

# The Families and Genera of Vascular Plants

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Edited by K. Kubitzki

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*Volume X*

## Flowering Plants Eudicots

Sapindales, Cucurbitales, Myrtaceae

THE FAMILIES  
AND GENERA  
OF VASCULAR PLANTS

Edited by K. Kubitzki

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**X**

*Flowering Plants · Eudicots*

*Sapindales, Cucurbitales, Myrtaceae*

Volume Editor:  
K. Kubitzki

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With 93 Figures

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## Preface

The present volume includes treatments of the families of the orders Sapindales and Cucurbitales and of the family Myrtaceae as an appendage to the Myrtales, which were dealt with in the previous volume. The contributions once more reflect the enormous progress plant systematics has witnessed since the publication of the first volumes of this series now two decades ago. This can be seen in the greatly improved understanding of the demarcations between and of the relationships among and within the families treated in this volume. The increase in our understanding of the age of the lineages of the flowering plants in connection with the interest of contemporary practitioners in the use of molecular clocks has led to the inclusion, in several contributions, of hypotheses on past dispersal events, often resulting in claims of unexpected long-distance-dispersal events.

Altogether, the volume contains an enormous wealth of interesting information, and I am deeply indebted to all authors for their scholarly contributions. I am also very grateful to all copyright holders who so kindly gave permission to reproduce illustrations published under their responsibility, including the Director and Board of Trustees, Royal Botanic Gardens, Kew; Publications Scientifiques du Muséum national d'Histoire naturelle, Paris; and the editors of *Blumea* (Leiden, the Netherlands) and of *Nuytsia* (Perth, Western Australia). The artist Bobbi Angell, New York, deserves my special thanks for the generosity with which she authorized the use of the illustration published under her authorship.

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Hamburg, August 2010

Klaus Kubitzki



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# Introduction to Sapindales

K. KUBITZKI

## CONSPECTUS OF FAMILIES

1. Herbs or low-growing shrubs 2  
– Erect shrubs or trees (some Anacardiaceae herbaceous) 4

2. Perennial herbs; nectary glands 5, at base of antese-palous stamens; carpels with distinct stylochia arising from base of ovarioles; ovules solitary, pendulous, epitropous; embryo sac tetrasporic, 16-celled;  $n = 5$ . 1/4 or 5. E Mediterranean to C Asia

### Biebersteiniaceae

- Low shrubs of saline habitats, rarely (*Tetradiclis*) annual herbs; intrastaminal nectary disk annular or angular; ovary with simple style; ovules 1 or several per carpel, epitropous or apotropous; embryo sac, as far as known, of Polygonum type 3

3. Ovule 1 per carpel, apotropous; fruit drupaceous;  $n = 12, 30$ . 1/5–8. Old World, Australia

### Nitrariaceae

- Ovules several to many per carpel, epitropous; fruit a loculicidal capsule or a berry;  $n = 7, 12, 13$ . 3/7–8. E and S Europe to Middle Asia, Mexico

### Tetradiclidaceae

4. Plants usually strongly resinous, with vertical resin canals in the bark and also with resin ducts in the phloem of the larger veins of the leaves and sometimes in wood rays; producing biflavonyls 5

- Plants resinous or not, but without resin ducts in the bark, rays, and leaf veins; biflavonyls 0 6

5. Ovules 2 in each locule, epitropous, collateral or (*Beiselia*) superposed; nodes mostly 5-lacunar 5-trace; flowers actinomorphic and obdiplostemonous, or with the antesepalous stamen whorl reduced; gynoecium of (2)3–5(9–13 in *Beiselia*) connate carpels; style simple with 2–3-lobed or capitate stigma; fruits drupes with 1–5 one-seeded pyrenes or pseudocapsules releasing pyrenes; endotesta lignified; seeds exalbuminous, with hemicellulosic reserves; embryo minute, with folded, usually palmately lobed cotyledons.  $n = 11, 13, 23$ . 19/640. Pantropical

### Burseraceae

- Ovule solitary in each locule, apotropous, more rarely epitropous; nodes mostly 3-lacunar 3-trace; flowers often monosymmetric, obdiplostemonous or with (1)5–10+ stamens; gynoecium of 4–12 distinct carpels of which usually only one is fertile, or of (2)3(–5) connate carpels; stylochia distinct or more or less connate into a simple style; fruit usually

drupaceous with resinous mesocarp; seeds with oily and starchy endosperm; endotegmen lignified, usually thickened; embryo curved, with fleshy cotyledons.  $n = 7–12, 14–16, 21$ . 81/c. 800. Pantropical, also temperate

