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SYSTEMATICS, PHYLOGENY & FLORISTICS - REVIEW ARTICLE

Neotropical Anacardiaceae (cashew family)

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Abstract
Anacardiaceae is an ecologically and economically important plant family of about 200 species in 32 genera in the Neotropics. The family is particularly diverse in leaf architecture and fruit morphology, making it a model family to study the evolution of structural diversity as it correlates with lineage diversification. This fruit diversity is the primary reason 11 of the Neotropical genera are monotypic and that so many genera are recognized in the Anacardiaceae. The economic value of the family is driven by the global markets for cashews, mangoes, and pistachios, but there is great potential value in its medicinal properties. At least 10 Neotropical genera cause contact dermatitis, which is a rich area for research in the family. Here presented is a review of the systematics and structural diversity of the family. Particular attention is given to the morphology, economic botany, paleobotany, ecology, and taxonomy of native and naturalized genera. Keys to Neotropical Anacardiaceae subfamilies and genera are provided along with descriptions of native genera.

Keywords Anacardioideae · Economic botany · Morphology · Phytochemistry · Spondioideae

1 Introduction

Accounting for nearly 200 species and 32 genera in the Neotropics (ca. 800 species and more than 80 genera globally), the Anacardiaceae is an ecologically and economically important plant family. The family includes valuable global fruit and seed crops such as cashew (*Anacardium occidentale* L.), mango (*Mangifera indica* L.), pink peppercorn (*Schinus areira* L. and *Schinus terebinthifolia* Raddi), and pistachio (*Pistacia vera* L.), and Neotropical fruit crops such as jocote/ciruela/siriguela (*Spondias purpurea* L.), cajá/jobo (*Spondias mombin* L.), umbu (*Spondias tuberosa* Arruda), and jobo dos Indios/pomme cythére (*Spondias dulcis* Parkinson). Members of the family are also used for medicine, timber, industrial applications, and much more. Anacardiaceae are notorious for causing contact dermatitis, but many of the toxic species are also useful.

The family is distributed from temperate North America, Asia, and Europe to temperate South America, Africa, and Australia. However, the greatest diversity of lineages occurs in the world's tropical areas and the center of diversity for the family is Southeast Asia. Approximately one quarter of all Anacardiaceae species are native to the Neotropics, with *Schinus* being the largest genus with 42 species. Eleven of the 32 Neotropical genera are monotypic, which is primarily a reflection of the great fruit diversity in the family, and seven genera are disjunct between the Old and New Worlds, presenting excellent opportunities for testing biogeographic hypotheses.

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Here, we present an overview of the Neotropical Anacardiaceae. Synopses are provided for evolution, taxonomy, morphology, anatomy, ecology, paleobotany, phytochemistry, and economic and ethnobotany. John Mitchell and Susan Pell edited the entire manuscript, while the numerous authors have each contributed their Anacardiaceae expertise in individual sections and provided key insights across the manuscript. Some of the text presented here is adapted and updated from the two lead authors' Anacardiaceae treatment for the Families and Genera of Vascular Plants series (Pell et al. 2011).

2 Phylogenetic and taxonomic overview

The family Anacardiaceae has a rich history of evolutionary and taxonomic study beginning before Linnaeus and extending to the present day. The family was first recognized by Lindley in 1830 upon his subdivision of Terebinthaceae, a large family described by Jussieu (1789) that included genera from taxa now classified in Anacardiaceae, Burseraceae, Simaroubaceae, Rutaceae, Connaraceae, Euphorbiaceae, and Averrhoaceae. The taxonomic history of Anacardiaceae is complex, with Anacardiaceous taxa historically placed in other families including Blepharocaryaceae, Comocladiaceae, Julianiaceae, Pistaciaceae, Podoaceae, Rhoaceae, Schinaceae, and Spondiadaceae (Pell et al. 2011). Bentham and Hooker (1862) were the first to propose generic groupings within Anacardiaceae, dividing the family into two tribes—Anacardieae and Spondieae—based on the number of ovary locules and ovule insertion on the placenta. These characters were then used in Marchand's (1869) classification in which he recognized nine tribes (Spondieae, Thyrsodieae, Tapirieae, Semecarpeae, Astronieae, Rhoideae, Pistacieae, Mangifereae, and Buchananieae). This tribal classification was modified by Engler in 1876 in his treatment of Brazilian Anacardiaceae, then later in 1881, 1883 and finally in 1892 where he recognized five tribes: Mangifereae (= Anacardieae), Rhoideae (= Rhoeae), Semecarpeae, and Spondieae (= Spondiadeae), and Dobineeae (= Dobineae). Like Bentham and Hooker, Engler used the number of ovary locules and ovule insertion on the placenta to circumscribe these tribes, in addition to other characters including the phyllotaxy, leaf morphology, presence of a perianth in the female flower, number of staminal whorls, stylar insertion on the ovary, carpel number, and embryo morphology.

Engler's tribal classification was generally accepted in subsequent treatments of Anacardiaceae (see additional references) and was most recently revised by Mitchell and Mori (1987). However, based on pericarp structure, wood anatomy, and biflavonoid data, Wannan and Quinn (1990, 1991) suggested that Engler's tribal classification was artificial, and that the small families previously considered to be sister to Anacardiaceae—Julianiaceae and Blepharocaryaceae—should be sunk into Anacardiaceae. They tentatively identified two major groups of genera, each divided into two subgroups. The genera previously included in Julianiaceae (*Amphipterygium* and *Orthopterygium*) and Blepharocaryaceae (*Blepharocarya*), as well as Engler's tribes Anacardieae, Dobineae, Rhoeae, and Semecarpeae, were placed in Group A, with the exception of *Androtium*, *Buchanania*, *Campnosperma*, and *Pentaspadon*. These four genera and all Spondiadeae were placed in Group B. Two genera—*Faguetia* and *Pseudoprotorhus* (= *Filicium,* Sapindaceae)—were not assignable to either group in this treatment.

Terrazas (1994) used *rbcL* sequences and morphological and wood anatomical data to study the phylogeny of the family. Her combined *rbcL*-morphology phylogeny elucidated a monophyletic Anacardiaceae of two major clades. One clade (A1) contains taxa from tribes Anacardieae, Dobineae, Rhoeae, and Semecarpeae and is supported by two synapomorphies: unicellular stalked leaf glands and having both septate and nonseptate fibers in the wood. The other clade (A2) contains Spondiadeae plus *Pentaspadon* and is supported by the synapomorphy of leaves with multicellular stalked glands. Terrazas (1994) proposed, but never formally named, these two clades as subfamilies Anacardioideae and Spondioideae, respectively. Pell (2004) found support for these subfamilies based on phylogenetic analysis of three plastid genes and formally circumscribed and described them. Each of Engler's tribes (sensu Mitchell and Mori 1987) was assigned to a subfamily, with Anacardieae, Dobineae, Rhoeae, and Semecarpeae grouped into Anacardioideae, and Spondiadeae ranked as Spondioideae; however, it was noted that some tribes were polyphyletic in some gene trees. This subfamilial classification was altered in Mitchell et al. (2006; see also Pell et al. 2011), where *Buchanania* was recognized as a member of Spondioideae on the basis of unpublished molecular data, in line with the morphological groupings of Wannan and Quinn (1990, 1991). It was also noted in Pell et al. (2011) that the unpublished molecular analysis retrieved Spondioideae as polyphyletic, although without complete resolution of Anacardiaceae relationships the two-subfamily classification system was maintained in the treatment.

The placement of *Buchanania* in Spondioideae and polyphyly of Spondioideae was later supported in the molecular analysis of one nuclear and three chloroplast markers by Weeks et al (2014). This study also challenged the tribal classification of Anacardiaceae, and as in previous studies, retrieved only Dobineae and Semecarpeae as monophyletic. Recent, target sequence capture data of 353 nuclear genes and 83% of Anacardiaceae genera generally support the subfamilial classification of Pell et al. (2011), retrieving Spondioideae as monophyletic (Joyce 2021, Joyce et al. unpublished). However, these data suggest Anacardioideae is polyphyletic, retrieving *Campnosperma* as an early diverging lineage in Spondioideae in support of the findings of Wannan and Quinn (1990, 1991) and Weeks et al. (2014). Like the molecular analyses of Pell (2004) and Weeks et al. (2014), this recent molecular data indicate that all tribes are polyphyletic with the exception of Dobineae (*Campylopetalum* and *Dobinea*) and Semecarpeae (including samples of *Semecarpus*, *Drimycarpus*, *Nothopegia,* and *Melanochyla*, but missing *Holigarna*), suggesting that the tribal classification of the family is in need of revision in order to be reflective of resolved clades (Joyce 2021; Joyce et al. unpublished). At the genus level, the phylogenetic data (Joyce 2021; Joyce et al. unpublished) and morphological analyses (Herrera et al. 2018) also suggest that *Cyrtocarpa* and *Poupartia* are polyphyletic and confirm the findings of previous authors that *Rhus* is polyphyletic and in urgent need of taxonomic revision (Yi et al. 2007).

Androtium, Haematostaphis, Haplospondias, Holigarna, Koordersiodendron, and *Solenocarpus* have never been included in molecular studies, and their relationships within Anacardiaceae as defined by morphology are yet to be corroborated with molecular data. The classification of *Pentaspadon* remains controversial because morphological studies have placed the genus contrastingly in Anacardioideae (Mitchell and Mori 1987) and Spondioideae (Wannan and Quinn 1991), and the molecular study of Weeks et al. (2014) retrieved it as sister to all Anacardiaceae. Further study of *Pentaspadon* and inclusion in a next-generation molecular study is needed to elucidate the placement of this genus.

At higher taxonomic levels, Anacardiaceae is most closely related to Burseraceae, sharing vertical intercellular secretory canals in the primary and secondary phloem and the ability to synthesize biflavonyls (Wannan et al. 1985; Wannan and Quinn 1990, 1991; Terrazas 1994). Additionally, members of these families are often resinous and possess ovules whose funicles typically have a dorsal bend projecting toward the base of the style, referred to as a ponticulus (Robbertse et al. 1986; Bachelier and Endress 2009; Pell et al. 2011). The close relationship of Anacardiaceae and Burseraceae has been supported by numerous morphological, anatomical, biochemical, and molecular studies (Gadek et al. 1996; Pell 2004; Bachelier and Endress 2009; Weeks et al. 2014; APG 2016; Joyce 2021, Joyce et al. unpublished). Morphological similarities between the gynoecia of some Spondioideae and *Beiselia*, which is sister to all other Burseraceae, support a close relationship between the two families and support their affinities with Kirkiaceae (Bachelier and Endress 2007, 2009). However, Anacardiaceae can be distinguished from Burseraceae by the presence of a single apotropous (syntropous) ovule per locule instead of two epitropous (antitropous) ovules per locule as in Burseraceae. Some Anacardiaceae members can also be separated from most Burseraceae members by the presence of 5-deoxyflavonoids and contact dermatitis-causing compounds, indehiscent fruits, and a lack of stipules, pseudostipules, and terminal pulvinuli subtending the leaflet laminae (Pell et al. 2011). Historically, Anacardiaceae has variously been classified within the orders of Burserales, Rutales, Sapindales, or Terebinthinae; molecular studies support its placement within Sapindales (Gadek et al. 1996; APG 2016; Muellner et al. 2016; Joyce 2021).

3 Anatomy and morphology

Vegetative morphology – *Growth forms*. Neotropical Anacardiaceae are all woody and primarily trees and shrubs, with a few subshrubs, scandent trees (e.g., *Attilaea abalak* E. Martínez & Ramos), and lianas (e.g., *Toxicodendron radicans* (L.) Kuntze). Plants exhibit monopodial or sympodial stem growth and at least two architectural models are present in the family. The model of Scarrone with monopodial trunk and orthotropic sympodial branches was reported in *Anacardium excelsum* (Kunth) Skeels and *Mangifera indica* (Hallé et al. 1978 and additional references), and the model of Rauh with sympodial modular growth in *Rhus* spp.; Hallé et al. 1978). Some taxa in arid habitats have succulent stems (e.g., *Cyrtocarpa, Pachycormus discolor* (Benth.) Coville, *Spondias purpurea, Spondias tuberosa*) or thorns (e.g., *Schinopsis, Schinus*). Short shoots bearing flowers and leaves are found in some taxa (e.g., *Pachycormus, Schinus*). Several taxa (e.g., *Anacardium corymbosum* Barb. Rodr*., A. humile* A. St.-Hil*., A. nanum* A. St.- Hil.) in the Cerrado of central South America are geoxylic suffrutices with large underground woody trunks that are fire-adapted (López-Naranjo 1977; Mitchell and Mori 1987). Water storage roots are characteristic of *Spondias tuberosa* (Cavalcanti et al. 2002).

Bark and wood anatomy of Anacardiaceae has been extensively studied by many authors (e.g., Dadswell and Ingle 1948; Kryn 1952; Roth 1969; Young 1974; Terrazas 1994, 1995; Giménez and Moglia 1995). Bark varies from smooth to rough or scaly; and in some cases, it is shed in peeling sheets (e.g., *Pseudosmodingium perniciosum* (Kunth) Engl*., Pachycormus*) or flaking plates (e.g., *Astronium graveolens* Jacq.), or is prominently ridged (e.g., *Amphipterygium, Spondias*). In *Pachycormus discolor*, the phelloderm (inner bark) is photosynthetic (Gibson 1981). The exudate in Neotropical Anacardiaceae may be milky, red, orange, brown, or clear, and often smells like turpentine. Some taxa have thick, gummy exudate (e.g., *Anacardium, Spondias, Tapirira*), and those that cause contact dermatitis usually have exudate that turns black with exposure to air (e.g., *Comocladia, Metopium, Toxicodendron*).

Leaves. Leaves in the family are deciduous or evergreen, estipulate and usually alternate. Most taxa have imparipinnate leaves (rarely paripinnate; e.g., *Schinus lentiscifolia* Marchand), usually with opposite leaflets (rarely alternate, e.g., *Thyrsodium*), while others have trifoliolate leaves (e.g., *Amphipterygium, Rhus, Toxicodendron*) or simple or unifoliolate leaves (e.g., *Amphipterygium, Anacardium, Cotinus, Lithrea, Malosma, Rhus, Schinopsis, Schinus*). Some taxa (e.g., *Bonetiella*, *Rhus, Schinopsis,* and *Schinus*) are heterophyllous. Leaf or leaflet margins can be entire, crenate, dentate, lobed, or serrate, prominently revolute (e.g., *Anacardium*), or rarely spinose (e.g., *Comocladia*), and when toothed they sometimes display rosoid teeth (Hickey and Wolfe 1975). Cataphylls have been reported in *Astronium, Campnosperma, Comocladia, Cyrtocarpa,* and *Pistacia*, but they are caducous and seasonal and thus, their presence is not always captured in herbarium specimens.

Leaf architecture within Anacardiaceae is extremely diverse (Martínez-Millán and Cevallos-Ferriz 2005; Ellis et al. 2009), and the terminology used here to describe it is based on the *Manual of Leaf Architecture* (Ellis et al. 2009). Primary leaf venation is pinnate, and secondary venation is most commonly eucamptodromous, brochidodromous (usually festooned), craspedodromous, semi-craspedodromous, or cladodromous (when present in Sapindales, the latter is usually diagnostic of Anacardiaceae; e.g., *Astronium*, *Comocladia, Cotinus, Pseudosmodingium, Rhus, Schinus*). Some authors have noted the need to reevaluate cladodromous venation to further distinguish it into different categories (Martínez-Millán and Cevallos-Feriz 2005). A relatively rare but quite distinctive character is craspedodromous with an intramarginal secondary vein, which occurs in *Attilaea* and *Spondias*, and has recently been reported in *Lithrea* (Mercado et al. 2014). Marginal secondary veins are rarely present (e.g., *Lithrea, Spondias radlkoferi* Donn. Sm.). Venation in *Spondias* exemplifies the utility of leaf architecture for distinguishing species in the family (Mitchell and Daly 2015).

Some genera have mixed secondary venation patterns either throughout (e.g., in *Comocladia*, craspedodromous, and cladodromous veins often alternate) or directionally (e.g., *Campnosperma* laminas are often apically brochidodromous and basally eucamptodromous). Intercostal tertiary venation is frequently random reticulate, irregular polygonal, mixed alternate-opposite percurrent, or opposite percurrent. Intersecondary veins are often present, but their frequency varies in many taxa.

Epimedial tertiaries are commonly perpendicular to the primary vein (e.g., *Comocladia*) or vary from parallel to variously angled relative to the secondary veins (e.g., *Actinocheita*, *Cardenasiodendron*), or rarely absent (e.g., *Attilaea*, *Spondias*). Their exmedial course is reticulate, ramifying, or basifixed. In several genera (e.g., *Spondias*), the tertiary veins can be admedially branched. In *Comocladia*, the intercostal tertiary veins are perpendicular to the secondary veins. In some Anacardioideae (e.g., *Comocladia, Pseudosmodingium, Rhus, Toxicodendron*), the transversely ramifying tertiary veins are interconnected (anastomosed) with quaternary veins. In *Malosma,* the tertiaries are truly freely ramified (i.e., areoles absent).

A fimbrial tertiary vein is typically present, and occasionally the marginal ultimate tertiary venation is looped or incompletely looped (e.g., *Spondias*). Areoles vary from being clearly and regularly defined (e.g., *Anacardium, Tapirira*) to being highly irregular in size and shape (e.g., *Spondias*), or absent (*Malosma*). Freely ending veinlets (FEVs) are diverse in Anacardiaceae. They are most commonly highly branched (either dichotomously or dendritically), but can also be one- to two-branched, terminated by highly branched sclereids (e.g., *Spondias radlkoferi*), or terminated by prominent tracheoid idioblasts (e.g., *Comocladia*, *Spondias*).

Trichomes in Neotropical Anacardiaceae may be simple, lepidote, or stellate; unicellular or multicellular; sessile or stalked; and 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 occur in some taxa (e.g., *Campnosperma, Pseudosmodingium*) (Aguilar-Ortigoza and Sosa 2004a). Lepidote scales are rarely present in the family, but are characteristic of *Campnosperma* and *Tapirira lepidota* Aguilar & Hammel.

Leaf anatomy in Anacardiaceae has been researched by many authors, including Metcalfe and Chalk (1950), who provided an overview, and Wilkinson (1971) who studied epidermal features. Many others covered specific genera or habitats (Paula and Alves 1973; Silva 1973; Gibson 1981; Muñoz 1990). Hairy tuft domatia (e.g., *Mauria, Spondias, Toxicodendron*) or marsupiform domatia (e.g., *Anacardium*, *Schinus*) are sometimes present in the secondary vein axils abaxially or associated with the petiole or the base of the leaflet (Mitchell and Daly 2015).

Leaf extrafloral nectaries have also been documented in the secondary vein axils of the leaves and on the adaxial surface of the petiole where it meets the blade of *Anacardium humile* and *A. occidentale*. They are composed of several multicellular and multiseriate nectariferous trichomes that produce glucose—for this reason, they have sometimes been interpreted as extrafloral nectaries rather than as domatia (e.g., Lacchia et al. 2016).

Reproductive morphology – *Inflorescences and flowers*. Inflorescences of Anacardiaceae can be terminal or axillary and tend to be clustered with the leaves toward the tips of the branches. They are often branched and range from panicles to thyrsoids or thyrses and racemes, ending in lax to compact cymose units sensu Endress (2010), or are spicate. In two dioecious Neotropical genera of Anacardioideae, female inflorescences can also develop into a cupular involucre formed by the subtending bracts of the (female) flowers in *Amphipterygium* and *Orthopterygium* (Wannan and Quinn 1991, 1992; Bachelier and Endress 2007; Herrera and Bachelier 2016). Extrafloral nectaries have also been reported at the junctions of the panicle branches in *Anacardium occidentale*.

