THE FAMILIES
AND GENERA
OF VASCULAR PLANTS

Edited by K. Kubitzki
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**Volume VIII**  
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The Families and Genera of Vascular Plants

Edited by K. Kubitzki

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With 174 Figures

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The present volume contains treatments of various eudicot orders which all are strongly supported in molecular analyses. A first group comprises Proteales, Buxales and the enigmatic Sabiaceae which, together with Ranunculales and Trochodendrales, treated earlier in Vol. II of this series, represent the basal grade of early-diverging eudicots. Although all of them have clearly tri-orate pollen, making them eudicots, they otherwise lack the strict eudicot floral organisation, particularly with regard to flower merosity, phyllotaxis and perianth structure. The same is true for the order Gunnerales which, however, according to findings of molecular systematics, forms part of the strongly supported core eudicots. All these orders to some extent bridge the morphological gap between basal angiosperms and typical core eudicots. Plesiomorphic floral traits, although less pronounced, are also found among the isolated but clearly core eudicotyledonous Saxifragales, treated in this volume, and particularly in the early-diverging woody families of this order. Some of these latter families were included in Vol. II, which followed a classification used prior to the discovery of the modern concept of Saxifragales. The exact interrelationships among the early-diverging eudicot orders still remain largely unresolved. This is even more true for many of the core eudicot orders included in the present volume, i.e. Vitales, Crossosomatales, Geraniales, Zygophyllales and Myrtales, and also for two of the families not assigned to order, i.e. Huaceae and Picramniaceae. A possible relationship between Dilleniacae and woody Caryophyllales, as suggested by recent studies, opens an interesting new perspective on the evolution of this family.

Included in this volume are two subclades of the vast Malpighiales. These are Passifloraceae with two satellite families, and Clusiaceae/Hypericaceae with Podostemaceae, which recently have been identified as very close relatives.

My deep thanks go to all authors of this volume, who have provided such highly interesting and scholarly contributions, and to all those who have freely shared additional information and/or have commented on earlier drafts of the contributions. These include B.G. Briggs, T. Clifford, G. Jordan, B. Makinson, P. Olde, R. Barker, J.A. Doyle, P.J. Rudall and C.A. Furness (Proteaceae); H. Manitz (Aphanopetalaceae); A.E. Orchard (Haloragaceae); P.H. Linder and M. Weigend (Geraniales); A. Bernhard and W.J.O. de Wilde (Passifloraceae); the late M. Ricardi S. (Malesherbiaceae); I. Jäger-Zürn and T. Philbrick (Podostemaceae); and S. Renner, P.G. Wilson and J. Schönenerberger (Myrtales). I am also grateful to M.L. Matthews and P.K. Endress for showing me their papers prior to publication elsewhere. Mark C. Chase is thanked for always making available the newest results of his pathbreaking studies. The copyright holders of the illustrations included in this volume are thanked for their generous permission to use their valuable material. As always, it is a pleasure to acknowledge the agreeable collaboration with the staff of Springer-Verlag, who kindly responded to all requests I had in connection with the production of this volume, and to thank Monique T. Delafontaine for her meticulous copy editing of the manuscript.

Hamburg, September 2006

K. Kubitzki
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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 calyptate 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, pentameros 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, 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 pentameros 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 relic 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 (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**


**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 pantporate; 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 (*Didymelas*, 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 *Didymelas* from Madagascar (cf. Fig. 11D), 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


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 under water; [pollination autogamous or cleistogamous, rarely allogamous; female gamophyte 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, Marilia); 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 xanthones, and bitemgic and tenuinucellate ovules.

References

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

Introduction to Crossosomatales

1. Perianth biseriate
   - Perianth uniseriate; [flowers solitary] 2

2. Leaves opposite, pinnately compound, rarely unifoliolate; embryonic green; [ovary syncarpous or apocarpous; ovules anatropous]. 2/40–50, temperate to tropical regions, mainly of the northern hemisphere Strasburgeriaceae
   - Leaves alternate, simple (if opposite and simple to slightly trilobate and gynoecium apocarpous, see Apacheria in Crossosomataceae); embryo achlorophyllous 3

3. Flowers solitary
   - Flowers in panicles, racemes or spikes 4

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 Ixerbaceae
   - Sepals (3)4–5(6); stamens 4–50 (flower haplostemonous, diplostemonous or polystemonous); anthers basifixed; gynoecium apocarpous, 1–5(–9)-carpellate; ovules 1–many per carpel, campylotropous; fruit foliaceous; seed arillate; embryo curved; vessel element perforation mostly simple; T-shaped trichomes 0. 4/10, North America, with Mexico Crossosomataceae
   - Flowers strictly 4-merous; ovules many per locule; pollen 4(-5)-colporate; fruit capsular; aril rudimentary; vessel element perforation scalariform; T-shaped unicellular trichomes present. 1/1, New Zealand Strasburgeriaceae
   - 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 stylodia; 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 unicocular; style simple; ovules campylotropous; fruit a berry; seeds arillate, incurved with hippocrepiform embryo. 1/1, E and southern Africa, islands of Indian Ocean. **Aphloiacae**

Until very recently, these apparently disparate families had been placed in different rosid orders and some had been “dumped” in larger families such as the broadly construed Saxifragaceae (**Ixerba** or Flacourtiaceae) 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 {[(Crossosoma + Stachyurus) Staphylea] Geissoloma}, albeit without significant support. Strong support for [(Crossosoma + Stachyurus) Staphylea] was adduced by further *rbcL* studies (Savolainen, Fay et al. 2000; Sosa and Chase 2003) and multigene analyses (Soltis et al. 2000; Cameron 2003), and for *Ixerba + Strasburgeria* by *rbcL* (Savolainen, Fay et al. 2000; Sosa and Chase 2003) and multigene 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 previously 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 Ixerbaeaceae 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; Aphloiacaeae and Crossosomataceae have campylotropous ovules. Pollen grains are colporate and usually have lalongate endoapertures; the gynoecium 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. Ixerbaeaceae 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. Aphloiacaeae, Geissolomataceae, Ixerbaeaceae and Strasburgeriaceae share pollen grains with pronounced protruding endoapertures (“pollen buds”). Crossosomataceae, Stachyuraceae and Staphyleaceae have polygamous or functionally unisexual flowers, and Crossosomataceae and Aphloiacaeae (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 *Surianna* known); endosperm 0 or sparse; nectary only rarely present; vented pits in *Recchiah*]. S/8, in warm-temperate and tropical regions, widely distributed

   Surianaceae

   - Style or stylodia not gynobasic

2. Gynoecium syncarpous, 2–8-carpellate (sometimes 1-locular); pollen grains 7–28-colporate; seeds mainly endotetral; leaves stipulate; [woody or herbaceous; nodes unilacunar with a single trace; vessel element perforations usually simple; vented 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 exotetral; leaves stipulate; [NECTARIFEROUS disk usually present]

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; vented 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 vented; [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 eudicots 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 ellagittannins (which are, however, present in Leguminosae) as common traits.