### Anacardiaceae

6. Fruit dehiscent with 4 or 8 one-seeded mericarps from a central column; flowers isomerous, 4-merous; testa thin; endosperm 0; trees with alternate, imparipinnate leaves; ellagic acid present. 1/6. Africa, Madagascar

### Kirkiaceae

- Fruit not dehiscent from central column 7

7. Pericycle containing a cylinder of sclerenchyma (*Xanthoceras*, *Guindilia*, and some *Aceraceae* excepted); plants containing saponins in idioblasts but no bitter nortriterpenoids; leaves alternate or less often (*Aceraceae*, *Hippocastaneae*) opposite; flowers actinomorphic or obliquely zygomorphic; disk extrastaminal or less often intrastaminal, annular (in *Xanthoceras*, with orange horn-like appendages) or unilateral; petals sometimes (*Hippocastaneae*, *Sapindoideae*) with basal scale-like appendage concealing nectary; ovules 1 or 2 per carpel or rarely more, usually apotropous.  $n = 10–16, 20$ . 141/c. 1,900. Pantropical, with some temperate genera

### Sapindaceae s.l.

- Pericycle without a cylinder of sclerenchyma; producing bitter nortriterpenoids (limonoids or quassinoids) 8

8. Leaves pellucid-punctate and secretory schizogenous cavities scattered through the parenchymatous tissue (not in all *Cneoroideae*); flowers mostly actinomorphic and obdiplostemonous, sometimes stamens in one cycle and antesepalous; nectary disk intrastaminal; carpels (2)4–5+, more or less connate proximally and usually held together by the joined stylochia, less often completely connate; ovules (1)2–many in each locule, usually epitropous; fruits follicles, drupes, berries, or samaras; producing limonoids, canthin-6-ones, and alkaloids of different types.  $n = 7–11, 18+$ . 154/c. 1,800. Pantropical and temperate

### Rutaceae

- Leaves not pellucid-punctate 9
9. Stamen filaments not appendaged, usually connate into a staminal tube with anthers in one or two whorls, less often filaments distinct; nodes mostly 5-lacunar 5-trace; ovary (1)2–6(–20)-carpellate, syncarpous; style simple; ovules 1–2 or more per carpel, usually epitropous; seeds often sarcotestal or arillate; seed coat exotegmic with fibres or pachychalazal;

producing limonoids.  $n = 8(-180)$ . 50/c. 575. Pantropical, some temperate  
**Meliaceae**

- Stamen filaments distinct, usually with scaly appendage; nodes 3-lacunar; carpels (1)2–5, distinct or basally or ventrally connate; stylodia distinct, conglomerate or connate into a common style; ovule 1 per carpel, epitropous; seeds not fleshy; seed coat usually nondescript, pachychalazal in *Quassia* and *Picrasma*; producing bitter quassinoids, limonoids, and canthin-6-ones.  $n = 10-13$ . 22/100. Pantropical, some temperate  
**Simaroubaceae**

Nineteenth century botanists, such as Bentham (in Bentham and Hooker 1862) and Engler (e.g., 1931), tended to treat Sapindales and Rutales (the latter sometimes as Geraniales) as distinct orders, a concept followed by Takhtajan (2009) to the present day; however, a wider ordinal concept with Rutales included in Sapindales, as Terebinthales (Wettstein 1901) or Sapindales (Cronquist 1968), is now broadly supported and accepted. Gene sequence studies (Sheahan and Chase 1996; Gadek et al. 1996; Muellner et al. 2007, among others) have contributed to shaping the present concept of the order and provided support for its monophyly, with increasing indications for Malvales and Brassicales and the little known Huerteales as close relatives of Sapindales (Worberg et al. 2009). The multigene analysis of Wang et al. (2009) has recovered the strongly supported relationship Crossosomatales [Picramniaceae [Sapindales [Huerteales [Brassicales + Malvales]]]]. Insights from morphology and molecular work, particularly a two-gene analysis with a broader sampling of Sapindales (Muellner et al. 2007), suggest the topology presented here (Fig. 1), in which, however, the precise relationship between Simaroubaceae and Meliaceae remains weakly supported.

