
Asterales: Introduction and Conspectus

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Asterales (incl. Campanulales of many authors), with Alseuosmiaceae, Argophyllaceae, Compositae (= Asteraceae), Calyceraceae, Campanulaceae (incl. Cyphiaceae, Lobeliaceae, Nemacladaceae), Carpodetaceae (included in Rouseaceae by APG II 2003), Goodeniaceae, Menyanthaceae, Pentaphragmataceae, Phellinaceae, Rouseaceae and Stylidiaceae (incl. Donatiaceae), contain about 26,300 species in c. 1,720 genera. The large majority of species and genera belong to Compositae and Campanulaceae. The order is well supported in all major molecular phylogenetic analyses (APG II 2003), and is part of the Euasterids II or Campanulids sensu Bremer et al. (2002).

Phylogenetic structure within Campanulids (also containing Apiales, Aquifoliales, Dipsacales and several families of uncertain ordinal placement; APG II 2003) is not sufficiently well resolved to identify the sister group of Asterales. It appears to be evident, however, that of all representatives of the Campanulids, Aquifoliales are least closely related to Asterales (Savolainen et al. 2000a, b; Soltis et al. 2000; Albach et al. 2001; Bremer et al. 2001, 2002).

Although several of the constituent families of the order had been recognized to be closely related to one another long ago (for discussion, see Lammers 1992), the recognition of the relationship of others to Asterales (Lundberg and Bremer 2003) is the result mainly (but not only) of recent molecular phylogenetic work. This applies particularly to Alseuosmiaceae (Backlund and Bremer 1997; Gustafsson and Bremer 1997; Kårehed et al. 1999; Cronquist 1981: Rosales; Thorne 1992: Saxifragales; Takhtajan 1997: Hydrangeales), Argophyllaceae (Kapil and Bhatnagar 1992; Gustafsson et al. 1996; Kårehed et al. 1999; Olmstead et al. 2000; Cronquist 1981: Rosales; Takhtajan 1997: Hydrangeales), Carpodetaceae (Gustafsson and Bremer 1997; Lundberg 2001; Takhtajan 1997: Hydrangeales), Phellinaceae (Backlund and Bremer 1997; Gustafsson and Bremer 1997; Kårehed et al.

1999; Cronquist 1981: Celastrales; Thorne 1992: Theales; Takhtajan 1997: Icaciniales) and Rouseaceae (Lundberg 2001; Takhtajan 1997: Brexiales), and partly also to Menyanthaceae (Downie and Palmer 1992; Olmstead et al. 1992; Cronquist 1981: Solanales; Thorne 1992: Campanulales; Takhtajan 1997: Menyanthales) and Stylidiaceae (Cronquist 1981: Campanulales; Thorne 1992: Saxifragales; Takhtajan 1997: Stylidiales). Further sampling may identify other taxa from distant corners of the traditional angiosperm system which should be included in the order. On the other hand, Sphecocleaceae, as a family often associated with Asterales/Campanulales (e.g. Lammers 1992), do not belong here but rather in Solanales (APG II 2003).

Members of Asterales are mostly herbaceous and in most cases have alternate leaves without stipules. Flowers are very rarely solitary but mostly aggregated in sometimes axillary but more commonly terminal inflorescences which are capitulate and involucrate in most of the closely related Goodeniaceae, Calyceraceae and Compositae, and also in some Campanulaceae. The mostly zoophilous flowers typically are tetracyclic and pentamerous but variation of organ number per whorl is known from several families. Flower symmetry is actinomorphic or zygomorphic with bilabiate or unilabiate flowers – actinomorphic and zygomorphic flowers are both found in the capitula of many Compositae – and resupination of flowers is known from Campanulaceae-Lobelioideae and some Stylidiaceae. The sepals are commonly fused (not in Alseuosmiaceae and some Menyanthaceae), and in Compositae the calyx commonly is replaced by a pappus of variable structure assisting in fruit dispersal. Petals are free only in Carpodetaceae, Phellinaceae and some Argophyllaceae, Pentaphragmataceae and Stylidiaceae (*Donatia*). The androecium normally is isomerous with calyx and corolla, and the stamens alternate with the petals. Reduction of stamen number is largely limited to Stylidiaceae. Stamens can be inserted on the corolla or not, and