Introduction to Geraniales

1. Embryo small, straight, aehlorophyllous; 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 ± zygomorphic flowers (*Melianthus, Bursara*), or herbs with mostly 4-merous flowers and commissural stigmas (*Francoa, Tetilla*)]. $n = 19$, subsaharan Africa, southern South America

   Melianthaceae

   - Embryo large, circinate, twisted, or cochlear, rarely (*Rhynchotheca*) straight, chlorophyllous; endosperm usually scant; secondary xylem often rayless

2. Pollen grains tricolporate or inaperturate; style elongate, with 5 style branches or (*Hyposocaris*) unbranched with capitulate stigma; fruits schizocarpic with 1-seeded awned mericarps or (*Hyposocharis*) loculicidal capsules; seed coat with crystaliferous endotesta and thickened but not lignified exotegmen. $c = 800$, nearly worldwide

   Geraniaceae

   - Pollen grains pantoporate or inaperturate; style very short, with 5–3 elongate stigmatic branches; fruits septical or septifragous capsules with 1–many-seeded locules; seed coat usually lacking mechanical layers (*Viviania*, exotegmic); *Balbisia* with mucilaginous exotesta. 4/16, South America, mostly Andean

   Ledocarpaece

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 Rutales, 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

References


Fernando, E.S. et al. 1993. See selected bibliography of Suri-

Morgan, D.R. et al. 1994. See selected bibliography of Quil-


Stevens, P.F. 2005. See general references.
Chase et al. (1993), the five genera of Geraniaceae s.str. grouped with Hypseocharis and, in some analyses, also with Viviania, Greyia and Francoa, and often also with Crossosoma, whereas other families of the erstwhile Geraniales were clearly excluded. More recent molecular work (Soltis et al. 2000; Savolainen, Fay et al. 2000; Sosa and Chase 2003) has resolved Geraniales and Crossosomatales (see treatment in this volume) as sister groups placed at the base of eurasiid II orders, but the statistical support is tenuous and the Angiosperm Phylogeny Group (APG II 2003) lists both orders among the unresolved rosids. Evidence for a sister group relationship of Melianthaceae and Ledocarpaceae and, in turn, of both of these with Geraniaceae is provided by the rbcL analyses of Savolainen, Fay et al. (2000) and Sosa and Chase (2003). This is notable, as morphologically Ledocarpaceae and Geraniaceae seem to have more in common than any of them have with Melianthaceae (see below). Support is also strong for recognising Melianthaceae and Geraniaceae in the circumscription adopted in this volume but it is less strong for the morphologically more diverse Ledocarpaceae.

Biebersteinia, a Eurasian monotype which often had been related to Geraniaceae (e.g. Knuth 1931), agreeing with this family in some details of fruit and seed morphology (Boesewinkel 1988), in molecular studies is resolved as sapindalean (APG II 2003).

A morphological characterisation of Geraniales is difficult because the genera of Melianthaceae and, less so, of Ledocarpaceae are diverse. It is true that all Geraniales have anomocytic stomata, vessels with simple perforation, 5- or 4-merous hypogynous flowers with a persistent calyx, and either haplosteremonous or more often obdiplostemonous androecia with paired antepetalous stamens, 5–3–carpellate syncarpous gynoecia with simple styles (extremely short in Balbisia) terminating in 3–5 stigmatic lobes or branches, axile or rarely basal placentation, anatropous to campylotropous bitegmic and crassinucellar ovules and, where known, a Polygonum type embryo sac and Nuclear endosperm. All Melianthaceae have copious endosperm, and Melianthus, Bersama and Greyia share multilacunar nodes. Francoa and Tetilla, formerly included in Saxifragaceae, differ from this family in the commissural stigma, the 4-merous flowers, Nuclear endosperm and the lack of myricetin. Otherwise, multilacunar nodes are not known in Geraniales, and the endosperm is absent or scanty in Geraniaceae. Ledocarpaceae and Geraniaceae agree, however, in numerous traits, such as rayless wood, acuminate to awned sepals, broadened filaments and sometimes basal nectariferous appendages, tanniniferous seed coats, green embryos and (Rhynchotheca excepted) curved or cochlear embryos. Differences between the two families exist in growth habit, pollen morphology and seed coat anatomy (Boesewinkel 1997).

Anthecologically, Geraniales families are diversified. Nectaries are present in all families, and Geraniaceae depend on a broad variety of insect groups as pollinators and only occasionally on bird, whereas Melianthaceae rely strongly on bird pollination. In Ledocarpaceae, Viviania produces copious nectar as reward for insect and other pollinators whereas the remaining genera, Balbisia and Rhynchotheca, lack nectaries. Balbisia has pollen flowers, and its showy corolla indicates that it is also zoophilous; one species, B. gracilis, may be anemophilous. Rhynchotheca has apetalous flowers with large, pendulous anthers and shows synchronous mass-flowering, all indicative of anemophily (Weigend 2005). Thus, the morphological disparity of Ledocarpaceae appears to be related to their range of pollination syndromes, which may explain the difficulties morphological workers had in recognising the circumscription and affinities of the family.

Phytochemically, Geraniales are characterised by the typical presence of ellagitannins; ellagic acid has been recorded from all genera (Tetilla not studied); gallotannins are also present in Geraniaceae, and geraniin, an ellagitannin based on dehydroxyhexahydroxydiphenic acid, is a prominent compound in Geranium. Proanthocyanidins are uniformly lacking from aerial parts but occur in seed coats and are recorded also from the rootstocks of Geraniaceae. Other biodynamic compounds include the bufodienolides and pentacyclic triterpenoids in Melianthaceae (Hegnauer 1969, 1989).

References

APG II 2003. See general references.


Takhtajan, A. 1997. See general references.


Takhtajan, A. 1987. See general references.


Introduction to Gunnerales

1. Poikilohydric shrubs; nodes trilacunar; axial parenchyma 0; rays uniseriate; leaves opposite; flowers unisexual, hypogynous; perianth of up to 4 scales; stamens 3–8; ovary 3-4-locular; stylodia 3–4, broad, recurved, with ventrally decurrent stigma; pollen in tetrads; embryo sac Allium type (bisporic, 8-celled); fruit a septical capsule; sieve-element plastids S type. 1/2, E and South Africa, Madagascar

Myrothamnaceae (see Vol. II)

Perennial herbs, often giant and nearly acaulescent, with endosymbiotic Nostoc cells; nodes multilacunar; vascular system nearly always polystelic; leaves alternate; flowers epigynous, 2-merous; ovary 1-locular; stylodia subulate; pollen in monads; embryo sac Peperomia type (tetrasporic, 16-celled); stylodia 2; fruit a drupe; ellagitanins present; sieve-element plastids Pcf type. 1/c. 60, mainly in southern hemisphere

Gunneraceae

Traditionally, Gunneraceae were included in Haloragaceae; Takhtajan (1997) placed them in Saxifraganae. Numerous molecular studies recovered the family in close association with the desert shrub Myrothamnus at the base of core eudicots, where they form a strongly supported clade. There is also evidence for the position of this clade as sister to all remaining core eudicots (cf. Fig. 1), a grouping indicated in various analyses and strongly supported particularly by Soltis et al. (2000, 2003) and Hilu et al. (2003).