The androecium is often (basically?) obdiplostemonous (with the carpels in antepetalous position), and the two stamen whorls sometimes (in Burseraceae, Rutaceae, and Sapindaceae) appear in a single cycle (meta-obdiplostemony, Lam 1931), or one cycle is missing. The herbaceous and shrubby, early diverging Nitrariaceae, Tetradiclidaceae, and Biebersteiniaceae are still little known but exhibit variation in ovule curvature and in seed and fruit structure, obviously in adaptation to the challenges of their saline or semiarid habitats. *Kirkia*, formerly included in Simaroubaceae, is now recognised as sister to

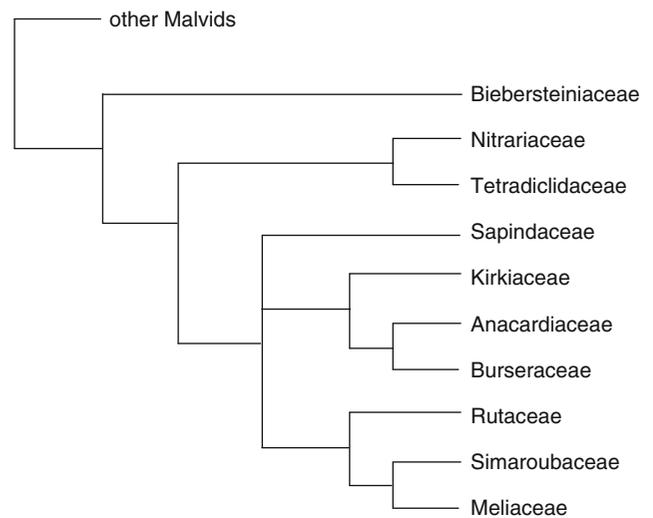


Fig. 1. Phylogenetic relationships of Sapindales families, based on *rbcL* sequence data from Muellner et al. (2007) and Sheahan and Chase (1996)

the Burseraceae/Anacardiaceae clade, with which it shares important similarities in floral structure (Bachelier and Endress 2008). Burseraceae are traditionally distinguished from Anacardiaceae by having two collateral ovules (except for *Beiselia* in which the two ovules are superposed) that are epitropous, in contrast to all other Sapindales. Bachelier and Endress (2009) report, however, that in the earliest developmental stages the ovules in Burseraceae appear apotropous. Thus, the rationale for the use of ovule curvature as a criterion for ordinal distinction becomes questionable.

The close relationship between Burseraceae and Anacardiaceae is well established both by anatomical (Takhtajan 2009), floral morphological (Bachelier and Endress 2009), and molecular evidence. Sapindaceae are treated here to include Aceraceae and Hippocastanaceae, in a return to the practice of several nineteenth century authors (for historical aspects, see the family treatment) and in conformity with the results of recent molecular studies (e.g., Harrington et al. 2005; Buerki et al. 2009), which have also brought to light the peculiar position of *Xanthoceras* as a basal branch of Sapindaceae. Rutaceae, Meliaceae, and Simaroubaceae share the possession of unusual bitter compounds, the limonoids and quassinoids, which are based on degraded triterpenes, the nortriterpenoids. The simplest

limonoids are found in Rutaceae, and occur in increasing complexity in Meliaceae and in Rutaceae/Cneoroideae. Cneoroideae comprise genera that until recently had been treated as belonging to either Rutaceae or Simaroubaceae, or had been separated into small satellite families, but the presence of triterpenoid bitter compounds and particularly the results of gene sequence studies have yielded strong arguments for combining them with the Rutaceae. The peculiar apocarp of Rutaceae and Simaroubaceae, thought by some to be inherited directly from basal angiosperms or Ranunculales, has been revealed to be a phylogenetically secondary condition, as is evidenced by the peculiar postgenital connation of the stylodia that hold together the carpels in the flowering stage (Ramp 1988).

Sapindales are an ancient lineage with a fossil record dating back to the Cretaceous. At least from the Paleocene onward, Meliaceae, Rutaceae, Sapindaceae, Anacardiaceae, and Burseraceae are represented by reliable fossils in the northern hemisphere, particularly in North America and Europe; Simaroubaceae follow in the early Eocene (for documentation, see family treatments in this volume). It is likely that the early evolution of Sapindales took place in North America, and that in the Eocene they dispersed eastward through the warm-temperate belt north of the Sea of Tethys (often erroneously called “paratropical”, see Kubitzki and Krutzsch 1996), and from there invaded and diversified in tropical regions.

