessile or petiolate, entire. Inflorescences terminal and/or axillary panicles, often pendulous. Perianth 5-parted; calyx very small, sepals more or less basally connate; corolla imbricate, white, cream-colored, yellow, pink, or red; androecium haplostemonous; filaments straight to sigmoid; anthers dorsifixed; pistillode reduced; staminodes reduced; disk glabrous, annular to cup-shaped; carpels 3; style 3-branched, lateral; stigmas capitate; ovule apical. Drupe small, sigmoid, 1-locular; exocarp with longitudinal striations visible when dry; mesocarp fleshy.

Ten species endemic to Madagascar.

37. *Mosquitoxylum* Krug & Urb.

Mosquitoxylum Krug & Urb., Notizbl. Königl. Bot. Gart. Berlin 1: 78 (1895); F.A. Barkley & M.J. Reed, Am. Midl. Nat. 24: 666–679 (1940), rev.

Polygamodioecious (androdioecious) trees. Leaves evergreen (more or less), alternate, imparipinnate; leaflets opposite or subopposite, short-petiolulate, entire. Inflorescences terminal and/or axillary panicles with spicate branches. Flowers sessile or short-pedicellate, each subtended by 3 deltoid bracts; perianth 5-parted, imbricate; corolla greenish white, or cream-colored; androecium haplostemonous; pistillode reduced; staminodes in female flower very reduced; disk glabrous, 5-lobed; carpels 3; style short, distally 3-branched, excentric; stigmas 3; ovule sublateral. Drupe obliquely ovoid, compressed, 1-locular; exocarp red, glabrous.

A single species, *M. jamaicense*, southern Mexico south to northwestern Ecuador and Jamaica.

Morphological and molecular evidence suggests that *Mosquitoxylum* is closely related to *Rhus*.

38. *Myracrodruon* Allem.

Myracrodruon Allem. in Trab. Comm. Sc. Expl. Ceará, Secc. Bot. 3, tt. 1, 2 (1862); D.A. Santin & H. de F. Leitão Filho, Revista Brasil. Bot. 14: 133–145 (1991), rev.
Astronium Jacq. (1760), p. p.

Dioecious trees with contact dermatitis-causing exudate. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets petiolulate, entire or serrate. Inflorescences terminal and/or axillary thyrsoids. Flowers pedicellate, articulate; perianth 5-parted, imbricate; corolla greenish-white or cream-colored to purplish; androecium haplostemonous; pistillode reduced; staminodes reduced; disk glabrous, 5-lobed in male flowers and annular in female flowers; carpels 3; stylodia 3, apical; stigmas capitate; ovule lateral or basal. Drupe subglobose, subtended by persistent stiffened and expanded sepals, 1-locular; exocarp brown.

Two or more species in sub-Amazonian Brazil, Bolivia, Paraguay, and northern Argentina.

This genus is segregated from *Astronium* by its ovule position and fruit morphology.

39. *Nothopegia* Blume

Nothopegia Blume, Mus. Bot. Lugd. Bat. 1: 203 (1850).
Glycycarpus Dalz. (1849).

Dioecious (androdioecious) trees with contact dermatitis-causing, milky exudate turning black with exposure to air. Leaves alternate to subopposite, simple, petiolate, entire, lanceolate to elliptic. Inflorescences axillary or pseudoterminal racemes. Flowers short pedicellate; perianth 4-parted, imbricate; corolla of distinct, twisted white petals; androecium haplostemonous; filaments pubescent to nearly glabrous; anthers pubescent; pistillode very reduced; staminodes reduced; disk glabrous, 4–5-lobed; carpels 3; style apical; stigma 1–3-lobed; ovule pendulous, apical to lateral. Drupe depressed globose or pyriform with persistent calyx and style, 1-locular; exocarp red to dark purple, sometimes longitudinally striate; mesocarp fleshy.

Ten or more species in India and Sri Lanka.

40. *Ochoterenaea* F.A. Barkley

Ochoterenaea F.A. Barkley, Bull. Torrey Bot. Club 69: 442 (1942).

Dioecious trees with milky exudate. Leaves alternate, imparipinnate, petiolate; leaflets opposite, sessile to very short petiolulate, entire, lanceolate, membranaceous, puberulent ab- and adaxially. Inflorescences terminal corymbose thyrsoids. Flowers pedicellate; perianth 5-parted, valvate; androecium haplostemonous; pistillode reduced, stylode simple; staminodes reduced; disk glabrous, annular; carpels 3, 1 fertile; stylodia 3, basally connate, lateral; stigmas capitate; ovule basal. Samara laterally compressed with long, violet trichomes on the margins, 1-locular by abortion.

A single species, *O. colombiana*, in Panama, Andean Venezuela and Colombia south to Bolivia.

Without nomenclatural conservation, the species name may change if *Rhus samo* is shown to be an earlier basionym as expected.

41. *Orthopterygium* Hemsl.

Orthopterygium Hemsl. in Phil. Trans. R. Soc. London B, 199: 190 (1907).

Dioecious shrubs or trees with milky exudate. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite, sessile to very short petiolulate, crenate. Inflorescences terminal; male flowers arranged in pendent or erect panicles, female flowers tightly arranged in 3-flowered clusters subtended by an involucre (2 flowers abort); male flowers pedicellate, females sessile; calyx 3–8-parted in male flowers, 0 in female

flowers; corolla 0; androecium haplostemonous; pistillode and staminodes 0; disk 0; carpels 3; stylodia slightly basally connate, apical; stigmas 3; ovule pendulous, basal. Syncarp samaroid, with little-dilated peduncle with parallel margins, 1-locular; exocarp brown.

A single species, *O. huaucui*, endemic to western Peru.

Together with *Amphipterygium*, this genus is often segregated into the family Julianiaceae, but morphological and molecular data place it well within Anacardiaceae.

42. *Ozoroa* Delile

Ozoroa Delile in Ann. Sci. Nat. II, 20: 91, t. 1 (1843); R.B. Fernandes, Garcia de Orta (Lisboa) 14: 19–60 (1966), rev.
Heeria Meissn. (1837), p. p.
Anaphrenium E. Mey. ex Endl. (1841), p. p.

Dioecious subshrubs, shrubs, or trees, with milky exudate. Leaves evergreen, alternate, opposite, or whorled, simple, petiolate, entire. Inflorescences terminal and/or axillary panicles. Flowers pedicellate, articulate; perianth 5-parted, imbricate; corolla patent or inflexed at the apex, white, yellow, or reddish, often pubescent; androecium haplostemonous; filaments subulate; anthers dorsifixed; pistillode very reduced; staminodes reduced; disk glabrous, crenulate; carpels 3; stylodia 3, slightly connate at base or distinct; stigmas capitate; ovule pendulous, lateral or basal. Drupe transversely reniform, subglobose or globose, 1-locular; exocarp black shiny or red turning black; mesocarp fleshy; endocarp bony. Seed obovate, compressed.

Forty or more species in sub-Saharan Africa and Yemen.

43. *Pachycormus* Coville

Pachycormus Coville in Cent. Dict., rev. ed., 6708 (1911).
Rhus L. (1753), p. p.
Bursera Jacq. ex L. (1762), p. p.

Dioecious trees with short trunk and crooked branches, caudiciform; outer white to yellow bark exfoliating, revealing green inner bark, with milky exudate drying clear. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite to subopposite, sessile to short-petiolulate, entire to irregularly lobed, elliptic. Inflorescences axillary panicles. Flowers pedicellate; perianth 5-parted, white to dark pink; calyx subvalvate; corolla exduplicate-valvate; androecium diplostemonous; pistillode very reduced; staminodes reduced; disk present but not well known, may be alternating with stamens; carpels 3; stylodia 3; stigmas capitate. Utricle pubescent; 1-locular.

A single species, *P. discolor*, endemic to central Baja California, Mexico.

44. *Parishia* Hook. f.

Parishia Hook.f., Trans. Linn. Soc. 23: 169, t. 26 (1860); Ding Hou, Flora Males. I, 8: 541–545 (1978).