Gunnera very probably has dimerous flowers and the same may apply to Myrothamnus (see Conspicetus). Dimery is not only widespread in early-diverging eudicots such as Proteaceae and many Ranunculaceae but usually also co-occurs with trimerism in basal angiosperms (Kubitzki 1987) or even with pentamery in early-diverging eudicots (Soltis et al. 2003). This is not seen in character reconstructions if only a single exemplar per family is included in a tree, as in the reconstruction of perianth merosity in Fig. 3 of Soltis et al. (2003). Indeed, both in basal angiosperms and early-diverging eudicots, there is pronounced variation in floral merosity, and the stereotyped pentameric floral structure with diplostemony or haplostemony occurs only above the node to Gunnerales. Thus, in Ranunculaceae, pentamery, where it occurs, is restricted to the perianth and, in pentamerosus Sabia (Sabiaeae), the sepals, petals and stamens stand on the same radius, a clear violation of Hofmeister’s rule but quite common in “basal” eudicots, as in Gunnera itself (see also Doust and Stevens 2005). Yet, following the node to Gunnerales, the typical pentamerosus eudicot pattern is strictly conserved, and further variation is limited to processes such as fusion, reduction and multiplication of stamens and/or carpels and of perianth parts. Gunnerales, although forming part of the core eudicot clade, have not achieved (or have lost?) the pentamerosus pattern, but agree with many core eudicots in possessing potent allelochemicals based on ellagic acid.

References


Takhtajan, A. 1997. See general references.

Introduction to Myrtales

1. Ovary unilocular with apical placentation, inferior (half-inferior in Strephanema); indumentum almost always of slender, unicellular, thick-walled, pointed hairs with a distinctive basal compartment; inflorescences indeterminate; [stamen whorls 1 or 2, the
outer sometimes with 2 or 3 times the normal number of stamens; pseudocolpi + (0 in Strephonema); intrastaminal disk often +; fruit 1-seeded, a drupe, usually flattened, ridged and/or winged; cotyledons twisted (massive and hemispheric in Strephonema)]. 14/500, pantropical

**Convallariaceae**

- Ovary usually multifloral with axile placentation, more or less inferior; fruit 1-many-seeded, usually a capsule or berry; indumentum various but not as above

**Combretaceae**

- Leaves with secretory cavities usually containing essential oils (0 in Psiloxylon), spirally arranged or opposite; pollen oblate, breviloquent, lacking pseudocolpi; style base often sunken in apex of gynoecium 3
- Leaves lacking secretory cavities, not aromatic; pollen often with pseudocolpi; style base generally not sunken (sunken in some Vochysiaceae) 4

3. Dioecious; leaves spiral; stamens ≥ 2. Leaves with secretory cavities usually containing essential oils (0 in Psiloxylon), spirally arranged or opposite; pollen oblate, breviloquent, lacking pseudocolpi; style base often sunken in apex of gynoecium 3
- Leaves lacking secretory cavities, not aromatic; pollen often with pseudocolpi; style base generally not sunken (sunken in some Vochysiaceae) 4

3. Dioecious; leaves spiral; stamens ≥ 10, erect in bud; anders tetralocular at anthesis, dehiscing by slits; embryo sac bisplicoid. 2/4, south-eastern Africa, Mascarenes

**Myrtaceae–Psiloxylidaceae**

- Flowers bisexual, rarely androgeious; leaves spiral or opposite; stamens (few–)usually many, in-fused in bud; anders bilocular at anthesis, dehiscing with longitudinal or apical slits or pores; embryo sac monosporic; [ovary (nearly superior–)inferior, (1)2–(4(–18))-locular; fruits capsular, indehiscent, or fleshy]. c. 140/over 5,500, tropical to warm-temperate regions mainly of southern hemisphere, with greatest diversity in the Australasian region Myrtaeae–Myrtoidae 10

4. Flowers strongly mono- or asymmetric; fertile stamen 1, staminodes 0–several; pollen without pseudocolpi; [petals (0)1–3(5); style base ± sunken in apex of gynoecium; fruit a loculicidal capsule or samaroid]. 8/200, most neotropical, 2/5 of them in West Africa

**Vochysiaceae**

- Flowers unusually not strongly zygomorphic; stamens > than 1; pollen often with pseudocolpi 5

5. Pollen with viscin threads on proximal surface and unique paracrystalline beaded exine, the central body of the grain circular to triangular with (2)(3)(–6) protruding apertures, pseudocolpi 0; embryo sac monosporic, 4-nucleate; endosperm diploid; [flowers (2)(4(5, 7))-merous; stamens usually arising from rim of the well-developed hypanthium; fruit a capsule, or dry and indehiscent; interzygous phloem often present; vegetative parts rich in oxalate raphides; exotegmen fibrous]. 17–24/675, widely distributed from tropics to arctic-alpine regions

**Onagraceae**

- Viscin threads 0, exine different; pollen apertures usually not protruding but pseudocolpi often present; embryo sac 8-nucleate, endosperm triplodial 6

6. Pollen grains 3-porate, lacking pseudocolpi; [ovary superior to partly inferior; branched foliar sclereids +17
- Pollen grains (23)-colporate; pseudocolpi present or not 8

7. Gynoecium 4–8-carpellate and -locular; petals shortly clawed; stamens 12 or numerous; tall trees with drooping, 4 angled ultimate branches. x = 10. 1/2, Southeast Asia, New Guinea

**Lythraceae** p.p. (Duabanga)**

- Gynoecium 10–20-carpellate and -locular; petals linear (lanceolate) or 0; stamens numerous; swamp and mangrove trees with pneumatophores. x = 12. 1/5, coastal Africa to Pacific islands

**Lythraceae** p.p. (Sonneratia)

8. Annual aquatic with floating leaves and submerged filiform-dissected stipules; flowers emergent, 4-merous; sepal basally connate into a tube, 2 or 4 of them accrescent in fruit as hornlike or spine-like projections; stamens 4, alternipetalous; gynoecium 2-carpellate, ovary partly inferior; fruits 1-seeded; endosperm 0 but one cotyledon starchy, very large, retained within the fruit. 1/3 (or 15), temperate to tropical regions of Old World, except Australia

**Lythraceae** p.p. (Trapa)

- Terrestrial

9. Endothelium present (at least, in Axinandra); [glabrous trees, often with quadrangular twigs; inflorescences indeterminate; flowers hypogynous to perigynous, 4–5–merous, obhaplostemonous or rarely diplostemonous; anther endothecium ephemeral; pollen tricolporate-pseudocolpate or (Crypteronia) bisyncolporate; petals 0 or (Axinandra) small and connate apically, falling off as a cup when the flower opens; ovary ± inferior, 2–6-locular; capsule woody or chartaceous]. 3/10, South and Southeast Asia, Malaysia Crypteroniaceae

- Endothelium 0

10. Flowers strictly obhaplostemonous; [plants woody; anther endothecium ephemeral]

11. Flowers usually diplostemonous or multistaminate; Melastomataceae and Lythraceae rarely (ob)haplostemonous

11. Hypanthium rim ending with some blunt teeth ("epicalyx"); ovary inferior, 3–5–locular; pollen heteropolar with unequal colpi and "half pseudocolpi" restricted to one polar face; sepal conspicuous, white or pinkish, inserted on margin of hypanthium; petals scale-like, minute, closing the hypanthium in bud; [stamens inserted on inner rim of tube below petals; fruit drupaceous]. x = 10. 1/c. 8, southern and eastern Africa, from Ethiopia to South Africa

**Oliniaceae**

- Epicalyx 0; ovary superior; pollen isopolar; petals, if present, not closing the hypanthium

