

Introduction to the Groups Treated in this Volume

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Introduction to Berberidopsidales

1. Dioecious tree, young parts covered with ferruginous scales; leaves conduplicate, entire; flowers 5(6)-merous, enveloped in bud by firm calyprate bract; stamens 5, alternating with nectary glands; gynoecium 1-carpellate; ovules 2, pendulous from apex of locule; style apically bifid; fruit dry, indehiscent; seed with ruminant endosperm and embryo of about half the length of seed. 1/1, S Chile and adjacent Argentina

Aextoxicaceae

- Scandent shrubs, largely glabrous; leaves involute (*Berberidopsis*), spiny-toothed or entire; flowers hermaphrodite, acyclic and with disk, or cyclic, pentamerous and without disk; gynoecium 3-5-carpellate; ovules several to many, each on 3-5 placentas; style not bifid; fruit berry-like; embryo small. 2/3, S Chile and SE Australia

Berberidopsidaceae

A close relationship between Berberidopsidaceae and Aextoxicaceae has never been considered until gene sequence studies provided strong support for a relationship between them (see family treatments). In the four-gene analysis of eudicots (Soltis et al. 2003), Gunnerales and subsequently Berberidopsidales are sister to all other core eudicots, the latter being strongly supported by molecular data and isolated from all other clades (Fig. 1). *Aextoxicum* has long been known for its peculiar wood anatomy, particularly the high number of bars of the vessel element perforations. A recent study by Carlquist (2003) has revealed many important similarities in the wood anatomy of the two families, although these are plesiomorphic. Pollen grains are relatively small and tricolpate to indistinctly colpate. The two families share encycloctytic stomata (Soltis et al. 2005), a rare character in angiosperms, stout filaments, and a ring of vascular bundles in the petiole (Judd and Olmstead 2004).

Unfortunately, many important characters are not known for both taxa but available information shows that Berberidopsidales are very plastic in their floral structure, combining (even within the same family, Berberidopsidaceae) both spiral and whorled patterns, and 1-, 3- and 5-merous

gynoecia. The spiral sequence of initiation of floral organs in *Berberidopsis*, with a tendency of arrangement in alternating groups of five, may represent an incipient case of pentamery (Ronse DeCraene 2004) but this is problematic, in view of the firmly established pentamerous floral structure characteristic for core eudicots which exists in parts of Berberidopsidaceae and in the closely related *Aextoxicum* (see Berberidopsidaceae and Aextoxicaceae, this volume).

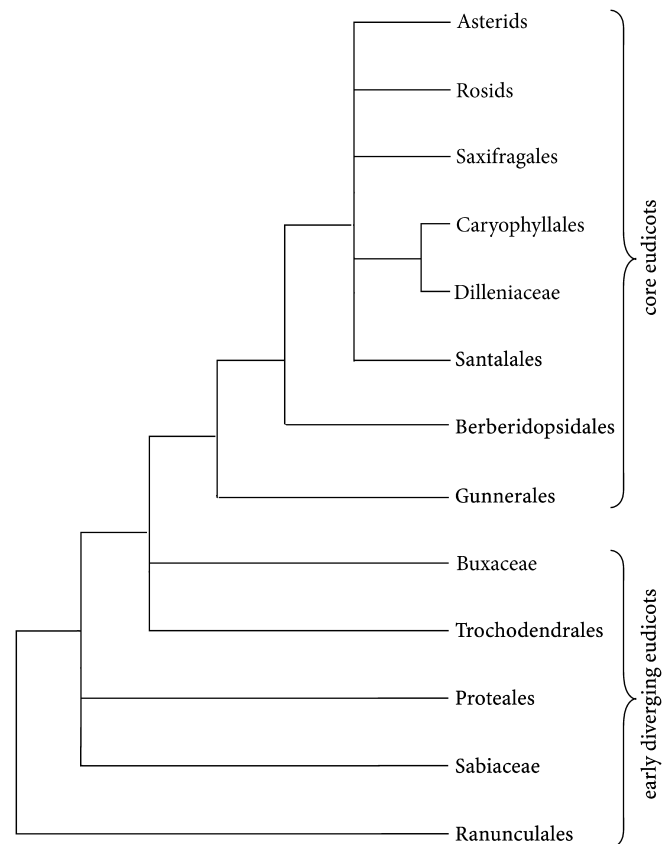


Fig. 1. A phylogenetic hypothesis of eudicot relationships, based on a four-gene dataset (Soltis et al. 2003)

