# Introduction to the Groups Treated in this Volume

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## Introduction to Berberidopsidales

1. Dioecious tree, young parts covered with ferrugineous scales; leaves conduplicate, entire; flowers 5(6)-merous, enveloped in bud by firm calyptrate 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 ruminate 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 colporate. The two families share encyclocytic 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, Berberidospidaceae) 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).

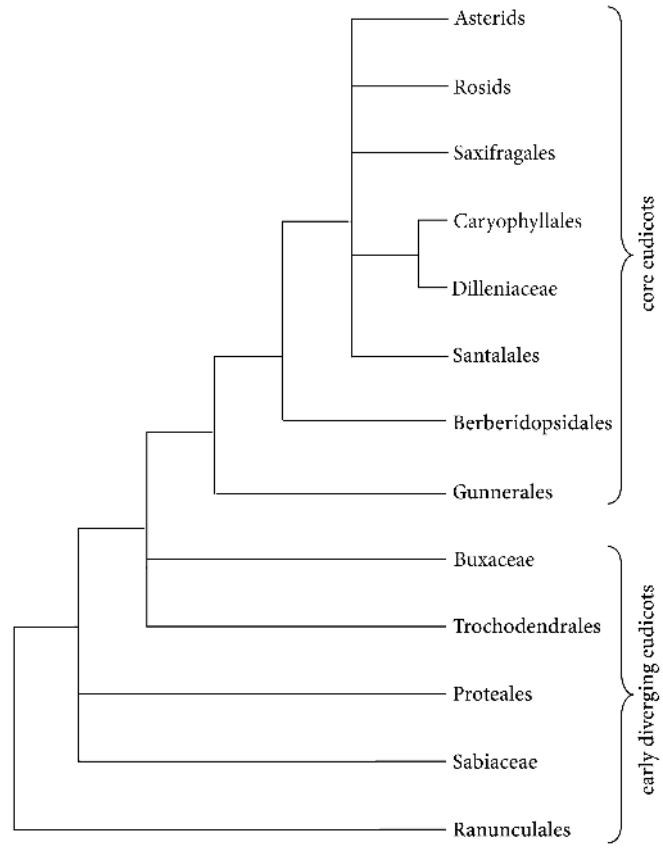


**Fig. 1.** A phylogenetic hypothesis of eudicot relationships, based on a four-gene dataset (Soltis et al. 2003)

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

Balthazar, M. von, Pedersen, K.R., Friis, M.E. 2005. *Teixeira lusitanica*, a new fossil flower from the Early Cretaceous of Portugal with affinities to Ranunculales. Pl. Syst. Evol. 255:55–75.

Carlquist, S. 2003. Wood anatomy of Aextoxicaceae and Berberidopsidaceae is compatible with their inclusion in Berberidopsidales. Syst. Bot. 28:317–325.

Judd, W.S., Olmstead, R.G. 2004. A survey of tricolpate (eudicot) phylogenetic relationships. Amer. J. Bot. 91:1627–1644.

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.

Soltis, D.E. et al. 2005. See general references.

## 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 antesepalous 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