12. Flowers (5)(6-7)-merous; hypanthium stellate; petals minute, hood-like, lobate and unguiculate, arising from hypanthial rim; sepals between the two microsporangia of each theca persistent; pollen 3-colporate with pseudocolpi; gynoecium 2(3)-carpellate, ovary 1-locular/partly bilocular; embryo sac monosporic/8-nuclear; fruit capsular. n = 10. 1/1

**Rhynchocalycaceae**

- Flowers 4–5(6)-merous; hypanthium tubular; petals strongly reduced or 0; sepals between the two microsporangia not persistent; embryo sac bisporic or tetrasporic

13. Flowers 4-merous; nodes unilacunar; foliar sclereids 0; hypanthium large, often conspicuously coloured; ovary 4-locular; pollen with pseudocolpi isomerous with apertures; embryo sac tetrasporic, 16-nucleate. n = 10. 7/23, Cape Province of South Africa

**Penaeaceae**

- Flowers 5(6)-merous; nodes trilacunar; branched foliar sclereids +; pollen without pseudocolpi; hypanthium green to yellow, 4–6 mm long; ovary 2-locular; embryo sac bisporic. 1/1, Costa Rica to Bolivia

**Alzateaceae**
14. Stamen connectives dorsally enlarged and often massive; anther dehiscence often ± poricidal; [pollen with pseudocolpi; leaves opposite; crystal druses and/or styloids +]

15. Leaf venation pinnate or brochidodromous (very rarely, acrodromous); plants woody; flowers strictly epigynous, diplostemonous; stamen connectives without dorsal glands; anthers mostly poricidal, endothecium 0; terminal leaf sclereids 0; stomata anemocytic, polycytic or encyclocytic; secondary xylem generally without included phloem islands; fruit capsular or baccate; seed coat without fibrous exotegmen; seeds 1–few, generally with well-developed storage cotyledons.

Memecylaceae*

16. Herbaceous or woody; ovary superior (to inferior); flowers usually diplostemonous or flowers (ob)haplostemonous; petals crumpled in bud; stamens inserted at the base of floral tube or above, whorls of unequal length; heterostyly widespread; pollen grains tricolporate, pseudocolpi 0 or isomerous with or double the number of apertures; fruit capsular or baccate. 30/c. 600, worldwide, mainly in subtropical and tropical regions

Lythraceae p.m.p.

- Woody; ovary inferior; stamens many, covering the inner floral tube surface from the rim to the ovary; homostylous; pollen tricolporate, with indistinct pseudocolpi; ovary 7–9(–15)-loculate, carpels in 1 whorl or in 2–3 superposed layers; fruit a leathery berry; seeds many, with translucent sarcotesta. 1/2, from Balkan Peninsula to Himalayas and on Socotra

Lythraceae p.p. (Punica)

Fig. 2. A phylogenetic hypothesis of relationships of Myrtales families, mainly based on Clausing and Renner (2001), Sytsma et al. (2004) and Wilson et al. (2005)
are characterised by the combination of vestured pits and bicolateral vascular bundles in the primary xylem, resulting in the appearance of phloem included within the secondary xylem (van Vliet and Baas 1984), and also by several embryological features (Tobe and Raven 1983). Additional characters found in part throughout the order include opposite leaves with undivided laminas, even in the aquatic members; small or rudimentary stipules; short to elongate hypanthia; stamens incurved in bud; vessel elements with simple perforations, paratracheal axial parenchyma and usually non-septate fibres; secondary phloem stratified in young twigs; unilacunar nodes; simple styles; pollen with subsidiary “colpi” (“pseudocolpi”, i.e. meridional invaginations in the intercolpial regions, apparently with a harmomegathic function); 2-celled pollen; a crystalliferous endotesta; scarce or no endosperm; and copious amounts of gallo-and ellagitannins, the latter often methylated. Morphological studies significantly contributed to our knowledge of Myrtales in the 1970s and 1980s, and many of these appear in the Myrtales symposium volume published in the Annals of the Missouri Botanic Garden (vol. 71, 1984). Following the comparative analysis of inflorescence structure by Briggs and Johnson (1979), Weberling (1988) analysed the inflorescences from a typological point of view. Monotelic thyrsopaniculate inflorescences, postulated to be basic in the order, predominate in Myrtaceae, Melastomataceae, Oliniaceae and other smaller families whereas Combretaceae and Onagraceae are polytelic throughout. Nevertheless, the aspect of character polarity of inflorescences is yet not completely settled, and recent work shows that within Lythraceae alone the monotelic condition is derived at least four times from the polytelic (Graham et al. 2005).

The so-called pseudocolpi are a peculiar character of the pollen grains of many Myrtales, and the distribution and different expressions of these structures are problematic. The absence of pseudocolpi from part of Lythraceae is striking, as is the occurrence of “double” pseudocolpi in another part (Patel et al. 1984). Their complete absence from Onagraceae and the Myrtaceae clade have led earlier authors (Dahlgren and Thorne 1984; see also Johnson and Briggs 1984) to postulate the origin of the pseudocolpi after the branching off of these two families. In view of recent phylogenetic hypotheses (Fig. 2), however, it seems more parsimonious to consider pseudocolpi as ancestral for the order as a whole.

Modern phylogenetic studies in Myrtales started with the seminal work of Johnson and Briggs (1984), and many of their findings have later been confirmed by molecular studies (Conti et al. 1996, 1997, 2002; Clausing and Renner 2001; Sytsma et al. 2004; Wilson et al. 2005). Molecular analyses generally provided strong support for the monophyly of individual families, and also interfamilial relationships have been greatly clarified. The morphological circumscription of families and larger clades turned out to be more difficult (see Conspectus of families). The exact position of the order within the eudicots is not clear and, together with Crossosomatales and Geraniales, Myrtales are left unplaced within the rosids (APG II 2003; see also the angiosperm-wide analysis of marK sequences by Hilu et al. 2003).

Combretaceae often appear to be sister to the rest of the order but statistical support for this is still tenuous. Onagraceae and Lythraceae are sister taxa, the former possessing raphides, the latter alkaloids. Onagraceae are highly autapomorphic (see Conspectus). Among the remaining families, Melastomataceae, Memecylaceae and their sister group, the CAROP families (Crypteroniaceae, Alzateaceae, Rhynchocalycaceae, Oliniaceae and Peneaeaceae), are characterised by dorsally massive anther connectives. Renner (1993) and Clausing and Renner (2001) determined the acrodromous leaf venation and lack of a fibrous anther endothecium as being synapomorphic for Melastomataceae, and the terpenoid-producing connective glands as synapomorphic for Memecylaceae. The few genera of Melastomataceae which lack the peculiar, arching leaf venation are nested within the family and thus are clearly derived, and the occurrence of an anther endothecium in the basal melastom genus *Pternandra* is interpreted as a plesiomorphy (Clausing and Renner 2001). Interestingly, *Pternandra* also has the interxylary phloem islands (included phloem) which generally occur in Memecylaceae. This trait is interpreted as parallelism, and not as plesiomorphy, because *Pternandra* agrees with Melastomataceae in most other wood characters.