Morphologically, basal eudicots exhibit considerable structural disjunctions, which underlines their relict nature. This is also corroborated by the remarkable angiospermous fossil from the Early Cretaceous, *Teixeira lusitanica*, which shows affinities to members of Ranunculales, and to Berberidopsidaceae, Hamamelidaceae and Daphniphyllaceae (von Balthazar et al. 2005). Characters such as the dimerous floral structure, known from *Gunnera*, and presumably plesiomorphic traits (decurrent stigmas, antepetalous stamens, etc.), known from other basal eudicot families such as Proteaceae and Sabiaceae, are not found in Berberidopsidales.

References

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- Ronse DeCraene, L.P. 2004. Floral development of *Berberidopsis corallina*: a crucial link in the evolution of flowers in the core eudicots. *Ann. Bot.* 94:741–751.
- Soltis, D.E. et al. 2003. See general references.
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Introduction to Buxales

1. Dioecious trees; flowers apetalous, male with one stamen pair, female often paired, a single carpel; pollen grains tricolpo-di-orate; seeds exalbuminous. 1/2, Madagascar **Didymelaceae**
- Monoecious, rarely dioecious shrubs or herbs; flowers with weakly differentiated perianth, male with decussate tepals and 4, 6 or more stamens, female with spiral tepals and a 2–4-carpellate, syncarpous gynoecium; pollen grains 3–7-colporate with 3–6 pores per colpus, or pantoporate; seeds albuminous. 5/c. 100, all continents, except Australia **Buxaceae**

Buxales comprise Buxaceae and Didymelaceae, grouped together by traits such as cyclocytic stomata, leaf venation pattern, wood anatomical peculiarities including many sclereids, racemose inflorescences, small, imperfect, often dimerous flowers with decurrent stigmas extending the entire length of the stylodia, stamens with more or less basifixed anthers and conspicuous connective anther protrusions, and the occurrence of very

peculiar steroidal pregnan alkaloids. The most obvious trait of Buxales is the plasticity and simplicity of perianth organisation. In some of their members (*Didymeles*, male *Styloceras*), a perianth is completely lacking and, in Buxaceae, the tepals hardly differ from vegetative bracts below the flower (von Balthazar and Endress 2002a) and in female flowers they are spirally arranged, making the delimitation of flowers difficult. The stamens are always antesealous and the stamen-sepalum complex of Buxaceae is similar to that of Proteaceae, also in the supply of the sepals by a single trace. Stamens, when occurring in low number, are arranged in dimerous whorls but, for higher numbers (in *Notobuxus* 6, 8, and up to more than 40), less regular arrangements prevail.

Palynologically, Buxales are highly diverse (Bessedik 1983; Doyle 1999). An early fossil attributable to Buxales (Doyle 1999) is a pollen from the Aptian/Albian of northern Gondwana, which has simple colpate apertures and a striate(-reticulate) sculpture and has been related to the buxaceous megafossil *Spanomera* (Drinnan et al. 1991). In the late Albian of Gabon and Brazil, the tricolpodiorate pollen *Hexaporotricolpites* (Boltenhagen 1967) appears. This pollen type may be related to extant *Didymeles* from Madagascar (cf. Fig. 36), which has left a fossil record in the southern Indian Ocean, Australia, New Zealand and New Caledonia. Similar pollen grains with an increasing number of pores and meridional colpi, later in pantocolporate and eventually pantoporate configuration, the latter combined with a crotonoid exine pattern (cf. Fig. 11D), appear both in the fossil record and in extant *Buxus* (Köhler 1981; Köhler and Brückner 1982; Bessedik 1983).