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# Introduction to Cucurbitales

K. KUBITZKI

## CONSPECTUS OF FAMILIES

1. Cambium initials not storied; flowers with lobed or crenate, intra- or interstaminal nectary disk on top of ovary (but see *Octomeles*/Datiscaceae); anthers dorsifixed; [flowers obdiplostemonous; fruit a drupe, samara, or capsule; endosperm 0; cotyledons reduced or 0]. 4/34. Pantropical **Anisophylleaceae**
- Cambium initials and secondary xylem and phloem storied; floral nectaries 0 (*Octomeles* excepted); anthers usually basifixed 2
2. Flowers hypogynous; ovule 1 per carpel, pendent; placentation apical; stylodia unbranched; stipules present, caducous; ellagitannins present 3
- Flowers (hemi)epigynous; ovules usually many per carpel; placentation parietal; stylodia sometimes branched; stipules present or not; ellagitannins 0 4
3. Leaves opposite or whorled; stipules lateral, small, caducous; fertile stamens 10; carpels 5 or 10, each with a long, slender stylodium stigmatic over its entire surface; pollen 3-aperturate. 1/15+. Worldwide **Coriariaceae**
- Leaves alternate; stipules intrapetiolar, caducous; fertile stamens 5; carpel 1(2); stylodium (stylodia) with capitate stigma(s); pollen 2-colporate. 1/6. Southwest Pacific region **Corynocarpaceae**
4. Tendril-bearing dioecious or less often monoecious climbers or trailers, rarely tendrils 0; young stems nearly always with 2 rings of bicollateral bundles; stamens 3–5, often 4 of them joined or connate in 2 pairs; gynoecium(1)3(–5)-carpellate, (semi)inferior; stylodia free or connate into a single style; fruit usually a soft- or hard-shelled berry; seeds flat; bitter cucurbitacins widespread. About 97/960, tropical, some reaching temperate regions **Cucurbitaceae**
- Tendrils 0; bundles never bicollateral; fruit capsular or rarely (*Begoniaceae*) baccate; seeds not flat; seed coat with operculum; cucurbitacins absent, except for roots of *Datisca* 5
5. Leaves simple with mostly large stipules, usually asymmetrical; monoecious, rarely dioecious perennials or rarely annuals or halfshrubs; placentation axile, sometimes parietal; seeds with collar cells arranged in transverse ring around operculum.  $2n = 16$ –156 (no clear base number recognisable).  $2n > 1,500$ . Tropical and subtropical regions of the World and temperate parts of Asia, but not in Australia **Begoniaceae**

- Leaves estipulate, simple, lobed, pinnate or pinnatifid, not asymmetrical; (andro)dioecious trees or perennial herbs; placentation parietal; seeds without collar cells around operculum.  $n = 11$ ,  $c. 23. 3/4$ . E Mediterranean to SE Asia and Papuasia, and California, Baja California **Datiscaceae**

Recognition of the close relationship among the core families of Cucurbitales (*Datiscaceae* incl. *Tetramelaceae*, *Begoniaceae*, and *Cucurbitaceae*) dates back to the 19th century, although in the more recent pre-molecular era these families usually have been included in more comprehensive groupings named *Violales* or *Parietales* (for more details, see Matthews and Endress 2004, and Zhang et al. 2006). The addition of *Coriariaceae*, *Corynocarpaceae*, and *Anisophylleaceae* to the core Cucurbitales is an outcome of molecular studies (Chase et al. 1993; Swensen 1996; Setoguchi et al. 1999; Schwarzbach and Ricklefs 2000, among many others). The inclusion of *Apodanthaceae*, recently favoured by several authorities (e.g., Stevens 2001), is presently not supported (APG III; S.S. Renner, Oct. 2009).

In early molecular studies of the order, using the *rbcl* gene, these families were not fully resolved and topologies were often contradictory. Still, in recent multigene analyses covering also other orders, statistical support for the branches within Cucurbitales is generally lower than in other angiosperm clades (e.g., Wang et al. 2009). Nevertheless, the analysis of nine loci from three genomes of all Cucurbitales families by Zhang et al. (2006) has resolved Cucurbitales as monophyletic and served as a basis for an understanding of morphological and sexual system evolution within the order, but did not resolve the relationships among all families (Fig. 2). *Fagales* are now generally viewed as the closest relatives of Cucurbitales; both orders share the essentially unisexual and epigynous flowers.