The CAROP families share the loss of an anther endothecium (probably evolved independently from Melastomataceae) with obhaplostemonous flowers (Schönenberger and Conti 2003) and the presence of stipules (Johnson and Briggs 1984). Apart from these features, the four families are strongly diversified. Particularly Crypteroniaceae, with their variable androecium and gynoecium
structure, defy any attempt for a sound morphological family characterisation; the circumscription of this family follows largely molecular findings. The melastom/CAROP clade is sister to the Myrtaceae/Vochysiaceae clade. Myrtaceae represent the largest, most diverse family of the order, for which a detailed classification has recently been established (Wilson et al. 2005). The inclusion of the somewhat aberrant genera *Psiloxylon* and *Heteropyxis* in Myrtaceae increases the support for the monophyly of the family, compared to a separate treatment of these two taxa as monogeneric families. The great size of Myrtaceae encompasses much variation in inflorescence, floral and fruit structure, which has been explored by numerous studies subsequent to the seminal contributions by Briggs and Johnson (1979) and Johnson and Briggs (1984). Until the advent of molecular systematics, the close relationship of Vochysiaceae and Myrtaceae had been camouflaged by the distinct floral organisation of the former family but Vochysiaceae have many myrtalean traits, and share the plesiomorphic (see the hypothetic “Protomyrtales” of Johnson and Briggs 1984) sunken styles and 1–2-celled hairs with many Myrtaceae (Stevens 2005).

Much work has been dedicated to the elucidation of the biogeographic history of Myrtaceae. This task is complicated due to the ancient origin of the order and its poor fossil record (see Sytsma et al. 2004). Recent dating analyses have estimated the crown group of Myrtaceae to be 107 million years old (Sytsma et al. 2004), corresponding to the Cretaceous. This implies that Gondwanan vicariance had already rifted c. 80 million years ago in the equatorial region (Sytsma et al. 2004). The initial radiation of Melastomataceae is hypothesised to have occurred during the Palaeocene/Eocene along the northern shore of the Sea of Tethys (Renner et al. 2001). From there, the family may have dispersed to North America and throughout Eurasia, later also to South America and from there with repeated long-distance dispersal events to Africa, Madagascar, India and Indochina.

**References**

APG II 2003. See general references.


Conti, E. et al. 1996. See general references.


Conti, E. et al. 2002. See general references.


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


Introduction to the Passifloraceae Alliance (“Passiflorales” = Malpighiales)

1. (Andro)gynophore 0; petal aestivation contorted; corona rarely present and then weakly developed; calyx and corolla separating from developing fruit and falling together; seeds arillate, pitted. 10/+200, Africa, America
   - (Andro)gynophore usually present; petal aestivation cochllear; corona often present and strikingly coloured in various seeds, cyclopentenoid cyanogenic glucosides (aporphines) present; myricetin and condensed tannins 0; carpel closure by secretion; flowers thermogenic. 1/1 or 2, North America, Asia, Australia

   Malesherbiaceae
   - Stylodia inserted beneath the top of ovary; stamens 5; pollen grains 3-colporate; seeds exarillate; calyx persistent in fruit; tendrils 0. 1/24, Chile, Peru

   Turneraeaceae
   - Stylodia inserted on top of ovary; stamens 4, 5, or many; pollen grains 3–12-colporate or -foraminate; seeds arillate; tendrils often present. 17/700–750, pantropical

   Passifloraceae

These three families are closely related and also could be merged into one, as suggested as an option by the Angiosperm Phylogeny Group (APG II 2003); here, they are treated separately because their authors prefer the traditional family circumscription. Whereas the molecular data of Chase et al. (2002) confirm that these families form a clade, at the time of writing of these accounts this introduction (Sept. 2005), it still remains unclear whether the separation of these families involves paraphyly. They share important characters such as an extrastaminal corona, exotestal seeds, cyclopentenoid cyanogenic glucosides and/or cyclopentenyl fatty acids, and biparental or paternal transmission of plastids (the latter not observed in Malesherbiaceae). Whereas seed structure and chemical make-up appear quite constant in the group, a corona is not always present and its expression is quite diverse. It is developed in its full-fledged form in Passifloraceae, mainly Passiflora, but is only weakly in the possibly basal Adenias and also in Turneraeaceae and Malesherbiaceae; it is difficult to decide whether this represents an anagenetic or reductional transformation. Accessory or superposed buds, as in Passifloraceae, are found also in various members of Salicaceae and Achariaceae (de Wilde 1971b, at that time included in Flacourtiaceae) where, however, no cyanogens are present; still, a corona is known from Abatia, which led earlier researchers to include the genus in Passifloraceae. Its placement in Salicaceae on the basis of molecular evidence (Chase et al. 2002) is corroborated by morphological evidence. Thus, in contrast to Passifloraceae, Abatia has opposite leaves, valvate calyx aestivation and extorse anthers, and both the coronal threads and stamens are irregularly arranged whereas in Passifloraceae the corona elements are in distinct whorls and the stamens in the polystemonous genera of this family are in a single whorl (Bernhard 1999); the corona may not be homologous in both groups.

References

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

Introduction to Proteales

1. Herbaceous, cambial activity 0; sepals 2, stamens numerous, spirally arranged; carpel closure by secretion; ovule 1 per carpel, anatropous; pollen grains variously furrowed or rarely sulcate or tricolporate; simple benzylisoquinoline alkaloids (aporphines) present; myricetin and condensed tannins 0; carpel closure by secretion; flowers thermogenic. 1/1 or 2, North America, Asia, Australia

   Nelumbonaceae (see Vol. II)
   - Woody; sepals or tepals > 2, stamens whorled; carpels postgenitally fused; ovules 1 or 2, rarely more per carpel, usually orthotropous; pollen grains triaperturate(-derived); benzylisoquinoline alkaloids 0; myricetin and condensed tannins present but gallate 0; [seeds lacking starch but containing fat oil and protein]

2. Stipules 2, often fused; flowers small, unisexual, in globular heads; perianth 3–4(–7)-merous, the petals vestigial; carpels 3–8, distinct, ovules 1(2); pollen grains tricolporate; triterpenes +. 1/c. 7, North America and Asia Minor to East Asia

   Platanaceae (see Vol. II)
   - Stipules 0; flowers usually bisexual, in racemes, panicles, or condensed, often paired; perianth of 4 (very rarely 3 or 5) valvate tepals; stamens antetepalous, often adnate to tepals, alternating with hypogynous nectar secreting glands; carpel 1; ovules 1–2(–many); pollen grains tricolporate, rarely tricolporate or diporate; triterpenes 0. 80/1,700, mainly southern hemisphere, best developed in Australia

The three families united in this order form an unexpected alliance, which was discovered by early molecular work and since has received support in
various multigene analyses. Sabiaceae, here left unplaced as to ordinal allocation (see family treatment), are also often found together with Proteales (cf. Fig. 1). As is evident from the characters given in the Conspectus, Nelumbonaceae appear quite out of place in this alliance. Their ranunculalean chemistry (see Gottlieb et al. 1993) is accompanied by completely ascidiate carpels without any postgenital fusion, which *Nelumbo* shares only with Berberidaceae; the ovules are anatropous (Igersheim and Endress 1998). *Nelumbo* has a dimerous calyx (Hayes et al. 2000; in contrast to information given erroneously by Kubitzki 1993), but dimerous whorls are widespread in basal eudicots (Drinnan et al. 1994; Doyle and Endress 2000; Soltis et al. 2003) and are by no means exclusive for early-diverging eudicots.

Nelumbonaceae are remarkable with regard to pollen development. Whereas in basal angiosperms (monosulcates) there is much variation between the simultaneous and successive type of microsporogenesis, almost all eudicots (triaperturates) have simultaneous microsporogenesis, with the notable exception of Nelumbonaceae (Kreunen and Osborn 1999) and Proteaceae (Furness et al. 2003) and are by no means exclusive for early-branching Proteaceae. The ultrastructural analysis of *Nelumbo* shares only with *Nelumbo*.