Flowers can be few to numerous, or rarely solitary in a few *Schinus* species (Barkley 1957; Silva-Luz et al. 2019), and are relatively small (< 1 cm in diameter in the Neotropics). They are usually bisexual to functionally or morphologically unisexual, with an isomerous pentamerous perianth and androecium, and a fleshy annular or lobed intrastaminal disk (lobed extrastaminal disk in *Mangifera*). Both the perianth and/or disk can be absent or severely reduced in wind-pollinated taxa (e.g., *Amphipterygium, Orthopterygium, Pistacia*), which are found only in Anacardioideae that primarily occur in at least seasonally dry habitats (see below for more information on the disk). The gynoecium is syncarpous (or rarely monomerous) with a superior ovary and as many carpels as there are styles and stigmas or stigmatic lobes (Wannan and Quinn 1991; Bachelier and Endress 2007, 2009; Tölke et al. 2021a). The flowers in Neotropical Spondioideae are usually obdiplostemonous with as many carpels as there are petals facing them and usually have an ovary with as many locules as styles and stigmas (Wannan and Quinn 1991; Bachelier and Endress 2009; Tölke et al. 2021a). In contrast, in Anacardioideae the androecium is usually haplostemonous (e.g., *Astronium*, *Comocladia*, *Cotinus, Pseudosmodingium, Rhus*), diplostemonous (*Lithrea, Mauria, Schinus*), or reduced to four stamens (*Anacardium excelsum*) or a single (*Mangifera indica,* other *Anacardium* spp.) fertile stamen. In some taxa (*Anacardium, Mangifera*), additional sterile stamens are present. The gynoecium of Anacardioideae is typically trimerous and the ovary pseudomonomerous formed by one carpel with a fertile locule and ovule and two sterile carpels reduced to more or less well-developed styles and stigmas (Wannan and Quinn 1991; Bachelier and Endress 2009; Tölke et al. 2021a). However, pseudomonomerous gynoecia have also been reported in Neotropical Spondioideae, in which species usually have carpel dimorphism and reduction in the number of fertile ovules (e.g., some *Cyrtocarpa* s.l. spp*., Tapirira*). Truly monomerous gynoecia have been reported in both subfamilies (e.g., *Campnosperma* in Spondioideae, or *Anacardium* and *Mangifera* in Anacardioideae) (Wannan and Quinn 1991; Bachelier and Endress 2009; Tölke and Demarco 2020; Tölke et al. 2021a).

In all Anacardiaceae, each fertile locule typically contains a single apotropous ovule (or also syntropous, see Endress 2011). The ovule is regularly bitegmic and crassinucellate with a round inner integument and a hood-shaped outer integument that sometimes has large lateral flaps. However, some Anacardioideae are unitegmic, as in *Mangifera* and *Anacardium* where the ovule is also pachychalazal, or in *Pistacia*, *Amphipterygium*, and *Orthopterygium* where the funicle tends to increase dramatically in size after fertilization and form large spongy tissue (Bachelier and Endress 2007; Herrera and Bachelier 2016). After fertilization, the development of the endosperm is free nuclear (Copeland 1959, 1961). However, the endosperm is usually entirely consumed during embryo development and mature seeds are typically exalbuminate. The dicotyledonous embryos are usually well-developed and are up to 5 cm in length and weigh about 20 g in some cultivars of *Mangifera* (Kennard 1955).

Breeding systems. In both subfamilies, flowers can be functionally unisexual with rudimentary stamens or carpels (type I sensu Mitchell and Diggle 2005) and are thus more or less cryptic (Wannan and Quinn 1991; Bachelier and Endress 2007, 2009). Herein, we refer to vestigial gynoecia as pistillodes because this term is used much more widely than carpellodes, which may sometimes be more accurate and is somewhat gaining popularity in use. Flowers that are morphologically and functionally unisexual with no vestigial stamens or carpels (type II sensu Mitchell and Diggle 2005) are only found in *Astronium* section *Astronium* and in a few other Anacardioideae taxa (*Pistacia, Amphipterygium, Orthopterygium*) that are strictly wind-pollinated (Barkley 1968; Bachelier and Endress 2007; Pell et al. 2011; Weeks et al. 2014; Mitchell and Daly 2017, Joyce unpublished data).

There is a tremendous diversity of flower morphologies and breeding systems in Neotropical Anacardiaceae. In *Spondias*, for example, breeding systems include hermaphrodite in *S. dulcis,* andromonoecious in *S. tuberosa* (Nadia et al. 2007) and *S. macrocarpa* Engl. (Tavares et al. 2020), and dioecious in *S. purpurea* (Bachelier and Endress 2009; Pell et al. 2011; Mitchell and Daly 2015). The literature for *S. mombin* is even more complicated with some studies describing it as gynodioecious (Tavares et al. 2020) and others as andromonoecious (Ramos 2009). In *Pistacia*, where unisexual flowers are of type I (Mitchell and Diggle 2005), a study recently found a range of breeding systems across the genus and even within species (Bai et al. 2019). These included hermaphrodite, dioecious, monoecious, gynomonoecious, and trimonoecious.

Perianth. In both subfamilies, sepals tend to be connate at the base, whereas petals are usually entirely free. The perianth is most commonly glabrous, although in some taxa it is pubescent only on the sepals (e.g., *Tapirira*) or on both petals and sepals (e.g., *Actinocheita*, *Campnosperma, Thyrsodium*) (Wannan and Quinn 1991; Bachelier and Endress 2009; Pell et al. 2011). Peltate scales are reported on the flowers of *Tapirira lepidota* and on the ovary of *Campnosperma* (Bachelier and Endress, 2009; Hammel et al. 2014).

In most Anacardiaceae, petals often become longer than the sepals during floral development and take over the protection of the inner reproductive organs. However, the sepals are persistent and greatly enlarged in the fruits of *Astronium* (Leite 2002; Mitchell and Daly 2017) and aid dispersal. In some wind-pollinated members of Anacardioideae, the perianth can be reduced to a single whorl of organs interpreted as tepals in *Haplorhus* (Pell et al. 2011), sepals in male flowers of *Amphipterygium* and *Orthopterygium*, and sepals or bracts in *Pistacia* (Bachelier and Endress 2007). Only rarely is the perianth entirely lacking, as in female flowers of *Amphipterygium* and *Orthopterygium* (Bachelier and Endress 2007; Herrera and Bachelier 2016).

Androecium. In virtually all Anacardiaceae, stamens are free, and only in *Anacardium* the bases of the filaments fuse together and form a short staminal tube around the ovary. In all members of the family with a diplostemonous androecium, stamens often appear to be arranged in a single whorl around the disk, with antepetalous stamens regularly shorter than the antesepalous ones (Wannan and Quinn 1991; Bachelier and Endress 2009). In haplostemonous flowers, the single whorl of stamens is usually facing the sepals and alternating with the petals (e.g., *Actinocheita*, *Astronium*, *Comocladia*, *Cotinus, Loxopterygium, Pseudosmodingium, Rhus, and Toxicodendron*). Even in flowers with a single perianth whorl, stamens are either facing sepals (or bracts) like in *Pistacia,* or alternating with perianth lobes interpreted as sepals in male flowers of *Amphipterygium* and *Orthopterygium* (Bachelier and Endress 2007). In *Mangifera* and *Anacardium*, the fertile androecium comprises only one fertile antesepalous stamen that is distinctively larger than the others, which are often reduced or sterile (Wannan and Quinn 1991; Bachelier and Endress 2009; Tölke and Demarco 2020).

Stamens are usually glabrous, but the filaments of some species (e.g., *Anacardium excelsum*, some *Thyrsodium*) and the anthers of others (e.g., *Amphipterygium, Orthopterygium*) are pubescent (Bachelier and Endress 2007; Herrera and Bachelier 2016). Anthers of all Anacardiaceae are bithecal, tetrasporangiate, and usually H-shaped or sometimes sagittate. The dorsal side of the theca is often more or less larger than the ventral one, and anther dehiscence is latrorse to ventrorse with a longitudinal dehiscence line extending from the tip down to the base of each theca. The connective can be conspicuous as in some *Cyrtocarpa*. Anthers are either connected at the base (basifixed) or on the median dorsal side (dorsifixed) and may be more or less versatile as in *Spondias* and *Tapirira* in Spondioideae*,* or *Anacardium* and *Mangifera* in Anacardioideae (Bachelier and Endress 2009; Tölke et al. 2021a).

Pollen is usually tricolporate and spheroidal with long, narrow colpi, with or without ornamentation. In part because of their distinct pollen morphologies, the wind-pollinated genera *Amphipterygium, Orthopterygium*, and *Pistacia* have historically been segregated as the distinct families Julianiaceae (*Amphipterygum* and *Orthopterygium*) and Pistaciaceae (*Pistacia*). Adapted for wind dispersal, their pollen grains thus have a large number of small, shallow colpi, much like a golf ball, in contrast to those more typical of insect-pollinated genera which typically have a combination of striations and reticulations. For additional information on Anacardiaceae pollen, see Heimsch (1940), Marticorena (1968), Anzótegui (1971), and Olivera et al. (1998).

Intrastaminal disk, osmophores, and secretions. The flowers of most Anacardiaceae have an intrastaminal disk, often referred to as a nectary disk. In the Neotropics, it is missing in *Amphipterygium, Anacardium, Orthopterygium,* and *Pistacia* and is extrastaminal in *Mangifera* (Bachelier and Endress 2007). When present, the disk is typically more or less fleshy and lobed between the bases of the filaments and the gynoecium, and smooth to extremely papillate. The surface is usually glabrous and may be densely covered in stomata that are sometimes referred to as nectarostoma because of their secretory function (Wannan and Quinn 1991; Bachelier and Endress 2009; Tölke et al 2018b; Tölke and Demarco 2020). *Mangifera* has an extrastaminal nectary disk that is sometimes described as five antesepalous fleshy lobes. *Anacardium* flowers lack a disk, but have multicellular glandular trichomes. Both genera have osmophores on the base of their petals, which were recently reported for the first time in the family (Tölke et al. 2018a).

The role of the intrastaminal disk as a nectary has long been assumed. A comparative study in seven genera and thirteen species encompassing both subfamilies of Anacardiaceae recently confirmed this by showing that the secretions contain at least three sugars (Tölke et al. 2018a, b, 2021b). They found that relative concentrations of fructose, glucose, and sucrose are more or less the same in different floral morphs of the same species, but vary strongly from one species to another. In most species, other substances such as lipids and/or phenolic compounds are also part of these mixed secretions, and in *Tapirira guianensis*, the disk persists in young fruits but produces only lipids and no sugars (Tölke et al. 2015, 2018b). However, whether these mixed secretions could also produce a floral scent remains unknown, and their potential evolutionary and ecological significance needs to be evaluated in the context of the most recent phylogenies of the family.

Gynoecium. In Anacardiaceae, the gynoecium is typically syncarpous and comprises a single ovary with as many styles and stigmas as there are carpels. In addition, there are usually as many carpels as there are petals in Spondioideae; whereas, in Anacardioideae the gynoecium typically comprises three carpels, out of which only one is fertile and forms a locule and the other two are reduced each to a style and stigma. Anacardioideae gynoecia are thus typically pseudomonomerous, whereas truly pseudomonomerous (unilocular) gynoecia are relatively rare in Spondioideae and, to date, have been documented in New World taxa only in *Tapirira* (Wannan and Quinn 1991; Bachelier and Endress 2009; Tölke et al. 2021a) and some species of *Cyrtocarpa* (Herrera et al. 2018). In some Spondioideae (e.g., *Attilaea* and some *Cyrtocarpa*), not all carpels are fertile and often only one seed is produced, while in others (e.g., *Antrocaryon* and *Spondias*) all carpels typically produce seed (Herrera et al. 2018; Tölke et al. 2021a). The gynoecium can be truly monomerous in both subfamilies, as in *Campnosperma* in Spondioideae, and in *Anacardium, Mangifera* (Wannan and Quinn 1991; Pell 2004; Bachelier and Endress 2009; Tölke and Demarco 2020), and other members of Anacardioideae (e.g., *Orthopterygium*; Herrera and Bachelier 2016).

In Anacardioideae, the asymmetric development of the carpels makes it difficult to compare their pseudomonomerous gynoecia to other syncarpous gynoecia in Spondioideae, where all carpels usually develop more or less symmetrically (at least up to ovule initiation or rarely earlier). In most Anacardioideae, the bases of the three styles are usually united above the ovary and form a symplicate zone with an internal compitum. Whereas in *Schinopsis*, the unusual development of the ovary above the single locule and the displacement and separation of the three styles and stigmas prevents the formation of a symplicate zone and internal compitum. There is also no symplicate zone or internal compitum in any syncarpous gynoecia of Spondioideae, in which all carpels either form a locule and share a well-developed synascidiate zone or like in *Tapirira,* they form a pseudomonomerous gynoecium (Bachelier and Endress 2009; Tölke et al. 2021a). Sometimes, as in *Spondias purpurea*, the synascidiate zone exposes the former center of the floral apex between the free styles and stigmas (Bachelier and Endress 2009).

Ovule and ponticulus. A defining feature of Anacardiaceae is the presence of a single ovule per locule. It is typically pendulous and anatropous (syntropous), and curved with the micropyle facing the base of the funicle below its connection to the median axile and apical placenta. Only in some taxa the insertion of the ovule is lower, toward the base of the inner ventral side of the locule, as in *Anacardium*, *Mangifera*, or *Pistacia* (Bachelier and Endress 2007, 2009). In all Anacardiacaeae studied to date, the funicle always appears relatively long and with a bend on the dorsal side that comes in close contact with the base of the style and the pollen tube transmitting tract and sometimes even forms a dorsal projection resembling the fin of a shark (Bachelier and Endress 2009). This zone of contact is called the ponticulus because it may function as a bridge in the pollen tube pathway between the base of the style and the ovule. In contrast with other angiosperms in which the pollen tube enters the locule and follows the morphological surface of the ovule until it reaches the micropyle, in some Anacardiaceae one pollen tube can penetrate directly inside the funicle via the ponticulus and follow the trace of procambium up to the chalaza and the female gametophyte (de Wet et al. 1986; Gonzalez 2016, Lora et al. 2021). To date, the ponticulus has only been looked for and documented in a few genera of Anacardioideae and seems not to be functional in Spondioideae studied to date (Robbertse et al. 1986). More research on the ponticulus is needed to determine whether or not it is a synapormophy for any Anacardiaceae clades and has any functional or evolutionary significance.

In Anacardiaceae, ovules are crassinucellar and regularly bitegmic. Unitegmic ovules have only been reported in a few genera of Neotropical Anacardioideae (*Amphipterygium, Anacardium, Mangifera, Orthopterygium*, *Pistacia*), and while the developmental origin of their single integument is still debated, it seems to be often associated with pachychalazy (Bachelier and Endress 2007, 2009, and references therein). However, pachychalazal seeds have also been reported in genera with bitegmic ovules (see below). In bitegmic ovules, the inner integument is typically circular and forms a straight endostome, while the outer integument is rather hood-shaped, sometimes with two more or less flattened "flaps" and an exostome that is variable in form (Bachelier and Endress 2009). In some genera, the funicle is massive (*Amphipterygium* and *Pistacia*) and develops a basal (lower) appendage, sometimes with lobes, that expands dramatically after fertilization (Bachelier and Endress 2007).

Fertilization is typically porogamous (through the micropyle). However, in some Anacardioideae it is chalazogamous, especially in genera where a functional ponticulus has been documented (Copeland 1961; Aleksandrovski and Naumova 1985). The function of the ponticulus has not yet been investigated in all species in which it has been documented. In *Schinopsis balansae*, an intermediate pathway called chalazoporogamy was described recently for the first time in the family (Gonzalez 2016). All species studied to date typically have a single monosporic *Polygonum*-type female gametophyte, which after fertilization yields a single embryo and a triploid free nuclear endosperm (Johri 1963).

Fruits and seeds. In Neotropical Anacardiaceae, fruits are typically drupes or samaras (rarely syncarps, utricles, nutlike, or baccate) that are fleshy or dry. Fruits of the family are often edible (e.g., *Antrocaryon, Cyrtocarpa, Mangifera, Rhus, Schinus, Spondias, Tapirira).* The exocarp varies in thickness and may be soft to lignified, pubescent or glabrous, and variously colored. It is brittle and separates from the mesocarp at maturity in some taxa (*Lithrea, Schinus, Toxicodendron*). The mesocarp is typically fleshy or fibrous and varies in thickness; it is edible in a number of species. In taxa that cause dermatitis, the mesocarp often has resin canals appearing brown or black, also called secretory ducts (e.g., *Anacardium, Comocladia, Lithrea, Metopium, Toxicodendron*).

Endocarps can be chartaceous, fibrous, cartilaginous, or bony, sometimes with opercula in Spondioideae. Wannan and Quinn (1990) described two anatomically distinct endocarp types that corresponded to the two subfamilies. The *Spondias* type typically has irregularly oriented sclerenchyma and is lignified, and the *Anacardium* type is regularly oriented into discrete layers including palisade-like sclereids. However, a recent comparative study of fruit anatomy in Spondioideae showed that the endocarps of *Campnosperma* (and Paleotropical *Buchanania*) are quite distinct from those found in other members of the subfamily (Herrera et al. 2018). Another study detailed the endocarp secretions produced in various stages of development in *Tapirira guianensis* Aubl. (Tölke et al. 2017), highlighting their potential role in seed protection and dispersal.

All Anacardiaceae typically produce a single seed per locule. Thus, in Anacardioideae, the fruit typically contains a single seed, whether the locule is derived from a pseudomonomerous or monomerous gynoecium (Wannan and Quinn 1990, 1991; Bachelier and Endress 2007, 2009). In contrast, the number of fertile carpels varies from one to several in Spondioideae. *Attilaea* and some *Cyrtocarpa* have more than one locule but produce only one seed (Martínez and Ramos 2007; Herrera et al. 2018), whereas *Antrocaryon* and *Spondias* have five or more locules and typically produce five seeds. In species of *Pistacia* (Verdù and Garcia-Fayos 1998), *Schinopsis* (González and Vesprini 2010), and *Spondias* (Juliano 1932), parthenocarpic development of seedless fruits is common and a study of a member of the sister family Burseraceae suggests that parthenocarpy may be more common in both families and may have an adaptive value to avoid seed predation (Ramos-Ordoñez et al. 2012).

Native Neotropical Anacardiaceae seeds vary in length from 2 mm to more than 4 cm and are typically straight or curved. Endosperm is generally lacking, and the seeds are exalbuminate, with a well-differentiated dicotyledonous embryo. Germination occurs through irregular or regular splitting of the endocarp or via specialized mechanisms (many of which are opercula) that open small portions of the endocarp (Hill 1933, 1937). Opercula are found only in Spondioideae; they are usually apparent on the endocarp surface, but are covered by fibrous endocarpic and mesocarpic projections in some *Spondias* taxa. In Neotropical Anacardiaceae, the whole operculum detaches with the emerging radicle (e.g., *Antrocaryon, Cyrtocarpa, Spondias*; Hill 1933, 1937; Herrera et al. 2018). Germination in Neotropical Anacardiaceae is typically epigeal, as in the rest of the family, but may be hypogeal, and in both types the plano-convex (rarely flat) cotyledons are equal in size, free, and may be either cryptocotylar or phanerocotylar, typically straight or curved (Carmello-Guerreiro and Paoli 1999; Garwood 2009).

Secretory ducts. In all Anacardiaceae, secretory ducts (resin canals) are derived either from the phloic procambium in vegetative and reproductive structures, or from the ground meristem behind the shoot or root apical meristem (medullary meristem). Their development can also vary from schizogenous to lysigenous, and authors often have different interpretations of similar results. For instance, their development is described as schizolysigenous in stems of Anacardioideae, such as *Anacardium, Rhus* (Copeland 1961; Paula and Alves 1973), and the invasive *Toxicodendron succedaneum* (L.) Kuntze (Harada 1937). Other studies of *Anacardium* (Nair et al 1983), *Toxicodendron* (McNair 1918), and *Schinus* (Venning 1948) reported their development as being schizogenous. However, *Anacardium* hypocarp secretory ducts were reported to be lysigenous (Varghese and Pundir 1964), as were vegetative and reproductive organs of *Mangifera* (Venning 1948; Fahn and Joel 1976), and shoots of *Schinus* (Joel 1978).