Buxales form part of the grade of early-diverging tricolpate(-derived) dicots or eudicots, which also comprises Ranunculales, Sabiaceae, Proteales and Trochodendraceae (cf. Fig. 1). With several early-diverging eudicots, and partly also with some basal core eudicots (Gunneraceae, Myrothamnaceae and some basal families of Saxifragales), Buxales share characters which are known also from the eumagnoliids. Particularly remarkable are the dimerous flowers, the supply of the sepals by a single trace, and the stamen-sepalum complex, in which Buxaceae agree with Proteaceae. Conspicuous connective protrusions are known from other early-diverging eudicots and some basal core eudicots, including Proteaceae, Platanaceae, Trochodendraceae, Myrothamnaceae; basifixed anthers are widespread in early-diverging

eudicots. Elongate stigmas decurrent in two crests are shared with Platanaceae, Myrothamnaceae and Trochodendraceae but are also found in some Saxifragales. Nectary disks are rare in early-diverging eudicots and, apart from the intrastylodial nectariferous structures in Buxaceae, are known only from Proteaceae and Sabiaceae.

References

Doyle, J.A. 1999. The rise of angiosperms as seen in the African Cretaceous pollen record. In: Heine, K. (ed.) *Palaeoecology of Africa and the surrounding islands*. Rotterdam: Balkema, pp. 3–29.

For other references, see the selected bibliographies of Buxaceae and Didymelaceae, and the General References (this volume).

Introduction to the Clusiaceae Alliance (Malpighiales)

1. Annual cataract-dwellers with unclear differentiation of stems, roots and leaves (roots often crustaceous, ribbon-like; leaves sometimes terminal and double-sheathed); fertile pollen and fertilisable embryo sacs developed underwater; [pollination autogamous or cleistogamous, rarely allogamous; female gametophyte reduced Allium type; no double fertilisation and no endosperm; seed set high]. 49/c. 280, worldwide, tropical and warm-temperate regions **Podostemaceae**
 - Woody or herbaceous land plants 2
2. Leaves alternate, serrulate, initially setulose, convolute; latex 0; stamen connective glands 0; capsule with persistent column. 3/40, northern South America, West Indies, and SE Asia to New Guinea **Bonnetiaceae**
 - Leaves opposite or alternate, entire, not setulose, not convolute; latex often present in glands or secretory canals; stamen connectives often with glands producing oil or resin; fruit, if capsular, then rarely with persistent column 3
3. Stylodia free, at least distally; flowers perfect; sepals and petals 3–5; aril 0; trichomes, if multicellular, then stellate; woody or herbaceous. 9/540, worldwide **Hypericaceae**
 - Stylodia free or fused to form a simple style; flowers perfect or unisexual; sepals 2–20, petals 0–8; aril sometimes present; stellate hairs very rare (*Caraipa*, *Marila*); woody. 27/1090, pantropical **Clusiaceae**

Although these families have been intensely studied by generations of botanists, recent work has considerably modified our understanding of their phylogenetic relationships and details of their family and tribal delimitation. Molecular studies have revealed one enigma of long standing – the systematic position of Podostemaceae. Their close relationship with Clusiaceae s.l. (i.e. including Hypericaceae) is

now well established (Soltis et al. 2000; Savolainen, Fay et al. 2000), and Podostemaceae appear sister to Hypericaceae or perhaps nested inside this family (Gustafsson et al. 2002). As the sinking of Podostemaceae in the broadly delimited Clusiaceae would lead to a highly heterogeneous unit, it appears preferable to “save” an independent family Podostemaceae by segregating Hypericaceae from Clusiaceae s.l., following the approach of many earlier authors such as Takhtajan (1997), although the separation in terms of contrasting characters between the latter two is not very strong. Characters common to the three families include resin cells and secretory ducts, containing xanthonenes, and bitegmic and tenuinucellate ovules.

References

For references, see the Selected Bibliography of Clusiaceae-Guttiferae and the General References (this volume).