Proteaceae pollen is known for differing from the widespread developmental pattern in eudicots, in which apertures are formed in pairs at six points in the developing tetrad, following Fischer’s Rule. In Proteaceae, the apertures are formed in groups of three at four points in the tetrad (Garside 1946). Furness and Rudall (2004), who quoted Illiciales, Proteaceae and Olacaceae as the only examples in angiosperms for pore orientation according to Garside’s Rule, argued for origins of this developmental mode of triaperturate pollen independent from the developmental pattern following Fischer’s Rule which characterises the majority of the eudicots. Illiciales are, however, irrelevant in this context because their “tricolpate” condition is an extension of the trichotomosulcate arrangement, which is often found among monosulcates in which Illiciales are embedded (Huynh 1976; Doyle et al. 1990). The pollen grains of some Olacaceae, which are formed according to Garside’s Rule, appear autapomorphic because this family is deeply embedded within the triaperturate group. Also for Proteaceae, it is difficult to envisage a completely independent origin of the triaperturate condition from a monosulcate/trichotomosulcate ancestor: even if Proteales were basal in eudicots, Proteaceae are nested within Proteales, in which Platanaceae and Nelumbonaceae produce “normal” triaperturates. Any hypothesis of an independent origin within this order would then require one or two additional origins of the normal Fischer’s Rule tricolpate type, a non-parsimonious assumption. Rather, these considerations all favour an origin of the proteaceous condition from normal tricolpates, much as concluded for Olacaceae. This view is shared by Blackmore and Crane (1998) who tend to view the Garside’s Rule arrangement in Proteaceae as derived.

A triporate fossil pollen from the Cenomanian (mid-Cretaceous) of the Northern Gondwana Province, *Triorites africanaensis*, has often been related to Proteaceae. The ultrastructural analysis of
Priorites by Ward and Doyle (1994) suggests that Priorites pollen is not tricolpate-derived, as usually is the case with tritoparates, but perhaps directly from tricolpate. Ward and Doyle (1994) considered this as an additional piece of evidence against a derivation of the family from a rosid ancestor – of course, amply confirmed by molecular data. A number of Late Cretaceous (Late Santonian–Early Campanian) follicular fruits from southern Sweden (Leng et al. 2005) exhibit several similarities with Proteaceae, particularly with the first branching lineages in the family. These include a plicate carpel structure with a vascular system of three bundles, several anatropous, probably bitegmic ovules, and a more or less sessile stigmatic area which is located at the distal-most part of the ventral slit and extends over the topological apex to the abaxial side of the follicle. Although these fossils differ from extant Proteaceae in having unisexual and obviously perianth-free flowers and several ovules, they represent an extinct lineage of basal eudicots which probably was close to modern Proteaceae.

Johnson and Briggs (1975), with admirable intuition, anticipated that Proteaceae are not only an “isolated” but also a fairly basal family, rather than belonging somewhere in the rosids, this having been fully confirmed by the evidence available 30 years later.

References


### Introduction to Saxifragales

1. Trees; stigmas decurrent; pollen colporate or pentaporate; [anthers with protruding connectives] 2
2. Trees or herbs; stigmas subulate, capitate or spatulate; pollen colporate, rarelyporate 5

2. Flowers mostly hermaphroditic; anthers mostly dehiscent with valves; [trichomes mostly stellate or tufted; flowers (2–)4–5–(7–)merous, calyx rarely 0, petals often adaxially circinate; ovary inferior to superior, 2-carpellate with straight stylodia; iridoids 0]. n = 8, 12, 18, 27/82, tropical to temperate, C and E North America, SE Europe through S, E and SE Asia to New Guinea and NE Australia

### Hamamelidaceae (see Vol. II)

1. Dioecious; anthers dehiscent with slits or rudimentary valves 3

3. Ovary unicarpellate with axilary suture [but the solitary carpels (= female flowers) united into pseudanthial]; iridoids 0; [fruit a samara; seed with large embryo]. n = 19. 1/2, China and Japan

### Cercidiphyllaceae (see Vol. II)

1. Ovary bicarpellate; no pronounced shoot dimorphism; iridoids present 4

4. Female flowers in globose heads, male in terminal globose racemes; stipules present; pollen pantporate; embryo > half the length of the seed; secretory ducts in all vegetative tissues. n = 8. 1/13, C America, E Mediterranean, E Asia to Malesia

### Altingiaceae (see Vol. II under Hamamelidaceae)

1. Flowers in elongate racemes; stipules 0; pollen tricolpate; embryo minute; secretory ducts 0, n = 8. 1/10, E Asia, Malesia

### Daphniphyllaceae

5. Flowers polyanthrous 6
6. Flowers haptorosemonious or diplotosemonious.

### Core Saxifragales 7

6. Apocarpous; stamens in 5 fascicles; seeds with shining sarcotesta; perennial herbs or (half)shrubs. 1/40, northern hemisphere

### Paoniaceae

7. Syncarpous, ovary unilocular; stamens not distinctly fasciculate; seeds with black crustaceous coat; trees. 3/11, South America, Africa

### Peridiscaceae

7. Flowers essentially 4-merous; [leaves estipulate; nodes unilacunar] 8
8. Ovary superior, nearly apocarpous; anther wall without fibrous endothecium; [pollen tricolporate; fruit follicular; seeds very small, winged; low glabrous shrub]. 1/1, Tasmania

### Tetracarpaeaceae

1. Ovary inferior or semi-inferior, the carpels at least basally connate; anther wall with fibrous endothecium

9. Leaves alternate, opposite, or verticillate; ovary inferior, 4–(2–)carpall; stylodia free with penicillate stigmas; vessel elements with simple perforation; pollen 4–6–(20)-colpate or -porate, often aspidiate; [tanniniferous terrestrial or aquatic herbs, shrubs or small trees]. n = 7 (6, 9, 21, 29). 8/150, worldwide but mainly Australia

### Haloragaceae

1. Ovary opposite or semi-inferior, 4–carpellate; style shortly 4–lobed; stigmas papillate; vessel elements with scalariform perforation; pollen tricolporate; [petals small or 0; climbing shrubs]. 1/2, Australia

### Aphanopetalaceae

10. Shrubs; [leaves alternate; vessel element perforation mainly scalariform; ovary syncarpous] 11

### Pterostemonaceae

11. Gynoecium 5–carpellate; style shortly 5-lobed; [ovary largely inferior with 4–6 ascending ovules/locule; stigmas radiate; stipules minute; pollen 3-colpate; vessel elements also with simple perforations]. 1/3, Mexico

### Grossulariaceae

12. Ovary inferior, 1-locular; fruit a berry; seeds usually numerous, small, mucilaginous; embryo small; pollen 8-zonocolporate, pentacolpo-di-orate, or pantporate; erect, arching, trailing or prostrate shrubs often with 3- or 2-forked or simple nodal spines and smaller internodal bristles, and long-petiolate, basally 2-veined leaves; [seed coat with exotestal mucilaginous palisade, endotesta crystalliferous]. n = 8. 1/150–200