The development of secretory ducts seems to be independent from their origin, but there appears to be a correlation between their derivation and the type of secretions they produce. Tölke et al (2021a, b) found that in *Anacardium, Lithrea, Spondias,* and *Tapirira*, ducts originating from phloic procambium tend to secrete lipids (resin sensu stricto of Tölke et al. 2021b), and those derived from ground meristem tissue tend to secrete mostly carbohydrates (gums). In addition, they showed that the composition of phloic duct secretions also tends to be similar in both vegetative and reproductive structures and are often a mix of compounds (e.g., lipids and carbohydrates) that are collectively referred to as resin sensu lato, like those of the medullary ducts of *Tapirira*. However, gums comprising only polysaccharides were also identified in medullary ducts of *Anacardium* and *Spondias*, and a resin sensu stricto comprising only lipids was found in fruits of *Anacardium*. Given these results, the current classification of mixed secretions should not be used for taxonomic inferences (Tölke et al. 2021b).

4 Ecology

Distribution and habitats – Neotropical Anacardiaceae are distributed from southern Canada and the USA in North America south to the West Indies and South America. All Spondioideae occur in subtropical and/or tropical habitats, while Anacardioideae are found in temperate, subtropical, and/or tropical habitats. Some species, such as *Malosma laurina* (Nutt.) Nutt. ex Abrams, *Metopium toxiferum* (L.) Krug & Urb., *Pistacia mexicana* Kunth, multiple species of *Rhus, Toxicodendron radicans,* and *T. diversilobum* (Torr. & A.Gray) Greene, occur primarily in temperate and/or subtropical areas of the USA and extend into the Neotropics. Of these, *Metopium toxiferum, Rhus copallinum* L., and *Toxicodendron radicans* occur on both the mainland and in the West Indies. *Lithrea, Schinopsis,* and *Schinus* are the southernmost genera, occurring primarily in the subtropics and tropics, but also reaching temperate areas in southern South America. *Schinus* occurs as far south as Patagonia with taxa distributed in lowland habitats and a few reaching an altitude up to 4000 m.

Some Neotropical Anacardiaceae genera, such as *Actinocheita*, *Amphipterygium*, *Apterokarpos*, *Astronium*, *Attilaea, Cardenasiodendron, Comocladia, Cyrtocarpa, Lithrea, Pseudosmodingium*, and *Schinopsis,* are primarily distributed in tropical dry forests (including the Chaco), while *Bonetiella, Orthopterygium*, and *Pachycormus* inhabit desert habitats (Barkley and Meyer 1973; Santin 1989; Mitchell and Daly 1991; Pell et al. 2011; Mitchell and Daly 2017). Species of *Comocladia*, *Cotinus*, *Lithrea, Malosma*, *Rhus,* and *Schinus* occur in open scrubland, including chaparral. *Pistacia mexicana* and many *Rhus* species are associated with pine-oak forest, often on calcareous soils. Species of *Anacardium, Antrocaryon, Campnosperma, Mosquitoxylum, Tapirira,* and *Thyrsodium* are commonly found in areas of lowland tropical moist forests and gallery forests, mainly in Amazonian and eastern Brazil (Mitchell and Mori 1987; Mitchell and Daly 1993; Mitchell 1999; Pell et al. 2011; Silva-Luz et al. 2019). Species of *Anacardium, Loxopterygium*, *Schinus,* and *Spondias* occur in both moist and tropical dry forests (Mitchell and Mori 1987; Mitchell and Daly 2015). *Anacardium* and *Tapirira* also extend their occurrence to cerrado, campo rupestre and restinga vegetation, in forest patches or coastal forests (Pirani 1987, 2003). *Mauria, Ochoterenaea,* and some species of *Schinus* and *Tapirira* are most commonly found in montane forests in the Andes (Silva-Luz et al. 2019).

Anacardiaceae adapted to living in dry habitats in the Neotropics are particularly rich in morphological diversity, which corresponds to greater taxonomic diversity in these habitats versus in wet habitats. The number of Anacardiaceae species in Neotropical dry habitats (e.g., caatinga, chaco, chaparral, campo rupestre, desert, grassland, matorral, Patagonian steppe, pine-oak forest, restinga, savanna, tropical dry forest) is nearly double the number in wet habitats (e.g., flooded forest, gallery forest, wet lowland and montane forests, tropical wet, and moist forests).

Organismal and ecological interactions – Ecological interactions occur between Neotropical Anacardiaceae and numerous other organisms including ants and other insects, mites, endophytic, and endomycorrhizal fungi, and a diversity of vertebrates. *Anacardium* has associations with endomycorrhizal and endophytic fungi (Faria et al. 2016), and endophytic fungi have been isolated from leaf blades of *Astronium* (mentioned as *Myracrodruon*), *Schinus,* and *Spondias* (Rodrigues and Samuels 1999; Lima et al. 2012; Pádua et al. 2019). Ants forage nectar from extrafloral nectaries of *Anacardium* and protect the plant against herbivores in this mutualistic relationship (e.g., Lacchia et al. 2016).

A great diversity of galls can be observed on South American Anacardiaceae, including barrel-shaped leaf rolls, lenticular, nipple-shaped, or pit galls on the leaves, or globoid or spindle-shaped galls enclosed within swollen stems. *Anacardium, Astronium, Lithrea, Schinopsis, Schinus, Spondias, Tapirira,* and *Thyrsodium* are particularly heavily attacked by insects, in some cases with host-specific gall-inducing insect species (Burckhardt and Basset 2000; Hodgson et al. 2009; Moura et al. 2010; Jesus et al. 2012; Dias et al. 2013; Avila and Oleques 2016).

Pollination syndromes. Most Neotropical Anacardiaceae are entomophilous, but wind pollination occurs in some members of Anacardioideae, such as *Amphipterygium, Orthopterygium,* and *Pistacia.* Some *Anacardium, Astronium,* and *Schinus* species are ambophilous (combination of insect and wind pollination; Torretta and Basilio 2009). *Haplorhus* appears to be at least partially wind-pollinated and may also be ambophilous, but additional study is needed for confirmation. Insects important for Anacardiaceae pollination in the Neotropics include bees (frequently stingless bees), wasps, and flies, with an assortment of other insects pollinating flowers to a lesser degree. Most Anacardiaceae flowers attract generalist pollinators, and in some cases multiple orders of insects have been found carrying the pollen of one taxon (Lenza and Oliveira 2005; Chiapero et al. 2021).

Anacardium species are typically pollinated by moths and butterflies (Mitchell and Mori 1987), and secondarily by bats (Gardner 1977). Heteranthery has been documented in *Anacardium* and *Mangifera* where some species have emergent large stamens and a set of smaller stamens, both of which have pollen (Mitchell and Mori 1987).

Dispersal. Both animal and wind dispersal are prevalent in Neotropical Anacardiaceae. Nineteen of the 32 genera have fleshy, vertebrate-dispersed drupes. The rest of the genera are wind-dispersed, or their mechanism of dispersal is yet to be determined.

Like wind pollination, wind dispersal is found exclusively in Anacardioideae, but the two only occur together in *Amphipterygium* and *Orthopterygium*. Wind-dispersed taxa display a variety of morphological adaptations that evolved for this purpose (Weeks et al. 2014). These include subtending enlarged sepals (*Astronium*), trichome-covered margins on a globose fruit (*Actinocheita*), laterally compressed samaras with trichome-covered margins (*Ochoterenaea*), samaras with two lateral wings (*Cardenasiodendron*, *Pseudosmodingium*), samaras with a single lateral wing (*Loxopterygium*, *Schinopsis*), and dry samaroid syncarps of nutlets (multiple fruit, *Amphipterygium*, *Orthopterygium*; Augspurger 1986, Burnham and Carranco 2004). Wind is the most likely dispersal mechanism of the small, dry fruit of *Apterokarpos* (a dry achene-like drupe without a wing) and *Pachycormus* (dry utricle fruits), but reports for these are lacking and further research must be done to confirm this conjecture.

Wind-dispersed Anacardiaceae genera are often associated with tropical dry forests (*Actinocheita, Amphipterygium, Apterokarpos, Astronium, Cardenasiodendron, Loxopterygium, Pseudosmodingium, Schinopsis*) or other types of arid habitats (*Orthopterygium*; Weeks et al. 2014). Some of these wind-dispersed genera have species that occur in moist habitats like tropical moist forests and tropical rain forests as well. In these habitats, the species tend to be emergent or canopy trees (e.g., *Astronium concinnum* Schott, *A. glaziovii* Mattick, *A. graveolens, A. lecointei* Ducke, *A. obliquum* Griseb., *A. ulei* Mattick, *Loxopterygium sagotii* Hook.f.). The winged fruits of *Schinopsis balansae* Engl. have been recorded as traveling 60–150 m away from the parent tree (Galarza 1915). In some cases, wind-dispersed fruits are consumed by animals that may or may not also disperse the seed (macaws, Pitter and Christiansen 1995; parrots, Villaseñor et al. 2010).

Birds are the primary dispersers of fleshy-fruited genera, including *Comocladia*, *Haplorhus*, *Lithrea, Malosma, Mauria, Metopium, Mosquitoxylum*, *Pistacia*, *Rhus*, *Schinus*, *Tapirira*, *Toxicodendron* (Eguiarte and Martínez de Rio 1985; Silva and Melo 2011; Athiêa and Dias 2016; Carlo and Morales 2016; Acosta and Mugica 2019). In addition, some primarily wind-dispersed genera (e.g., *Astronium*) are secondarily bird-dispersed (Silva and Melo 2011). Bats are an important dispersal agent for *Anacardium,* feeding on the fleshy hypocarp, and for *Spondias* and *Thyrsodium* (Lobova et al. 2009), feeding on the fleshy drupes. Primates disperse the fruits of *Anacardium, Antrocaryon*, *Astronium*, *Spondias,* and *Tapirira* (van Roosmalen 1980; Estrada and Coates 1984; Stevenson 2000; Di Fiore et al. 2008). There are also reports in the literature of additional important animal dispersers of Neotropical Anacardiaceae: coatis, coyotes, ctenosaurs, deer, foxes, iguanas, kinkajou, maned wolf, peccaries, tapirs, and tortoises (Janzen 1985; Castro et al. 1994; Fragoso 1997; Altrichter et al. 1999; Motta-Junior and Martins 2002; Alves-Costa and Eterovick 2007). Leafcutter ants have been observed carrying fruits of *Cyrtocarpa velutinifolia* (R.S. Cowan) J.D. Mitch. and Daly into their refuse piles where they germinate at a higher rate than in other nearby areas where they fall (Brener and Silva 1996). These ants have also been observed dispersing *Schinopsis balansae* (Barberis et al. 2012). In both cases, the ants are secondary dispersers as these fruits are primarily vertebrate- and wind-dispersed, respectively.

Rodents and parrots mostly function as seed predators rather than dispersers, but they do occasionally effectively disperse seeds (e.g., agoutis; Smythe 1970). Bearded capuchin monkeys in Brazil have been reported as seed predators, and they have been observed using tools to open the endocarps of *Anacardium* (Luncz et al. 2016). Some birds, such as macaws and parrots, have beaks strong enough to break open even very hard Anacardiaceae endocarps and eat the seeds inside (e.g., Ragusa-Netto 2011).

Anacardium has an especially interesting adaptation that facilitates animal dispersal: an enlarged edible hypocarp that subtends the drupe. This vegetative structure is a fleshy, expanded pedicel and is the source of cashew juice. One species of *Anacardium*, *A. microsepalum* Loes., grows in the flooded forests of the Amazon and lacks a hypocarp. The fruits fall into the water at maturity and may be fish-dispersed (Mitchell and Mori 1987), but are more likely fish-predated and water-dispersed (Gottsberger 1978).

Conservation – As with other threatened plants, the primary drivers endangering Neotropical Anacardiaceae are habitat loss and overexploitation, primarily for wood and charcoal harvesting. There are eight species of Neotropical Anacardiaceae currently listed as Endangered (EN) by the International Union for Conservation of Nature (IUCN); however, some of these are in need of further evaluation. *Haplorhus peruviana* Engl. occurs in inter-Andean valleys on the western slope of the Andes from central Peru south to northern Chile and has been determined by the IUCN to be Endangered. Similarly, *Orthopterygium huaucui* (A. Gray) Hemsl. is endemic to the western slope of the Andes in central Peru at mid-elevations and, although it has not yet been evaluated by IUCN, it is a Species of Concern due to habitat destruction (León et al. 2013). Species that are restricted to the Caatinga and other dry habitats in Central and South America are also under great pressure from habitat destruction and conversion to agricultural use. Taxa endemic to islands are also under particular threat due to habitat loss. For example, numerous taxa in Jamaica are listed as Near Threatened to Critically Endangered (e.g., *Comocladia cordata* Britton, *C. parvifoliola* Britton, *C. velutina* Britton). *Tapirira chimalapana* T. Wendt and J.D. Mitch. from Mexico is listed as Critically Endangered by the IUCN due to habitat loss in the wet forests in the area around the Isthmus of Tehuantepec.

Species that have not been evaluated by IUCN but are Species of Concern are *Apterokarpus gardneri* (Engl.) Rizzini, *Cardenasiodendron brachypterum* (Loes.) F.A. Barkley, *Loxopterygium huasango* Spruce ex Engl., *Spondias admirabilis* J.D. Mitch. and Daly, and *Spondias expeditionaria* J.D. Mitch. and Daly. Much work remains to be done to evaluate the conservation status of Neotropical Anacardiaceae. Many of the Caribbean islands have been particularly neglected, including most dramatically Cuba and Hispaniola.

Mauria provides a good case study for the importance of resolving taxonomic questions in preparation of conservation assessments. Several species of *Mauria* are listed by IUCN, but the genus is in need of taxonomic revision. Unfortunately, some IUCN assessments are based on incorrect or unresolved taxonomy. *Schinopsis haenkeana* Engl. is listed as vulnerable, but it is a synonym of *Schinopsis marginata* Engl., which is not listed (Hunziker 1998). Further confusing this issue is that *Schinopsis quebracho-colorado* (Schltdl.) F.A. Barkley and T. Mey. is listed as being of Least Concern by the IUCN, but the correct name for this taxon is *Schinopsis lorentzii* (Griseb.) Engl. (Mogni et al. 2017), and *Schinopsis marginata* is recognized within it by some authorities.

5 Paleobotany

Due to its fossil diversity, prevalence, and uniquely identifying characters, Anacardiaceae have been the focus of many paleobotanical studies. The family is well-represented in the fossil record by wood, leaves, flowers, pollen, and fruits. Studies of these fossils have contributed to a better understanding of the family's evolution and biogeography (e.g., Weeks et al. 2014). This evidence points to a Cretaceous origin of the family, which is present in the fossil record through the Cenozoic. Martínez-Millán (2000) proposed a Southeast Asian origin for the family, but this finding is somewhat controversial given the fossil record that has been discovered to date and some contradictory phylogenetic data (see Phylogeny, Taxonomy and Evolution section above).

As with all organisms, not all Anacardiaceae fossil identification should be treated with the same degree of confidence. Because our taxonomic system is based on reproductive characters, fruit and flower fossils are somewhat easier to assign to an extant taxon than are vegetative fossils. Within Anacardiaceae, wood fossils have proven to be particularly challenging due to the similarity of Burseraceae and Anacardiaceae wood (Kryn 1952; Terrazas 1994). For these reasons, some fossils identified in the literature as Anacardiaceae need to be reevaluated.

The fossil record shows that Anacardiaceae were an important component of Paleogene floras in various parts of the world (Manchester 1999). The family was particularly widespread during climatically warm intervals of the Eocene in Europe and North America (Manchester 1994; Collinson and Cleal 2001). As with other organisms, some Anacardiaceae fossil evidence reported in the literature is suspect and requires reevaluation (see Supplementary Information for additional references).

Anacardiaceae are an important element of the Paleocene flora of the Salamanca Formation in Chubut Province, Argentina (Iglesias et al. 2021). This flora was first interpreted by Berry in 1937, but some of his identifications are questionable. Iglesias et al. (2021) used a more robust set of morphological characters to taxonomically compare and assign the fossils in this flora to extant genera. For example, diagnostic leaf architectural characters, such as admedial branching of the tertiary veins and the presence of an intramarginal secondary vein, were used for identifications. Iglesias et al. (2021) assigned some of the fossil specimens to extant genera currently restricted to the Paleotropics including *Sorindeia*, *Dracontomelon*, and *Micronychia*.

Fossils of *Rhus*, a currently widely distributed genus in the Northern Hemisphere, are found as fossilized wood, leaves, pollen, and fruit from the Eocene through the Miocene-Pliocene from the Northern Hemisphere (see additional references). This stratigraphic range includes the Eocene in Western North America, the Oligocene of North America and Europe, and the Miocene-Pliocene of Europe (Wolfe and Wehr 1987; Meyer and Manchester 1997; Tosal et al. 2019). *Rhus* has been reported from various fossiliferous localities, such as the Florissant (MacGinitie 1953; Manchester 2001), Green River (MacGinitie 1969), and the Bridge Creek in Oregon, USA (Meyer and Manchester 1997).

Various early Eocene samples of *Rhus* fossil leaves have also been described from the Republic flora of Washington, USA that have leaf characteristics comparable with extant species (Flynn and DeVore 2019). These include shape, margin, venation, and a winged petiole. This study provides the earliest documentation (early Eocene) of hybridization within *Rhus* (Flynn and DeVore 2019). Manchester (1994) described silicified endocarps of sumac fruits (*Rhus rooseae* Manchester) from the middle Eocene Nut Beds Flora, Clarno Formation, Oregon. His work was the first report of fossilized Anacardiaceae fruits in North America.

Several other Anacardiaceae genera also make their appearances in the Eocene. In the Florissant deposits in Colorado (USA), a fossil leaf was identified as *Cotinus fraterna* (Lesquereux) Cockerell due to its cladodromous secondary venation (Meyer 2003). From the early Middle Eocene of Messel, Germany, there are reports of compressed fruits of *Anacardium* (Manchester et al. 2007), a genus that is today restricted to the Neotropics (Mitchell and Mori 1987). The fossil shares characters with extant *Anacardium* that in combination are diagnostic: a reniform drupe with a subtending enlarged pedicel called a hypocarp (''cashew apple''). Previous reports of *Anacardium* were described from leaves by Berry (e.g., 1924a, b) in the fossil record of Texas, USA and in northern South America. Manchester (1977) described fossil wood of *Tapirira* from the Eocene of the Clarno Formation in Oregon, USA. This is the oldest record for the genus. The form genus *Bosquesoxylon* from the Eocene of Chiapas, Mexico, is based on wood fossils (Pérez-Lara et al. 2017).

Diverse Oligocene fossil leaves of Anacardiaceae have been reported from Tepexi de Rodríguez, Puebla, Mexico. These samples were assigned to *Pseudosmodingium*, *Haplorhus*, *Rhus*, *Comocladia,* and *Pistacia*. The diagnostic characters include several leaf architectural features: asymmetrical lamina, pinnate primary venation, craspedodromous or cladodromous secondary venation, poorly developed areolation, and entire or serrate margin. These fossils indicate that Anacardiaceae were a diverse and important component of the Oligocene flora (Ramírez et al. 2000; Ramírez and Cevallos-Ferriz 2002). The form genus *Llanodelacruzoxylon* from the Oligocene–Miocene of Panama is based on fossilized wood (Rodríguez-Reyes et al. 2020). *Tapirira* has also been reported from permineralized wood from the Oligocene–Miocene of Baja California Sur, Mexico (Martínez-Cabrera and Cevallos-Ferriz 2004), and Miranda (1963) depicted a complete flower embedded in amber from the late Oligocene and early Miocene of Simojovel de Allende, Chiapas, Mexico.