Dioecious trees with contact dermatitis-causing, white to brown exudate turning black with exposure to air. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite to subopposite, petiolulate, entire. Inflorescences terminal and/or axillary panicles. Flowers pedicellate, articulate; perianth 4-parted, imbricate; androecium haplostemonous; filaments filiform, thin, glabrous; anthers dorsi- to basifixed; pistillode very reduced; staminodes reduced; disk pubescent; carpels 3; stylodia 3(4), very short; stigmas 3(4); ovule 1. Drupe wind-dispersed by persistent, enlarged calyx with 4 wing-like lobes, 1-locular; exocarp yellowish to reddish to brown, covered with dense brown trichomes; endocarp cartilaginous. Seed with straight embryo.

Five species in Myanmar, Thailand, and western Malesia.

45. *Pentaspadon* Hook. f.

Pentaspadon Hook.f., Trans. Linn. Soc. 23: 168, t. 24 (1860); Ding Hou, Flora Males. I, 8: 520–524 (1978).
Microstemon Engl. (1881).

Hermaphrodite trees with contact dermatitis-causing exudate turning black with exposure to air. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite to subopposite, sessile or petiolulate, entire, with hairy tuft domatia in secondary vein axils abaxially. Inflorescences axillary panicles. Flowers very short pedicellate, articulate; perianth 5-parted, imbricate; corolla white to pink; androecium diplostemonous or haplostemonous, sometimes (Malesian taxa) in two series with a whorl of stamens alternating with a whorl of staminodes, staminodes with or without antherodia; filaments subulate, papillose; anthers basi- or dorsifixed; disk glabrous,

10-lobed; carpels 1; style short; stigma subglobose or slightly 2-lobed; ovule pendulous, lateral. Drupe elongate ovoid, 1-locular; exocarp tan or purple turning black; mesocarp resinous; endocarp thin, seed oily.

Six species in Southeast Asia, Malesia, and the Solomon Islands.

This genus is of somewhat uncertain subfamilial affiliation, and may actually belong in subfamily Spondioideae.

46. *Pistacia* L.

Pistacia L., Sp. Pl.: 1025 (1753).
Lentiscus (Tourn.) L. (1735).
Terebinthus P. Br. (1735).

Dioecious shrubs or trees with clear exudate. Leaves evergreen or deciduous, alternate, paripinnate and/or imparipinnate, rarely simple or trifoliolate, petiolate; rachis sometimes alate; leaflets opposite or subopposite, petiolulate; cataphylls sometimes present. Inflorescences axillary thyrsoids, panicles, racemes, or spikes; perianth 0, but flowers surrounded by 1–3 small bracts and (1)2–7 tepal-like bracteoles; androecium: 3–5(–8) stamens; filaments short; anthers basifixed; pistillode reduced or 0; staminodes reduced or 0; disk glabrous, often reduced to a patch or 0; carpels (2)3; style short, 3-branched, apical; stigmas (2)3, bilobed or simple, recurved; ovule pendulous from a basal funicle. Drupe globose or ovoid, 1-locular; exocarp chartaceous, red to purplish; mesocarp thin; endocarp woody. $n = 12$, 14, 15.

Twelve species in Texas, USA, south to Nicaragua; Mediterranean Europe, and North and East Africa; Southwest and Central Asia (former Soviet Republics) east to Afghanistan and temperate central and southern China, south to peninsular Malaysia and the Philippines. *Pistacia vera* is cultivated worldwide in dry, warm climates.

47. *Protorhus* Engl.

Protorhus Engl., Bot. Jahrb. 1: 420 (1881).
Anaphrenium E. Mey. ex Endl. (1841), p. p.

Polygamodioecious shrubs or trees with milky, possibly contact dermatitis-causing, exudate. Leaves evergreen, opposite to subopposite, simple, petiolate, linear oblong or narrowly elliptic; young leaves bright orange. Inflorescences terminal and/or axillary panicles. Flowers pedicellate, non-articulate; perianth 5-parted, imbricate; corolla greenish white to yellow; androecium haplostemonous; pistillode reduced; staminodes reduced, pink; disk glabrous, urceolate in males, saucer-shaped and orange in females; carpels 1–3, only 1 fertile; stylodia 3, basally connate or distinct; stigmas capitate; ovules 1–3, pendulous, subapical, only 1 fertile. Drupe reniform, asymmetrical, 1-locular; exocarp purple to black, slightly ridged at maturity, wrinkled when dry; mesocarp fleshy, resinous; endocarp chartaceous to cartilaginous. Seed cotyledons easily separable; embryo oblong.

A single species, *P. longifolia*, endemic to eastern South Africa.

48. *Pseudosmodingium* Engl.

Pseudosmodingium Engl., Bot. Jahrb. 1: 419 (1881); F.A. Barkley & M.J. Reed, Am. Midl. Nat. 24: 666–679 (1940), rev.; C.J. Aguilar-Ortigoza & V. Sosa, Rhodora 106(928): 348–359 (2004), rev.

Dioecious or polygamodioecious trees with contact dermatitis-causing exudate. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite or alternate, sessile or petiolulate, entire to serrate. Inflorescences axillary panicles. Flowers pedicellate, non-articulate; perianth 5-parted, imbricate; corolla white and prominently veined; androecium haplostemonous; filaments filiform; pistillode extremely reduced; staminodes slightly reduced; disk glabrous; carpels 3; style 3-branched; stigmas 3; ovule pendulous, apical. Samara with two broad lateral wings, reniform in outline, 1-locular; exocarp yellow to brown or reddish brown, glabrous. Seed reniform; cotyledons slender.

Four species endemic to central and southern Mexico.

49. *Rhodosphaera* Engl.

Rhodosphaera Engl., Bot. Jahrb. Syst. 1: 423 (1881).

Polygamodioecious trees with bark shedding in scaly patches; exudate white, gummy. Leaves alternate, imparipinnate (paripinnate), petiolate; leaflets opposite to subopposite, petiolulate, entire, oblong or elliptic, base asymmetrical; hairy tuft domatia sometimes present in secondary vein axils abaxially. Inflorescences terminal and/or axillary panicles, pyramidal, dense. Flowers

pedicellate; perianth 5-parted, imbricate; corolla dark pink to red; androecium diplostemonous; anthers dorsifixed; pistillode present or 0, reduced; staminodes reduced; disk glabrous, cupular, 10-lobed; carpels 3; stylodia 3, distinct, short, apical; stigmas capitate; ovule pendulous, basal. Drupe 1-locular; exocarp shiny brown; mesocarp woody; endocarp bony. Seed cotyledons flat.

A single species, *R. rhodanthema*, endemic to Queensland and northern New South Wales, Australia.

50. *Rhus* L.

Rhus L., Sp. Pl. 1: 265 (1753); F.A. Barkley, Ann. Missouri Bot. Gard. 24: 265–499 (1937), rev.; D. Young, Systematics of *Rhus* subg. *Lobadium* sect. *Styphonia*. Ph.D. dissertation, Claremont Graduate School, Claremont, CA, (1975); Ding Hou, Flora Males. I, 8: 534–541 (1978).
Rhus subg. *Rhus* L. (1754).
R. sect. *Sumac* DC. (1825), p. p.
R. subg. *Lobadium* (Raf.) Torr. & A. Gray (1838), p. p.
R. sect. *Trichocarpae* Engl. (1881), p. p.
R. subg. *Schmaltzia* (Desvaux ex de Candolle) C.K. Schneider (1907).
Schmaltzia Desv. ex Small emend. F.A. Barkley & Reed (1940).
Excluding: *R.* sect. *Baronia* H. Perrier (1944); *R.* sect. *Gerontogeae* Engl. (1881); *R.* sect. *Melanocarpae* Engl. (1881); *R.* sect. *Venenatae* Engl. (1881); *R.* subg. *Melanococca* (Blume) Brizicky (1963); *R.* subg. *Thezera* (DC.) K. Koch (1853).

Polygamodioecious or rarely hermaphrodite shrubs or trees, rarely sarmentose, sometimes with dichotomous branching. Leaves evergreen or deciduous, alternate, imparipinnate, trifoliolate, or unifoliolate, petiolate; rachis sometimes alate; leaflets opposite or subopposite, subsessile to petiolulate. Inflorescences terminal and/or axillary thyrsoids or compound spikes. Flowers sessile or short pedicellate; perianth 5-parted, imbricate; androecium haplostemonous; filaments subulate; anthers dorsifixed; pistillode reduced; staminodes reduced; disk glabrous; carpels 3, only 1 fertile; stylodia 1–3, united at base; stigmas 3; ovule basal (pendulous, apical or lateral). Drupe globose, 1-locular; exocarp red to brown, usually with both glandular and non-glandular trichomes. $n = 15$ or 16, polyploidy is common.