anthers are mostly tetrasporangiate, basifixed and commonly introrse. Pollen grains are mostly tricolporate, but both colpate or porate pollen grains with an increased number of apertures are known. *Carpodetus* (Carpodetaceae) and *Lechenaultia* (Goodeniaceae) are unusual in having pollen tetrads. The pluri- to unilocular ovary is commonly inferior (or semi-inferior) but superior ovaries are found in some Carpodetaceae, some Goodeniaceae, some Campanulaceae, and in Menyanthaceae, Phellinaceae and Rouseaceae. Ovules usually are anatropous (hemi- to campylotropous in Phellinaceae), unitegmic and tenuinucellate and, where known, endosperm formation is mostly cellular, but nuclear in some Compositae. Fruits are commonly capsules or achenes (= cypselae), rarely berries or drupes. Inulin is found in several families (Calyceraceae, Campanulaceae, Compositae, Goodeniaceae, Menyanthaceae and Stylidiaceae), and iridoids or seco-iridoids are common, but absent from Campanulaceae and Compositae, and apparently also from Alseuosmiaceae, Phellinaceae and Rouseaceae.

A tight integration of stamens and style is found in several families. In most Stylidiaceae, the two stamens are fused with the style to form a pressure-sensitive gynostemium. In Calyceraceae, Campanulaceae, Compositae and Goodeniaceae, the interaction of style and either fused or free anthers results in various forms of secondary pollen presentation (Carolin 1960; Leins and Erbar 1990, 2003; Erbar and Leins 1995). Erbar and Leins (1995) classified these as (1) brushing or pump mechanism in Compositae and Campanulaceae-Lobelioideae (pollen is removed from an anther tube by the elongating style which is hairy or not), (2) deposition (or rarely brushing) mechanism in Campanulaceae-Campanuloideae (pollen from free anthers is deposited on hairs on the outside of the style, these hairs can invaginate or not), (3) cup and cup/brushing mechanism in Goodeniaceae (pollen is deposited in a cup-like outgrowth below the stigma, the indusium; in addition to this cup, hairs can be present on the style) and (4) deposition mechanism of Goodeniaceae (deposition of pollen grains on top of the style). Detailed summaries of character distribution in Asterales have been provided by Lammers (1992; excl. Alseuosmiaceae, Argophyllaceae, Carpodetaceae, Phellinaceae, Rouseaceae) and, covering the entire order, particularly by Lundberg and Bremer (2003).

In spite of the very high molecular support for the order, it is difficult to identify synapomorphies.

Following Lundberg and Bremer (2003), valvate corolla aestivation and the absence of apotracheal wood parenchyma can be identified as synapomorphic. Both these characters, however, are not unique for the order and are variable within it. Previously identified synapomorphies, such as secondary pollen presentation (which is present in the form of different mechanisms and is likely to have arisen more than once; see above) and the presence of inulin, are characteristic only of subgroups of Asterales.