Introduction to Crossosomatales

1. Perianth biseriolate 2
 - Perianth uniseriate; [flowers solitary] 6
2. Leaves opposite, pinnately compound, rarely unifoliate; embryo green; [ovary syncarpous or apocarpous; ovules anatropous]. 2/40–50, temperate to tropical regions, mainly of the northern hemisphere **Staphyleaceae**
 - Leaves alternate, simple (if opposite and simple to slightly trilobate and gynoeceium apocarpous, see *Apacheria* in Crossosomataceae); embryo achlorophyllous 3
3. Flowers solitary 4
 - Flowers in panicles, racemes or spikes 5
4. Sepals 4–10; stamens 5 + 5; anthers dorsifixed; pistil 4–7-carpellate; style simple; ovules 1 per locule, anatropous; fruit indehiscent, fibrous; seed with rudimentary aril; embryo straight; vessel element perforation scalariform; T-shaped unicellular trichomes present. 1/1, New Caledonia **Strasburgeriaceae**
 - Sepals (3)4–5(6); stamens 4–50 (flower haplostemonous, diplostemonous or polystemonous); anthers basifixed; gynoeceium apocarpous, 1–5(–9)-carpellate; ovules 1–many per carpel, campylotropous; fruit follicular; seed arillate; embryo curved; vessel element perforation mostly simple; T-shaped trichomes 0. 4/10, North America, with Mexico **Crossosomataceae**
5. Flowers strictly 5-merous; ovules 2 per locule; pollen 4(5)-colporate; fruit capsular; aril rudimentary; vessel element perforation scalariform; T-shaped unicellular trichomes present. 1/1, New Zealand **Ixerbaceae**
 - Flowers strictly 4-merous; ovules many per locule; pollen 3-colporate; fruit berry-like; seed with soft

funicular aril; vessel element perforation simple; T-shaped trichomes 0. 1/c. 16, E Asia **Stachyuraceae**
 6. Leaves decussate, entire; tepals 4; stamens 4 + 4; anthers dorsifixed; ovary 4-locular, with 4 twisted stylopodia; ovules anatropous; fruit capsular; seeds with swollen funicle; embryo straight; T-shaped unicellular trichomes present. 1/1, South Africa

Geissolomataceae

- Leaves alternate, serrate; tepals 4–5(6); stamens many; anthers basifixed; ovary unilocular; style simple; ovules campylotropous; fruit a berry; seeds arillate, incurved with hippocrepiform embryo. 1/1, E and southern Africa, islands of Indian Ocean **Aphloiaceae**

Until very recently, these apparently disparate families had been placed in different rosoid orders and some had been “dumped” in larger families such as the broadly construed Saxifragaceae (*Ixerba*) or Flacourtiaceae (*Aphloia*). The taxonomic history of the individual families is briefly described in the family treatments, and has been treated in more depth by Matthews and Endress (2005). Although Takhtajan (1987) for the first time used the name of the order Crossosomatales which, in his approach, comprised only the name-giving family, a broader concept of the order was not achievable in the pre-molecular era largely because the characters traditionally used in higher-level classification are very variable in these seven families (see *Conspectus*).

During recent years, several molecular studies have contributed to the recognition of the relationships in the entourage of Crossosomataceae. In their *rbcL* and combined morphological and *rbcL* studies, Nandi et al. (1998) found a clade of $\{[(\textit{Crossosoma} + \textit{Stachyurus}) \textit{Staphylea}] \textit{Geissoloma}\}$, albeit without significant support. Strong support for $[(\textit{Crossosoma} + \textit{Stachyurus}) \textit{Staphylea}]$ was adduced by further *rbcL* studies (Savolainen, Fay et al. 2000; Sosa and Chase 2003) and multi-gene analyses (Soltis et al. 2000; Cameron 2003), and for *Ixerba* + *Strasburgeria* by *rbcL* (Savolainen, Fay et al. 2000; Sosa and Chase 2003) and multi-gene studies (Cameron 2003). When included in the analysis, *Ixerba* + *Strasburgeria*, *Aphloia* and *Geissoloma* usually appeared in the same clade as *Crossosoma*, *Stachyurus* and *Staphylea*, although statistical support for this was low. The concept of Crossosomatales proposed by Savolainen, Fay et al. (2000) and Soltis et al. (2000), comprising Crossosomataceae, Stachyuraceae and Staphyleaceae, has later been extended to include all seven aforementioned families (see also Stevens 2005). This concept is now confirmed by the broad-based comparative study of Matthews and Endress (2005), which has revealed structural traits, particularly previ-

ously neglected floral characters, which are shared in different constellations by groups of two, three or more families of the whole alliance.

