Asteraceae and relationships within Asterales

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THE SEARCH FOR THE SISTER OF ASTERACEAE

At the Compositae Conference at Kew in 1994 ("Compositae: Systematics, Biology, Utilization"), DeVore and Stuessy (1995) argued in favor of a sister group relationship between Asteraceae and Calyceraceae, mainly drawing evidences from morphology. Even if a close relationship between Asteraceae and Calyceraceae had been repeatedly suggested ever since Cassini described the latter family (as Boopideae; Cassini 1816), it was perhaps not until the Compositae Conference at Reading in 1975 ("The Biology and Chemistry of the Compositae"), that this relationship was seriously corroborated (Turner 1977), mainly based on similarities in pollen morphology (Skvarla et al. 1977). This hypothesis further gained strength with the identification of the subtribe Barnadesiinae (now subfamily Barnadesioideae) in Mutisieae as the sister group to the rest of the family (Bremer 1987; Jansen and Palmer 1987; Bremer and Jansen 1992; Olmstead et al. 1992). However, the Asteraceae-Calyceraceae sister group relationship was soon challenged by Goodeniaceae (all these taxa, except Asteraceae of course, will be presented in some detail below). Since then there have been three competing hypotheses: a clade of Asteraceae + Calyceraceae with Goodeniaceae (if sampled) as its their sister group (Gustafsson and Bremer 1995; Kim and Jansen 1995; Downie et al. 1996; Jansen and Kim 1996; Bremer and Gustafsson 1997; Carlquist and DeVore 1998; Kårehed et al. 1999; Olmstead et al. 2000; Albach et al. 2001; K. Bremer et al. 2001; B. Bremer et al. 2002; Lundberg and Bremer 2003; Winkworth et al. 2008), or a clade of Goodeniaceae + Calyceraceae with Asteraceae as its sister group (Michaels et al. 1993; Olmstead et al. 1993; Cosner et al. 1994; Savolainen et al. 2000; Soltis et al. 2000, 2007), or a clade of Asteraceae + Goodeniaceae with Calyceraceae (if sampled) as its sister group (Gustafsson and Bremer 1995; Gustafsson et al. 1996). It is possible to find at least some characters in favor of any of these relations (as well as contradicting them), but as shown by DeVore and Stuessy (1993), Hansen (1997), and Lundberg and Bremer (2003), the morphology is mainly in favor of the Calyceraceae-Asteraceae sister group relationship, while it is largely some molecular markers that suggested the other two alternatives. Furthermore, the two best-sampled analyses to date (Lundberg and Bremer 2003; Winkworth et al. 2008) both support the Calyceraceae-Asteraceae sister group relationship. This contribution does not argue for this sister group relationship, but instead gives an overview of what I think is the most likely phylogeny of the Asteraceae alliance, covering the entire order Asterales (sensu APG II 2003; Fig. 10.1; Table 10.1).