### Penthoraceae

13. Fruit a 5–7–carpall; -beaked stellate capsule, the beak of each carpell circumsiscile above the syncarpous region; nodes unilacunar; vessel element perforation scalariform; [rizomatous perennials; petals 0 or very small]. n = 8, 9. 1/2, E North America, E and SE Asia

### Italeaceae

14. Succulent herbs, subshrubs or rarely shrubs; stipules 0; nodes trilacunar or unilacunar; leaves usually simple and entire; gynoeceum isomerous with perianth; nectariferous scale near base of each carpel (petaloid and entire; gynoecium isomerous with perianth; nodal spines and smaller internodal bristles, and long-petiolate, basally 2-veined leaves; [seed coat with exotestal mucilaginous palisade, endotesta crystaliferous]. n = 8. 1/150–200

### Crassulaceae

15. Succulent herbs, subshrubs; stipules present or leaf basis sheathing; nodes trilacunar or unilacunar; leaves simple or pinnately or
palmately compound or decompound; gynoecium 2(–5)-carpellate; nectariferous disk mostly present. \( n = (5, 6) \{11, 12, 15, 17, 18\} \). 33/1,410, nearly cosmopolitan but mainly in northern temperate zone and centred in North America

Saxifragaceae

Saxifragales, in the circumscription followed in this volume, are the result of a series of molecular analyses carried out over the past 15 years or so (Chase et al. 1993; Morgan and Soltis 1993; Soltis and Soltis 1997; Fishbein et al. 2001; APG II 2003; Davis and Chase 2004; Fishbein and Soltis 2004, among others). The monophyly of this clade is strongly supported. Moreover, there is a 1 bp insertion common to all members of the order (Soltis and Soltis 1997). In addition to the Core Saxifragales traditionally considered to belong to this order (see Fig. 3), it comprises also Haloragaceae, the controversial Paeoniaceae, some woody "hamamelidid" families (Cercidiphyllaceae, Hamamelidaceae, Altingiaceae, Daphniphyllaceae), and the enigmatic Peridiscaceae. Outgroup relationships of Saxifragales are weakly supported (Savolainen, Chase et al. 2000; Soltis et al. 2000) but the group is often found together with Vitaceae at the base of the large eurrosid clade.

A group comprising the families now constituting the order Saxifragales has never before been recognised in traditional systematic studies. In comparison with older concepts such as of those of Bentham (1865), Engler (1891, 1930) and Cronquist (1981), and partly also with the more recent but essentially morphologically based classifications by Huber (1991), Takhtajan (1997) and Thorne (2001), the present circumscription differs in three major points, first, in the exclusion of the lineages having tenuinucellate ovules and containing iridoids; second, in the inclusion of Haloragaceae, Peridiscaceae and Paeoniaceae (included in Saxifragales by Huber 1991); and third, in the addition of several woody families showing presumably plesiomorphic characters such as valvate anther dehiscence, apiculate connective protrusions and tricolpate pollen, some of which persist here and there in the Core Saxifragales.

ad 1. The first to recognise the systematic significance of ovules was Warming (1878), and the bitegmic ovules of Itea led van Tieghem (1898) to propose the transfer of Itea from Escalloniaceae to Saxifragaceae. He later (van Tieghem 1901) used the distinction between bitegmic and unitegmic ovules as a rigorous criterion in the classification of the whole plant kingdom, which resulted in a system containing inconsistent and unnatural groupings, discrediting the use of this character. Consequently, his views were wholly rejected by other botanists and Engler (1930), when commenting on Hydrangioideae and Escalloniodeae which he included in his Saxifragaceae, argued that the number of integuments had little systematic significance because, among otherwise clearly related genera of Ranunculaceae, their number

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Fig. 3. A phylogenetic hypothesis of relationships of Saxifragales families, based on Fishbein et al. (2001), Fishbein and Soltis (2004) and, for Peridiscaceae, on Davis and Chase (2004). Note that resolution among the basal woody families is weekly supported. Hamamelidaceae, Altingiaceae and Cercidiphyllaceae were treated in Vol. II (Kubitzki et al. 1993) of this series.
can be variable. However, Mauritzon (1933), in his embryological studies of Saxifragales, found ovule characters to be useful, and Philipson (1974) suggested that a distinction be made between families in which the ovular characters are constant, as opposed to those in which some variation in this respect occurs sporadically. Taxa such as Escalloniaceae, Hydrangeaceae, Phyllonoma, Montinia and Eremosyne, transferred to the asterids by Soltis and Soltis (1997) on the basis of molecular evidence, are all unitegmic and iridoid-positive. Some unitegmic genera (Darmera, Micranthes) persist in Saxifragaceae but these are embedded in broader bitegmic lineages and lack iridoids, whereas the few iridoid-positive Saxifragales are bitegmic.

ad 2. Haloragaceae traditionally have been related with Myrtales but Takhtajan (1997) demonstrated that they have more characters in common with Saxifragales. Peridiscaceae have often been related to Flacourtiaceae but the three-gene analysis of Davis and Chase (2004) adds the family, with the inclusion of Soyauxia, to the Saxifragales where they come out with Daphniphyllaceae and the other woody groups at the base of the Saxifragales clade, albeit with low support (M.W. Chase, pers. comm. Nov. 2003). A close relationship between these three taxa is not reflected by morphological traits, although the anther flaps of Soyauxia are found in some basal Saxifragales families as well. Paeoniaceae, large-flowered, apocarpous, with striking seed-presentation and strongly autapomorphic, in the analysis of Fishbein and Soltis (2004) are basal to Core Saxifragales.

ad 3. Within the Saxifragales, but outside the Core Saxifragales, iridoids occur in two families, Altingiaceae and Daphniphyllaceae, where they are poorly diversified chemically (Kaplan and Gottlieb 1982), perhaps due to the small size of these families. These are the only reports of iridoids outside the asterids.

The tricolpate pollen predominating in Ceridiphyllaceae, Hamamelidaceae and Daphniphyllaceae is likely to be a plesiomorphic trait; in fact, the apertures of Ceridiphyllum appear quite archaic, and are intermediate between the poroidate and colpoidate condition (Praglowski 1975); however, there are transitions to compound (colporoidate or colporate) apertures known from within Daphniphyllum. In the Core Saxifragales, elabo-

rate compound apertures (with well-differentiated exo- and endoapertures) are the rule but sometimes (Saxifragaceae) they are not fully developed. On the whole, the woody basal families of (“non-Core”) Saxifragales appear as isolated remnants of formerly more richly developed, archaic lineages, as is particularly well documented for Ceridiphyllaceae. Resolution within the Core Saxifragales is better supported, mainly due to the efforts of Fishbein et al. (2001), and even a cursory glance at the topology reproduced in Fig. 3 reveals that a broader concept of Saxifragaceae (with the inclusion of Tetracarpaea and Penthorum) is untenable, unless Crassulaceae and Haloragaceae were to be incorporated, too. The topology of Fig. 3 is also useful for a comparison with character transformations which can be recognised in the Core Saxifragales. The transition from woody to herbaceous growth, usually accompanied by the loss of scalariform perforation plates of the vessel elements, has taken place some five times within Saxifragales – in Paeoniaceae, Saxifragaceae, Crassulaceae (the few woody members of which are definitely secondarily woody; see Crassulaceae, this volume), Penthoraceae and the woody/herbaceous Haloragaceae. Penthoraceae are remarkable for having “retained” scalariform perforation in spite of being herbaceous. Grossulariaceae are strictly woody whereas their sister group Saxifragaceae is largely herbaceous – a remarkable difference, although both agree in details of shoot morphology and growth dynamics, as is well described by Weigend under “Affinities” of Grossulariaceae (this volume).