Relationships within the order are clear and well supported in some parts but not in others (Lundberg and Bremer 2003). One well-supported clade identified in several analyses (Chase et al. 1993; Morgan and Soltis 1993; Cosner et al. 1994; Gustafsson and Bremer 1995; Olmstead et al. 2000; Soltis et al. 2000; Bremer et al. 2001; Lundberg and Bremer 2003) consists of Menyanthaceae, Goodeniaceae, Calyceraceae and Compositae (MGCA clade; Fig. 1). This clade is characterized by the presence of petal lateral veins (Gustafsson 1995), the loss of micropylar endosperm haustoria (Cosner et al. 1994), and a thick and multilayered (> 10 cells) integument (Inoue and Tobe 1999). Within this clade, the sister-group relationship between Calyceraceae and Compositae is supported by several potential synapomorphies in wood anatomical (Carlquist and De Vore 1998), inflorescence, flower and fruit morphological and anatomical (Hansen 1992; Gustafsson 1995), and pollen (Hansen 1992) characters. Goodeniaceae are sister to these two families, and the clade consisting of Goodeniaceae/Calyceraceae/Compositae may be supported by pollen grains with a prominent layer with branched columellae and secondary pollen presentation involving fused anthers (Lundberg and Bremer 2003). Lundberg and Bremer (2003) suggested that Stylidiaceae incl. Donatiaceae, a strongly supported clade in their study, are sister to the MGCA clade. A close relationship between Donatiaceae and Stylidiaceae, however, was not found in other analyses (Albach et al. 2001; Bremer et al. 2002), and neither Donatiaceae nor Stylidiaceae were sister to the MGCA clade in these two analyses. Instead, Stylidiaceae were sister to Campanulaceae (Albach et al. 2001; Bremer et al. 2002), and Donatiaceae sister to Alseuosmiaceae/Argophyllaceae/Phellinaceae (Bremer et al. 2002) or to all families except Stylidiaceae/Campanulaceae (Albach et al. 2001). A second possible clade of the order consists of Alseuosmiaceae, Phellinaceae and Argophyllaceae (APA clade; Fig. 1), where

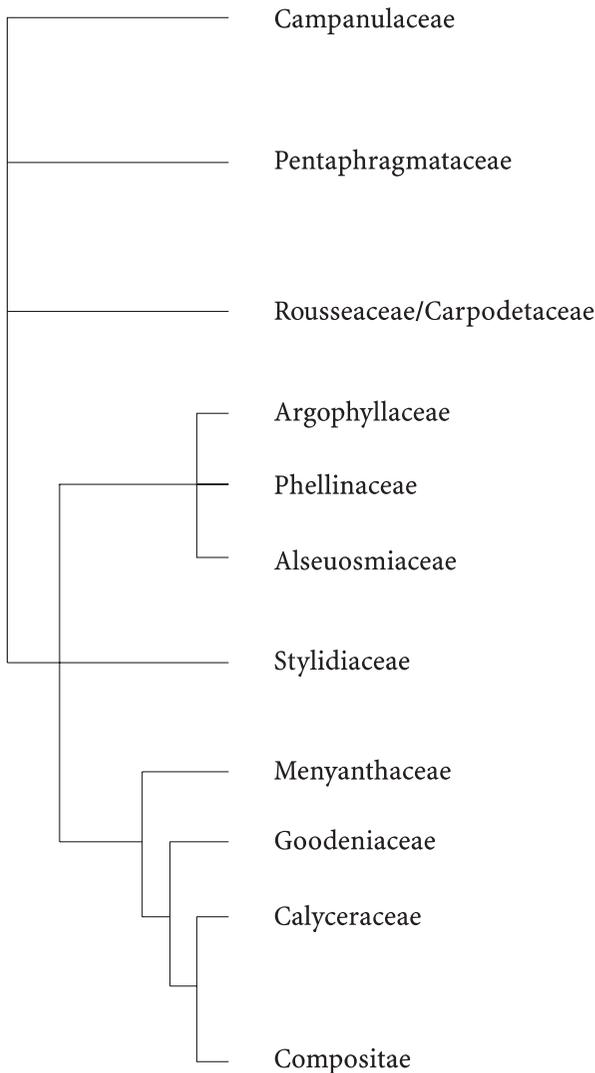


Fig. 1. A phylogenetic hypothesis for the families of Asterales. (Modified from Lundberg and Bremer 2003)