PLESIOMORPHIC ASTERACEAE

The family Asteraceae, the focus of this volume, hardly needs any introduction. Instead I will try to give a review of possible plesiomorphic character states that might be
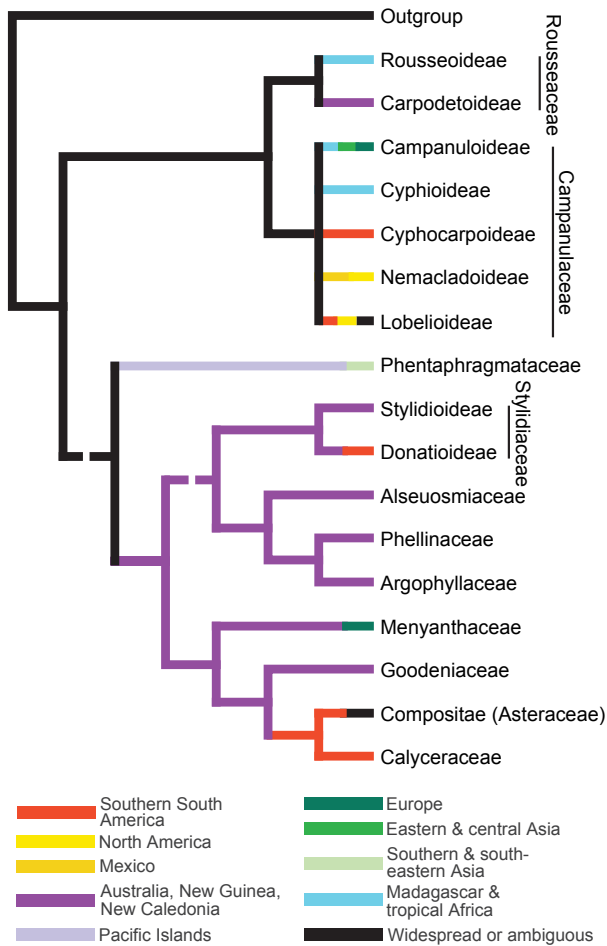
Fig. 10.1. Suggested phylogeny of Asterales, mainly based on the phylogeny presented by Winkworth et al. (2008). The two dotted branches are well supported (posterior probabilities least 0.95) in the Winkworth et al. (2008) Bayesian analysis, but the position of Pentaphragmataceae relative to Core Asterales and Campanulaceae/Rousseaceae, and that of Stylidiaceae relative to the MGCA clade and the APA clade, differ in other analyses of Asterales phylogeny (e.g., Kårehed et al. 1999; K. Bremer et al. 2001; B. Bremer et al. 2002; Lundberg and Bremer 2003).

of interest when discussing the clades most closely related to Asteraceae. Much information is obtained from Jeffrey (2007), some also from Stevens (2001 onwards), Hellwig (2007), and Carolin (2007a).

Spirally, alternate leaves are probably plesiomorphic; opposite leaves are found in some younger clades (e.g., Heliantheae, Liabeae, and some other), and also in some Barnadesioideae (e.g., *Schlechtendalia*, *Duseniella*, and some *Chuquiraga*), but not in Calyceraceae and only in a few Goodeniaceae (some *Scaevola*). It is somewhat more difficult to establish the plesiomorphic growth form; in both Barnadesioideae and Goodeniaceae there are annual and

perennial herbs as well as shrubs (and in Barnadesioideae even trees up to 20 m tall), but in Calyceraceae perennial herbs dominate (in addition to a few annual herbs). The *wood* in Asteraceae is, with the exception of obviously secondary woody members, more or less indistinguishable from that of other woody sympetalous families, indicating that at least some woodiness is plesiomorphic, perhaps shrubs or subshrubs. In many Asteraceae, *internal secretory systems* are present, either as articulated laticifers or laticiferous cells (with a triterpene-rich latex), or as schizogenous secretory canals (resins). These are absent from some genera of Barnadesioideae and Mutisioideae, as well as Calyceraceae and Goodeniaceae, and it is possible that their absence is the ancestral state for Asteraceae.

The capitulum is perhaps the most prominent feature of the family. Capitula are, however, also known from Calyceraceae (in various forms from all genera) and from Goodeniaceae (most well known is *Brunonia*, but some *Dampiera* and *Scaevola* species also have tight head-like inflorescences), as well as many other more distantly related families. The capitula of Asteraceae are indeterminate, in contrast to most capitula of Calyceraceae that are determinate. However, the capitulum of *Acicarpha* differs from all other Calyceraceae in being indeterminate, but the position of this genus within Calyceraceae is still not known with certainty, and the plesiomorphic state for Calyceraceae is uncertain. It seems quite likely, however, that an indeterminate inflorescence is the plesiomorphic state for Asteraceae. The *corolla is initiated* as a ring meristem (Erbar and Leins 1996). This state is shared with nearly all investigated members of the campanulids and is most certainly the plesiomorphic state, with the irregular successive development that has been reported for bilabiate and ligulate corollas in non-asteroid tribes (Harris 1995) only recently evolved. Asteraceae have five stamens with connate anthers (only some wind-pollinated species have free anthers) and free filaments (with very few exceptions, among others some *Barnadesia*). Also Calyceraceae have anthers that are connate, although often only at the base, but with the filaments partly united forming a tube. In Goodeniaceae the filaments are free, but the anthers might be more or less connate (*Anthotium*, *Brunonia*, *Dampiera*, *Diaspasis*, and *Lechenaultia*) or free (all other genera). At least partly connate anthers (and free filaments?) thus seem to be the plesiomorphic state for Asteraceae. The upper part of the filaments form a filament collar, also reported from Calyceraceae and thus probably plesiomorphic for Asteraceae. The plesiomorphic *ovary wall vascularization* (Jeffrey 2007) may consist of a ring of ten vascular bundles (with five fused laterals, and five median bundles), in addition to the four carpellary bundles extending into the style. This pattern can be found in some Barnadesioideae (e.g., *Schlechtendalia*), Stifftieae, and Vernonieae. A similar