Thirty-five or more species: twenty-seven or more from southern Canada south to Panama and Cuba; one in North Africa to Mediterranean Europe east to Asia where six or more species are found east to China, Japan and Korea, south to Java and the Philippines; one endemic to the Hawaiian islands.

In much need of taxonomic revision. One species recognized here within *Rhus*, *R. chiangii*, may be a distinct genus from Mexico. Infrageneric classification includes subgenera *R.* subg. *Rhus* with pedicellate flowers and thyrsoid inflorescences, and *R.* subg. *Lobadium* with sessile or subsessile flowers and pseudospicate inflorescences. Much taxonomic work remains to be done within *Rhus*, particularly in Mexico and Asia. See Yi et al. (2004, 2007) for recent molecular and biogeographical assessments of *Rhus*. Useful taxonomic revisions of *Rhus* are cited above, but many treatments include taxa that should be or have since been segregated.

51. *Schinopsis* Engl.

Schinopsis Engl. in Mart., Fl. Brasil. 12(2): 403 (1876); T. Meyer & F.A. Barkley, Lilloa 33(11): 207–257 (1973), rev.
Quebrachia Griseb. (1874).
Loxopterygium Hook.f., p. p.

Dioecious or monoecious trees, sometimes with thorns, and with contact dermatitis-causing exudate turning black with exposure to air. Leaves usually evergreen, alternate, imparipinnate or unifoliolate (rarely both on the same plant) or rarely trifoliolate or paripinnate, petiolate; rachis sometimes alate; leaflets opposite, sessile or petiolulate, entire. Inflorescences terminal and/or axillary panicles. Flowers sessile or pedicellate, articulate or non-articulate; perianth 5-parted, imbricate; corolla greenish to white; petals with a prominent midvein; androecium haplostemonous; anthers dorsifixed; pistillode very reduced; staminodes reduced; disk glabrous, 5-lobed; carpels 3; stylodia 0 or 3, lateral; stigmas 3 or solitary and sessile; ovule pendulous, subapical. Samara 1-locular; exocarp and mesocarp expanded into a flattened lateral wing, green or red to brown; endocarp bony; calyx persistent. n=14.

Seven species in dry forests of northern Peru, and sub-Amazonian and eastern Brazil south to central Argentina. Often the dominant canopy tree in Chaco forests of Bolivia, Paraguay, and northern Argentina.

52. *Schinus* L.

Schinus L., Sp. Pl.: 388 (1753); F.A. Barkley, Brittonia 5: 160–198 (1944), and in Lilloa 28: 5–110 (1957), rev.
Duvaua Kunth (1824), p. p.

Dioecious shrubs or trees, rarely subshrubs, rarely with thorns, and with contact dermatitis-causing exudate. Leaves evergreen or deciduous, alternate, unifoliolate or imparipinnate (paripinnate), petiolate; rachis often alate; leaflets opposite or alternate, sessile to subsessile. Inflorescences terminal and/or axillary, spike-like pseudoracemes, panicles, or pleiothyrses, rarely reduced to a few fascicles. Flowers pedicellate, articulate; perianth (4–)5-parted, imbricate; androecium diplostemonous, in two whorls distinctly unequal in length; filaments subulate; pistillode very reduced; staminodes reduced; disk glabrous, 8–10-lobed, patelliform in male flowers, disk-shaped in female flowers; carpels 3; stylodia (1–)3; stigmas capitate; ovule pendulous, lateral to apical. Drupe small, globose, 1-locular; exocarp light purple to dark red, sometimes densely pubescent, thin at maturity, separating from rest of pericarp; mesocarp resinous, fleshy, adhering to the bony endocarp. Seed compressed. n=14, 15.

Thirty or more species from Ecuador south to Patagonia but excluding Amazonia. Two species, *S. molle* and *S. terebinthifolia*, are cultivated throughout the tropical, subtropical, and warm temperate regions of the world.

Barkley (l.c. 1944, see also l.c. 1957) recognized two subgenera: *S.* subg. *Duvaua* with unifoliolate leaves, often thorny, and subg. *Schinus* (as subg. *Euschinus*) with compound leaves and lacking thorns.

53. *Searsia* F.A. Barkley

Searsia F.A. Barkley, Am. Midl. Nat. 28: 472 (1942); R.O. Moffett, Bothalia 37: 165–175 (2007), rev.
Terminthia Bernh. (1838).
Rhus sect. *Sumac* DC. (1825), p. p.
Rhus subg. *Thezera* (DC.) K. Koch (1853); R.O. Moffett, Fl. South Africa 19, 3 (1993), rev.
Rhus sect. *Gerontogeae* Engl. (1881).

Monoecious (polygamous) subshrubs, shrubs, or trees, stems conspicuously lenticellate, thorns sometimes present. Leaves evergreen or deciduous, alternate, imparipinnate, usually trifoliolate; leaflets opposite or subopposite, sessile or petiolulate. Inflorescences terminal and/or axillary (one sp. cauliflorous) panicles or racemes. Flowers subsessile to pedicellate, non-articulate; perianth (4)5(6)-parted, imbricate; calyx greenish to red; corolla greenish yellow to whitish or red; petals generally twice as long as sepals; androecium haplostemonous; anthers dorsifixed; filaments subulate; pistillode usually 0, rarely present in male flowers, reduced; staminodes reduced; disk glabrous, 5(–10)-crenulate, cup-shaped; carpels 3; stylodia 3 (very rarely 4), distinct or connate basally, apical, erect or patent; stigmas capitate; ovule 1(–3), basal, pendulous. Drupe globose, ovoid, or laterally compressed, 1(–3)-locular; exocarp shiny light brown to black or red; mesocarp resinous and adhering to endocarp; endocarp bony; stylodia persistent or caducous. Seed ovoid or reniform, compressed. n=14, 15, 16.

One hundred-twenty or more species, in Sicily, the Middle East, Arabian Peninsula, Socotra, Africa, India, Nepal, Bhutan, Myanmar, and China. *S. lancea* is widely cultivated in warm regions.

This genus was formerly recognized within *Rhus* but was segregated by Barkley (1942). Moffett (2007) published most of the necessary new combinations in *Searsia*. It is separated from *Rhus* by a combination of having ternate leaves and a mesocarp adherent to the endocarp at maturity.

54. *Semecarpus* L. f.

Semecarpus L. f., Suppl. Pl.: 285 (1781).
Oncocarpus A. Gray (1854).

Dioecious (polygamous) shrubs or trees, rarely monopodial, with contact dermatitis-causing, milky exudate turning black with exposure to air. Leaves evergreen or deciduous, alternate, simple, petiolate, entire, coriaceous; leaf shape and size vary widely. Inflorescences terminal and/or axillary (cauliflorous) panicles. Flowers sessile or pedicellate, articulate; perianth (4) 5-parted; calyx imbricate (rarely valvate); corolla imbricate, rarely valvate; androecium haplostemonous; filaments subulate and glabrous; anthers dorsifixed; pistillode present or 0 in male flowers; staminodes reduced; disk glabrous to densely pubescent; ovary sometimes seemingly semi-inferior due to envelopment by hypocarp; carpels

3; stylodia 3, basally adnate, apical; stigmas variously shaped; ovule apical. Drupe subglobose, ovoid to oblong (rarely transversely elongate), immersed in a cupular, obconical, or disk-shaped hypocarp, 1-locular; exocarp yellow, gray, or brown; mesocarp fleshy, resinous; endocarp crustaceous; hypocarp yellow to red. Seed with straight embryo. n=29, 30.

Seventy to seventy-five species in moist or dry forests, along the banks of fast-flowing rivers (rheophytes), or on cliffs, in India and Sri Lanka, Nepal, Bhutan, tropical and subtropical East Asia to Melanesia, Micronesia, and tropical Australia.

55. *Smodingium* E. Mey.

Smodingium E. Mey. in Drège, Zwei Pfl. Docum.: 222 (1843).