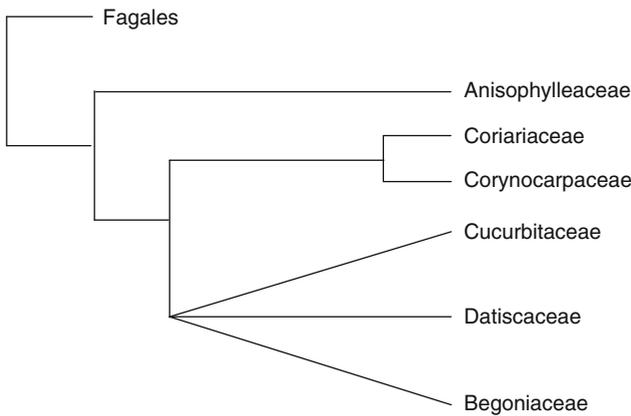


Fig. 2. Phylogenetic relationships of Cucurbitales families, based on the multigene sequence analysis of Zhang et al. (2006)

The strongly supported multigene analysis of Wang et al. (2009) has recovered the relationship Fabales[Rosales[Cucurbitales + Fagales]].

Anisophylleaceae, formerly included in Rhizophoraceae, are firmly established as the sister group to all remaining Cucurbitales, from which they differ significantly in reproductive and vegetative morphology (Schwarzbach and Ricklefs 2000). Matthews et al. (2001) and Matthews and Endress (2004) have pointed to similarities in floral structure that exist between Anisophylleaceae and Cunoniaceae, but at the same time have also revealed morphological traits in common between Anisophylleaceae and core Cucurbitales, such as unisexual flowers and inferior ovaries. Anisophylleaceae share with other Cucurbitales some anatomical characters of the wood, such as nonbordered or minimally bordered perforation plates and wide rays not accompanied by uniseriate rays, traits that are conservative and less likely affected by ecology. Anisophylleaceae have retained, however, characters that are more conservative than those in the other families of the order, such as absence of storying, presence of tracheids, and heterogeneous rays (Carlquist and Miller 2001). Thus, it appears that this family is correctly placed in Cucurbitales, and that its similarities with Cunoniaceae are due to convergence.

Among the remaining families, Coriariaceae and Corynocarpaceae stand out with 1-ovulate carpels, apical placentation, and superior ovaries, the latter trait, in view of the topology of Zhang

et al. (2006), certainly derived. Cucurbitaceae, Datisceae s.l. (i.e., including Tetramelaceae), and Begoniaceae have epigynous flowers (as do Anisophylleaceae), essentially basifixed introrse (or latrorse) anthers, trimerous gynoecia, bifurcate carpels, and a peculiar extended neck over the roof of the ovaries or instead (in *Begonia* and many Cucurbitaceae) a narrow neck at this site (Matthews and Endress 2004). It is notable that Cucurbitaceae share with *Coriaria* and *Corynocarpus* a rare combination of wood anatomical traits (vertical parenchyma scanty vasicentric, banded, and ray adjacent, and rays with upright cells strongly predominant; Carlquist and Miller 2001). In the molecular topology, Cucurbitaceae place as sister to Datisceae and Begoniaceae, but the precise relationship between the latter remains unresolved.

In view of the amount of morphological differentiation both in Cucurbitaceae and in Begoniaceae, the difference in the numbers of genera recognised in the two families is surprising, if not paradoxical. By the middle of the nineteenth century, the development of taxonomic concepts in both families had reached a comparable level. Further development in Cucurbitaceae led to a steady consolidation of taxonomic concepts, and until the present, the family has remained a field of dynamic systematics activities. Begoniaceae, in contrast, never recovered from A. de Candolle's degradation of Klotzsch's 41 genera to sections, in which he has been followed by all students of the family to the present day. Although in principle Klotzsch's concept survives in the sectional classification of the family, this never has attracted much interest by botanists (for a notable exception, see Doorenbos et al. 1998); instead, they sometimes resorted to an alphabetic sequence of the 1,400 species of *Begonia*, and the family became a field mainly of floristic, rather than systematics activity. It is true that the decisive differences among begonias are difficult to observe and put into words, many of them being included in the unpopular area of inflorescence morphology. Nevertheless, I am convinced that Klotzsch's generic concepts would have been further developed had his genera not disappeared out of the focus of botanists through their degradation to sections.

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## Anacardiaceae

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

S.K. PELL, J.D. MITCHELL, A.J. MILLER, AND T.A. LOBOVA

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

utracles, or baccates), fleshy or dry, occasionally subtended by a fleshy hypocarp or an accrescent, chartaceous or fleshy calyx or corolla; mesocarp sometimes with prominent black resin canals. Seeds 1–5(–12); endosperm scant or absent; embryo curved or straight (rarely horse-shoe-shaped or pyramidal); cotyledons usually planoconvex or flat and distinct, usually equal in size, rarely fused or ruminant, sometimes bilobed.