Anacardiaceae Miocene fossil fruits have been reported from Panama and Ecuador. Permineralized endocarps belonging to the subfamily Spondioideae have been found in Panama (Herrera et al. 2019), including *Spondias*, *Antrocaryon,* and *Dracontomelon*. The first two have extant disjunct distributions between the Neotropics and Paleotropics, while the third is currently restricted to the Paleotropics. From Ecuador Burnham and Carranco (2004) described laterally winged fossil fruits with a remnant stigma on the backbone of the wing as a new species of *Loxopterygium* (*L. laplayense* Burnham and Carranco). This record is the only known fossil evidence of wind dispersal in the Anacardiaceae, and the authors suggest that their findings support the hypothesis that tropical dry forests date back to the Miocene in this area.

In Patagonia, Argentina, fossil leaves/leaflets from the middle Miocene were identified as *Lithrea*, which is extant and endemic to South America. The identification was possible because of leaf architectural features, such as craspedodromous secondary venation, several secondary veins (some of them forming exmedial branching), parallel intersecondaries, and acute cuneate to decurrent base (Passalia et al. 2019).

6 Economic botany and phytochemistry

The Anacardiaceae have a rich diversity of uses, primarily involving their edible fruits, phytochemistry, and wood (Sweet and Barkley 1936; Gillis 1975). Indigenous people have utilized Neotropical Anacardiaceae for millennia for food, firewood, timber, medicine, and many other purposes. These plants have also been the subject of much research investigating compounds that are useful and/or injurious to humans.

Edible plants – Neotropical Anacardiaceae include a few fruits of global significance, with cashew, *Anacardium occidentale,* being the most well known and widely utilized. The seed of *A. occidentale* (cashew nut) is a valuable agricultural commodity, with an estimated global value reaching over \$2.75 billion USD in 2018 (FAOSTAT). Despite cashew being native to Brazil, global production of cashew nut is highest in South and Southeast Asia and sub-Saharan Africa. Beyond direct consumption of cashew nuts, cashew milk, oil, and butter are important food products, and trends toward plant-based diets have also highlighted cashew's utility in vegan alternatives to animal products like cashew cheese. The hypocarp of *A. occidentale,* commonly called cashew apple, is also an important crop, with an estimated value of \$272 million USD in 2018 (FAOSTAT). Cashew apples are eaten fresh or used to make juice, jam, or jelly. Widely popular in Brazil, cashew apple is beginning to gain popularity in other regions of the world (Strom 2014). On a more local scale, other *Anacardium* species are cultivated and consumed in the Neotropics, particularly *A. giganteum* J. Hancock ex Engl.*, A. humile,* and wild *A. occidentale* (Lévi-Strauss 1952; Pereira et al. 2019).

Since its introduction in the 1700s, mango (*Mangifera indica*) has become one of the most economically important species of Anacardiaceae in the Neotropics, with a combined regional production value of over \$1 billion USD in 2018 (FAOSTAT). Along with cashew and mango, the fruits of the Neotropical species *Spondias mombin* and *S. purpurea* are also global crops. The introduced range of cultivation of *S. purpurea* is limited to the Philippines, where the species was introduced by the Spanish in the sixteenth century, while *S. mombin* is cultivated throughout Southeast Asia and in parts of sub-Saharan Africa. Other species of *Spondias* are consumed locally in the Neotropics, including *S. tuberosa* (umbu), *S. globosa* J.D. Mitch. and Daly (taperibá), *S. testudinis* J.D. Mitch. and Daly (cajarana, cajá do jabuti), and the non-native *S. dulcis* (cajarana, jobo dos Indios) (Lévi-Strauss 1952; Mitchell and Daly 2015). Fruits of *Spondias* species can be eaten fresh, but are typically processed into juice, jam, pulp, and ice cream, or are sometimes used to make a slightly fermented alcoholic beverage (Ramírez-Guzmán et al. 2019). A minor yet noteworthy global product, pink peppercorn, is a gourmet spice produced from the dried drupes of two *Schinus* species, *S. areira* and *S. terebinthifolia* (Giuffrida et al. 2020). The drupes of these *Schinus* species are prized for their complex flavor profile with fruity, evergreen/pine, citrus, and spicy notes, and are an alternative to black peppercorn. Additionally, the essential oils derived from pink peppercorns are marketed for aromatherapy and used in perfumery (Giuffrida et al. 2020).

Numerous other species of Neotropical Anacardiaceae are important local sources of food and medicine. Fruits consumed fresh or processed for pulp/juice include those of *Antrocaryon amazonicum* (Ducke) B.L. Burtt & A.W. Hill (ameixa, jacaiacá), *Cyrtocarpa edulis* (Brandegee) Standl. (ciruela de monte), *Cyrtocarpa procera* Kunth (chupandio, chupandilla, copalcojote), *Rhus aromatica* Aiton (agrito), and *R. ovata* S. Watson (Casas et al. 2001; Wilken 2012; Rangel-Landa et al. 2016). Fruits of many *Schinus* species, particularly *S. areira* (pirú) and *S. molle* L., but also including *S. fasciculata* (Griseb.) I.M. Johnst., *S. johnstonii* F.A. Barkley (molle, michí), *S. odonellii* F.A. Barkley, *S. polygama* (Cav.) Cabrera, *S. patagonica* (Phil.) I.M. Johnst., and *S. roigii* Ruiz Leal and Cabrera, are consumed fresh or turned into drinks such as the traditional alcoholic beverage chicha de molle (Kramer 1957; Casas et al. 2001; Chamorro and Ladio 2020).

Phytochemistry – Compounds identified in and isolated from Anacardiaceae are used in traditional and Western medicine, industrial applications, cosmetics, nutrition, textile dyes, leather and wood preservation, and cultural applications and have been the basis of taxonomic publications. Anacardiaceae are also well known for causing contact dermatitis (see review below and Mitchell 1990) and nut allergies (cashew and pistachio seeds; see Weinberger and Sicherer 2018 for a review).

Numerous broad surveys of Neotropical Anacardiaceae phytochemistry have revealed a diversity of compounds, many of which are of potential use to humans. Among the more commonly reported compounds are terpenoids (including triterpenoids), flavonoids (including biflavonoids), quinones, polysaccharides, catechols, alkylresorcinols, amino acids, tannins, phenols, phenolic acids, alkaloids, saponins, sterols, and other volatile organic compounds (Correia et al. 2006, Ferrero et al. 2006; dos Santos et al. 2009). Certain types of 5-deoxyflavonoids are apparently unique to the Anacardiaceae, and the family is particularly rich in biflavonoids. Interestingly, subfamily Spondioideae lacks biflavonoids (Aguilar-Ortigoza et al. 2003; Aguilar-Ortigoza and Sosa 2004b).

Prior to the invention of PCR and widespread application of DNA-based phylogenetic studies, phytochemistry was an important taxonomic tool for understanding the evolution of the Anacardiaceae. For example, comparative analysis of flavonoids was used in placing Julianiaceae (*Amphipterygium* and *Orthopterygium*) in the cashew family (Wannan and Quinn 1988). Serotaxonomy was another line of evidence used to place the Julianiaceae within Anacardiaceae (Peterson and Fairbrothers 1983). David Young combined the study of flavonoids and morphology in his taxonomic study of *Rhus* subgenus *Lobadium*, which is particularly diverse in Mexico (Young 1976, 1979).

There is a diversity of industrial uses for extracts of Neotropical Anacardiaceae, especially of the exudate extracted from cashew mesocarp (cashew nutshell liquid), for which the global market value is predicted to reach $489.63 million by 2026 (Fior Markets 2020). Uses of cashew nutshell liquid are primarily petrochemical alternatives such as plant-based plastics and fuel (Lomonaco et al. 2017; Krishnan 2020), but also include other applications such as larvicides (Vani et al. 2018). Other Anacardiaceae have been investigated for industrial product development, such as insecticides, cosmetics, meat additives, nematicides, chromatographic gels, and adhesives (Lima et al. 2002; Ferrero et al. 2006, and see additional references). Tannin extracts from *Schinopsis* are used in a variety of applications from food additives to improve color and shelf life (Fruet et al. 2020), to tanning agents to dye and preserve wood and leather, to dietary supplements to reduce bovine flatulence (Beauchemin et al. 2007). The high tannin content of *Schinopsis* (Streit and Fengel 1995) makes it a popular rot-resistant wood for outdoor applications such as posts, poles, and railroad ties (Barberis et al. 2012). *Schinopsis* wood has many interesting properties that make it useful. The specific gravity of some taxa is so high (1.00 to 1.28) that the wood sinks in water (Muñoz et al. 2019a, b), and it is an excellent source of dendroclimatological data (López and Villalba 2016).

Medicinal uses – Traditionally and today, Neotropical Anacardiaceae are used, or have been investigated for potential use, as interventions for a variety of medical conditions. One of the most important traditional medicinal plants of this group is *Amphipterygium adstringens* (Schltdl.) Schiede ex Standl. (cuachalalate), the bark of which is widely used in

Mexico and has also developed an international market as an anti-inflammatory, anti-bacterial, and obesity treatment (Oviedo-Chávez et al. 2004; Alonso-Castro et al. 2015). Both *Schinus areira* and *Spondias mombin* have been used as stimulants (Casas et al. 2001, wherein *Schinus areira* is called *Schinus molle* sensu lato, which we are recognizing as a synonym of *Schinus areira* in most cases and recognizing *Schinus molle* sensu stricto as being restricted to southern Brazil, Uruguay and northeastern Argentina). Other species of *Schinus* (*S. fasciculata, S. longifolia* (Lindl.) Speg.*, S. molle, S. terebinthifolia*) appear commonly in surveys of folk medicine and are used for a wide range of ailments, including as an analgesic, anti-inflammatory agent, antiseptic, antiparasitic, sedative, digestive, and even (in the case of *S. terebinthifolia,* as an antidote for ciguatera fish poisoning (Kramer 1957, Casas et al. 2001, Ferrero et al. 2006, Trillo et al. 2010, Medeiros et al. 2018). Other commonly used taxa include species of *Rhus* (e.g., *R. aromatica, R. ovata, R. pachyrrhachis* Hemsl., *R. standleyi* F.A. Barkley and *R. terebinthifolia*), *Schinopsis* (e.g., *S. balansae, S. brasiliensis* Engl.*, S. lorentzii, S. marginata*)*,* and *Spondias* (e.g., *S. mombin, S. purpurea, S. tuberosa*) (Casas et al 2001; Albuquerque et al. 2007; Trillo et al. 2010; Wilken 2012; Alonso-Castro et al. 2015; Marisco and Pungartnik 2015).

Additional genera with documented uses in traditional medicine include *Anacardium, Astronium, Cyrtocarpa, Lithrea, Malosma, Mangifera, Mauria, Mosquitoxylum, Pseudosmodingium, Tapirira,* and *Thyrsodium* (Casas et al. 2001; Trillo et al. 2010; Wilken 2012). The uses for these species include anti-bacterial, antifungal, antiviral, antiplasmodial, anti-leishmania, antidiabetic, immunomodulation, molluscicidal, anthelmintic, antiepileptic, antipsychotic, anticancer, analgesic, antioxidant, antiulcer, anticlotting, antigingivitis, anti-inflammatory, wound healing, and other dermatological applications (Dikshit et al. 1986; Corthout et al. 1991, Esquivel-García 2019, and see additional references). Studies on the medicinal efficacy of Anacardiaceae have mostly been restricted to isolation of compounds and testing of these compounds for cytotoxicity on microorganisms in culture, against tumor cell lines, and in mice and rat studies—very few human trials have been conducted. Medically active compounds in Anacardiaceae have been isolated from leaves, bark, exudate, roots, and fruit. In addition, antimicrobial secondary metabolites produced by endophytic fungi have been identified in *Spondias mombin* (Rodrigues et al. 2000).

Toxicity – Toxicity of Neotropical Anacardiaceae has been widely investigated (see review in Aguilar-Ortigoza and Sosa 2004b), and 10 genera cause dermatitis, with five additional genera having anecdotal evidence of causing dermatitis (*Actinocheita*, *Campnosperma*, *Loxopterygium*, *Mosquitoxylum*, and *Spondias*). Genera that are confirmed to cause dermatitis and for which associated phytochemicals have been isolated include *Anacardium* (Sampietro et al. 2013), *Astronium* (Vilar et al. 2004), *Comocladia* (Potthoff and Brockmeyer 2009)*, Lithrea* (Alé et al. 1997), *Mauria* (Hurtado et al. 1982), *Metopium* (Rivero-Cruz et al. 1997), *Pseudosmodingium* (Aguilar-Ortigoza and Sosa 2004a), *Schinopsis* (Sampietro et al. 2017), *Schinus* (Morton 1978), and *Toxicodendron* (Moreno 2008) and have been included in many survey papers (Gross et al. 1975; Lampe 1986; Hurtado 1986; Mitchell 1990; Aguilar-Ortigoza et al. 2003). For most of these genera, the offending compounds are urushiols, which are oily mixtures of alkyl catechols (primarily pentadecyl- and heptadecyl-catechols). The toxic compounds in *Anacardium* responsible for causing contact dermatitis are not urushiols but rather alkylresorcinols (e.g., anacardic acids, anacardol, and cardanol) (Sampietro et al. 2013). Contact dermatitis caused by Anacardiaceae is a T cell-mediated delayed hypersensitivity reaction resulting from skin coming in contact with exudate (that specifically binds to Langerhans cells; Gladman 2006). Cross-reactivity to different species of Anacardiaceae has been well documented in both humans and guinea pigs (Hurtado et al. 1982; Alé et al. 1997).

For several genera, data are lacking in either the phytochemical analysis supporting the ability to cause contact dermatitis, or in reports of cases of contact dermatitis. For *Actinocheita* and *Mosquitoxylum*, urushiols have been isolated, and in *Campnosperma* alkylquinols have been found (Lamberton 1959), but we could find no Neotropical cases of contact dermatitis documented in the literature for *Mosquitoxylum* or *Campnosperma*. For *Actinocheita*, there are some reports of it causing a rash similar to other Neotropical Anacardiaceae genera (Medina-Lemos and Fonseca 2009). In *Spondias*, there are many reports of contact dermatitis, but no phytochemicals have been isolated that are known to cause this condition in humans.

Timber – The most important timber-producing taxa within Neotropical Anacardiaceae are species of *Astronium*, commonly called gonçalo alves, muiracatiara, aroeira, or tigerwood because of characteristic dark stripes that run through the reddish wood (Molinos et al. 2021). *Astronium* species are widely available in the international market and have a variety of uses, including as flooring and veneers in furniture and cabinetry, and in knife handles, bows, pool cues, craft jewelry, and guitars (Meier 2021). The wood of *Schinopsis* is also harvested for timber, along with species of *Anacardium*, *Antrocaryon amazonicum*, *Campnosperma panamense* Standl., *Loxopterygium sagotii*, *Metopium brownei* (Jacq.) Urb., *Schinus areira*, *Schinus molle*, *Spondias mombin*, and *Tapirira guianensis* (Molinos et al. 2021).

Anacardium, *Astronium*, *Comocladia*, *Cyrtocarpa*, *Pseudosmodingium*, *Rhus*, *Spondias*, and *Tapirira* have documented uses as living fences, which separate livestock and agricultural fields or line people's yards and serve as sources of food and wood (Casas et al. 2001; Aguilar-Ortigoza and Sosa 2004a). The fruits and/or leaves of some species also provide forage/fodder for livestock, including *Actinocheita filicina* (DC.) F.A. Barkley, *Cyrtocarpa procera*, *Pistacia mexicana*, *Pseudosmodingium andrieuxii* (Baill.) Engl., *Schinopsis marginata*, *Schinus areira*, *Schinus microphylla* I.M. Johnst., *Spondias mombin*, and *S. tuberosa* (Casas et al. 2001; Rangel-Landa et al. 2016). Many taxa of Neotropical Anacardiaceae are used locally as firewood (e.g., *Actinocheita, Anacardium*, *Cyrtocarpa*, *Pseudosmodingium*, *Rhus*, *Schinus*, *Spondias*, and *Tapirira*), and an unknown number of species are also used in the illegal production of charcoal (van Andel 2000; Gonçalves and Scheel-Ybert 2016; Rangel-Landa et al. 2016).

Horticultural and invasive plants – A few species of Neotropical Anacardiaceae are common in the horticulture trade. *Pachycormus discolor* is a popular species for bonsai and succulent enthusiasts (Rowley 1975), and seed is widely available from online retailers. *Rhus integrifolia* (Nutt.) Benth. & Hook.f. is used for hedges, *Schinus areira* is a popular ornamental tree that has become invasive in some areas, and *Schinus polygama* is also planted and of concern for its tendency to escape. *Anacardium excelsum* is planted in some Neotropical cities as a street tree. *Rhus aromatica* is planted widely, and there are numerous cultivars on the market; one of the most popular is *Rhus aromatica* "Gro-Low." Several Neotropical Anacardiaceae have great potential to be successful horticultural plants. Examples include numerous *Schinus* and *Rhus* species, *Anacardium spruceanum* Benth. ex Engl. with its beautiful white to pink bracts that subtend the inflorescence and give a similar appearance as poinsettia, *Ochoterenaea colombiana* F.A. Barkley has large purple-fringed infructescences, and *Actinocheita filicina* has fern-like leaves and large red to purple infructescences.

Some horticultural species have the potential to become invasive in their introduced ranges. This is the case for the Asian species *Toxicodendron succedaneum,* a popular street tree with bright fall foliage that is now considered invasive in Brazil and Cuba as well as other parts of the world (Rojas-Sandoval 2016). Native to central and eastern South America, *Schinus terebinthifolia* was introduced into the horticultural trade and has since become an extremely problematic invasive in many parts of the world including California, Florida, and Hawaii in the USA and in parts of the Caribbean, Australia, New Zealand, Portugal, and Spain (Morton 1978). Some evidence suggests that the success of *S. terebinthifolia* may in part be due to allelopathy (Morgan and Overholt 2005). Much research has been done to identify and test the effectiveness of biological controls for *S. terebinthifolia* (Wheeler et al. 2016). *Schinus areira* has also become naturalized and potentially invasive in parts of its introduced range (Bañuelas et al. 2019), and naturalization of *S. polygama* has been noted in California (Martin 2000). *Lithrea caustica* (Molina) Hook. and Arn. appears to be naturalizing at the University of California Santa Cruz Arboretum and Botanic Garden and is a taxon to watch as a nascent invasive (Mitchell personal observation).

Other uses – Beyond the uses stated above, Neotropical Anacardiaceae possess other attributes that make them an important component of ethnobotanical practices throughout their range. Species of *Mauria* contain a resin that is used to make candles, while the fruits of *Cyrtocarpa* were used to make a soap in the Aztec empire (Janick and Tucker 2018). Handicrafts are made from *Pseudosmodingium andrieuxii* and *Spondias mombin* (Casas et al. 2001)*,* while *Rhus aromatica* is used for basketry (Wilken 2012) and *Toxicodendron* species are used for basket and textile dyes (Senchina 2006). Some Neotropical Anacardiaceae have religious significance, such as *Astronium lecointei,* which, in parts of northwestern Guyana, is used to drive away evil spirits (van Andel 2000). The macerated bark of *Anacardium excelsum* can reportedly be used as fish bait (Allen 1956), while *Schinus fasciculata* has been used in traditional veterinary medicine (Scarpa 2000). There are even historical accounts of *Toxicodendron* species being used in tattooing and other skin marking/dyeing practices, though the veracity of these reports may be questioned (Senchina 2006).