Dioecious subshrubs to small trees, sometimes semiscandent, with contact dermatitis-causing exudate turning black with exposure to air. Leaves alternate, trifoliolate, petiolate; leaflets petiolulate, lanceolate, sharply toothed. Inflorescences terminal and/or axillary thyrses. Flowers pedicellate, articulate; perianth 5-parted; corolla imbricate, reflexed at maturity, white to cream-colored; androecium haplostemonous; anthers dorsifixed; pistillode reduced; staminodes reduced; disk glabrous, orange, 10-crenulate; carpels 3; stylodia 3, basally adnate, recurved, lateral; stigmas capitate; ovule pendulous, lateral. Samara dry, laterally compressed with a marginal wing, suborbicular in outline, 1-locular; exocarp light brown; calyx and stylodia persistent. Seed reniform.

A single species, *S. argutum*, endemic to eastern South Africa.

56. *Sorindeia* Thou.

Sorindeia Thou., Gen. Nov. Madag.: 23 (1806); Breteler, Adansonia III, 25: 93–113 (2003), rev.
Dupuisia A. Rich. (1832).

Dioecious or possibly very rarely monoecious trees, usually small and slender, branched or monopodial, shrubs or lianas, with light-colored contact dermatitis-causing exudate. Leaves alternate, imparipinnate (unifoliolate), petiolate; leaflets opposite to alternate, petiolulate; in most species tertiary veins collect into an oblique vein that is directed admedially toward the secondary vein axil. Inflorescences terminal and/or axillary, or cauliflorous thyrsoids. Flowers pedicellate, articulate or non-articulate; perianth 5-parted; calyx fused in lower half or more; corolla valvate or rarely imbricate; color widely variable: white, yellow, greenish-yellow, pink, or red when open; red to purple or green in bud; androecium of 10–20 stamens; filaments subulate, inserted outside of and on the disk, shorter than anthers; anthers dorsifixed; pistillode 0; staminodes 5–10; disk glabrous, crenulate; carpels 3; style short; stigma capitate or 3-lobed; ovule pendulous, subapical or apical. Drupe ellipsoid or asymmetrically ovoid, 1-locular; exocarp yellow, orange, red to black-purple; mesocarp fleshy, thin; endocarp chartaceous or woody; stigma persistent. Seed ellipsoidal. $n = 16$.

Nine species in tropical Africa and Madagascar. The species number was reduced from 80+ by Breteler (l.c.).

57. *Swintonia* Griff. Fig. 3C

Swintonia Griff. in Proc. Linn. Soc. 1: 283 (1846).

Andromonoecious trees with contact dermatitis-causing exudate. Leaves evergreen, alternate, simple, petiolate, entire, papillose abaxially. Inflorescences terminal and/or axillary panicles. Flowers pedicellate, articulate or non-articulate; perianth 5-parted, imbricate; corolla white to light green or yellowish, turning red when enlarged (prior to drying in mature fruit); androecium haplostemonous; filaments filiform or subulate; anthers dorsifixed; pistillode very reduced, pubescent; staminodes 0; disk glabrous, extrastaminal, 5-lobed; gynoecium pseudomonomerous; style cylindrical, distinct; stigma capitate; ovule basal. Drupe wind-dispersed by persistent, enlarged, wing-like petals, 1-locular; endocarp coriaceous. Seed with straight embryo.

Twelve species, Andaman Islands, Myanmar east to Malesia (Sumatra, Malay Peninsula, Borneo, and Philippines).

58. *Thyrsodium* Salzm. ex Benth. Fig. 5

Thyrsodium Salzm. ex Benth., Hook., J. Bot. Kew Gard. Misc. 4: 17 (1852); Mitchell & Daly, Brittonia 45: 115–129 (1993), rev.
Garuga Roxb. (1814), p. p.
Kunthia Benth. & Hook. (1862), p. p.

Dioecious trees with milky exudate. Leaves evergreen, alternate to subopposite, imparipinnate, petiolate; leaflets opposite or alternate, petiolulate, entire. Inflorescences terminal and/or axillary thyrsoids. Flowers non-articulate, perigynous; perianth 5-parted; calyx valvate; corolla imbricate; white, greenish, yellow; androecium haplostemonous; stamens opposite the sepals; filaments very short; anthers sometimes pubescent; pistillode reduced; staminodes reduced; disk glabrous, adnate to the hypanthium, or 0; carpels 3; style simple or 2–3-branched, apical; stigmas 1–3 or 2–3-lobed; ovule lateral. Drupe globose, obovoid, oblong or ellipsoid, 1-locular; mesocarp fleshy; endocarp crustaceous. Seed with straight embryo.

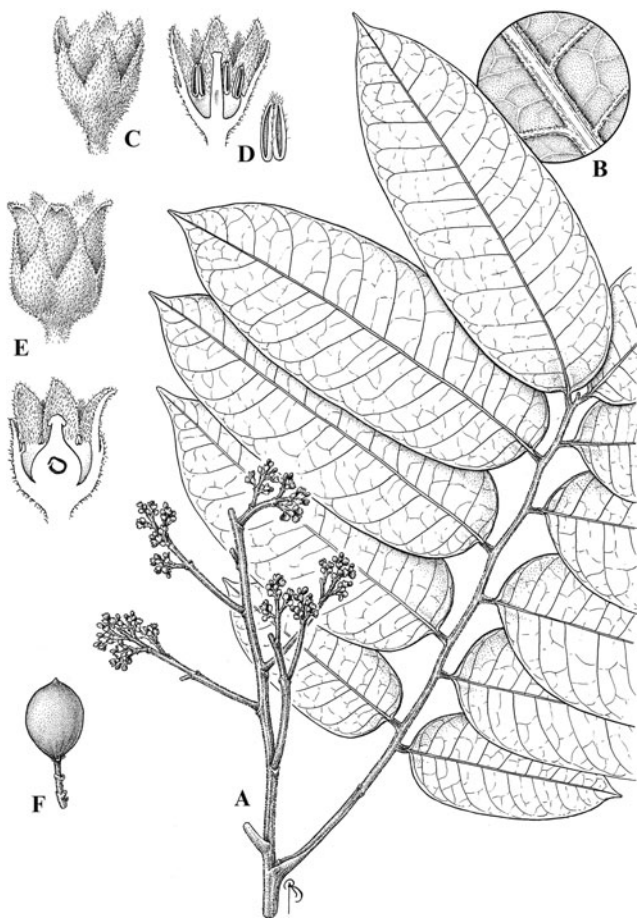

Fig. 5. Anacardiaceae. *Thyrsodium bolivianum*. **A** Flowering branchlet. **B** Abaxial leaflet surface. **C** External view and vertical section of male flower, showing cupular hypanthium. **D** Anther. **E** External view and vertical section of female flower. **F** Fruit. (Reproduced with permission of the artist Bobbi Angell)

Six to seven species east of the Andes in Colombia, Peru, Bolivia, southern and eastern Venezuela, the Guianas, and Amazonian and eastern Brazil.

59. *Toxicodendron* Mill.

Toxicodendron Mill., Gard. Dict. Abr. Ed., 4 (1754); Gillis, Rhodora 73: 72–159, 161–237, 370–443, 465–540 (1971), rev.
Rhus sect. *Sumac* DC. (1825), p. p.
Rhus subg. *Toxicodendron* (Mill.) K. Koch (1853); emend. Schneider (1907).
Rhus sect. *Trichocarpae* Engl. (1881), p. p.
Rhus sect. *Venenatae* Engl. (1881).

Polygamodioecious shrubs, trees, or lianas with contact dermatitis-causing, white exudate turning black with exposure to air. Leaves deciduous, rarely evergreen, alternate, imparipinnate, usually multifoliolate, often trifoliolate, very rarely unifoliolate, petiolate; leaflets opposite to subopposite, sessile or petiolulate, entire, serrate or lobed; hairy tuft domatia sometimes present in secondary vein axils abaxially. Inflorescences axillary panicles. Flowers pedicellate, non-articulate; perianth (4)5(6)-parted; calyx fused at base; corolla imbricate; white to greenish; androecium haplostemonous; anthers dorsifixed; pistillode reduced, stylodium 1; staminodes reduced; disk glabrous, annular and lobed; carpels 3; stylodia 3, short; stigmas capitate; ovule basal. Drupe globose, often laterally compressed, 1-locular; exocarp yellowish to white or pale gray, sometimes pubescent, separating from mesocarp at maturity; mesocarp white waxy, striated with resin canals; endocarp bony. n=15, polyploidy is common.