the latter two families probably are sister to each other (Lundberg and Bremer 2003). This clade had already been identified in earlier analyses (Gustafsson et al. 1996; Backlund and Bremer 1997; Gustafsson and Bremer 1997; Källersjö et al. 1998; Kårehed et al. 1999; Savolainen et al. 2000b; Lundberg 2001) and may be supported by pollen being 3-celled at anthesis and the presence of ellagic acid (not known in all groups; Lundberg and Bremer 2003). Stevens (2001 onwards) further records the presence of subepidermal cork as well as serrate and gland-toothed leaf blades as possible synapomorphies. In the analysis of Lundberg and Bremer (2003), the APA clade is sister to the Sty-

liaceae/MGCA clade. All three groups together constitute the “Core Asterales” of these authors and are characterized by having a non-intrusive placenta (Lundberg and Bremer 2003). Sister to this in the analysis by Lundberg and Bremer (2003) is a clade consisting of Rouseaceae (incl. Carpodetaceae), Pentaphragmataceae and Campanulaceae. This clade was resolved as a basal grade (incl. Stylidiaceae as sister to Campanulaceae) by Bremer et al. (2002). The close relationship between *Roussea* and Carpodetaceae is well supported (Savolainen et al. 2000b; Lundberg 2001; Bremer et al. 2002). The possible sister-group relationship between Pentaphragmataceae and Campanulaceae found by Lundberg and Bremer (2003) but not in several other analyses (Cosner et al. 1994; Jansen and Kim 1996; Backlund and Bremer 1997; Olmstead et al. 2000; Savolainen et al. 2000b) may be supported (Lundberg and Bremer 2003) by the presence of a free hypanthium and petal veins which form a dense reticulum (Gustafsson 1995).

In summary, relationships within the order should be viewed (Fig. 1), as by Stevens (2001 onwards), as a polytomy consisting of four lineages. These are (1) Campanulaceae, (2) Pentaphragmataceae, (3) Rouseaceae/Carpodetaceae and (4) a trichotomy of the APA clade, Stylidiaceae (incl. Donatiaceae), and the MGCA clade.

Although the earliest fossils of the order are of Oligocene (c. 29 Ma B.P.) age (Magallón et al. 1999), consideration of phylogenetic relationships and molecular evidence led to the conclusion that the order must have originated c. 100 Ma B.P. in the Cretaceous (Bremer and Gustafsson 1997; Wikström et al. 2001). Stem node and crown node ages of 112 and 93 Ma B.P. respectively were recently estimated by Bremer et al. (2004). The notion of a Cretaceous origin of Asterales certainly requires revision of the observation by Magallón and Sanderson (2001) that Asterales have the highest diversification rate of all angiosperm orders. This inference was based on the assumption of an Oligocene age of Asterales.

Apart from the cosmopolitan Campanulaceae, Compositae and Menyanthaceae, of which Compositae have been postulated to have originated in South America (Bremer 1994) and Campanulaceae which have centres of diversity in southern Africa and Andean South America but also in Eurasia between the Mediterranean region and the Himalayas, all other families of the order have an almost exclusively southern hemispherical distribution, mostly in Australasia and partly in South America. Based on an analysis of ancestral

areas, Bremer and Gustafsson (1997) concluded that the order originated in Australasia. Although this interpretation was based on a rather terminal position of the cosmopolitan Campanulaceae in the phylogeny of the order these authors used, the placement of this family in a basal polytomy (see above) probably will not change the outcome of an ancestral area analysis. Many species of the small families of the order are found in either temperate forest or more open, often humid to wet habitats.

