

# 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 stylodia 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 antesealous 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; stylodia 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 *Acereae* excepted); plants containing saponins in idioblasts but no bitter nortriterpenoids; leaves alternate or less often (*Acereae*, *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 antesealous; nectary disk intrastaminal; carpels (2)4–5+, more or less connate proximally and usually held together by the joined stylodia, 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 Benthham (in Benthham and Hooker 1862) and Engler (e.g., 1931), tended to treat Sapindales and Rurales (the latter sometimes as Geraniales) as distinct orders, a concept followed by Takhtajan (2009) to the present day; however, a wider ordinal concept with Rurales 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, Tetradielidaceae, 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

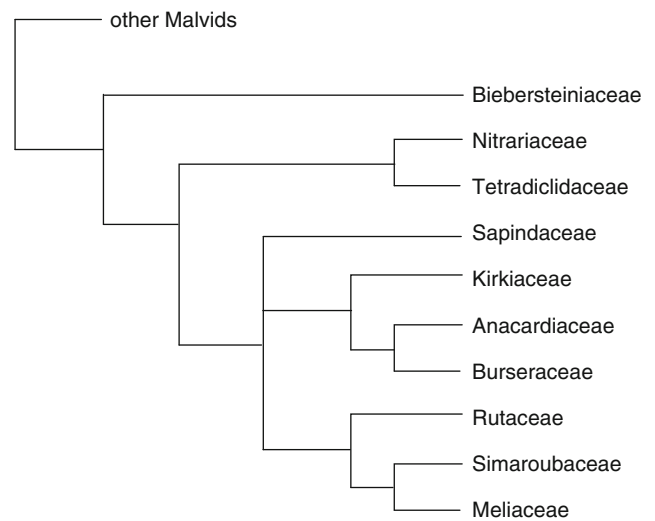


Fig. 1. Phylogenetic relationships of Sapindales families, based on *rbcL* sequence data from Muellner et al. (2007) and Sheahan and Chase (1996)

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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