Twenty-two species from southern Canada south to Bolivia; India and Nepal; Bhutan and Myanmar; and temperate East Asia to New Guinea.

Several taxa belonging to *Toxicodendron* have not yet been transferred and are currently recognized in other genera including *Rhus*. Three sections are recognized within the genus: *Simplicifolia*, *Toxicodendron*, and *Venenata* (Gillis l.c.).

60. *Trichoscypha* Hook. f.

Trichoscypha Hook.f. in Benth. & Hook.f., Gen. Pl. 1: 423 (1862); Breteler, Adansonia III, 23: 247–264 (2001) et ibid. 26: 97–127 (2004), rev.
Emiliomarcelia Th. & H. Dur. (1909).

Dioecious trees, sarmentose trees, shrubs or lianas with white to pink, contact dermatitis-causing exudate turning black with exposure to air. Leaves evergreen, alternate, imparipinnate (unifoliolate), petiolate; leaflets opposite or alternate, petiolulate, lanceolate to oblong, entire. Inflorescences terminal and/or axillary, or cauliflorous thyrsoid panicles; the female inflorescence with a thicker, shorter axis than the male inflorescence. Flowers sessile or pedicellate; non-articulate; perianth 4(5, very rarely 6)-parted; calyx valvate, basally fused; corolla imbricate to valvate, reflexed at maturity; white to red; androecium haplostemonous; filaments filiform; anthers dorsifixed; pistillode present or 0 in male flowers; staminodes reduced; disk glabrous to densely pubescent, cup-shaped; carpels 3–4 (very rarely 6); stylodia (1–)3–4 (very rarely 6), erect or patent, compressed; stigmas capitate to shallowly bilobed (sessile); ovule pendulous, apical. Drupe ellipsoid, slightly oblique, ovoid, subglobose, or turbinate, 1-locular; exocarp red to purple or black, glabrous to densely pubescent; mesocarp fleshy; endocarp thin, coriaceous or crustaceous. n=24.

Thirty-two species in Tropical West and central Africa, and eastern to southern Africa. Breteler (l.c. 2001, 2004) completed a revision of the genus in which he recognized fourteen species in Upper Guinea, and eighteen in Lower Guinea and Congolia.

II. Subfam. Spondioideae Kunth ex Arn. (1832).

61. *Allospondias* (Pierre) Stapf

Allospondias (Pierre) Stapf in Hook., Icon. Pl.: 2667 (1900).
Spondias L. (1753), p. p.
Poupartia Comm. ex Juss. (1789), p. p.

Trees, dioecious (androdioecious) or with hermaphrodite flowers. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite or alternate, sessile to petiolulate, entire. Inflorescences terminal panicles, pubescent. Flowers pedicellate, articulate; perianth 5-parted; calyx imbricate; corolla valvate, white; androecium diplostemonous; pistillode reduced; staminodes reduced; disk glabrous; ovary prominently lobed (carpels only fused on one plane); carpels 5; stylodia 4–5, apically connate or distinct; stigmas capitate or spathulate; ovules 5, apical, 1–4 fertile. Drupe subglobose, 2–5-locular; exocarp red; mesocarp fleshy; endocarp woody with matrix of fibers expanding into mesocarp.

Two species, Myanmar, Thailand, Indochina, southern and tropical China.

A. laxiflora may represent a distinct genus due to differences in the connation of the stylodia (distinct), shape of stigmas (capitate), absence of endocarp lobing, number of locules (2), and the absence of four parenchyma-filled cavities.

62. *Antrocaryon* Pierre

Antrocaryon Pierre in Bull. Mens. Soc. Linn. Paris II, 3: 23 (1898); R.B. Fernandes, Garcia de Orta, Bot., Lisboa, 2: 107–110 (1975), rev.
Poupartia Comm. ex Juss. (1789), p. p.

Polygamodioecious trees. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite or subopposite, sessile or petiolulate, entire. Inflorescences axillary panicles, often emerging with new leaves. Flowers pedicellate; perianth 5-parted; calyx slightly imbricate or apert; corolla imbricate (valvate in *A. klaineanum*), pubescent; androecium diplostemonous; pistillode very reduced; staminodes reduced; disk glabrous, 10-lobed; carpels 5; stylodia 5, recurved, subapical and excentric; stigmas capitate; ovules 5, apical or subapical. Drupe plum-like or apple-shaped and depressed at apex, 5-locular; mesocarp strong smelling and edible; endocarp woody, angled with 5 apical opercula. $n = 12$.

Three species in tropical Africa, 1 in Amazonian Brazil, Colombia, and Peru.

63. *Buchanania* Spreng. Fig. 3A

Buchanania Spreng. in Schrad., J. Bot. 2: 234 (1800).
Launzan Buch.-Ham. (1799).
Cambessedea Kunth (1824).
Coniogeton Blume (1826).

Hermaphrodite trees. Leaves alternate, simple, sessile to petiolate, entire, subcoriaceous to coriaceous; cataphylls sometimes present. Inflorescences terminal and/or axillary panicles. Flowers hermaphrodite, pedicellate, articulate or non-articulate; perianth (4)5(6)-parted, imbricate; corolla greenish to white; androecium diplostemonous; filaments articulated in some species; anthers basifixed and usually sagittate; disk glabrous, cupular and crenulate; carpels 4–6, basally connate, only 1 fertile, the fertile one sometimes pubescent; stylodia 4–6, short; stigmas oblique,

truncate, sterile carpels with functional stigmas, fertile carpel without functional stigma (stigma vestigial); ovules 4–6, basal or sublateral, only 1 fertile. Drupe lentiform, 1-locular, with persistent or caducous calyx; exocarp red or brown; endocarp bony, splitting vertically in half at maturity in some species. $n = 11$.

Twenty-five to thirty or more species in tropical Asia, Malesia, Australia, Micronesia, Melanesia, and Samoa, with greatest diversity in Malesia.

64. *Choerospondias* B.L. Burtt & A.W. Hill

Choerospondias B.L. Burtt & A.W. Hill, Ann. Bot. II, 1: 254 (1937).
Spondias L. (1753), p. p.
Poupartia Comm. ex Juss. (1789), p. p.

Polygamodioecious trees. Leaves evergreen or deciduous, alternate, imparipinnate, petiolate; leaflets opposite, petiolulate, entire or sometimes serrate; hairy tuft domatia present in secondary vein axils abaxially. Inflorescences terminal and/or axillary; female flowers in racemes (or solitary), male flowers in panicles. Flowers pedicellate; calyx cupular with tiny lobes; corolla imbricate; petals 5, purplish; androecium diplostemonous; filaments connate at the base and connate with the disk; anthers dorsifixed; pistillode reduced; staminodes reduced; disk glabrous; carpels 5; stylodia 5, short; stigmas capitellate to capitate; ovules 5, apical. Drupe ovoid or oblong, 5-locular; exocarp yellow; mesocarp thin, fleshy; endocarp woody with 5 apical shallow orifices, each covered by a membrane (possibly rudimentary opercula).

A single species, *C. axillaris*, in northeastern India, Nepal east to China, Taiwan, Thailand, Vietnam, and Japan.

65. *Cyrtocarpa* Kunth in Humb., Bonpl. & Kunth

Cyrtocarpa Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp., Qu. Ed., 7: 20, t. 609 (1824); Mitchell & Daly, Ann. Missouri Bot. Gard. 78: 184–189 (1991), rev.
Bursera Jacq. ex L. (1762), p. p.

Polygamodioecious trees with somewhat succulent branchlets and exudate. Leaves deciduous, alternate, imparipinnate (paripinnate), petiolate; leaflets opposite, occasionally subopposite, sessile to short-petiolulate, entire. Inflorescences terminal and/or axillary panicles or pseudospikes. Flowers pedicellate; perianth 5-parted, imbricate; petals usually patent at anthesis; androecium diplostemonous; anther sometimes with glandular connective; pistillode reduced to five stylodes; staminodes reduced; disk glabrous, annular, crenulate and fleshy; carpels 5; stylodia (3–)5, short; stigmas capitate; ovule pendulous, subapical or apical. Drupe obliquely obtuse-oblong, 1–3(–5)-locular; exocarp purple or yellow to orange; mesocarp fleshy; endocarp bony with 1–5 opercula. Seed cotyledons reniform.