pattern is also found in Calyceraceae (Gustafsson 1995). In most other Asteraceae, a more reduced pattern with five ovary wall bundles (two entering the style), in addition to one bundle entering the ovule, is found. Further reductions are also present. The style is single in all Asteraceae, generally with two style arms and papillose, dry stigmatic areas. Since also Calyceraceae (with a single club-like stylar head) and Goodeniaceae (with their peculiar stylar indusia) have a papillose, dry stigma, it is quite safe to assume that this is the plesiomorphic state for Asteraceae. The ovules are anatropous, unitegmic and tenuinucellate and the inner epidermis of the integument differentiates into an integumentary tapetum, all states shared with many other Asterales (Tobe and Morin 1996). The endosperm development is *ab initio* cellular in most Asteraceae, but nuclear in Cardueae and some other groups. In Calyceraceae the endosperm development is likewise *ab initio* cellular, but both nuclear and cellular

developments are found in Goodeniaceae (Tobe and Morin 1996). The *ab initio* cellular endosperm development is, however, the most common state also in the rest of Asterales (but note that the endosperm development, as many other embryological characters, are not known for some of the smaller, less well-known families), and it seems fairly clear that this is the plesiomorphic state for Asteraceae. As in Calyceraceae and Goodeniaceae (as well as Menyanthaceae) no endosperm haustoria are formed (Tobe and Morin 1996).

The mature pollen grains are 3-celled, in contrast to Calyceraceae and Menyanthaceae where the pollen grains are 2-celled when shed (Tobe and Morin 1996), and the 3-celled pollen grains might be an apomorphy for Asteraceae. Spinulate (or smooth) pollen grains are shared between Barnadesioideae and Mutisioideae; they are also found in Calyceraceae and some other families, and are thus probably plesiomorphic in Asteraceae (Hansen 1991;

Table 10.1. The major clades of Asterales, with information on number of genera, species, and distribution.

Clade name	Genera	Species	Distribution
Rousseaceae	4	6	
Carpodetoideae	3	5	E Australia, New Guinea, New Zealand, Solomon Is.
Rousseoideae	1	1	Mauritius
Campanulaceae	84	ca. 2400	
Campanuloideae	50	ca. 1050	Cosmopolitan (Old World)
Cyphioideae	1	64	Africa
Cyphocarpoideae	1	3	Chile
Lobelioideae	29	ca. 2000	Cosmopolitan (New World)
Nemacladoideae	3	15	SW USA, NW Mexico
Pentaphragmataceae	1	30	SE Asia to New Guinea
Core Asterales			
Stylidiaceae	6	ca. 245	
Donatioideae	1	2	Australia, New Zealand, South America
Stylidioideae	5	ca. 245	Australia, New Zealand, (SE Asia, S America)
APA clade			
Alseuosmiaceae	5	10	E Australia, New Zealand, New Caledonia, New Guinea
Argophyllaceae	2	ca. 20	E Australia, Lord Howe Is., New Caledonia, New Zealand, Rapa Is.
Phellinaceae	1	11	New Caledonia
MGCA clade			
Menyanthaceae	5	ca. 60	Almost cosmopolitan
Goodeniaceae	11	ca. 440	Mainly Australia
Calyceraceae	4	ca. 60	Southern South America
Asteraceae	>1600	ca. 23,000	Cosmopolitan