The group as a whole is only weakly characterised. Stomata are usually anomocytic. Leaf margins are usually toothed. Stipules are lacking only in Ixerbaceae and some Crossosomataceae. Vessel elements have scalariform perforation, Crossosomataceae and Stachyuraceae excepted. Sepal and petal aestivation is imbricate throughout, and stamens are always incurved in bud; anthers are tetrasporangiate; nectary disks are present. Ovules are bitegmic and crassinucellar, mostly anatropous; Aphloiaceae and Crossosomataceae have campylotropous ovules. Pollen grains are colpate and usually have lalongate endoapertures; the gynoeceum is often stalked; the carpel tips are often postgenitally united to form a compitum. The seed coat is testal. Sieve element plastids are S type throughout. Ellagitannins and gallotannins, but no proanthocyanidins, are known from Crossosomataceae. More restricted are the following traits. Ixerbaceae and Strasburgeriaceae have large flowers with petals forming a tight, pointed cone in bud, stamens with sagittate anthers, and a rudimentary aril. These families share with Geissolomataceae T-shaped unicellular trichomes and a punctiform stigma on postgenitally united and twisted carpel tips, and only one or two ovules per carpel. Aphloiaceae, Geissolomataceae, Ixerbaceae and Strasburgeriaceae share pollen grains with pronounced protruding endoapertures (“pollen buds”). Crossosomataceae, Stachyuraceae and Staphyleaceae have polygamous or functionally unisexual flowers, and Crossosomataceae and Aphloiaceae (although not resolved as sisters in molecular studies) share polyandrous flowers, basifixed anthers, a stigma with two or more decurrent crests, campylotropous ovules and reniform seeds (data from Matthews and Endress 2005).

Crossosomatales are core eudicots but otherwise their relationships are still unclear: they appear at the base of eurosids II (Savolainen, Fay et al. 2000; Soltis et al. 2000) or eurosids I (Hilu et al. 2003), or in a polytomy with Geraniales, Myrtales, eurosids I and eurosids II (APG II 2003), but always with low statistical support.

References

For references, see the General References (this volume).

Introduction to Fabales

1. Stylodia gynobasic; [woody; flowers regular; gynoecium apocarpous, 1–5-carpellate; ovule unitegmic (only *Suriana* known); endosperm 0 or sparse; nectary only rarely present; vestured pits in *Recchia*]. 5/8, in warm-temperate and tropical regions, widely distributed
Surianaceae
– Style or stylodia not gynobasic 2
2. Gynoecium syncarpous, 2–8-carpellate (sometimes 1-locular); pollen grains 7–28-colporate; seeds mainly endotestal; leaves estipulate; [woody or herbaceous; nodes unilacunar with a single trace; vessel element perforations usually simple; vestured pits sometimes present; flowers actinomorphic to zygomorphic; nectary a disk, a gland, or 0; seeds often arillate]. $n = 6–23$. 21/800–1,000, widely distributed in tropical, subtropical and temperate regions
Polygalaceae
– Gynoecium (nearly) apocarpous; pollen grains mostly 3-aperturate; seeds exotestal; leaves stipulate; [nectariferous disk usually present] 3
3. Flowers strictly actinomorphic; carpels 5, only basally connate; pollen grains in monads; seeds exarillate; endosperm thin; cotyledons convolute; stipules small; nodes unilacunar; vessel elements with simple and scalariform perforation; vestured pits 0; [woody; bark strongly saponiferous]. $n = 14$. 1/2, warm-temperate southern South America
Quillajaceae
– Flowers actinomorphic to zygomorphic; carpel usually 1 or very rarely more (and then each carpel with a terminal stylodium); pollen grains in monads, tetrads or polyads; seeds arillate or not; endosperm usually 0, rarely sparse or even copious; stipules sometimes modified into prickles or spines; nodes tri-(penta-)lacunar; vessel elements with simple perforations, the lateral pits often vestured; [roots very often with N-fixing root nodules]. 640/1800, widely distributed throughout the world
Leguminosae–Fabaceae s.l. (not treated in this volume)