7 Taxonomic treatment

Family description of native and naturalized Neotropical Anacardiaceae – Trees, shrubs, sometimes scandent, or rarely subshrubs or lianas. Bark smooth to rough, sometimes exfoliating. Secretory ducts present in bark, leaves, flowers, fruits, and/or other tissues; usually with watery to resinous or viscous exudate, in many species causing contact dermatitis and turning black with exposure to air. Leaves simple or imparipinnate, rarely paripinnate, trifoliolate, or unifoliolate; alternate, often clustered at tips of branches; sessile or petiolate; estipulate; simple leaves entire or serrate; leaflets opposite, subopposite, or alternate; leaflets entire, serrate, dentate, crenate, or lobate, rarely spinose; sessile or petiolulate; rachis rarely alate. Inflorescences terminal and/or axillary; thyrsoid, paniculate, racemose, or spicate, rarely flowers solitary. Flowers bisexual and/or unisexual and sexual systems ranging from hermaphrodite to (cryptically) monoecious or dioecious, andromonoecious, gynodioecious, polygamodioecious; actinomorphic; pedicellate or sessile, pedicels often articulated; hypanthium rarely present; perianth usually biseriate, rarely uniseriate or absent, imbricate or less often valvate; sepals (3-)4–5, usually basally fused, rarely fully connate and cup-shaped; petals (3-)4–5(-8), rarely absent; stamens (1-)5–10, mono- or biseriate, in some genera only 1 or 2(-4) stamens fertile, filaments free, rarely basally connate, anthers dorsi- or basifixed, sometimes versatile, usually longitudinally dehiscent, introrse/ventrorse to latrorse, rarely extrorse; staminodes present and reduced or absent in female flower, rarely in bisexual flowers; disk intrastaminal (extrastaminal in introduced *Mangifera*) or absent; gynoecium simple or syncarpous, sometimes pseudomonomerous; carpels 1–5, most commonly 3; ovary superior; ovule solitary, apotropous/syntropous, basal, apical, or lateral; style apical or lateral, erect or recurved, rarely sigmoid; stigma capitate, discoid, lobate, or spathulate, rarely punctiform; pistillode present and reduced or absent in male flowers. Fruits drupes or samaras (rarely syncarps, utricles, nut-like, or baccate), fleshy or dry, occasionally subtended by a fleshy hypocarp or an accrescent, chartaceous calyx; mesocarp sometimes with prominent black resin canals; endocarp cartilaginous to bony, rarely fibrous, sometimes with opercula (part of subfamily Spondioideae). Seeds 1–5, but always 1 per locule, curved or straight (rarely pyramidal); endosperm scant or absent; cotyledons usually plano-convex (rarely flat), free and equal in size. Thirty-two native genera (and 1 naturalized genus, *Mangifera*), consisting of 188 or more native species (and 3 naturalized species: *Mangifera indica, Spondias dulcis*, and *Toxicodendron succedaneum*).

Key to subfamilies – 1. Exudate usually not causing contact dermatitis (*Spondias* and *Campnosperma* cause dermatitis in a small subset of the human population); carpels 1–5 (-6); styles 1–5 (-6); fruits 1–5 seeded, never wind-dispersed; exocarp usually thick; germination pores, opercula, or valves in endocarp usually present (absent in *Campnosperma* and most *Tapirira*) Spondioideae

1. Exudate sometimes causing (severe) contact dermatitis; carpels 1–3; styles 1–3; fruits always 1-seeded, often wind-dispersed; exocarp usually thin; germination pores, opercula and valves in endocarp absent Anacardioideae

Key to Spondioideae genera – 1. Leaves simple, with peltate or lobed scales; unilocular but appearing bilocular in fruit *Campnosperma*

1. Leaves compound, without peltate or lobed scales (except *Tapirira lepidota*); multilocular or unilocular, but not as above 2.

2. Leaflets with intramarginal secondary vein (in *Spondias radlkoferi* sometimes with marginal secondary vein instead of intramarginal vein); secondary venation craspedodromous 3.

2. Leaflets lacking intramarginal secondary vein and marginal secondary vein; secondary venation brochidodromous, eucamptodromous, and/or cladodromous 4.

3. Small to very large trees; carpels (3–)5(–6); lowland habitats from northwestern Mexico south to southeastern Brazil and Bolivia *Spondias*

3. Scandent or erect shrubs or trees; carpels 2; restricted to tropical dry forests of the Yucatan Peninsula *Attilaea*

4. Leaves evergreen; fruits exocarp purple to black (sometimes green in *T. lepidota*); endocarp without opercula (*T. mexicana* Marchand with germination pores and valves); cotyledons with purple striations *Tapirira*

4. Leaves deciduous; fruits red, orange, yellow, or greenish when ripe; endocarp usually with 1–5 opercula; cotyledons without purple striations 5.

5. Ovary 5-locular; drupe plum-like or apple-shaped and depressed at apex; endocarp with 5 apical opercula; tropical moist forest *Antrocaryon*

5. Ovary 1–3(–5)-locular; drupe obliquely obtuse-oblong or obovoid; endocarp with (0–)1–5 apical to lateral opercula (opercula lacking in *C. caatingae* J.D.Mitch. and Daly); tropical dry forest or savanna *Cyrtocarpa*

Key to Anacardioideae genera –

1. Leaves simple or unifoliolate 2.

1. Leaves compound 13.

2. Style 1; disk extrastaminal or absent 3.

2. Styles 3 (1 in *Mauria*, sometimes reduced to one with two additional sessile stigmas in *Schinopsis*); disk intrastaminal 5.

3. Domatia often present in abaxial secondary vein axils; filaments basally connate into a staminal tube; drupe usually subtended by fleshy hypocarp *Anacardium*

3. Domatia absent; staminal tube absent; hypocarp absent 4.

4. Leaf entire; perianth present, with glandular ridges on petals; disk extrastaminal; style unbranched; fruit a fleshy drupe *Mangifera* (*M. indica* cultivated and naturalized)

4. Leaf crenate to serrate; perianth of only sepals in male flowers, perianth absent in female flowers; disk absent; style 3-branched; fruit a dry samaroid syncarp of nutlets *Amphipterygium* p. p.

5. Leaves linear to narrowly lanceolate 6.

5. Leaves elliptic, ovate, or obovate 7.

6. Exudate turning black with exposure to air, causing contact dermatitis; perianth biseriate; exocarp yellowish; mesocarp resinous *Bonetiella*

6. Exudate white and not causing contact dermatitis; perianth uniseriate; exocarp red; mesocarp fleshy *Haplorhus*

7. Inflorescence with pseudospicate terminal branches; exocarp with red glandular trichomes *Rhus* subgen. *Lobadium*

7. Inflorescences with clearly pedicillate flowers (terminal branches not pseudospicate); exocarp without red glandular trichomes (orange to red glandular trichomes rarely present in *Schinus*) 8.

8. Leaves conduplicate; S California (USA) south to Baja California (Mexico) *Malosma*

8. Leaves not conduplicate; north central to northeastern Mexico south to southern South America 9.

9. Leaves always entire with conspicuous marginal or intramarginal secondary vein; exocarp pale gray to whitish *Lithrea* p. p.

9. Leave usually entire or serrate without conspicuous marginal or intramarginal secondary vein; exocarp green, pink, red to purple 10.

10. Androecium diplostemonous; mesocarp fleshy 11.

10. Androecium haplostemonous; mesocarp not fleshy 12.

11. Calyx deeply lobed; corolla aestivation imbricate; exocarp generally separating from mesocarp at maturity, endocarp bony *Schinus* p. p.

11. Calyx shallowly lobed; corolla aestivation valvate or subvalvate; exocarp not separating from mesocarp at maturity, endocarp chartaceous *Mauria* p. p.

12. Style excentric to lateral; fruit a laterally winged samara; South America *Schinopsis* p. p.

12. Style terminal; fruit a drupe; Mexico *Cotinus*

13. Leaves trifoliolate 14.

13. Leaves multifoliolate 18.

14. Male flowers in pendent thyrses, female flowers tightly enclosed in a cupular involucre; corolla absent in female flowers, male flowers with perianth lobes (interpreted as sepals); disk absent; fruit a samaroid syncarp of nutlets subtended by a broad, asymmetrical wing that is curved and tapers to a narrow stalk, derived from a much-dilated secondary inflorescence branch *Amphipterygium* p. p.

14. Female and male inflorescences of the same type or if different, not as above; corolla present; intrastaminal disk present; fruit a drupe or samara 15.

15. Exudate not turning black with exposure to air nor causing contact dermatitis; inflorescence with pseudospicate terminal branches; exocarp reddish with glandular trichomes *Rhus* p. p. (*Rhus* subgen. *Lobadium*)

15. Exudate turning black with exposure to air and causing contact dermatitis; inflorescence with clearly pedicillate flowers (terminal branches not pseudospicate); exocarp green or red to brown, or white or gray to yellowish, without glandular trichomes 16.

16. Marginal or intramarginal secondary veins present; androecium diplostemonous *Lithrea* p. p.

16. Marginal and intramarginal secondary veins absent; androecium haplostemonous 17.

17. Trees; thorns often present; hairy tuft domatia absent; fruit a laterally winged samara with exocarp remaining attached at maturity; South America *Schinopsis* p. p.

17. Shrubs or lianas; thorns absent; hairy tuft domatia sometimes present abaxially in secondary vein axils; fruit a drupe with exocarp easily separating from mesocarp at maturity; Canada south to Guatemala, east to Cuba and the Bahamas *Toxicodendron* p. p.

18. Plants caudiciform; fruit a utricle; endemic to Baja California, Mexico *Pachycormus*

18. Plants not caudiciform; fruit not a utricle (various); not in Baja California 19.

19. Leaflets serrate, dentate, crenate, or lobate 20.

19. Leaflets entire 33.

20. Leaflets broadly pinnately lobed (leaf fern-like); fruit a globose drupe covered with very long, villous, violet-reddish trichomes *Actinocheita*

20. Leaflets not as above; fruits various, glabrous or trichomes not as above 21.

21. Corolla absent in female flowers, male flowers with perianth lobes (sometimes interpreted as a calyx); disk absent; fruit a samaroid syncarp of nutlets subtended by a wing derived from a much-dilated secondary inflorescence branch 22.

21. Corolla present; disk intrastaminal; fruit derived from a single ovary and baccate, nutlet-like, a drupe, or a samara 23.

22. Fruit a samaroid syncarp of nutlets subtended by a broad, asymmetrical wing that is curved and tapers to a narrow stalk, derived from a much-dilated secondary inflorescence branch, often in pairs; Mexico to Costa Rica *Amphipterygium* p. p.

22. Fruit a samaroid syncarp subtended by a slightly dilated, elongate secondary inflorescence branch with parallel margins, always solitary; endemic to western Peru *Orthopterygium*

23. Leaves with distal leaflets entire and basal leaflets lobed; flowers haplostemonous; fruit a samara with a single wing lacking conspicuous venation, consisting of exocarp and mesocarp tissue *Schinopsis* p. p.

23. Leaves with leaflets serrate, crenate, pinnatifid, or rarely lobate; flowers haplostemonous or diplostemonous; fruit various (if a samara, with more than one wing or single

wing with conspicuous venation, consisting of exocarp tissue) 24.

24. Leaflets with spinose teeth; flowers 3- to 4-merous; Greater and Lesser Antilles *Comocladia* p.p.

24. Leaflets lacking spinose teeth; flowers typically 5-merous, but 3- to 4-merous in non-spinose *Comocladia*; distribution various 25.

25. Trees typically unbranched; flowers 3- to 4-merous; petals red to purple; Mexico south to Guatemala and the Greater Antilles *Comocladia* p. p.

25. Trees and shrubs branching; flowers 5-merous; petals greenish to pinkish or white to cream-colored; distributed throughout the Neotropics 26.

26. Inflorescences and infructescences erect, pyramidal thyrses; fruits with red glandular trichomes *Rhus* p. p. (*Rhus* subgen. *Rhus*)

26. Inflorescences and infructescences not as above; fruits without red glandular trichomes 27.

27. Exudate turning black with exposure to air; fruit a samara 28.

27. Exudate not turning black with exposure to air; fruit not a samara, but sometimes subtended and dispersed by enlarged calyx 30.

28. Fruit with a single elongate wing; Bolivia south to northwestern Argentina *Loxopterygium* p. p.

28. Fruit with two lateral wings; Bolivia or Mexico 29.

29. Flowers sessile to long-pedicellate; styles 3, distinct; ovule basal; samara with two unequal, narrow lateral wings; Bolivia *Cardenasiodendron*

29. Flowers pedicellate; style 3-branched; ovule apical; samara with two equal, broad lateral wings; Mexico *Pseudosmodingium*

30. Flowers haplostemonous; fruits dry or resinous 31.

30. Flowers diplostemonous; fruits fleshy or resinous 32.

31. Inflorescences terminal and/or axillary thyrsoids, terminal branches not spike-like; drupe dry to resinous, wind-dispersed via a subtending enlarged, persistent calyx *Astronium* p. p.

31. Inflorescences terminal panicles with elongate primary and secondary branches, terminal branches widely spaced and spike-like; drupe dry with longitudinal grooves *Apterokarpos*

32. Leaflets petiolulate; corolla valvate or subvalvate; exocarp not easily separating from mesocarp at maturity *Mauria* p. p.

32. Leaflets sessile to subsessile; corolla imbricate; exocarp easily separating from mesocarp at maturity *Schinus* p. p.

33. Leaf rachis alate 34.

33. Leaf rachis not alate (terminal petiolule alate in *Mosquitoxylum*) 36.

34. Leaflets with a prominent marginal(or intramarginal) secondary vein; exocarp pale gray to whitish *Lithrea* p. p.

34. Leaflets lacking prominent marginal(or intramarginal) secondary vein; exocarp light purple to dark red or brown 35.

35. Flowers haplostemonous; exocarp with red glandular trichomes and not easily separating from mesocarp at maturity *Rhus* p. p.

35. Flowers diplostemonous; exocarp without red glandular trichomes and easily separating from mesocarp at maturity *Schinus* p. p.

36. Stems, leaves, and fruits with copious white exudate; leaflets frequently alternate; flowers perigynous; disk adnate to the hypanthium or absent *Thyrsodium*

36. Exudate, if present and milky, not copious; leaflets usually opposite to subopposite; flowers hypogynous; disk usually annular and lobate, sometimes absent or minute 37.

37. Flowers apetalous; styles plumose; fruit a drupe; Texas, USA, south to Nicaragua *Pistacia*

37. Flowers with petals; styles not plumose; fruit a drupe or samara; Mexico, the Caribbean, Central America and/or South America 38.

38. Flowers diplostemonous; fruit always a drupe 39.

38. Flowers haplostemonous; fruit a drupe, samara, baccate, or nutlet-like 40.

39. Calyx deeply lobed; corolla aestivation imbricate; exocarp generally separating from mesocarp at maturity, endocarp bony *Schinus* p. p.

39. Calyx shallowly lobed; corolla aestivation valvate or subvalvate; exocarp not separating from mesocarp at maturity, endocarp chartaceous *Mauria* p. p.

40. Fruit a samara, baccate, or nutlet-like 41.

40. Fruit a drupe 45.

41. Fruit baccate or nutlet-like and subtended by an enlarged calyx *Astronium* p. p.

41. Fruit a samara 42.

42. Samara with single lateral wing 43.

42. Samara otherwise 44.

43. Plants polygamodioecious; samara wing chartaceous with conspicuous venation, consisting of exocarp tissue; tropical moist forests of Guiana Shield *Loxopterygium sagotii*

43. Plants dioecious or monoecious; samara wing stiffened and thick, lacking conspicuous venation, consisting of exocarp and mesocarp tissue; dry forests of northern Peru,

and sub-Amazonian and eastern Brazil south to central Argentina *Schinopsis* p. p.

44. Inflorescence terminal corymbose thyrsoids; samara not lignified, laterally compressed with long, violet trichomes on the margins; Panama and Venezuela south to Bolivia *Ochoterenaea*

44. Inflorescence an axillary panicle; samara lignified, with two broad lateral wings with glabrous margins; central and southern Mexico *Pseudosmodingium* p. p.

45. Exudate turning black with exposure to air, evident on fresh and dried material; exocarp yellowish to white or pale gray, or orange to brown, glabrous 46.

45. Exudate not turning black with exposure to air; exocarp red, glabrous or with glandular trichomes 47.

46. Plants polygamodioecious; styles 3; exocarp white to gray or yellow, easily separating from mesocarp; mesocarp white or gray with black resin canals *Toxicodendron* p. p. (*T. striatum* (Ruiz and Pav.) Kuntze native southern Mexico south to northern Bolivia and Venezuela; *T. succedaneum* naturalized in extra-Amazonian Brazil)

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

47. Erect or scandent shrubs or small trees; drupe globose; exocarp with both red glandular and non-glandular trichomes; seed fills most of the locule *Rhus* p. p.

47. Medium to large trees; drupe obliquely ovoid, compressed; exocarp glabrous; seed fills only a small portion of the locule *Mosquitoxylum*

Genus descriptions Anacardioideae

Actinocheita F.A. Barkley

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

Rhus L. (1753), p. p.

Polygamodioecious shrubs or trees to 3-4 m tall with contact dermatitis-causing exudate. Leaves deciduous, alternate, imparipinnate, petiolate; lateral leaflets sessile, terminal leaflet petiolulate, leaflets linear to oblong, crenate to lobate, margin revolute, base truncate to rounded, apex rounded to obtuse, densely pubescent; secondary venation craspedodromous and cladodromous. Inflorescences axillary panicles. Flowers pedicellate; perianth 5-parted, densely pubescent; calyx deeply lobed, petals imbricate, yellowish white to pink; androecium haplostemonous; anthers ovoid; filaments thickened and longer than anthers, pilose; pistillode reduced; disk modified into a gynophore; gynoecium densely pubescent, trichomes often surpassing styles in length, pseudomonomerous; carpels 3; styles 3, short; stigmas capitate; ovule basal; staminodes reduced. Drupe globose; 1-locular; exocarp pink to reddish brown, covered with very long-villous, violet-reddish trichomes; wind-dispersed. Seed rhomboid.

A single species, *A. filicina*, endemic to tropical dry forest and pine-oak forest in south-central Mexico.

Amphipterygium Schiede ex Standl.

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

Hypopterygium Schltdl. (1843).

Juliania Schltdl. (1843).

Dioecious shrubs or trees, with milky exudate; bark smooth to wrinkled, sometimes with distinctive cork outgrowths. Leaves deciduous, alternate, imparipinnate, trifoliolate, or sometimes unifoliolate; leaflets opposite, lateral leaflets sessile or short-petiolulate; margin crenate, dentate or serrate; secondary venation usually cladodromous. Inflorescences axillary; male flowers arranged in lax pendent thyrses, female flowers tightly arranged in a cyme and subtended by a cupular involucre. Flowers pedicellate; perianth of male flowers 6–8(–9) sepals, connate at base; perianth absent in female flowers; androecium haplostemonous; pistillodes absent; disk absent; gynoecium glabrous to pubescent, pseudomonomerous; carpels 3; style 1 with 3 branches; stigmas 2-lobed, revolute; ovule unitegmic, basal; staminodes absent. Fruit a samaroid syncarp of nutlets enclosed in an involucre, subtended by a broad, asymmetrical wing that is curved and tapers to a narrow stalk, derived from a much-dilated secondary inflorescence branch; 1(2) fertile nutlets and 2(3) smaller sterile, empty nutlets; wing green to pink and turning brown, glabrous to pubescent; endocarp bony; wind dispersed. Seed curved.

Four to five species in tropical dry forests 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 (Pell 2004; Bachelier and Endress 2007; Weeks et al. 2014).

Anacardium L.

Anacardium L., Sp. Pl. 383 (1753); see also: Mitchell & Mori, Mem. N. Y. Bot. Gard. 42: 1–76 (1987); Mitchell, Brittonia 44: 331–338 (1992).

Acajou (Tournefort) Adans. (1763).

Rhinocarpus Bert. & Balb. ex Humb., Bonpl. & Kunth (1824).