Urtubey and Tellería 1998). In some Calyceraceae and Barnadesioideae, intercolpar concavities are found, but it is still uncertain if they represent a symplesiomorphy for the two families (and thus are plesiomorphic in Asteraceae). Associated with the *secondary pollen presentation*, the tapetum forms pollen kit that facilitates the presentation and transfer of the pollen to the pollinator. Pollen kit production is also found in Calyceraceae, a family that shares a similar pollen-presentation mechanism (Leins and Erbar 1990; DeVore and Stuessy 1995; Erbar and Leins 1995). Also Goodeniaceae have secondary pollen presentation, but involving a structure (the indusium) that is apomorphic for Goodeniaceae. Pollen kit and secondary pollen presentation are thus both probably plesiomorphic for Asteraceae.

The fruits of Calyceraceae and Asteraceae are achenes, that is single-seeded dry fruits formed by a unilocular, inferior ovary often described as indehiscent (but at least in some Asteraceae are split open by the growing embryo at preformed dehiscence lines), crowned by the persistent and more or less modified calyx. Also Goodeniaceae have dry fruits, but both indehiscent and dehiscent fruits (as well as drupes) can be found. In *Brunonia* (Goodeniaceae) a modified persistent calyx is present on top of the dry one-seeded fruit and aids in the dispersal. A dry inferior, one-seeded and basically indehiscent fruit with persistent and modified calyx thus seems to be plesiomorphic for Asteraceae.

The chemistry of Asteraceae is rich and complex, but much of this complexity has evolved after the origin of the family; the chemistry of early-branching clades such as Barnadesioideae seems to be less specialized than that of younger groups. Inulin is, however, found through the family, but it is also shared with most other members of Asterales and its presence is plesiomorphic for Asteraceae. Another family of compounds, often associated with Asteraceae, are the bitter, toxic sesquiterpene lactones, but these seem to be absent from Barnadesioideae, and are thus probably an apomorphy for the non-barnadesioid Asteraceae (they are particularly complex among the asteroid tribes). The antibiotic, toxic acetylenes (earlier often referred to as polyacetylenes), mainly present in the resin ducts are also present in Goodeniaceae (although apparently not in Calyceraceae), and their presence might be plesiomorphic for Asteraceae. On the other hand, iridoids, present in Calyceraceae and Goodeniaceae as well as other families of Asterales, are absent from Asteraceae, but their absence is strongly correlated with the presence of sesquiterpene lactones as they share the same metabolic pathway.

Although the *haploid chromosome numbers* in Asteraceae range from 2 up to 120, the most common number is 9, and this has been hypothesized also to be the plesiomorphic number (e.g., Jeffrey 2007), while in Calyceraceae the plesiomorphic number is $x = 8$ (Hellwig 2007) and in

Goodeniaceae both $x = 8$ and $x = 9$ are fairly common. The plesiomorphic number for Asteraceae is thus still uncertain (but see Chapter 4).

It has been suggested (e.g., DeVore and Stuessy 1995) that the ancestral, plesiomorphic distribution of Asteraceae is southern South America, the present-day distribution of many Barnadesioideae and Calyceraceae. The scanty early fossil record of Asteraceae, Calyceraceae and Goodeniaceae (Muller 1981; Graham 1996) make it difficult to date the split between Calyceraceae and Asteraceae. Based mainly on external evidence, DeVore and Stuessy (1995) and Stuessy et al. (1996) argued for the split to correlate with the increasing aridity and temperature fluctuations in southern South America during early Oligocene. Thus the area for the split could have been the zone between the northern tropical/subtropical forests and the cool temperate forests to the south, perhaps just north of the then partly submerged Patagonia (Stuessy et al. 1996). Molecular dating of the split between Asteraceae and Calyceraceae have given older time estimates for the split; Kim et al. (2005) dated the split to mid Eocene (approximately 42–49 Ma), with a major radiation within Asteraceae during the Oligocene, coinciding with the rapid cooling of the Antarctic region following the final separation of the Australian continental block from Antarctica ca. 35 Ma (Li and Powell 2001).