A clade comprising these four families was resolved as belonging to eurosoids I by early molecular studies (Chase et al. 1993; Fernando et al. 1993; Morgan et al. 1994) and is strongly supported in several multigene analyses (e.g. Soltis et al. 1999, 2000). Morphologically, the four families have little in common, apart from the basically core eudicot floral organisation. Stevens (2005) notes green embryos and often fluorescent wood, and absence of ellagitannins (which are, however, present in Leguminosae) as common traits.

References

- Chase, M.W. et al. 1993. See general references.
Fernando, E.S. et al. 1993. See selected bibliography of Surianaceae.
Morgan, D.R. et al. 1994. See selected bibliography of Quillajaceae.

Soltis, P.S., Soltis, D.E., Chase, M.W. 1999. Angiosperm phylogeny inferred from multiple genes as a tool for comparative biology. *Nature* 402:402–404.

Soltis, D.E. et al. 2000. See general references.

Stevens, P.F. 2005. See general references.

Introduction to Geraniales

1. Embryo small, straight, achlorophyllous; endosperm copious; secondary xylem always with rays; [either (sub)shrubs or small trees with mostly 5-merous flowers and simple leaves and regular flowers (*Greyia*), or with pinnate leaves and \pm zygomorphic flowers (*Melianthus*, *Bersama*), or herbs with mostly 4-merous flowers and commissural stigmas (*Francoa*, *Tetilla*)]. 5/19, subsaharan Africa, southern South America
Meliantaceae
– Embryo large, circinate, twisted, or cochlear, rarely (*Rhynchotheca*) straight, chlorophyllous; endosperm usually scant; secondary xylem often rayless 2
2. Pollen grains tricolp(or)ate; style elongate, with 5 style branches or (*Hypseocharis*) unbranched with capitate stigma; fruits schizocarpic with 1-seeded awned mericarps or (*Hypseocharis*) loculicidal capsules; seed coat with crystalliferous endotesta and thickened but not lignified exotegmen. 5/c. 835, nearly worldwide
Geraniaceae
– Pollen grains pantoporate or inaperturate; style very short, with 5–3 elongate stigmatic branches; fruits septicidal or septifragous capsules with 1–many-seeded locules; seed coat usually lacking mechanical layers (*Viviania*, exotegmic); *Balbisia* with mucilaginous exotesta. 4/c. 18, South America, mostly Andean
Ledocarpaceae

The former, broadly construed concept of the order Geraniales (e.g. Engler 1892) comprised 15–20 families including disparate groups such as Oxalidaceae, Tropaeolaceae, Zygophyllaceae, Rutaceae and Euphorbiaceae. Based on the work of many authors, notably Takhtajan (e.g. 1959, 1987) and Dahlgren (e.g. 1980), Geraniales were stepwise restricted by the exclusion of orders such as Rurales, Polygalales and Malpighiales. Yet, in a still more recent survey of dicotyledon families, Thorne (2001) merged Geraniales with Linales (= Malpighiales), mainly on account of these sharing a tendency for obdiplostemonous flowers with 10–15 stamens and a 5-partite gynoecium. It is difficult to understand why Oxalidaceae, for instance, were for so long considered to belong to Geraniales, although the former differ in possessing traits such as free stylodia, abundant endosperm, and capsular fruits (see treatment of Oxalidales in Vol. VI of this series).

In the pioneering molecular studies of Price and Palmer (1993), Morgan and Soltis (1993) and