Andromonoecious subshrubs, small to large trees with contact dermatitis-causing exudate that is clear or brown, turning black with exposure to air. Leaves usually evergreen, sometimes semi-deciduous with brief deciduous periods, alternate, simple, sessile to petiolate, chartaceous to coriaceous; domatia usually present in abaxial secondary vein axils (also interpreted as extrafloral nectaries); secondary venation brochidodromous, eucamptodromous, or cladodromous. Inflorescences terminal and/or axillary thyrsoids, subtended by foliaceous bracts (white or pink in *A. spruceanum*). Flowers pedicellate; perianth 5-parted; calyx imbricate, cylindrical to campanulate, connate at base; petals reflexed; stamens (6–)8–10(–12), fertile stamens 1(–4), much larger and exserted; filaments basally connate into a staminal tube; disk absent; pistillode reduced; gynoecium glabrous or pubescent, monomerous; style straight to sigmoid, apical or lateral (sometimes approaching gynobasic); stigma punctiform, obscure; ovule unitegmic, basal; staminodes absent or present and reduced in bisexual and male flowers. Drupe reniform; 1-locular; endocarp fused to mesocarp, woody with large rectangular cavities containing caustic oils; exocarp greenish to brown to black, usually glabrous, sometimes partially pubescent, not separating from mesocarp at maturity; subtended by sigmoid to pyriform hypocarp (rarely absent), white, green, yellow, or red; animal dispersed (those lacking hypocarps possibly water dispersed). Seed reniform. $n=12$, 29.

Twelve or more species in tropical moist forest (including restinga and along rivers in sandy soils in the Amazon basin), gallery forest, rocky outcrops, and savanna (including cerrado and campo rupestre) in Honduras south to Paraguay, Brazil, and Bolivia.

Anacardium occidentale is cultivated pantropically. See Fig. 1 for illustrations of *A. humile* and *A. occidentale*.

Apterokarpos C.T. Rizzini

Apterokarpos C.T. Rizzini, Leandra 5(6): 40 (1975).

Loxopterygium Hook.f. (1862), p. p.

Dioecious shrubs or trees with white exudate. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite to subopposite; subsessile; margin serrate; secondary venation cladodromous. Inflorescences terminal panicles with elongate branches upon which flowers and terminal branches are widely spaced and spike-like. Flowers subsessile to pedicellate; perianth 5-parted, imbricate; calyx deeply lobed; corolla white to yellowish; androecium haplostemonous; anthers dorsifixed; disk glabrous; pistillode absent; gynoecium glabrous, pseudomonomerous; carpels 3; style simple; stigma 3-lobed; ovule position unknown; staminodes reduced. Drupe dry; 1-locular; obovoid, laterally compressed, oblique, with persistent calyx; exocarp with longitudinal grooves; dispersal mechanism unclear.

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

Astronium Jacq.

Astronium Jacq., Enum. Syst. Pl. 10 (1760); see also: F.A. Barkley, Phytologia 16: 107–152 (1968); Mitchell and Daly, Brittonia 69: 457–464 (2017).

Myracrodruon Allem. (1862); Santin DL, Revista Brasileira de Botânica 14(2): 133–145 (1991).

Dioecious trees with clear contact dermatitis-causing exudate that is yellowish or brown, turning black with exposure to air; bark sometimes with exfoliating patches. Cataphylls sometimes present. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite (alternate), petiolulate; margin entire, serrate, or crenate; secondary venation cladodromous, craspedodromous, and/or brochidodromous. Inflorescences terminal and/or axillary thyrsoids. Flowers pedicellate; 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; disk glabrous, 5-lobed, very thin; pistillode present, absent, reduced, or minute; gynoecium glabrous, pseudomonomerous; carpels 3; styles 3, recurved; stigmas capitate; ovule apical, lateral or basal; staminodes reduced. Fruit fusiform, subglobose, or broadly ovoid and laterally lobed, baccate or nutlet-like; 1-locular; sepals persistent, accrescent, chartaceous; often with persistent styles; exocarp glabrous; mesocarp resinous; endocarp bony or thin and brittle when dry; wind dispersed. Seed straight to reniform. $n=15$.

Eleven species in tropical dry to moist forests and savannas in Mexico south to Paraguay and northern Argentina. See Fig. 1 for illustrations of *A. graveolens* and *Astronium urundeuva* (Allemão) Engl. and Fig. 2 for illustrations of *A. concinnum.*

Bonetiella Rzed.

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

Polygamodioecious shrubs with contact dermatitis-causing exudate turning black with exposure to air. Leaves deciduous, alternate, simple, petiolate, entire, linear to trifid or pinnatifid; secondary venation cladodromous. Inflorescences axillary panicles. Flowers subsessile to shortly pedicellate; perianth 5-parted, imbricate; calyx deeply lobed; corolla greenish white; androecium haplostemonous; disk glabrous, 5-lobed; pistillode reduced; gynoecium glabrous, pseudomonomerous; carpels 3; styles 3, short, subapical and unequal; stigmas 3; ovule basal; staminodes reduced. Drupe laterally compressed and subreniform, 1-locular; exocarp with numerous glands near remnant styles, yellowish; mesocarp thin, resinous; endocarp fibrous; dispersal mechanism unclear. Seed subreniform.

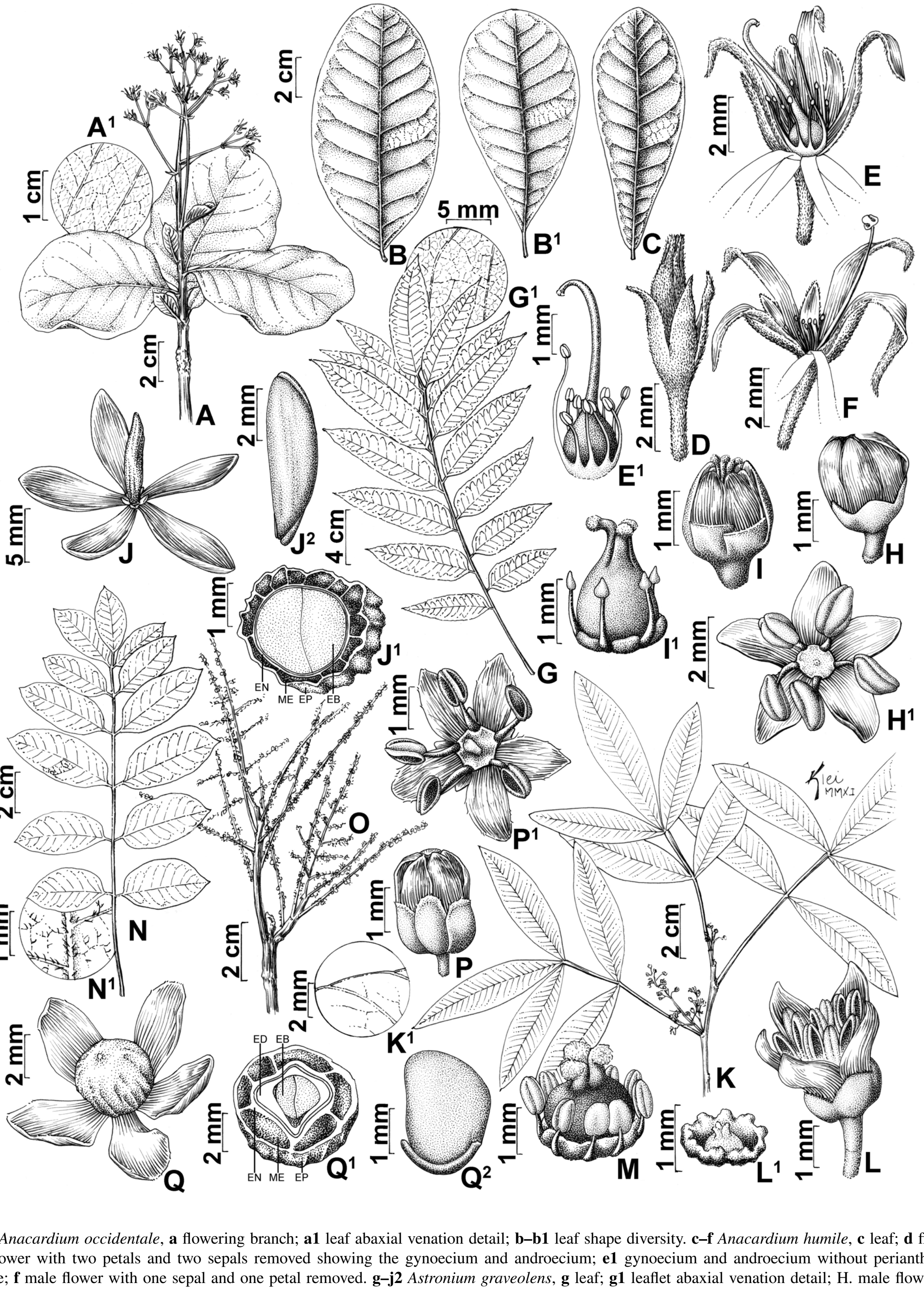


Fig. 1 **a–b1** *Anacardium occidentale*, **a** flowering branch; **a1** leaf abaxial venation detail; **b–b1** leaf shape diversity. **c–f** *Anacardium humile*, **c** leaf; **d** flower bud; **e** bisexual flower with two petals and two sepals removed showing the gynoecium and androecium; **e1** gynoecium and androecium without perianth, showing staminal tube; **f** male flower with one sepal and one petal removed. **g–j2** *Astronium graveolens*, **g** leaf; **g1** leaflet abaxial venation detail; H. male flower bud; **h1** male flower; **i** female flower bud with two sepals sectioned, showing imbricate aestivation; **i1** female flower with perianth removed; **j** fruit with enlarged calyx; **j1** fruit cross section showing exocarp (EP), mesocarp (ME), endocarp (EN), and cotyledons (EB); **j2** lateral view of the seed with seed coat removed. **k–m** *Lithrea molleoides*, **k** flowering branch; **k1** leaflet abaxial marginal venation detail; **l** male flower; **l1** male flower with androecium and perianth removed showing disk and reduced pistillode; **m** female flower with perianth removed. **n–q2** *Astronium urundeuva*, **n** leaf; **n1** leaflet abaxial indumentum detail; **o** flowering branch; **p** male flower bud; **p1** male flower; **q** fruit with enlarged calyx; **q1** fruit cross section showing exocarp (EP), mesocarp (ME), endocarp (EN), and the seed in endosperm (ED) enclosing the cotyledons (EB); **q2** lateral view of the embryo (**a** Loebmann SPF 201238; **b** Jorge SPF 165799; **b1** Pirani 4516; **c–e1** Hoehne 12536; **f** Naranjo 102; **g–g1** Gandolfi 365; **h–h1** Ivanauskas SPF 201247; **i–i1** Chaddad 250; **j–j2** Gandolfi 365; **k–l** Sasaki 680; **m** Tamashiro 708; **n–n1** Cipolla SP 14542; **o–p** Jaccoud 69; **q–q2** Assis 259). Illustrations by Klei Rodrigo Sousa (Silva-Luz and Pirani in press)

Fig. 2 *Astronium concinnum*, **a** flowering branch; **b** inflorescence detail; **c** male flower adaxial view showing reduced pistillode, abaxial view, and stamen detail; **d** developing fruit showing enlarging sepals and remnant petals, stigmas, and styles; E. longitudinal section of female flower with gynoecium removed showing staminodes and lobes of disk; **f** gynoecium whole and in longitudinal section showing basal ovule; **g** fruiting branch; **h** drupe with subtending enlarged sepals; **i** cross section of drupe showing two cotyledons in one locule; **j** two cotyledons from single seed (**a–c** Thomas 13514; **d–f** TSS 1903; **g, h** Thomas 13570; **i, j** Mori 12839). Illustrations by Bobbi Angell

A single species, *B. anomala* (I.M.Johnst.) Rzed., endemic to the Chihuahuan Desert in northern and central Mexico. Morphological and molecular evidence suggests that *Bonetiella* is closely allied with *Pseudosmodingium* (Aguilar-Ortigoza et al. 2004; Weeks et al. 2014).

Cardenasiodendron F.A. Barkley

Cardenasiodendron F.A. Barkley, Lloydia 17: 242 (1954).

Loxopterygium Hook.f. (1862), p. p.

Dioecious trees with white exudate. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite or subopposite, petiolulate; margin serrate; secondary venation craspedodromous and cladodromous. Inflorescences terminal and/or axillary, compound panicles with ultimate branches spicate. Flowers sessile to long-pedicellate, subtended by three triangular bracts; perianth 5-parted, imbricate; calyx not deeply lobed; corolla white to greenish yellow; androecium haplostemonous; stamens alternating with lobes of disk; disk glabrous, 5-lobed; pistillode minute; gynoecium pubescent, pseudomonomerous; carpels 3; styles 3; stigmas 3; ovule basal; staminodes present. Samara obovate to subreniform with two unequal, lateral wings and persistent calyx; 1-locular; wind dispersed. Seed obliquely curved.

A single species, *C. brachypterum*, endemic to tropical dry forest in Bolivia.

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. Cataphylls sometimes present. Leaves alternate, imparipinnate, petiolate; leaflets opposite, petiolulate, margin entire or toothed to spinose; secondary venation cladodromous or craspedodromous, sometimes a mix of the two or mixed with brochidodromous. 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; disk glabrous, cup-shaped, slightly lobed; pistillode very reduced; gynoecium glabrous, pseudomonomerous; carpels 3; styles absent or 3, short; stigmas 3; ovule basal, pendulous; staminodes very reduced. Drupe oblong-ellipsoidal with persistent calyx; 1-locular; exocarp yellow, red, or black; mesocarp fleshy; animal dispersed. Seed oblong; cotyledons fleshy.

Twenty species widespread in central Mexico south to Guatemala and Belize, and east to the Greater and Lesser Antilles. See Fig. 3 for illustrations of *Comocladia mayana* Atha, J.D. Mitch. & Pell.

Cotinus Miller, p. p.

Cotinus Miller, Gard. Dict. Abr. Ed., 4 (1754); Rzedowski and Calderón de Rzedowski, Acta Botánica Mexicana 47:23–30 (1999); Young, Bull. Torrey Bot. Club 104:241 (1977)

Rhus L. (1753), p. p.

Dioecious or gynodioecious (polygamodioecious or monoecious), shrubs or trees, exudate unknown. Leaves deciduous, alternate, simple, petiolate, margin entire or serrate, oblong, secondary venation cladodromous or craspedodromous. Inflorescences terminal panicles. Flowers pedicellate; perianth 5-parted, imbricate; calyx deeply lobed; corolla greenish or yellowish white; androecium haplostemonous; filaments subulate; disk glabrous; pistillode present; gynoecium sparsely to densely pubescent, pseudomonomerous; carpels 3; styles 3, terminal to sub-terminal; stigmas 3; ovule basal, pendulous; staminodes present or absent. Drupe globose to ovoid or obliquely ovoid, with persistent calyx; 1-locular; dispersal mechanism unclear; exocarp with purple glandular trichomes. Seed reniform. $n = 15$.

Two species in the Neotropics (*Cotinus chiangii* (Young) Rzedowski & Calderón and *Cotinus carranzae* Rzedowski & Calderón) are endemic to open scrubland on steep limestone slopes of northern to central Mexico. Four species occur outside of the Neotropics: one in the temperate southern USA; one in central to southern Europe, east to China; and two in southwestern China. The two Mexican taxa are so morphologically distinct from *Cotinus* elsewhere (including the type species of the genus) and from each other, that they warrant further study to reevaluate their recognition in the same genus. The species outside the Neotropics have fruiting panicles that are wind-dispersed, much like a tumbleweed, via elongated plumose pedicels of numerous aborted flowers.

Haplorhus Engl.

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

Dioecious trees with white exudate. Leaves evergreen, alternate, simple, sessile to very short-petiolate, linear to lanceolate; margin entire; secondary venation cladodromous. Inflorescences axillary panicles. Flowers sessile; perianth 5-parted; male flowers subtended by bracts, tepals pink, imbricate; epicalyx and red to purple tepals of female flowers imbricate; androecium haplostemonous; anthers basifixed; disk glabrous; pistillode absent; gynoecium glabrous, pseudomonomerous; carpels 3; styles 3, short; stigmas 3, capitate; ovule pendulous, basal; staminodes absent. Drupe obliquely ovoid; 1-locular; exocarp red; mesocarp thin, fleshy; endocarp cartilaginous; animal dispersed. Seed obovoid.

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

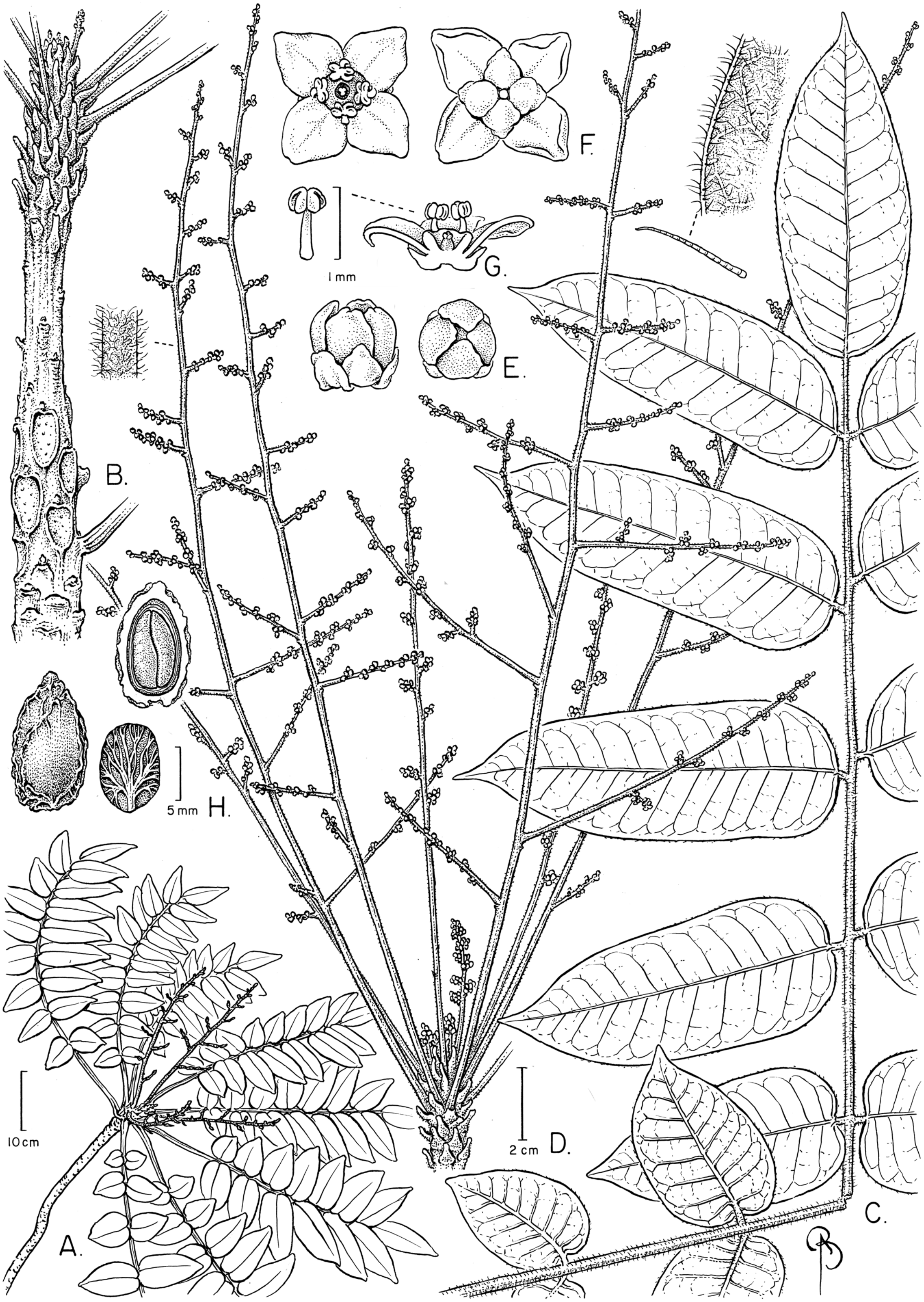


Fig. 3 *Comocladia mayana*, **a** habit; **b** stem showing leaf scars (below) and cataphylls (above); **c** leaf with indumentum detail and trichome; **d** male inflorescence; **e** male flower buds side view (left) and adaxial view (right); **f** male flower adaxial view (left) and abaxial view (right); **g** longitudinal section of male flower and enlarged stamen; **h** Fruit (left), fruit longitudinal section showing cotyledons (upper right), seed with seed coat (lower right) (**a–g** from the type specimen; **h** from Ortiz 989). Illustrations by Bobbi Angell (Atha et al. 2011)

Lithrea Hook.