Five species in dry forests to open arid habitats: 1 endemic to southern Baja California; 2 in western Mexico; 1 in northern Colombia east to Guyana, Venezuela, and northern Brazil; 1 endemic to the Caatinga of northeast Brazil.

66. *Dracontomelon* Blume

Dracontomelon Blume, Mus. Bot. Lugd. Bat. 1: 231, t. 42 (1850).
Comeurya Baill. (1872).
Dracontomelum orthographic variant

Hermaphrodite trees with buttresses and white exudate. Leaves evergreen, alternate, imparipinnate, petiolate; leaflets opposite, subopposite or alternate, petiolulate, entire; hairy tuft domatia sometimes present in secondary vein axils abaxially. Inflorescences terminal and/or axillary panicles. Flowers hermaphrodite, pedicellate, articulate; perianth 5-parted; sepals imbricate, essentially distinct; petals valvate, imbricate at apex, white, greenish, or yellow; androecium diplostemonous; filaments subulate; anthers dorsifixed or medifixed; disk glabrous or pubescent; carpels 5; stylodia 5, basally and apically connate; stigmas capitate, receptive face lateral; ovules 1–5, apical, usually not all fertile. Drupe globose, depressed globose, ovoid, or ellipsoid, 5-locular or appearing fewer due to abortion; exocarp orange, brown to black; mesocarp fleshy; endocarp woody with 5 apical opercula. Seed with straight embryo. $n = 18$.

Eight species, India to Myanmar, Indo-China, tropical China, Malesia, and Fiji.

67. *Haematostaphis* Hook. f.

Haematostaphis Hook. f., Trans. Linn. Soc. 23: 169, t. 25 (1860).

Dioecious trees with clear exudate. Leaves alternate, imparipinnate, prominently multifoliolate, petiolate; leaflets opposite or alternate, petiolulate, emarginate at apex; small hairy tuft domatia present in secondary vein axils abaxially. Inflorescences terminal panicles, large; perianth 3-parted, imbricate; corolla whitish; androecium diplostemonous, in two whorls distinctly unequal in length; anthers dorsifixed; pistillode present or 0 in male flowers; staminodes reduced; disk glabrous; carpels 3; styles 3; stigmas 3; ovules 1–2, apical. Drupe with red exocarp; mesocarp thin, fleshy; endocarp woody with a bipartite, apical operculum.

A single species, *H. barteri*, tropical West Africa south to Nigeria.

68. *Haplospondias* Kosterm.

Haplospondias Kosterm., Kedondong, Ambarella, Amra. The Spondiodeae (Anacardiaceae) in Asia and the Pacific area. Published by the author; printed by Bina Karya 78 Printing Works, Bogor, Indonesia (1991).
Spondias L. (1753), p. p.
Bouea Meisn. (1837), p. p.

Hermaphrodite trees. Leaves alternate, simple, petiolate, entire. Inflorescences terminal, pyramidal thyrses. Flowers hermaphrodite, pedicellate; perianth (4)5-parted; calyx cupular with tiny teeth-like lobes; corolla valvate, reflexed at maturity; androecium diplostemonous; filaments glabrous; anthers dorsifixed; disk glabrous, 10-lobed; carpel 1; style very thick and gradually forming from the apex of the ovary; stigma a long, bilobed extension of the style. Fruit unknown.

A single species, *H. brandisiana* (=*H. haplophylla*), endemic to Yunnan, China, and Myanmar. This species is known from a single collection.

69. *Harpephyllum* Bernh. ex Krauss

Harpephyllum Bernh. ex Krauss, Flora 27: 349 (1844).

Dioecious trees. Leaves evergreen, alternate, imparipinnate, petiolate; rachis narrowly alate; leaflets sessile, opposite, entire, falcately narrowly ovate; cataphylls present. Inflorescences axillary panicles. Flowers pedicellate, non-articulate; perianth 4–5-parted, imbricate; corolla white to yellow, androecium diplostemonous (7–10 stamens); filament apex subulate, base flattened; anthers oblong-ovate; pistillode reduced; staminodes reduced; disk glabrous, cup-shaped, crenulate; carpels 4–5; stylodia 4–5, short; stigmas capitate; ovules 2, pendulous. Drupe oblong-obovoid, 4-locular (2 fertile); exocarp red; mesocarp subfleshy; endocarp woody or bony with spinose projections and 1–2 internal opercula. Seed compressed.

A single species, *H. caffrum*, in the Cape Province, Transvaal, and Natal, South Africa. Cultivated outside its native range.

70. *Koordersiodendron* Engl.

Koordersiodendron Engl., Meded. Lands Plantent. 19: 411 (1898).

Hermaphrodite trees. Leaves evergreen, alternate, imparipinnate, petiolate; leaflets opposite or subopposite, petiolulate, entire. Inflorescences axillary panicles. Flowers hermaphrodite, pedicellate, articulate; perianth 5-parted; calyx fused at base; corolla imbricate, white, greenish, or yellow; androecium diplostemonous; anther connective slightly protruding; disk glabrous; carpels 5, incompletely connate; stylodia 5, short; stigmas small; ovules 1–5, apical, usually only 1 fertile. Drupe broadly ellipsoid, oblique at base, 1(–3)-locular by abortion; exocarp yellow; endocarp cartilaginous. Seed with straight embryo.

A single species, *K. pinnatum*, in Borneo, the Philippines, Sulawesi, Maluku, and New Guinea.

71. *Lannea* A. Rich. in Guillem.

Lannea A. Rich. in Guillem., Fl. Seneg. Tent.: 153, t. 42 (1831).
Odina Roxb. (1832).
Scassellatia Chiov. (1932).

Dioecious, androdioecious or polygamodioecious subshrubs, shrubs, or trees with inflorescences and young stems and leaves covered with stellate trichomes. Leaves deciduous, alternate, imparipinnate, trifoliolate, or rarely unifoliolate (rarely all leaf types on same plant), petiolate; leaflets opposite or subopposite, sessile or petiolulate, entire or rarely serrate. Inflorescences terminal and/or axillary; female flowers in racemes or spikes; male flowers in panicles that are reduced to appear spike-like; inflorescence often emerging before the foliage. Flowers pedicellate, articulate; perianth 4(5)-parted, imbricate; corolla recurved at maturity, white, greenish, yellow, or

red; androecium diplostemonous; filaments subulate; anthers dorsi- to basifixed; pistillode reduced; staminodes reduced; disk glabrous, patelliform, 8-crenulate; carpels 4, 1(2) fertile; stylodia 3–4, short, subapical; stigmas subglobose or capitate; ovules pendulous, apical. Drupe obovoid or ovoid, laterally compressed or subglobose, 1–4-locular (1–3 sterile); exocarp red to purple, brown, or black; mesocarp thin; endocarp woody, alveolate with ridges, 1–2 apical opercula; style bases persistent. Seed reniform, laterally compressed; embryo straight. $n = (14)\ 15\ (20)$.

Forty or more species from sub-Saharan Africa to Socotra; one of these (*L. coromandelica*) is distributed from Pakistan to Indo-China. Cultivated in Southeast Asia.

72. *Operculicarya* H. Perrier

Operculicarya H. Perrier, Mem. Mus. Hist. Nat. II, 118 (7): 248 (1944); Eggli, Bull. Mus. Natl. Hist. Nat., Paris IV, 17, sect. B, Adansonia: 149–158 (1995), rev.; Randrianasolo & Lowry, Adansonia III, 28: 359–371 (2006), rev.

Dioecious shrubs or small trees with swollen trunks (especially basally) and gummy exudate. Leaves deciduous, alternate, imparipinnate, nearly sessile to short petiolate, usually microphyllous; rhachis usually alate; leaflets opposite to subopposite, sessile to short-petiolulate, entire. Female inflorescence of up to 4 flowers or reduced to a solitary flower, rarely multiflorate, axillary or on tip of short shoot; male inflorescence arising from short shoots and often reduced to one flower or in spicate to paniculate solitary or fascicled inflorescences. Flowers sessile or pedicellate, articulate; perianth (4)5(6)-parted, imbricate or apert; corolla creamy-yellow; androecium diplostemonous; anthers introrse, dorsifixed; pistillode very reduced, 3–5-cleft; staminodes reduced; disk glabrous, crenate; carpels 5; stylodia 5, often 4 are very reduced; stigma 1, shortly glandular; ovule apical. Drupe subglobose, 1(2)-locular; endocarp stony, with one operculum; exocarp red to black. Seed with horseshoe-shaped embryo.