If we speculate, we can thus hypothesize an ancestral Asteraceae as a subshrub or small shrub with alternate, spirally inserted leaves, growing in what today is southern South America just north of Patagonia, sometime around middle or late Eocene. Secretory systems were absent (but some precursors might have been present). The flowers were numerous and in an indeterminate capitulum, with the corolla initiated as a ring meristem, and the sympetalous corolla had five lobes. The five stamens had free filaments but more or less connate anthers, and the upper parts of the filaments were differentiated into an anther-collar. The ovary vascularization consisted of five lateral and five median bundles in the ovary wall, and four carpellary bundles extending into the single style. There were two style arms, with papillose, dry stigmatic areas. The single ovule was anatropous, unitegmic, tenuinucellate with an integumentary tapetum and *ab initio* cellular endosperm development. The mature pollen grains were 3-celled, somewhat sticky by the presence of pollen kit, and presented to the pollinator by the style. The pollen were spinulate and had intercolpar concavities. The fruit was an achene, crowned by a modified calyx that aided in dispersal. Inulin was present as a storage compound. Sesquiterpene lactones were not present, but polyacetylenes might have been. Iridoids were probably absent. The basic chromosome number might have been $x = 8$ or $x = 9$.

With this very hypothetical first Asteraceae in mind, we will visit all the major clades in Asterales, discussing relevant characters.

CALYCERACEAE AND ASTERACEAE

The sister group to Asteraceae is the small family Calyceraceae (Fig. 10.2A; four genera and some sixty species). They are endemic to southern South America where they are mostly found in high-altitude arid habitats, especially in the Andes (Hellwig 2007). They are annual or perennial herbs, with the flowers in capitula surrounded by the involucral bracts. This is not the only similarity with Asteraceae; other potential synapomorphies can be found in the stamens (the filament collars), pollen (spinulate or smooth pollen with intercolpar concavities and presence of pollen kit), ovaries (unilocular ovaries with a single ovule), the mechanisms of the secondary pollen presentation, and the fruits (achene with a persistent, modified calyx). There are also dissimilarities that are not easily explained; most notable is the orientation of the single ovule in the ovary. Asteraceae have a basal and erect ovule, while Calyceraceae have a pendulous ovule, and this difference in orientation has been used as an argument against a sister group relationship between the two families (e.g., Cronquist 1981).

GOODENIACEAE, CALYCERACEAE AND ASTERACEAE

The sister to the Calyceraceae-Asteraceae clade is the medium-sized, largely Australian family Goodeniaceae (Fig. 10.2B; eleven genera including *Brunonia*, Brunoniaceae, ca. 440 species; Carolin 2007a). The species with a distribution outside Australia are mainly found in coastal subtropical and tropical areas, apparently the results of recent long-distance dispersals. Goodeniaceae are mostly herbs or shrubs, but small trees and scramblers are also known. The variation of inflorescences is greater in Goodeniaceae than in its sister-clade; here we find cymes, thyrses, racemes, spikes, heads, subumbels and solitary flowers. Based on some striking similarities (polysymmetric flowers in a dense head, connate anthers, lack of endosperm, ovary with a single and basal ovule), it has earlier been speculated that *Brunonia* may be the closest relative to Asteraceae, but with the more likely placement of *Brunonia* as sister to one of the two major clades of Goodeniaceae (see, e.g., Gustafsson et al. 1996), these similarities are better explained as parallelisms and thus apomorphies for *Brunonia*. The other Goodeniaceae have zygomorphic flowers with petal wings (i.e., delicate, marginal appendages of the corolla lobes; Gustafsson 1995),