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

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

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

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

Leaf architecture within Anacardiaceae is extremely diverse. Primary leaf venation is pinnate, rarely palmate (e.g., *Campylopetalum*). Secondary venation is most commonly eucamptodromous, brochidodromous (usually festooned), craspedodromous, semi-craspedodromous, or cladodromous (which is usually diagnostic of Anacardiaceae when present) and rarely exmedially reticulodromous (e.g., *Rhus thouarsii*). An intramarginal vein is rarely present (e.g., *Spondias*, *Solenocarpus*). Some genera have mixed secondary venation patterns either throughout (e.g., in *Comocladia glabra* lamina, craspedodromous alternates with brochidodromous veins) or directionally (e.g., *Gluta* and *Campnosperma* laminas are apically brochidodromous and basally eucamptodromous). Intercostal tertiary fabric is frequently random reticulate, polygonal-reticulate, mixed alternate-opposite, or opposite-percurrent. Intersecondary veins are frequently present, but the consistency varies in many taxa. Epimedial tertiaries are frequently present: they may be perpendicular to the primary vein, or varying from parallel to variously angled relative to the secondary veins. In several genera (e.g., *Abrahamia*, *Spondias*) the tertiary veins are admedially branched. A diagonally oriented, admedially branched, trunked tertiary is characteristic of several species of *Sorindeia* and *Buchanania*. In

*Comocladia*, the tertiary veins are perpendicular to the secondary veins in the intercostal region. In some Anacardiaceae (e.g., *Comocladia*, *Rhus*, *Toxicodendron*), the apparently blindly ramifying tertiary veins are interconnected by quaternary veins. Rarely (e.g., *Abrahamia*, *Rhus perrieri* (= *Baronia* or possibly segregate), *Melanococca*), the tertiaries are truly freely ramified (i.e., areoles absent). Marginal veins are rarely of secondary gauge (e.g., *Drimycarpus*, *Lithrea*). A fimbrial vein is typically present, and occasionally the marginal ultimate tertiary venation is looped (e.g., *Spondias bivenomarginalis*). Areoles vary from being clearly defined (e.g., *Anacardium*, *Tapirira*) to being highly variable in shape and pattern (e.g., *Spondias*). Freely ending veinlets (FEVs) are commonly highly branched (either dichotomously or dendritically) or rarely one- to two-branched. Sometimes the FEVs are terminated by highly branched sclereids (e.g., *Sorindeia*, *Spondias radlkoferi*). Some taxa are characterized by having FEVs terminated by prominent tracheoid idioblasts (e.g., *Comocladia*, *Harpephyllum*, *Melanococca*, *Pleiogynium*, *Spondias*). Terminology for leaf architecture is based on the *Manual of Leaf Architecture* (Leaf Architecture Working Group 1999) and subsequent revisions by the Leaf Architecture Working Group (Ellis et al. 2009).

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

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

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

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

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

Members of Anacardiaceae tend to have more condensed inflorescences as compared to Spondioideae. These are usually in the form of condensed panicles, thyrses, or thyrsoids, some being extremely condensed (e.g., *Blepharocarya*, *Laurophyllus*). The bracts subtending inflores-

cences may be very large (e.g., *Trichoscypha*), prominently foliose (e.g., *Anacardium*, *Dobinea*), condensed into a cupule in female flowers (*Blepharocarya*, *Laurophyllus*), or brightly colored (e.g. white to pink foliose bracts in *Anacardium spruceanum*). In some species there is a gradual transition from leaves to bracts subtending the terminal inflorescence (e.g., *Anacardium*, *Dobinea*, *Mauria*).