Eight species in Madagascar, the Comoros, and Aldabra.

73. *Pegia* Coleb.

Pegia Coleb., Trans. Linn. Soc. 15: 364 (1827).
Tapirira Aubl. (1775), p. p.
Phlebochiton Wall. (1835).

Polygamous or polygamodioecious scandent shrubs, sarmentose trees, or lianas. Leaves evergreen, alternate, imparipinnate, petiolate; leaflets opposite or subopposite, petiolulate, entire or crenate. Inflorescences terminal and/or axillary panicles. Flowers pedicellate, articulate; perianth (4)-5-parted; calyx valvate; corolla imbricate or subvalvate, whitish; androecium diplostemonous; filaments filiform; pistillode reduced; staminodes reduced; disk glabrous, 5-lobed; carpels (4)5, only 1 fertile; stylodia (4)5, apical; stigmas capitate; ovule 1. Drupe slightly reniform, 1-locular; exocarp red to purple; endocarp crustaceous. Seed with straight embryo.

Two species, India to Myanmar, Indo-China, tropical China, and Malesia.

74. *Pleiogynium* Engl.

Pleiogynium Engl. in DC., Monogr. Phan. 4: 255 (1883).

Dioecious trees. Leaves evergreen, alternate, imparipinnate (very rarely paripinnate), petiolate; leaflets opposite to subopposite, petiolulate, entire, sometimes with hairy marsupiform domatia. Inflorescences axillary panicles (sometimes female inflorescence racemose or spiciform). Flowers pedicellate, articulate; perianth (4)5(6)-parted; calyx valvate; corolla imbricate, green, white, yellow, or brown; androecium diplostemonous; filaments filiform-subulate; anther with glandular connective; pistillode reduced, of 5 carpellodes; staminodes reduced; disk glabrous; carpels (5)8–12; stylodia (5)8–12, short, forming a marginal ring; stigmas spathulate; ovules pendulous. Drupe depressed globose or turbinate, (5) 8–12-locular; exocarp membranous, red to brown or black and depressed at opercula locations; outer mesocarp fleshy, inner mesocarp woody; endocarp bony with 5–12 opercula. Seed with curved embryo.

Two species, from Indo-China to Malesia, South Pacific Islands, and northeastern Australia.

75. *Poupartia* Comm. ex Juss.

Poupartia Comm. ex Juss., Gen.: 372 (1789); H. Perrier, Mém. Mus. Natl. Hist. Nat. 18: 243–269 (1944), rev.; F. Friedmann, Flore des Mascareignes 77: 5–9 (1997).
Spondias L. (1753), p. p.
Shakua Bojer (1837).
Sclerocarya Hochst. (1844), p. p.

Polygamodioecious or dioecious trees with exudate. Leaves evergreen or deciduous, alternate, imparipinnate, petiolate; leaflets opposite, petiolulate, entire. Inflorescences axillary to pseudoterminal; male flowers arranged in spicate racemes; female flowers in few-flowered panicles or racemes; male flowers sessile, female flowers pedicellate; perianth (4)5(6)-parted, imbricate; androecium diplostemonous; filaments distinct; anthers dorsifixed; pistillode minute or 0 in male flowers; staminode reduced; disk glabrous; carpels (1)2–5; stylodia 2–5, short, subapical; stigmas capitate; ovules (1)2–5. Drupe (1)2–5-locular; mesocarp fleshy; endocarp bony with 2–5 apical opercula. Seed with curved embryo. $n = 12$.

Seven species in Madagascar and the Mascarene Islands.

Distinct from *Operculicarya* by its curved versus horseshoe-shaped embryo, and 2–5 versus 1 opercula.

76. *Poupartiopsis* Capuron ex J.D. Mitch. & Daly

Poupartiopsis Capuron ex J.D. Mitch. & Daly, Syst. Bot. 31: 338 (2006).

Dioecious trees with milky exudate. Leaves evergreen, alternate, imparipinnate, petiolate; rhachis narrowly alate; leaflets opposite or subopposite, petiolulate. Inflorescences terminal and/or axillary panicles. Flowers (sub)sessile; perianth imbricate, 5-parted; androecium diplostemonous; filaments subulate, inserted at base of disk; anthers dorsi- to basifixed, connective with discolorous, slightly bulbous apex; pistillodes in male flowers; staminodes reduced; disk glabrous; carpels 3; stylodia 3; stigmas 3; ovules pendulous, subapical. Drupe lightweight and buoyant, large oblong to ovoid, 3-locular; mesocarp thin; endocarp bony with long hooked spinose processes parallel to the axis of the fruit enclosed in a fibrous matrix.

A single species, *P. spondiocarpus*, endemic to coastal forests of eastern Madagascar.

77. *Pseudospondias* Engl.

Pseudospondias Engl. in DC., Monogr. Phan. 4: 258 (1883).
Haematostaphis Hook.f. (1860), p. p.

Dioecious shrubs or trees with exfoliating bark. Leaves alternate, imparipinnate, petiolate; leaflets opposite or alternate, petiolulate, lateral leaflets asymmetrical at base, with strongly arcuate venation. Inflorescences axillary panicles. Flowers pedicellate, non-articulate; perianth 3–4(5)-parted, imbricate; corolla whitish; androecium diplostemonous, often in two whorls of unequal length; pistillode reduced to four lobes; staminodes reduced; disk glabrous, annular, crenulate; carpels 3–4(5), usually only 1(2) fertile; stylodia 3–4(5), very short, subapical; stigmas nearly sessile; ovules pendulous, apical. Drupe oblong-obovoid, 3–4(5)-locular; exocarp blue-black; mesocarp resinous; endocarp woody with 3–4(5) bipartite, apical opercula. $n = 15$.

Two species in riverine forests and rain forests of sub-Saharan Africa.

78. *Sclerocarya* Hochst.

Sclerocarya Hochst. in Flora 27, Bes. Beil. 1 (1844).
Poupartia Comm. ex Juss. (1789), p. p.

Dioecious (very rarely gynodioecious) trees. Leaves deciduous, alternate, imparipinnate, rarely unifoliolate, petiolate; leaflets opposite or occasionally subopposite, petiolulate (sessile). Inflorescences terminal and/or axillary; female inflorescence often reduced to a solitary flower; male flowers arranged in spicate racemes. Flowers pedicellate, non-articulate; perianth 4–5-parted, imbricate; calyx yellow to red; corolla yellow to purplish-pink to red; stamens (8–10–)15–25(–30); filaments subulate; anthers basi-dorsifixed; pistillode barely evident to 0 in male flowers; staminodes many (21–26); disk glabrous, patelliform; carpels (1)2(–4); stylodia 2–3, short, subapical; stigmas capitate; ovules pendulous, apical, funicle very long. Drupe obovoid-subglobose, 2–3(4)-locular; exocarp yellow to orange; mesocarp fleshy, thick; endocarp bony with (1)2–3(4) apical opercula; stylodia often persistent. Seed obclavate, compressed; testa chartaceous, brownish. $n = 13$.

Two to three species in sub-Saharan Africa and Madagascar.

79. *Solenocarpus* Wight & Arn.

Solenocarpus Wight & Arn., Prodr.: 171 (1834); Kostermans, Kedondong, Ambarella, Amra, The Spondiodeae (Anacardiaceae) in Asia and the Pacific area. Published by the author; printed by Bina Karya 78 Printing Works, Bogor, Indonesia (1991), rev.
Spondias L. (1753), p. p.
Pegia Coleb. (1827), p. p.

Hermaphrodite hemi-epiphytes, sarmentose trees, or lianas. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite to subopposite, petiolulate, oblique; *S. indica* with intramarginal vein, *S. philippinensis* with eucamptodromous secondary venation. Inflorescences terminal panicles. Flowers pedicellate; perianth 5-parted; calyx cupular with tiny lobes; corolla valvate in bud, distally reflexed at maturity; androecium diplostemonous; anthers dorsifixed; disk glabrous; carpels 1; style partially lateral or apical, clavate; stigma bilobed; ovule pendulous. Drupe 1-locular, mesocarp thin, fleshy; endocarp woody.