bilocular and often more or less inferior ovaries, and a peculiar, unique form of secondary pollen presentation (lost in *Brunonia*): the pollen are collected in a cup-shaped structure, the indusium, at the top of the style, from where the pollen are presented to the pollinator. The often many-seeded fruits are variable within the family, but mostly consisting of laterally dehiscing capsules, although also drupes and nuts can be found. There are some possible synapomorphies for the Goodeniaceae-Calyceraceae-Asteraceae clade. The presence of secondary pollen presentation might be one (although the mechanisms differ within the clade, and as we will see it is also found in other more distantly related members of Asterales), as may a dry and more or less papillate stigma, and a persistent calyx (but in Goodeniaceae not modified). The split between Goodeniaceae and the Calyceraceae-Asteraceae clade might date back to the onset of the cooling at the end of the Early Eocene Climate Optimum (approximately 50 Ma; Zachos et al. 2001) and correlate with the break-up of Australia from Antarctica (starting 95 Ma, but with land contact between Australia and Antarctica maintained through the South Tasman Rise until about 40 Ma; Li and Powell 2001).

THE MGCA CLADE: MENYANTHACEAE, GOODENIACEAE, CALYCERACEAE AND ASTERACEAE

The sister clade to the three families described above is Menyanthaceae (Fig. 10.2C). This small family of five genera and ca. sixty species of aquatic and marshland herbs has an almost cosmopolitan distribution (Kadereit 2007). The two monotypic genera, *Menyanthes* and *Nephrophyllidium*, have an exclusively northern hemisphere distribution, and probably form a clade separated from the three remaining, mainly southern-hemispheric genera (Lundberg and Bremer 2003; *Liparophyllum* not sampled). *Villarsia* and the monotypic *Liparophyllum* are both nearly exclusively Australian, while *Nymphoides* is primarily tropical in distribution, but with a few species in the north temperate regions. Menyanthaceae are all glabrous herbs with rootstocks or rhizomes, and the leaves are often forming rosettes. The flowers are actinomorphic and in several species quite large (some *Nymphoides* species are cultivated as ornamentals in ponds and have thus been widely introduced) with sympetalous corolla and sometimes delicate petal wings similar to those in Goodeniaceae (Gustafsson 1995). The more or less superior ovary is unilocular (but bicarpellate), and the fruit is generally a capsule (rarely a berry) with few to many seeds. Not known from the other Asterales is the heterostyly found in all genera but *Liparophyllum*, often combined with self-incompatibility.

Fig. 10.2. Selected Asterales. **A** *Calycera herbacea* Cav. (Calyceraceae), Argentina; **B** *Lechenaultia formosa* R. Br. (Goodeniaceae), Western Australia; **C** *Nephrophyllidium crista-galli* Gilg (Menyanthaceae), northwestern North America; **D** *Argophyllum grunowii* Zahlbr. (Argophyllaceae), New Caledonia; **E** *Platyspermation crassifolium* Guillaumin (Alseuosmiaceae), New Caledonia; **F** *Phelline* sp. (Phellinaceae), New Caledonia; **G** *Donatia novae-zelandiae* Hook. f. (Stylidiaceae), Tasmania; **H** *Stylidium schoenoides* DC. (Stylidiaceae), Australia; **I** *Pentaphragma aurantiaca* Stapf (Pentaphragmataceae), Borneo; **J** *Carpodetus serratus* J.R. Forst. & G. Forst. (Rousseaceae), cultivated at University of Oxford Botanic Garden; **K** *Roussea simplex* Sm. (Rousseaceae) visited by a

Phelsuma cepediana gecko (Gekkonidae), Mauritius; **L** *Campanula persicifolia* L. (Campanulaceae), Sweden. [Photographs: A, J.M. Bonifacino; B, G. Watson, from Watson and Dallwitz 1992 onwards; C, A. Tasler; D, R. Amice; E, F, D. and I. Létocart; G, M.G. Hanna; H, P. Mann; I, T. Rodd; J, T. Waters; K, D. Hansen; L, C. Johansson.]