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

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

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

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

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

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

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

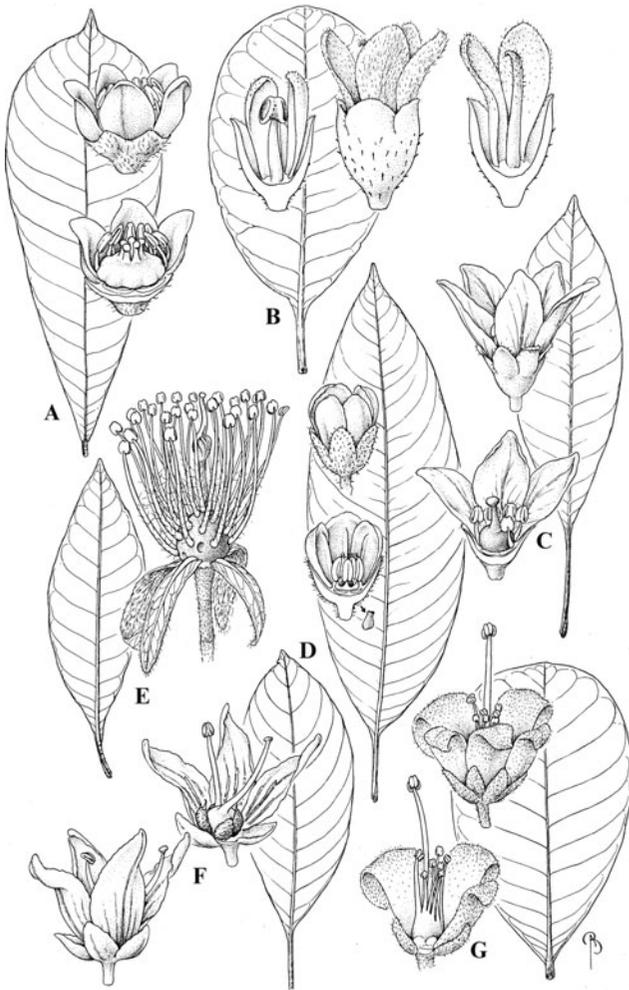


Fig. 3. Anacardiaceae. Flowers and leaves of selected genera. A *Buchanania sessifolia*. B *Fegimanra afzelii*. C *Swintonia acuta*. D *Bouea oppositifolia*. E *Gluta rugulosa*. F *Mangifera monandra*. G *Anacardium fruticosum*. (Reproduced with permission of the artist Bobbi Angell)

The ovule is solitary, anatropous or rarely campylotropous (*Semecarpus* in Bachelier and Endress 2009), apotropous (“syntropous” of Bachelier and Endress 2009), apical, lateral or basal, with dorsal or ventral raphe, crassinucellate, with one (e.g., *Anacardium*) or two either entirely or partially developed integuments (e.g., *Lannea*, *Pistacia*, *Rhus*, *Schinus*, *Toxicodendron*) (Geesink et al. 1981). The micropyle is formed by the inner integument, or by both, as in *Schinus molle*. The funicle is long, massive, and bent. A funicular obturator and a cup-like hypostase are present. In addition, a ponticulus (a

small bridge between the pollen tube track and the dorsal surface of the ovule) is present in all Anacardiaceae studied by Bachelier and Endress (2009). A nucellar cap of 2–4 cell layers is developed in *Anacardium*, *Lannea*, *Rhus*, *Schinus*, and *Toxicodendron* (Kelkar 1958a, 1958b; Copeland 1961; Grundwag and Fahn 1969; Aleksandrovski and Naumova 1985). The variations and details of ovule structure are summarized by Plisko (1996).

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

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

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

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

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

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

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

may explain their deviating morphology from the rest of the family.

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

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

canals, and often fiber bundles or sclerenchyma zones.

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

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

Seeds vary in size from 2 mm to more than 10 cm. They are generally ellipsoid, ovoid, falcate, lenticular, or reniform. Species of *Mangifera* have labyrinth seeds—the extreme form of rumination in which the seed coat deeply encroaches on the endosperm and embryo (Boesewinkel and Bouman 1984). The seed coat s.s. (derived from the integuments) is usually undifferentiated and/or reduced, while the chalaza is well developed and forms the greater part of the seed coat s.l.

Pachychalazal seeds with undifferentiated seed coat have been found in *Mangifera* and *Heeria*; partially pachychalazal seeds with some traces of lignification in the seed coat have been found in subfamily Spondioideae, *Camptosperma*, *Ozoroa*, *Pistacia*, and *Rhus*, and both types of seeds, some endotegmic, in subfamily Anacardioideae (von Teichman 1991). von Teichman (1991) suggested that the evolutionary trend of seeds within Anacardiaceae is from pachychalazal, to partially pachychalazal, and ultimately to seeds without extensive chalaza. The embryo of Anacardiaceae is oily, curved or straight, with two expanded cotyledons. Endosperm is scant.

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

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

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

**PHYTOCHEMISTRY AND TOXICITY.** Toxic compounds and other chemicals within members of Anacardiaceae have been widely investigated (see review in Aguilar-Ortigoza and Sosa 2004b). Several of these studies focused on the medicinal activity of phenolics (Corthout et al. 1994), esters (Corthout et al. 1992, Galvez et al. 1992), and tannins (Corthout et al. 1991; Galvez et al. 1991; Viana et al. 1997). Others have dealt with toxic components such as contact dermatitis-causing compounds (see Mitchell 1990 for a review; Rivero-Cruz et al. 1997; Drewes et al. 1998), and those responsible for causing nut allergies (Jansen et al. 1992; Fernandez et al. 1995).