Lithrea Hook., Bot. Misc. 3: 175 (1833), sphalm., nom. 2181 cons.

Lithraea Miers ex Hook. & Arn. (1826), partim.; see also: F.A. Barkley, Phytologia 8(7): 329–365 (1962).

Schinus L. (1753, 1754), p. p.

Dioecious shrubs or trees with contact dermatitis-causing exudate turning black with exposure to air. Leaves evergreen or semi-deciduous, alternate, imparipinnate or unifoliolate, petiolate; rachis often alate; leaflets sessile, entire; marginal secondary or intramarginal secondary vein present, secondary venation cladodromous or craspedodromous Inflorescences terminal and/or axillary panicles. Flowers pedicellate; perianth 5-parted; calyx apert to slightly imbricate, lobes minutely deltate; corolla valvate in bud, greenish white to greenish yellow; androecium diplostemonous; disk glabrous, 10-lobed; pistillode reduced; gynoecium glabrous, pseudomonomerous; carpels 3; styles 3, basally connate, apical; stigmas 3, capitate; ovule basal; staminodes reduced. 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; animal dispersed. Seed ovoid. $n = 15$.

Three species in Brazil, Bolivia, Paraguay, Argentina, Uruguay, and Chile. See Fig. 1 for illustrations of *Lithrea molleoides* (Vell.) Engl.

Loxopterygium Hook. f.

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

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

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* Hieron. and H.Lorentz ex Griseb. in Bolivia south to northwestern Argentina. See Fig. 4 for illustrations of *L. sagotii*.

Malosma Nutt. ex Abrams

Malosma Nutt. ex Abrams, Fl. Los Angeles 3: 220 (1917).

Rhus subgen. *Malosma* Nutt. ex Torr. & A. Gray (1838).

Rhus sect. *Venenatae* Engl. (1881), p. p.

Polygamodioecious shrubs or trees. Exudate clear, turning dark brown with exposure to air. Leaves evergreen, alternate, simple, petiolate, longitudinally plicate(conduplicate); margin entire; secondary venation cladodromous. Inflorescences terminal thyrsoids. Flowers pedicellate; perianth 5-parted, imbricate; corolla whitish; calyx deeply lobed; androecium haplostemonous; disk glabrous; pistillode reduced; gynoecium glabrous, pseudomonomerous; carpels 3; styles 3, short; stigmas 3; ovule basal; staminodes reduced. Drupe laterally compressed, glabrous; 1-locular; exocarp white; mesocarp thick, waxy; endocarp bony; animal dispersed. Seed unknown.

A single species, *M. laurina*, in chaparral and coastal sage scrub of southern California south to central Baja California, Mexico. It is segregated from *Rhus* on the basis of having a white exocarp and lacking glandular trichomes. *M. laurina* has subterranean lignotubers that enable it to resprout after fires or other above-ground damage.

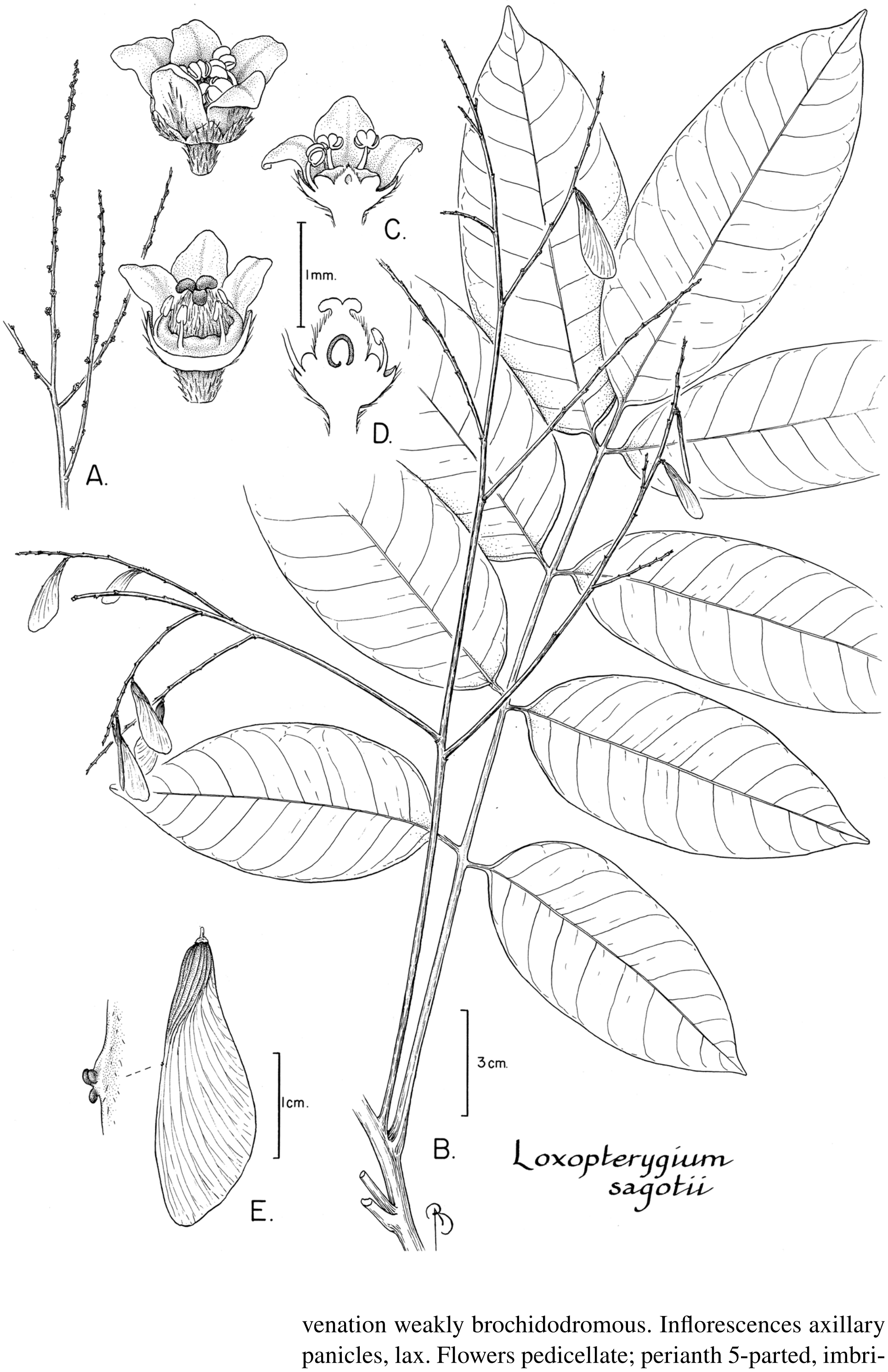
Mauria Kunth

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

Hermaphrodite, sometimes cleistogamous, or less frequently polygamodioecious shrubs or trees, with clear 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 abaxial secondary vein axils; secondary venation cladodromous or eucamptodromous. Inflorescences terminal and/or axillary panicles or pleiothyrsoids; flowers pedicellate; perianth 5-parted; calyx short-cupulate; corolla valvate or subvalvate, white to yellow, yellow-green, or pink; androecium diplostemonous; stamens sometimes of unequal lengths; filaments subulate; anthers dorsifixed, connective extended slightly above anthers; disk glabrous, 10-crenulate; gynoecium glabrous; carpels 3, ovary pseudomonomerous; style short; stigma 3-lobed; ovule pendulous, lateral or subapical. Drupe laterally compressed, oblique, crowned by vestigial style; 1-locular; exocarp orange or red to brown; mesocarp thin, fleshy; endocarp chartaceous; animal dispersed. Seed subreniform to oblong, flattened.

Sixteen Andean and Central American species from El Salvador south to eastern Venezuela and extreme northern Argentina, primarily in montane tropical forest.

Fig. 4 *Loxopterygium sagotii*, **a** inflorescence; **b** fruiting branch; **c** male flower with longitudinal section; **d** female flower with longitudinal section showing basal ovule; **e** samara with persistent style detail (**a** Cox & Hubbard 82; **d, e** Davidse & Gonzalez 16274; **c** A.C. Smith 3512; **d** BAFOG 7575). Illustrations by Bobbi Angell, copyright RBG Kew (Mitchell 1997)



Metopium P. Br.

Metopium P. Br., Civ. Nat. Hist. Jamaica: 177 (1756); see also: F.A. Barkley, Ann. Missouri Bot. Gard. 24: 265–499 (1937).

Rhus L. (1753), p. p.

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

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

Mosquitoxylum Krug & Urb.

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

Polygamodioecious (androdioecious) trees; exudate milky. Leaves evergreen (semi-deciduous), alternate, imparipinnate; leaflets opposite or subopposite, short-petiolulate with terminal petiolule alate, margin entire; secondary venation cladodromous, basally eucamptodromous. Inflorescences terminal and/or axillary panicles with spicate branches. Flowers sessile or short-pedicellate, each subtended by 3 deltoid bracts; perianth 5-parted, imbricate; calyx shallowly lobed; corolla greenish white or cream-colored; androecium haplostemonous; disk glabrous, 5-lobed; pistillode reduced; gynoecium glabrous, pseudomonomerous; carpels 3; style short, distally 3-branched, excentric; stigmas 3; ovule sublateral; staminodes very reduced. Drupe obliquely ovoid, compressed; 1-locular; exocarp red, glabrous; animal dispersed. Seed straight.

A single species, *M. jamaicense* Krug and Urb., southern Mexico south to northwestern Ecuador and Jamaica. Morphological and molecular evidence suggests that *Mosquitoxylum* is closely related to *Rhus*. There is one report of urushiol being present in this genus, but we can find no reports of *M. jamaicense* causing contact dermatitis (Aguilar-Ortigoza et al. 2003).

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, lanceolate, membranaceous, margin entire, puberulent ab- and adaxially; secondary venation brochidodromous. Inflorescences terminal corymbose thyrsoids. Flowers pedicellate; perianth 5-parted, valvate; corolla white; calyx deeply lobed; androecium haplostemonous; disk annular, glabrous; pistillode reduced, styllode simple; gynoecium pubescent, pseudomonomerous; carpels 3; styles 3, basally connate, lateral; stigmas capitate; ovule basal; staminodes reduced. Samara not lignified, laterally compressed with long, violet trichomes on the margin; 1-locular; wind dispersed. Seed unknown.

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

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

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, margin crenate; secondary venation cladodromous. Inflorescences terminal; male flowers arranged in pendent or erect panicles, female flowers tightly arranged in 3-flowered clusters subtended by a cupular involucre (2 flowers abort); male flowers pedicellate, female flowers sessile; perianth uniseriate (calyx), 3–8-parted in male flowers, absent in female flowers; androecium haplostemonous; disk absent; pistillode absent; gynoecium pubescent; carpels 1; style 1, apical, style of central flower larger; stigma 1, bilobed; ovule unitegmic, lateral; staminodes absent. Fruit a samaroid syncarp subtended by a slightly dilated, elongate secondary inflorescence branch with parallel margins; 1-locular; exocarp brown, pubescent; wind dispersed. Seed straight.

A single species, *O. huaucui*, endemic to mid-elevation arid slopes of the Andes of western Peru.

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

Pachycormus Coville

Pachycormus Coville in Cent. Dict., rev. ed., 6708 (1911).

Rhus L. (1753), p. p.

Bursera Jacq. ex L. (1762), p. p.

Veatchia A.Gray (1884)

Dioecious trees with short trunk and crooked branches, caudiciform; outer bark white to yellow, exfoliating, revealing green inner bark, with copious reddish brown to milky exudate drying clear. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite to subopposite, sessile to short-petiolulate, margin entire to crenate or serrate, irregularly lobed to pinnatifid, elliptic; secondary venation cladodromous. Inflorescences axillary panicles. Flowers pedicellate; perianth valvate, 5-parted, white to dark pink; calyx deeply lobed; corolla exduplicate-valvate; androecium diplostemonous; disk present but not well known, sometimes alternating with stamens; pistillode reduced; gynoecium pubescent, pseudomonomerous; carpels 3; styles 3; stigmas 3, capitate; ovule unknown; staminodes reduced. Utricle pubescent; 1-locular; wind dispersed. Seed unknown.

A single species, *P. discolor*, endemic to patches of lava fields and on hillsides in the Sonoran Desert of central Baja California, Mexico.

Pistacia L., p. p.

Pistacia L., Sp. Pl.: 1025 (1753); see also: L. Xie et al. Mol Phyl Evol 77:136–146 (2014).

Lentiscus (Tourn.) L. (1735).

Terebinthus P. Br. (1735).

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

One species in pine-oak forest, often associated with limestone, in Texas, USA, south to Guatemala. Eleven species in 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 in the Neotropics and worldwide in dry, warm climates.

Pseudosmodingium Engl.

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

Dioecious or polygamodioecious trees or caudiciforms with contact dermatitis-causing exudate turning black with exposure to air; bark brown to red, sometimes exfoliating in plates. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite or alternate, sessile or petiolulate, margin entire to serrate; stellate trichomes sometimes present; secondary venation cladodromous, often mixed with craspedodromous, sometimes eucamptodromous basally. Inflorescences axillary panicles. Flowers pedicellate; perianth 5-parted, imbricate; calyx deeply lobed; corolla white and prominently veined; androecium haplostemonous; filaments filiform; disk glabrous; pistillode extremely reduced; gynoecium glabrous, pseudomonomerous; carpels 3; style 3-branched; stigmas 3; ovule pendulous, apical; staminodes slightly reduced. Samara lignified with two broad lateral wings, reniform in outline; 1-locular; exocarp yellow to brown or reddish brown, glabrous; wind dispersed. Seed reniform; cotyledons slender.

Four species endemic to central and southern Mexico.

Rhus L., p. p.

Rhus L., Sp. Pl. 1: 265 (1753); see also: F.A. Barkley, Ann. Missouri Bot. Gard. 24: 265–499 (1937); D. Young, Systematics of *Rhus* subgenus *Lobadium* sect. *Styphonia*. Ph.D. dissertation, Claremont Graduate School, Claremont, CA, (1975).

Rhus subgen. *Rhus* L. (1754).

R. sect. *Sumac* DC. (1825), p. p.

R. subgen. *Lobadium* (Raf.) Torr. & A. Gray (1838), p. p.

R. subgen. *Schmaltzia* Schneider (1907).

Schmaltzia Desv. ex Small emend. F.A. Barkley & Reed (1940).

Excluding: *R*. sect. *Venenatae* Engl. (1881).

Polygamodioecious or rarely hermaphrodite shrubs or trees, rarely sarmentose or rhizomatous, sometimes with dichotomous branching; exudate clear to milky or yellowish. Leaves evergreen or deciduous, alternate, imparipinnate, trifoliolate, or unifoliolate, petiolate; rachis sometimes alate; leaflets opposite or subopposite, subsessile to petiolulate; margin entire to crenate, serrate, or lobate; secondary venation cladodromous or craspedodromous, or a mix of the two. Inflorescences terminal and/or axillary thyrsoids or compound spikes. Flowers sessile or short-pedicellate; perianth 5-parted, imbricate; sepals deeply lobed; petals white, yellowish, or pink; androecium haplostemonous; filaments subulate; anthers dorsifixed; disk glabrous; pistillode reduced; gynoecium glabrous to pubescent; carpels 3, ovary pseudomonomerous; styles 1–3, united at base; stigmas 3; ovule basal (pendulous, apical or lateral); staminodes reduced. Drupe globose; 1-locular; exocarp red to brown, usually with both glandular and non-glandular trichomes; mesocarp resinous or fleshy; animal dispersed. Seed straight. $n = 15$ or 16, polyploidy is common.

Twenty-four or more species from southern Canada south to Panama and Cuba; two additional species restricted to temperate North America; one in North Africa to Mediterranean Europe east to Asia; six or more species from South Asia and western China east to Japan and Korea, south to Java and the Philippines; one endemic to the Hawaiian islands.

Infrageneric classification includes *Rhus* subgen. *Rhus* with pedicellate flowers and thyrsoid inflorescences, and *R*. subgen. *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.

Schinopsis Engler.

Schinopsis Engler in Mart., Fl. Brasil. 12(2): 403 (1876); see also: T. Meyer & F.A. Barkley, Lilloa 33(11): 207–257 (1973); Mogni, Prado, Oakley, Bol Soc Argent Bot 52(1):185–190 (2017).

Quebrachia Griseb. (1874).

Loxopterygium Hook.f., p. p.

Dioecious or monoecious trees, sometimes with thorns, with clear to brown contact dermatitis-causing exudate turning brown or 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 or sometimes basal pair lobate; secondary venation cladodromous. Inflorescences terminal and/or axillary panicles. Flowers sessile or pedicellate; perianth 5-parted, imbricate; calyx deeply or shallowly lobed; corolla greenish to white; petals with a prominent midvein; androecium haplostemonous; anthers dorsifixed; disk glabrous, 5-lobed; pistillode reduced; gynoecium glabrous to pubescent, pseudomonomerous; carpels 3; styles 1–3, lateral; stigmas 3, sometimes two are sessile; ovule pendulous, subapical; staminodes reduced. Samara 1-locular; exocarp and mesocarp expanded into a stiffened and thick, flattened lateral wing, green or red drying to brown; endocarp bony; calyx persistent; wind dispersed. Seed oblong and reniform. $n = 14$.

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.

Schinus L.

Schinus L., Sp. Pl.: 388 (1753); see also: F.A. Barkley, Brittonia 5: 160–198 (1944); F.A. Barkley Lilloa 28: 5–110 (1957); C. Silva-Luz et al., Mol. Phyl. Evol. 133:302–351 (2019).

Duvaua Kunth (1824), p. p.

Dioecious shrubs or trees, rarely subshrubs, rarely with thorns, and with transparent contact dermatitis-causing exudate. Leaves evergreen or deciduous, alternate, unifoliolate or imparipinnate (paripinnate), petiolate; rachis often alate; leaflets opposite or alternate, sessile to subsessile; margin entire to serrate; secondary venation cladodromous or craspedodromous. Inflorescences terminal and/or axillary, spike-like pseudoracemes, panicles, or pleiothyrses, rarely reduced to a few fascicles or flowers solitary. Flowers pedicellate; perianth (4–)5-parted, imbricate; calyx deeply lobed; corolla white to green; androecium diplostemonous; filaments subulate; disk glabrous, 8–10-lobed, patelliform in male flowers, annular and lobed in female flowers; pistillode very reduced; gynoecium glabrous to densely pubescent, sometimes with glandular trichomes; carpels 3, ovary pseudomonomerous; styles (1–)3; stigmas capitate; ovule pendulous, lateral to apical; staminodes reduced. 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; animal dispersed. Seed compressed. $n = 14, 15$.

Forty-two or more species, endemic to South America, ranging from the central Andes to southern South America, with exception of *Schinus areira* and *S. terebinthifolia*, which are native to this region but have become widespread invasive species outside their native range. *Schinus* species are distributed along the Andes in Argentina, Bolivia, Chile and Peru, where they can be found in the inter-Andean valleys and cloud forests, as well as at low altitudes from eastern Brazil to Patagonia. A few endemic Chilean species occur also in sclerophyllous forests under a Mediterranean climate. *Schinus areira, S. polygama,* and *S. terebinthifolia* are cultivated throughout the tropical, subtropical, and warm temperate regions of the world.