The clade with Menyanthaceae, Goodeniaceae, Calyceraceae and Asteraceae (the MGCA clade of Lundberg and Bremer 2003) is well-supported both by molecular and morphological data, and there are several possible synapomorphies: the presence of petal lateral veins, the absence of (micropylar) endosperm haustoria, and a thick and multilayered integument (Inoue and Tobe 1999). Other suggested synapomorphies include the presence of scalariform perforation plates, the frequent occurrence of sclerified idioblasts, binucleate mature pollen and multinucleate tapetal cells, and the at least partial fusion of lateral veins of adjacent petals, but their occurrences are either not known in sufficient detail among other Asterales outside the MGCA clade, or can equally well be interpreted as parallelisms within the clade. The similarity in the petal wings of Goodeniaceae and Menyanthaceae suggests that they are an apomorphy for the clade, but structures reminiscent of petal wings are also found in other closely related clades.

THE CORE ASTERALES CLADE: MGCA, STYLIDIACEAE AND APA

If the MGCA clade is well supported and present in all recently published molecular phylogenies, its sister group is more difficult to identify. Kårehed et al. (1999), as did Lundberg and Bremer (2003), suggested that Stylidiaceae (including *Donatia*) are the sister group to the MGCA clade, with the three families Alseuosmiaceae, Phellinaceae, and Argophyllaceae (the APA clade of Lundberg and Bremer 2003) as their successive sister group. Albach et al. (2001), on the other hand, in a sparsely sampled analysis suggested a clade with the two families Argophyllaceae and Alseuosmiaceae as the sister group to the MGCA clade with *Donatia* as their successive sister (Phellinaceae not sampled), while B. Bremer et al. (2002) suggested the APA clade together with *Donatia* to form a clade sister to the MGCA clade (with Stylidiaceae s.str., i.e., without *Donatia*, in both Albach et al. (2001) and B. Bremer et al. (2002) as sister to Campanulaceae). In a recent large-scale Bayesian phylogeny of the angiosperms, Soltis et al. (2007) found the APA clade to be sister to the MGCA clade, with Stylidiaceae s.l. as their successive sister group. Another, but more densely sampled, Bayesian analysis focusing on the campanulids (Winkworth et al. 2008) obtained a clade with Stylidiaceae s.l. together with the APA clade as the sister group to the MGCA clade (Fig. 10.1). In summary, it seems quite likely that the sister group to the MGCA clade is either the APA clade (Albach et al. 2001; Soltis et al. 2007), Stylidiaceae (Kårehed et al. 1999; Lundberg and Bremer 2003), or a clade of Stylidiaceae (and/or *Donatia*) together with the APA clade (Bremer

et al. 2002; Winkworth et al. 2008). Even if the phylogeny suggested by Winkworth et al. (2008) is the most robust suggested up to now (a total of nine DNA markers, but not very densely sampled among Asterales), a trichotomy with the MGCA clade, the APA clade, and Stylidiaceae (incl. *Donatia*) is still the best representation of the present understanding of the phylogeny. These three major clades constitute the "Core Asterales" of Lundberg and Bremer (2003). This Core Asterales clade is well supported by molecular data (e.g., Lundberg and Bremer 2003; Soltis et al. 2007; Winkworth et al. 2008), although reliable morphological synapomorphies are yet to be identified.