Some of the compounds in Anacardiaceae have been shown to be defensive in function. These include antimicrobials (Saxena et al. 1994), and antifungal and/or insect- and herbivore-repelling compounds (Chen and Wiemer 1984; Cojocarú et al. 1986).

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

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

**TAXONOMY AND PHYLOGENY.** The family Anacardiaceae was first proposed by Lindley in 1830, but its members have been variously placed in other families including Blepharocaryaceae, Comocladaceae, Julianiaceae, Pistaciaceae,

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

In the first molecular investigation of Anacardiaceae, Terrazas (1994) used sequences of the chloroplast gene *rbcl*, together with data on morphology and wood anatomy to interpret the phylogeny of the family. Her combined *rbcl*-morphology phylogeny elucidated a monophyletic Anacardiaceae comprised of two groups. The first group, clade A2, contains Spondiaceae plus *Pentaspadon*, and is united by the morphological synapomorphy multicellular stalked glands on the leaves. The second group, clade A1, contains the remaining genera in the four other tribes, and is supported by the morphological and wood anatomical synapomorphies, unicellular stalked leaf glands and the presence of both septate and nonseptate fibers. Based on the combined phylogeny, Terrazas (1994) informally proposed splitting the family into two subfamilies, Anacardioidae and Spondioideae. Pell found a similar division of the family based on analysis

of three plastid genes, and described and circumscribed the two subfamilies (Pell 2004; Mitchell et al. 2006). This classification is followed herein, with the exception of the subfamilial placement of *Buchanania*: recent molecular data have helped resolve ambiguous morphological data, and suggest that this genus is a member of subfamily Spondioideae. It should be noted that recent, more extensively sampled analyses of cpDNA (*trnL*F and *rps16*) and nrDNA (ETS) data (Pell, unpublished data) indicate that subfamily Spondioideae (formerly recognized as tribe Spondiaceae) is polyphyletic. However, because the two subfamilies as circumscribed by Mitchell et al. (2006) are structurally recognizable, and formal subfamilial rankings have not yet been assigned to the newly resolved clades, the two-subfamily system is used here to divide the genera.

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

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

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

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

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

**PALEOBOTANY.** Anacardiaceae have rich fossil records because of their woody growth form, and past and current wide distribution. Anacardiaceae pollen and wood first appear in the Paleocene, 65 to 55 million years ago (Hsu 1983; Muller 1984), and are found throughout the world. Fossils occur mostly in the western United States south to Panama from the Eocene and Oligocene (Taylor 1990; Ramírez and Cevallos-Ferriz 2002).

Leaf fossil material of four species of *Rhus* and one putative species of *Cotinus* with its distinctive cladodromous secondary venation have been identified from the Eocene in the Florissant fossil beds of Colorado (Meyer 2003). Silicified wood fragments from the lower Miocene formations of central west Sardinia have been allied with *Sclerocarya birrea* (Biondi 1981). Many purported Anacardiaceae leaf and wood fossils have been determined to belong to taxa outside of the family, and many others are of dubious affinity.

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

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

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

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

Many Anacardiaceae species are also valued for their horticultural appeal. Specimens of *Cotinus*, *Harpophyllum*, *Lannea*, *Pistacia*, *Rhodospaera*, *Rhus*, *Schinus*, *Searsia*, *Smodingium*, and *Toxicodendron* are planted for their beautiful inflorescences, infructescences, evergreen foliage, and/or fall foliage. A few agricultural and horticultural species have escaped cultivation and become invasive in their non-native areas. Japanese wax tree, *Toxicodendron succedaneum*, is an Asian species that was originally cultivated in Brazil but escaped after introduction, and is now invasive. Brazilian pepper tree or pink

peppercorn, *Schinus terebinthifolia*, is another notoriously problematic species where it occurs in the Everglades of central and southern Florida, in the Hawaiian Islands, and various other parts of the subtropics and tropics (Gilman 1999; Mitchell 2004). More recently, *Pistacia chinensis* has become naturalized and invasive in Texas (McWilliams 1991).

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

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

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

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

#### KEY TO THE SUBFAMILIES

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

#### KEY TO THE GENERA OF ANACARDIOIDEAE

1. Leaves simple or unifoliolate 2
- Leaves compound 41
2. Leaves opposite 3

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

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