The generic name *Schinus* has variously been treated as masculine or feminine, but Zona (2015) established that the correct gender is feminine. Barkley (1944, see also 1957) recognized two subgenera: *S.* subgen. *Duvaua* with unifoliolate leaves, often thorny, and *S.* subg. *Schinus* (as subgen. *Euschinus*) with compound leaves and lacking thorns. Recent phylogenetic study of *Schinus* strongly supports the monophyly of the genus, but indicates that *S.* subgen. *Schinus* and the sections of *S.* subgen. *Duvaua* are polyphyletic. The phylogenetic relationships that emerged from the analyses include eight relatively well-supported lineages, in which the simple-leaved species were grouped in a strongly supported clade that was resolved into five internal clades, namely *Schinus* sect. *Atlantica*, *S.* sect. *Duvaua*, *S.* sect. *Montana*, *S.* sect. *Myrtifolia*, and *S.* sect. *Pilifera* (Silva-Luz et al. 2019). See Fig. 5 for illustrations of *Schinus engleri* F.A. Barkley, *Schinus weinmanniifolia* Engl., and *S. terebinthifolia.*

Thyrsodium Salzm. ex Benth.

Thyrsodium Salzm. ex Benth., Hook., J. Bot. Kew Gard. Misc. 4: 17 (1852); see also: Mitchell & Daly, Brittonia 45: 115–129 (1993).

Garuga Roxb. (1814), p. p.

Kunthia Benth. & Hook. (1862), p. p.

Dioecious trees, trunk sometimes buttressed, with copious milky exudate, Leaves evergreen, alternate to subopposite, imparipinnate or rarely paripinnate, petiolate; leaflets opposite or alternate, petiolulate, margin entire; secondary

Fig. 5 **a–d** *Schinus engleri*, **a** fruiting branch; **a1** leaf indumentum detail; **b** male inflorescence; **b1** pedicel detail showing bracts and articulation; **c** androecium and disk; **d** female flower with perianth removed. **e–e2**. *Schinus weinmanniifolia*, **e–e2** leaf morphological variation; **e** flowering branch; **e1** fruiting branch; **e2** leaf. **f–g** *Schinus terebinthifolia*, **f–f1** leaf morphological variation; **f** flowering branch; **f1** leaf; **g** infructescence branch showing separation of exocarp from mesocarp; **h–j1** *Spondias mombin*, **h** flowering branch; **i** leaflet abaxial detail showing intramarginal secondary vein; **j** bisexual flower; **j1** gynoecium and intrastaminal disk. **K–n1** *Tapirira obtusa*, **k** flowering branch; **l** abaxial leaf indumentum detail showing midvein and secondary vein; **m** female flower; **n** immature fruit; **n1** fruit indumentum detail. **o–r** *Tapirira guianensis*, **o** male flower; **o1** pistillode and intrastaminal disk from male flower; **p** female flower with two sepals and two petals removed; **q** gynoecium; **r** fruit longitudinal section showing apical placentation (**a–a1** Lima 1144; **b, c** Silva-Luz 161; **d** Silva-Luz 165; **e** Barreto 3211; **e1** Mattos 14298; **e2** Lima RB 69444; **f** Jung 427; **f1–g** Bernacci 1428; **h–j1** Moraes 2; **k–l** Hoehne SPF 13548; **m–n1** Nicolau 1797; **o** Tomasulo 42; **p–q** Hoehne 13939; **r** Bernacci 722). Illustrations by Klei Rodrigo Sousa (Silva-Luz and Pirani in press)

venation eucamptodromous and/or brochidodromous. Inflorescences terminal and/or axillary thyrsoids. Flowers pedicellate, perigynous; perianth 5-parted; calyx valvate, connate half or more of its length; corolla imbricate, greenish, white to yellow; androecium haplostemonous; filaments very short; anthers sometimes pubescent; disk glabrous and adnate to the hypanthium, or absent; pistillode reduced; gynoecium glabrous or pubescent, pseudomonomerous; carpels 3; style simple or 2–3-branched, apical; stigmas 1 and 0–3-lobed on simple styles, or stigmas 2–3 on branched styles; ovule lateral; staminodes reduced. Drupe globose, obovoid, oblong or ellipsoid; 1-locular; exocarp green to bluish-green, purple, brown, or black, glabrous or pubescent; mesocarp fleshy; endocarp crustaceous; animal dispersed. Seed straight.

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

Toxicodendron Mill. p. p.

Toxicodendron Mill., Gard. Dict. Abr. Ed., 4 (1754); see also: Gillis, Rhodora 73: 72–159, 161–237, 370–443, 465–540 (1971).

Rhus sect. *Sumac* DC. (1825), p. p.

Rhus subgen. *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 white contact dermatitis-causing 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; margin entire, serrate or lobed; hairy tuft domatia sometimes present in abaxial secondary vein axils; secondary venation cladodromous or brochidodromous, often mixed with craspedodromous, sometimes eucamptodromous basally. Inflorescences axillary panicles. Flowers pedicellate; perianth (4–)5(–6)-parted; calyx fused at base; corolla imbricate, white to greenish; androecium haplostemonous; anthers dorsifixed; disk glabrous, annular and lobed; pistillode reduced, style 1; gynoecium glabrous, pseudomonomerous; carpels 3; styles 3, short; stigmas capitate; ovule basal; staminodes reduced. Drupe globose, often laterally compressed; 1-locular; exocarp yellowish to white or pale gray, sometimes pubescent, separating from mesocarp at maturity; mesocarp white, waxy, striate with resin canals; endocarp bony; animal dispersed. Seed straight. $n = 15$, but polyploidy is common.

Three species: two from southern Canada south to Mexico, one from Mexico to Bolivia. Two additional species in temperate North America; seventeen species in India and Nepal; Bhutan and Myanmar; and temperate East Asia to New Guinea. One species, *Toxicodendron succedaneum*, is naturalized in Brazil.

Several taxa published in other genera, including *Rhus,* belong in *Toxicodendron* but have not yet been transferred. Three sections are recognized within the genus: *Simplicifolia*, *Toxicodendron*, and *Venenata* (Gillis 1971; Gandhi 2021). The genus has been included in numerous phylogenetic studies, which have consistently found it to be monophyletic and quite distinct from *Rhus* (Miller et al. 2001; Yi et al. 2007).

Spondioideae

Antrocaryon Pierre p. p.

Antrocaryon Pierre in Bull. Mens. Soc. Linn. Paris II, 3: 23 (1898); see also: R.B. Fernandes, Garcia de Orta, Bot., Lisboa, 2: 107–110 (1975).

Poupartia Comm. ex Juss. (1789), p. p.

Polygamodioecious trees. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite or subopposite, sessile or petiolulate, margin entire; secondary venation eucamptodromous. Inflorescences axillary panicles, often emerging with new leaves. Flowers pedicellate; perianth 5-parted; calyx slightly imbricate or apert, deeply lobed; corolla imbricate, pubescent, yellow; androecium obdiplostemonous; disk glabrous, 10-lobed; pistillode reduced; gynoecium glabrous; carpels 5; styles 5, recurved, subapical and excentric; stigmas capitate; ovules 5, apical or subapical; staminodes reduced. Drupe plum-like or apple-shaped and depressed at apex; 5-locular; exocarp yellow to light orange; mesocarp fleshy, with a sweet smell, edible; endocarp woody, angled, with 5 apical opercula; animal dispersed. Seed straight. $n = 12$.

One species in Amazonian Brazil, Colombia, and Peru (*A. amazonicum*) primarily in Amazonian tropical moist forest. Two species in tropical west and central Africa.

Attilaea E. Martínez & Ramos

Attilaea E. Martínez & Ramos in *Acta Botanica Hungarica 49:353–358.*

Hermaphrodite scandent or erect shrubs or trees, exudate unknown; some lower branches modified into thorns. Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite to subopposite, petiolulate, margin entire to shallowly crenate; secondary venation craspedodromous with intramarginal secondary vein. Inflorescences terminal and axillary thyrses, appearing before leaves. Flowers pedicellate; perianth 5-parted, calyx imbricate, deeply lobed; corolla valvate, red, cucullate; androecium obdiplostemonous;

filaments subulate; anthers dorsifixed; disk annular and lobed; gynoecium glabrous; carpels 2; styles 2; stigmas 2, capitate; ovules apical. Drupe ovoid to ellipsoid; 2-locular, only one fertile; exocarp red; mesocarp fleshy; endocarp bony; animal dispersed. Seed solitary.

One species, *Attilaea abalak*, in tropical deciduous forests in primarily calcareous soils of Mexico and Guatemala. This species is very similar to *Spondias purpurea,* but can be distinguished by its often scandent habit and by its bicarpellate gynoecium, which differs from all other Anacardiaceae.

Campnosperma Thwaites p. p.

Campnosperma Thwaites in Hook., J. Bot. Kew Gard. 1841 Misc. 6: 65, t. 1 (1854), nom. cons.

Polygamodioecious trees to 30 m tall, with *Terminalia*-branching, often trunk buttressed or with stilt roots, and with contact dermatitis-causing exudate. Cataphylls sometimes present. Leaves evergreen, alternate, simple, sessile to petiolate, elliptic, obovate to oblanceolate, entire, coriaceous, peltate or lobed scales present ad- and abaxially; apex rounded, emarginate, or short-acuminate; stellate trichomes sometimes present ad- and abaxially; secondary venation brochidodromous, eucamptodromous, or festooned-brochidodromous. Inflorescences axillary panicles. Flowers sessile to pedicellate; perianth (3–)4(–5)-parted, valvate to apert; calyx connate 1/3 of its length; corolla white, greenish, or yellow; androecium obdiplostemonous; anthers dorso-basifixed; disk glabrous; round and flat in male flowers, cupular in female flowers; pistillode reduced; gynoecium monomerous; style short or obscure; stigma flattened, discoid, irregularly lobed; ovule pendulous, apical; staminodes reduced. Drupe subglobose or ovoid, unilocular but appearing bilocular in fruit; exocarp generally red to black; endocarp woody; animal dispersed. Seeds spherical to ovoid, cotyledons faintly plano-convex or flat; embryo curved.

Two species in gallery forests and swamps from Honduras to northwest Ecuador (*C. panamense*) and in blackwater-flooded forests (igapó) in Amazonia (*Campnosperma gummiferum* (Benth.) Marchand). Eleven or more species in the Seychelles and Madagascar to Sri Lanka; southern Thailand and Malaysia, east to Micronesia and the Solomon Islands.

Cyrtocarpa Kunth in Humb., Bonpl. & Kunth

Cyrtocarpa Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp., Qu. Ed., 7: 20, t. 609 (1824); see also: Mitchell & Daly, Ann. Missouri Bot. Gard. 78: 184–189 (1991).

Tapirira Aubl. (1775), p. p.

Bursera Jacq. ex L. (1762), p. p.

Polygamodioecious trees with somewhat succulent branchlets and white exudate. Cataphylls sometimes present. Leaves deciduous, alternate, imparipinnate (paripinnate), petiolate (rachis usually alate in *C. procera*); leaflets opposite, occasionally subopposite, sessile to short-petiolulate, entire; secondary venation cladodromous, brochidodromous, or festooned brochidodromous, often with a mix of more than one type including eucamptodromous. Inflorescences terminal and/or axillary panicles or pseudospikes. Flowers pedicellate; perianth 5-parted, imbricate; calyx deeply lobed; petals usually patent at anthesis, color white, yellow, or pink; androecium obdiplostemonous; anther sometimes with glandular connective; disk glabrous, annular, crenulate and fleshy; pistillode reduced to 5 styles; gynoecium glabrous or pubescent (pseudomonomerous in *Cyrtocarpa caatingae* J.D.Mitch. & Daly); carpels 5; styles (3–)5, short; stigmas (3–)5, capitate; ovule pendulous, subapical or apical; staminodes reduced. Drupe obliquely obtuse-oblong or obovoid; 1–3(–5)-locular; exocarp reddish purple or yellow to orange; mesocarp fleshy; endocarp bony, with (0-)1–5 apical to lateral opercula, with an either smooth or sculpted surface; animal dispersed. Seed straight to 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.

Cyrtocarpa caatingae differs morphologically from the rest of the genus, as the fruit is unilocular and the endocarp lacks opercula, and it was found to represent a distinct lineage in a recent molecular phylogeny of the genus (Joyce et al., unpublished data). Its elevation to a distinct genus is currently in progress (Mitchell et al. unpublished).

Spondias L. p. p.

Spondias L., Sp. Pl.: 200 (1753); see also: 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); Mitchell & Daly, PhytoKeys 55(55):1–92 (2015).

Evia Commerson ex Blume (1850).

Warmingia Engl. (1874).

Polygamodioecious, hermaphrodite, or andromonoecious (rarely dioecious) trees with clear to cloudy exudate, sometimes drying black (rarely reported to cause contact dermatitis); rarely bark with cork protuberances (*S. mombin*) or thorns present (*S. purpurea*). Leaves deciduous, alternate, imparipinnate, petiolate; leaflets opposite, subopposite or alternate, sessile to petiolulate, margin entire to crenate or serrate; venation craspedodromous with intramarginal secondary vein. Inflorescences terminal and/or axillary panicles (racemes); often appearing before leaves or with young leaves. Flowers pedicellate; calyx slightly imbricate or apert; (4)5-lobed; corolla valvate, (4)5(6)-parted, cucullate; white, cream-colored, purple, or red; androecium obdiplostemonous; filaments filiform or subulate; anthers dorsifixed; disk

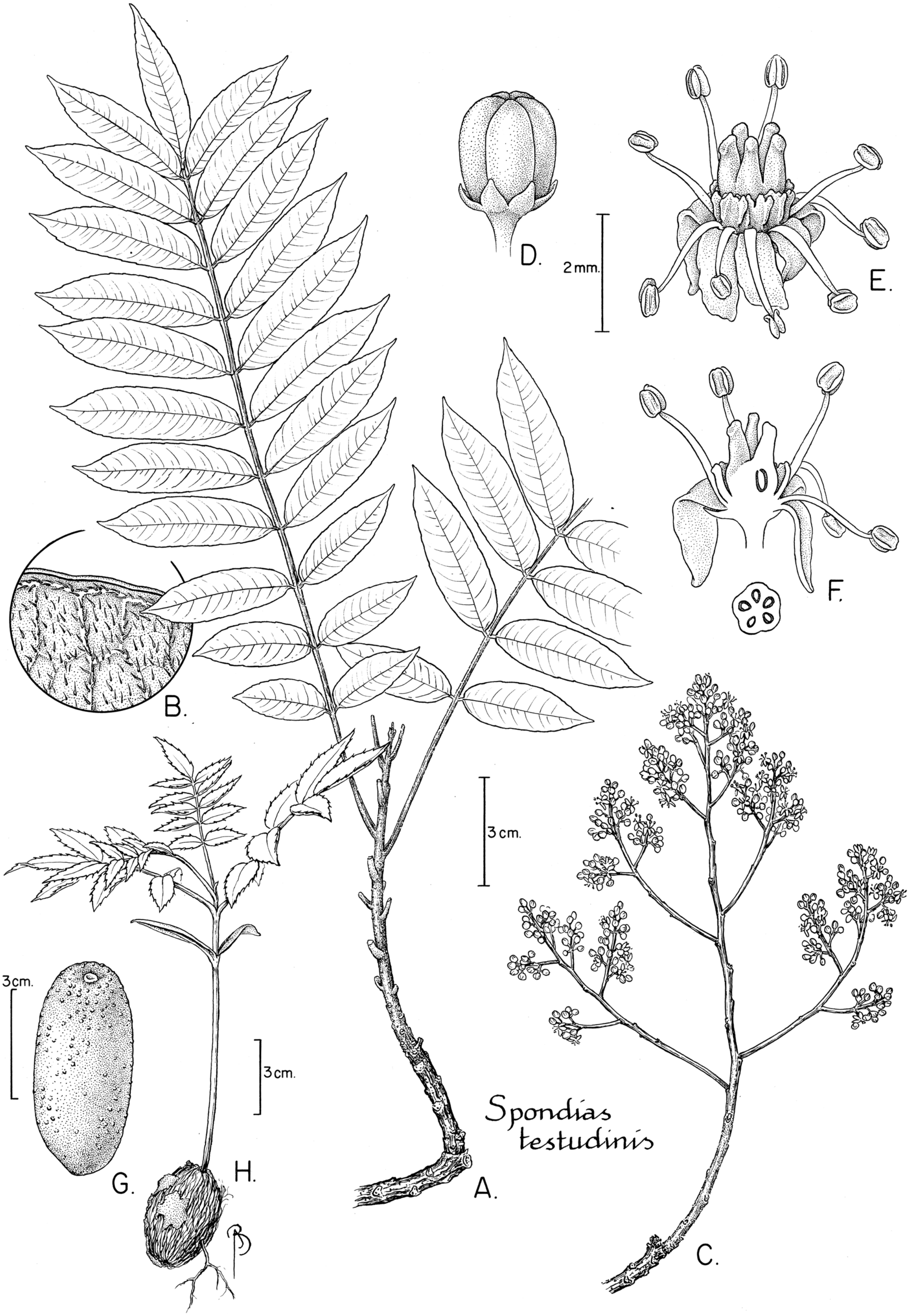


Fig. 6 *Spondias testudinis,* **a** branch with leaves; **b** leaflet indumentum abaxial detail showing intramarginal secondary vein; **c** inflorescence, **d** bisexual flower bud; **e** bisexual flower; **f** longitudinal section of flower showing apical ovule (above) and transverse section of ovary (below); **g** drupe; **h** seedling. Illustrations by Bobbi Angell (Mitchell and Daly 1998)

glabrous or papillose, annular and lobed; pistillode reduced; gynoecium glabrous; carpels (3–)5(–6); styles (3–)5; stigmas capitate to spathulate; ovules apical; staminodes reduced. 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 (spiny and projecting into the fleshy mesocarp in introduced *S. dulcis*); animal dispersed. Seed curved. $n = 16$.

Ten species native to tropical dry forests, moist forests, gallery forests, forest patches in savannas, caatinga, and coastal forests from Mexico south to southeastern Brazil and Bolivia. Nine species native to Madagascar and south Asia east to tropical China, south to the South Pacific. Two Neotropical species (*S. mombin* and *S. purpurea*) are naturalized in West Africa and the West Indies, and likely also in Southeast Asia; *S. dulcis* is naturalized in the Neotropics. Three species (*S. mombin, S. dulcis,* and *S. purpurea*) are cultivated pantropically. See Fig. 5 for illustrations of *S. mombin* and Fig. 6 for illustrations of *S. testudinis.*

Tapirira Aubl.

Tapirira Aubl., Hist. Pl. Guiane 1: 470, t. 188 (1775).

Mauria Kunth (1824), p. p.

Polygamodioecious trees, trunk sometimes buttressed, exudate clear, white, yellow, orange or reddish, sometimes turning brown with exposure to air. Leaves evergreen, alternate, imparipinnate to paripinnate, petiolate; leaflets opposite or subopposite, petiolulate, margin entire; secondary venation brochidodromous, festooned brochidodromous, or eucamptodromous. Inflorescences terminal and/or axillary panicles. Flowers pedicellate; perianth 5-parted, imbricate; calyx deeply lobed; corolla greenish yellow or cream-colored; androecium obdiplostemonous, stamens (8–)10; disk glabrous, (8–)10-lobed; pistillode reduced; gynoecium pubescent, pseudomonomerous; carpels (4)5; styles (3–4-)5; stigmas capitate; ovule apical or subapical; staminodes reduced. Drupe with persistent calyx; globose, oblong-oblique or ellipsoid; 1-locular; exocarp purple to black (sometimes green in *T. lepidota*); mesocarp thin, fleshy; endocarp cartilaginous and usually brittle when dry (bony in *T. mexicana*); animal dispersed. Seed curved; cotyledons with purple striations.

Ten or more species in tropical moist forests, montane forests, gallery forests, campo rupestre, white sand campinas, and restinga from southern Mexico to southeastern Brazil, Bolivia, and Paraguay.

Tapirira lepidota differs from the other species in having 3–4(-5) styles, leaves and flowers covered in lepidote scales, and green fruit. *Tapirira mexicana* Marchand has a distinctly different endocarp from the other species in the genus and instead resembles that of *Cyrtocarpa caatingae* (Herrera et al. 2018). See Fig. 5 for illustrations of *T. guianensis* and *Tapirira obtusa* (Benth.) J.D.Mitch.

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Conflict of interest The authors declare that they have no conflicts of interest.

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*See addendum for additional references not cited in text.

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