By far the largest amount of generic and species diversity is found in Campanulaceae and Compositae. Interestingly, these are the two major families of the order lacking iridoids or secoiridoids. In

Compositae, the biosynthetic pathway producing iridoids has been blocked and diverted to the production of sesquiterpene lactones (Zdero and Bohlmann 1990), and the diversification of secondary compounds in the family has been held responsible for its great success in terms of species diversity (Cronquist 1977; Lammers 1992). In Campanulaceae, iridoids are replaced by polysterols (particularly Campanuloideae), acetylenes and/or alkaloids (particularly Lobelioideae) which, however, have a biosynthetic origin unrelated to the iridoid pathway (Lammers 1992). It has not been claimed that the success of Campanulaceae is related to their biochemical diversification.

CONSPECTUS OF FAMILIES AS TREATED IN THIS VOLUME

1. Stamens as many as corolla lobes
2. Corolla lobes with distinct wings or appendages
 3. Corolla zygomorphic; herbs, shrubs or scramblers with zygomorphic flowers, fruit a drupe, nut or capsule; 11/400, southern hemisphere, mainly Australia **Goodeniaceae**
 3. Corolla actinomorphic
 4. Plants herbaceous, from wet habitats; flowers actinomorphic, petal lobes often fimbriate or crested; fruit a capsule or rarely a berry; 5/c. 60, subcosmopolitan **Menyanthaceae**
 4. Plants woody
 5. Sepals free, fruit a berry; shrubs or subshrubs, leaf axils with tufts of hairs; flowers actinomorphic; 4/9, Australia, New Zealand, New Guinea and New Caledonia **Alseuosmiaceae**
 5. Sepals fused, fruit a capsule or drupe; shrubs or small trees with actinomorphic flowers; 2/c. 20, Australia, New Zealand, Lord Howe and Rapa Islands, New Caledonia **Argophyllaceae**
2. Corolla lobes without distinct wings or appendages
 6. Petals free
 7. Fruit a drupe; shrubs or small trees with actinomorphic flowers; 1/11, New Caledonia **Phellinaceae**
 7. Fruit a berry or capsule; shrubs or trees with actinomorphic flowers; 3/5, Australia, New Zealand, New Guinea and Solomon Islands **Carpodetaceae**
 6. Petals fused, sometimes corolla tube short
 8. Ovary unilocular with one ovule, inflorescence capitulate
 9. Calyx mostly modified, anthers connate, ovule insertion apical; 1,621/c. 23,300, cosmopolitan **Compositae**
 9. Calyx not modified, anthers free, ovule insertion basal; annual or perennial herbs with actinomorphic flowers in involucre head, fruit an achene; 4/c. 60, South America and Falkland Islands **Calyceraceae**
 8. Ovary two- to multilocular, rarely unilocular with only one ovule, then inflorescence not capitulate
 10. Climbing shrub with opposite or verticillate leaves; flowers actinomorphic, fruit a berry; 1 sp., Mauritius **Rousseaceae**
 10. Not as above
 11. Shrub, flowers inclined, corolla tube short, stamens sessile, fruit a 2-locular capsule; 1 sp., New Caledonia **Platyspermatum (Alseuosmiaceae)**
 11. Not as above
 12. Leaf bases asymmetrical, plants without milky latex; mostly fleshy perennial herbs with asymmetrical leaf blades and actinomorphic flowers, fruit a berry; 1/c. 30, SE Asia **Pentaphragmataceae**
 12. Leaf bases not asymmetrical, plants with milky latex; herbs, lianas, rosette plants, subshrubs, shrubs, treelets or trees with actinomorphic or zygomorphic flowers, fruit a capsule or berry; 84/c. 2,400, cosmopolitan **Campanulaceae**
 1. Stamens fewer than corolla lobes
 13. Corolla lobes free, gynoeceum with separate stylochia; perennial herbs with solitary, actinomorphic flowers and capsular fruits; 1/2, South America, Tasmania and New Zealand **Donatia (Stylidiaceae)**
 13. Corolla lobes fused, gynoeceum with one style; herbs or subshrubs with mostly zygomorphic flowers, filaments and style fused into a column in most genera, fruits capsular; 6/c. 160, southern hemisphere, mainly Australia **Stylidiaceae**

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