Two species, one in southern India and one in Malesia.

80. *Spondias* L. Fig. 6

Spondias L., Sp. Pl.: 200 (1753); Kostermans, Kedondong, Ambarella, Amra. The Spondiodeae (Anacardiaceae) in Asia and the Pacific area. Published by the author; printed by Bina Karya 78 Printing Works, Bogor, Indonesia (1991), rev.
Evia Commerson ex Blume (1850).
Warmingia Engl. (1874).

Polygamodioecious or hermaphrodite (rarely dioecious), strongly protandrous trees (very rarely hemi-epiphytes) with contact dermatitis-causing exudate. Leaves deciduous, alternate, imparipinnate (bipinnate), petiolate; leaflets opposite, subopposite or alternate, sessile to petiolulate. Inflorescences terminal and/or axillary panicles (racemes); often appearing before leaves or with young leaves. Flowers pedicellate, articulate; calyx slightly imbricate or apert; (4)5-lobed; corolla valvate, (4)5(6)-parted, cucullate; white, cream-colored, purple, or red; androecium diplostemonous, sometimes in two whorls of unequal length; filaments filiform or subulate; anthers dorsifixed; pistillodes and staminodes reduced; disk glabrous or papillose, annular and lobed; carpels (3–)5; stylodia (3–)5; stigmas capitate to spathulate; ovules apical. Drupe globose, obovoid, oblong or ellipsoid, (1–)5-locular; exocarp yellow-orange, red-purple, or greenish; mesocarp fleshy; endocarp bony, usually with a fibrous outer layer (very rarely spiny) projecting into the fleshy mesocarp. Seed with curved embryo. $n = 16$.

Sixteen or more species: eight from Mexico south to southeastern Brazil and Bolivia; eight in India and Sri Lanka east to tropical China and South Pacific Islands; Neotropical species naturalized in West Africa, the West Indies, and Southeast Asia. Several species cultivated pantropically.

A new monotypic genus, ***Attilaea abalak*** E. Martinez & Ramos, has been described from the Yucatan Peninsula in Mexico, and was suggested to be closely related to *Spondias* (Martinez and Ramos 2007). This newly described taxon shares the ubiquitous intramarginal vein of *Spondias* and is very similar to *S. purpurea*, but differs from it by having two rather than five carpels, and being scandent rather than erect in habit. This bicarpellate gynoecium differs from all other Anacardiaceae. We have been unable to examine enough material to confirm the separate generic status of this taxon, but do believe it belongs within the family in subfam. Spondioideae.

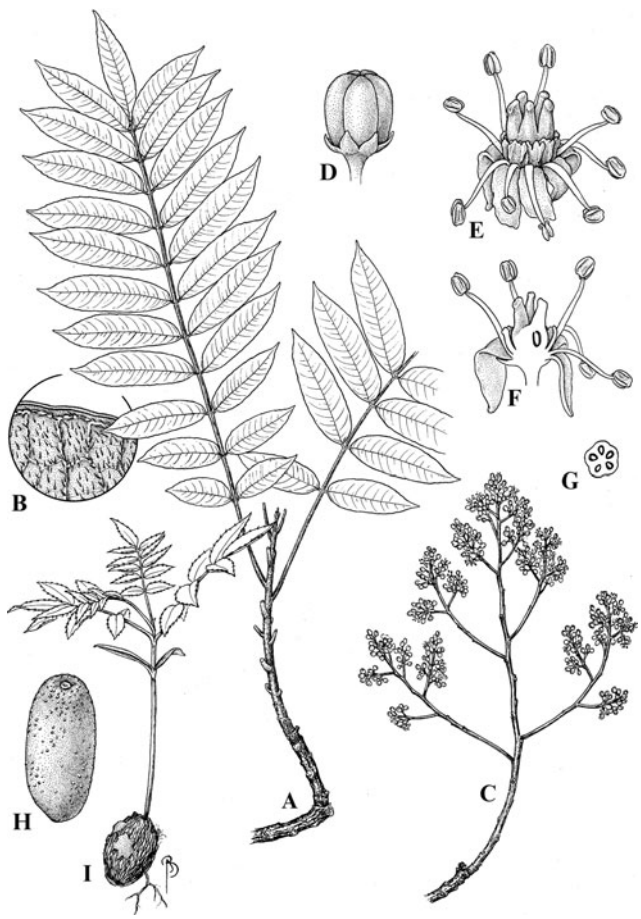

Fig. 6. Anacardiaceae. *Spondias testudinis*. **A** Leafy branchlet. **B** Abaxial leaflet surface. **C** Inflorescence. **D** Flower bud. **E** Flower. **F** Longitudinal section of flower. **G** Transverse section of ovary. **H** Fruit. **I** Seedling. (Reproduced with permission of the artist Bobbi Angell)

81. *Tapirira* Aubl. Fig. 7

Tapirira Aubl., Hist. Pl. Guiane 1: 470, t. 188 (1775).
Mauria Kunth (1824), p. p.

Polygamodioecious trees. Leaves evergreen, alternate, imparipinnate to paripinnate, petiolate; leaflets opposite or subopposite, petiolulate, entire. Inflorescences terminal and/or axillary panicles. Flowers pedicellate, non-articulate; perianth 5-parted, imbricate; corolla greenish yellow or cream-colored; stamens (8–)10, in two whorls of unequal length; pistillode reduced; staminodes reduced; disk glabrous, (8–)10-lobed; carpels (4) 5; stylodia (4)5; stigmas capitate; ovule apical or subapical. Drupe globose, oblong-oblique or ellipsoid, 1-locular, with persistent calyx; exocarp black or purple; endocarp bony or cartilaginous, usually brittle when dry; mesocarp thin, fleshy. Seed with curved embryo; cotyledons with purple striations.

Eight or more species from southern Mexico to southeastern Brazil, Bolivia, and Paraguay.

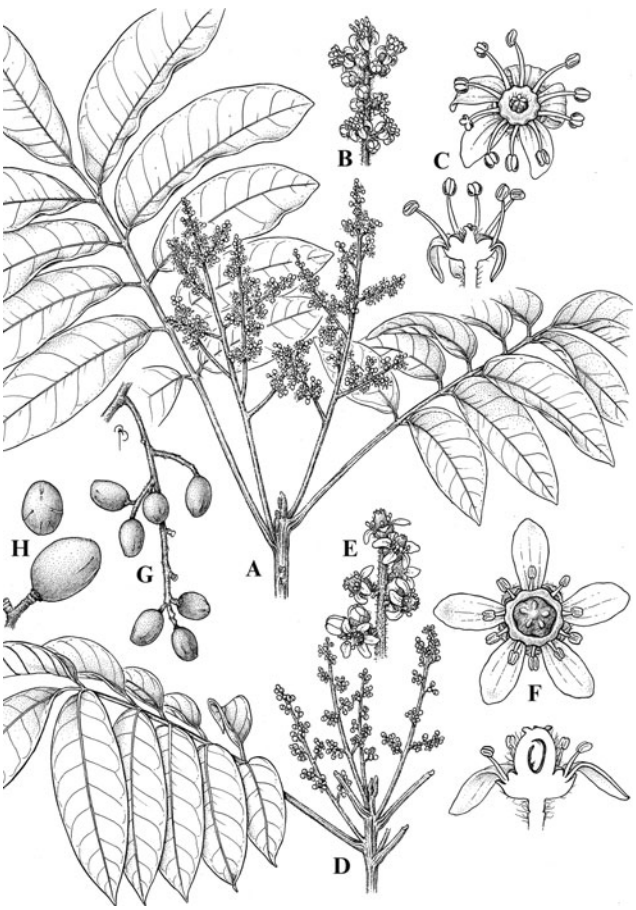

Fig. 7. Anacardiaceae. *Tapirira chimalapana*. **A–C** Male plant. **A** Flowering branchlet. **B** Portion of inflorescence. **C** Flowers, in plan and in longitudinal section. **D–F** Female plant. **D** Flowering branchlet. **E** Portion of inflorescence. **F** Flowers, in plan and in vertical section. **G** Part of infructescence. **H** Fruit, apical and side view. (Reproduced with permission of the artist Bobbi Angell)

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