Anthers in Saxifragales are remarkably uniformly basified but gynoecium structure, particularly in Core Saxifragales, is labile. Pterostemonaceae stand out with an isomerous and apocarpous gynoecium within an otherwise 2–3-carpellate Saxifragaceae alliance; the gynoecia of Crassulaceae and Tetracarpaeaceae are also (nearly) apocarpous. Free stylodia are widespread, and most groups with this character seem to lack a compitum. The functionally advantageous fusion of stylodia into a common style is uncommon (Grossulariaceae, Iteaceae, Aphanopetalaceae). Although there is no indication that apocarpy here, or in the (other) eurosids where it also occurs, is due to a reversal, it is difficult to imagine that this character expression should be plesiomorphic in these groups. Minute embryos characterise Peridiscaceae, Daphniphyllaceae, Paeoniaceae, Grossulariaceae and Tetracarpaeaceae; all other groups have medium-sized or large embryos.

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2 The record of iridoids sometimes indicated for Paeonia (e.g. in Stevens 2005) may be based on Nekratova et al. (1988, in Rast. Resur. 24:392–399), who may have mistaken monoterpenoid glucosides of the Paeonilin type for iridoids (Hegnauer 1990).
References

APG II 2003. See general references.


Cronquist, A. 1981. See general references.


Hegnauer, R. 1990. See general references.


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

Takhtajan, A. 1997. See general references.


Introduction to Vitales

1. Small trees, shrubs, or herbs; tendrils 0; stipular wings conspicuous, sheathing; inflorescences terminal; floral disk tubular, not producing nectar; due tosecondary septation, ovary 4–6–(–8)-locular, ovule 1per locule. 1/34, mainly southern Asia, extending toAfrica/Madagascar and Australia. Vitaceae– Woody lianas usually with leaf-opposite tendrils,rarely succulent small trees or erect herbs; stipulesnot sheathing the petiole margins; inflorescences oftenleaf-opposed; floral disk intrastaminal, ring-shaped,cupular, or gland-shaped, usually nectariferous; ovary2-locular, ovules 2 per locule. 14/c. 750, pantropicalVitaceae

Traditionally, Vitales were included in Rhamnales– both have antepetalous stamens – but Takhtajan (1997) dismembered this association because Vitaceae and Leeaceae differ from Rhamnaeae in theirberry-like fruits and seed structure, and in having raphide sacs in the parenchymatous tissue; he placed them as “Vitalanae” close to hisProteanae at the end of his Rosidae. Corner (1976) wasmuch impressed by the thick, lignified endotesta andsmall embryo of the seeds of Vitaceae, whichhe found “scarcely improved on that of Magnoliand… even more primitive”. Vitales also havethraceidal exotegmen, which is a rare feature inangiosperm seeds – apart from Dilleniaceae; it is listed only for Cunoniaceae by Nandi et al. (1998).Vitaceae, Leeaceae and Dilleniaceae are the onlyangiosperm families which share the lignified endotesta and tracheidal exotegmen.

The first to find an association betweenVitaceae and Dilleniaceae were Nandi et al. (1998) in a combined rbcL/morphological analysis. In an rbcL analysis (Savolainen, Fay et al. 2000), Vitales and Dilleniaceae appear in a sister position to Caryophyllales. The two-gene analysis ofSavolainen, Chase et al. (2000) and the three-gene analysis ofSoltis et al. (2000) place Vitales at the base of the rosid clade. In the matK analysis ofHilu et al. (2003), the rosids are sister to Vitis andTetracera (in turn, sister taxa) and to other taxa.
including Berberopsidales, Santalales (relative positions were uncertain), and Caryophyllales plus asterids. In the four-gene study of Soltis et al. (2003), Vitales occupy a position at the base of a Caryophyllales/Saxifragales clade. None of these associations is strongly supported. Thus, a closer relationship between Vitaceae/Leeaceae and Dilleniaceae can not be ruled out. Perhaps both families branched off at the base of the core eudicot tree and both, but Dilleniaceae more probably than Vitaceae/Leeaceae, may be related to Caryophyllales. Evidence for placing Vitales in rosids is tenuous because the molecular data are not convincing. Note, however, that Stevens (2005), citing Oxelman et al. (2004), mentions that the RPB2 gene may not be duplicated in Vitales, perhaps suggesting a position outside core eudicots.

Summarising, one may agree with Stevens (2005, on Vitales) that Vitales have no firm position as yet, although a more strongly supported association with Dilleniaceae and Caryophyllales would not come as a surprise.

References

Stevens, P.F. 2005. See general references.
Takhtajan, A. 1997. See general references.

Introduction to Zygophyllales

1. Hemiparasitic; stipules 0; flowers solitary or in botryoid panicles, zygomorphic; the two abaxial petals lipid-secreting, the three adaxial ones forming a flag; stamens \pm as many as petals; ovary 1-locular; pollen 3-porate; vessels with non-vestured pits; axial parenchyma usually with one cell per strand; storying absent or nearly so; crystals many per cell, mostly in axial phloem parenchyma; \( n = 6 \). 1/18, New World

Krameriaceae

– Autotrophic; stipules \(+\); flowers solitary, paired or in few-flowered cymes, regular or rarely slightly zygomorphic; nectar-secreting disk often \(+\); stamens 1 or 2 times as many as petals; ovary (2–)5–(12)-locular; vessels with vested pits; axial parenchyma usually with 2–4 cells per strand; storying present in axial parenchyma, sometimes in rays; crystals one per cell or septate portion of cell in wood or secondary phloem; \( x = 6–15 \). 22/230–240, in hot dry regions all over the world

Zygophyllaceae

Previously, Krameriaceae and Zygophyllaceae were placed in different orders, and no close relationship between them had been recognised. Molecular studies, particularly the multigene analyses of Soltis et al. (2000) and Savolainen, Chase et al. (2000), revealed a strongly supported clade consisting of the two families within eurosids I. Ordinal status for this clade, which appears not to fit in any other rosid order, was suggested by Soltis et al. (2000). Zygophyllaceae and Krameriaceae are quite diverse but have more or less pentameric and (ob-)diplostemonous(-derived) flowers, bitegmic/crassinucellate ovules, and simple styles, and thus conform to a generalised rosid pattern. They agree in various wood characters such as simple perforation plates in vessels, and the presence of tracheids (vasicentric, in the case of Zygophyllaceae), which are considered as plesiomorphous within eurosids whereas other characters, listed by Carlquist (2005) and partly included in the Conspectus above, are autapomorphic; the paedomorphic rays of Krameria are probably related to its hemiparasitism. The presence of anthraquinones may indicate their relationship to the nitrogen-fixing clade (Cucurbitales, Fagales, Fabales, Rosales) where these compounds are more often found (Savolainen, Chase et al. 2000), and to which they appear close in some analyses, although with low support.

Apart from the presence of harman alkaloids in both families, the remarkable diversification of lignans and neolignans is a strong link between them (see “Phytochemistry” in family treatments) although, according to our present knowledge, these compounds in Krameriaceae are localised in the roots but in Zygophyllaceae on the leaf surface and in the wood.

References

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