STYLIDIACEAE

The medium-sized family Stylidiaceae (Fig. 10.2G, H; five genera including *Donatia*, ca. 245 species) is mainly distributed in Australia (in particular its southwestern parts) and New Zealand, with a few species in southeastern Asia and South America. The family can be divided into two subfamilies (Lundberg and Bremer 2003; Carolin 2007b; but see Wege, 2007, for the alternative view of treating the subfamilies as separate families), Donatioideae with *Donatia* (two species) only, and Stylidioideae with the remaining four genera (*Forstera*, *Levenhookia*, *Stylidium* including *Oreostylidium*, and *Phyllachne*). There are some marked differences between the two subfamilies, but also possible synapomorphies. Most prominent of the latter are the imbricate petals (all other Asterales have valvate petal bud aestivation) and a reduction in the numbers of stamens (three stamens in *Donatia fascicularis*, and two stamens in all other Stylidiaceae). Other suggested synapomorphies include unilacunar nodes, the absence of wood rays, the presence of extrastaminal floral nectar disc, and extrorse anthers. The differences in favor of a recognition of the two subfamilies as distinct families include the sympetalous corolla in Stylidioideae in contrast to the free petals in *Donatia*, the floral column formed by the stamens united with the style and found only in Stylidioideae but not in *Donatia* (where the stamens are free but close to the style), and some differences in vegetative anatomy (Rapson 1953; e.g., the replacement of the stem epidermis by a hypodermis in *Donatia*, scalariform vessel element perforation plates in *Donatia* but simple perforations in Stylidioideae, and stomata paracytic in *Donatia* but anomocytic in Stylidioideae). Most if not all of these differences can be interpreted as apomorphies for either Donatioideae or Stylidioideae (with the contrasting states as plesiomorphies). The flowers of *Donatia* and a few Stylidioideae are actinomorphic, but in the other species more or less zygomorphic. The floral column, the most striking feature of Stylidioideae, is active in the

transfer of pollen to the pollinator, and very active indeed in the genus *Stylidium*, the trigger-plants. In this genus the column is touch-sensitive, so when the pollinator brushes the column it is triggered and very rapidly strikes the pollinator, at the same time depositing pollen from the anthers or picking them up onto the stigmata. Self-pollination is prevented in many species by protandry. After being triggered, the column slowly resets, to be triggered again by the next visitor. In *Levenhookia*, the column is released only once, and the pollen is sprayed over the pollinator. Within Stylidioideae, it appears that *Forstera* and *Phyllachne* are paraphyletic with respect to each other, and *Phyllachne* might better be merged into *Forstera* (Wagstaff and Wege 2002).

THE APA CLADE: ALSEUOSMIACEAE, PHELLINACEAE AND ARGOPHYLLACEAE

The third major clade in Core Asterales is the APA clade, consisting of the three small families Alseuosmiaceae, Phellinaceae, and Argophyllaceae. This clade is well-supported by molecular data (Kårehed et al. 1999; Lundberg and Bremer 2003; Winkworth et al. 2008), but it has been difficult to identify synapomorphies for it. This is at least partly due to lack of information on these three families, but so far serrate and gland-toothed leaves (Stevens 2001 onwards) and 3-nucleate mature pollen (Lundberg and Bremer 2003) have been suggested. All three families are woody (shrubs or small trees) with alternate leaves and a similar distribution: Alseuosmiaceae (five genera with ten species) are present in eastern Australia, New Zealand, New Caledonia, and New Guinea; Argophyllaceae (two genera with some twenty species) in eastern Australia, New Zealand, New Caledonia, Lord Howe Island, and Rapa Island; and Phellinaceae (one genus with eleven species) are endemic to New Caledonia. It is possible that Argophyllaceae and Phellinaceae are sister to each other, but also here only a few synapomorphies have been identified to date (presence of subepidermal cork, a short style, apotropous ovules, and crassinexinous and rugulose pollen; Stevens 2001 onwards; Lundberg and Bremer 2003). Alseuosmiaceae (Fig. 10.2E) are shrubs (or sometimes small trees or subshrubs) with spirally arranged leaves and, possibly a synapomorphy for the family, small tufts of rusty brown, multicellular uniseriate hairs in the leaf axils (in *Platyspermation*, probably sister to the rest of Alseuosmiaceae, these hairs are not restricted to the leaf axils but are more dense there). Except for *Platyspermation* with short corolla tube and spreading corolla lobes, the flowers are funnel-shaped or more or less bell-shaped, and the corolla lobes in all genera have more or less prominent appendages or papillae,

somewhat reminiscent of petal wings (Gustafsson 1995; Kårehed 2007a). Also Argophyllaceae (Fig. 10.2D) are shrubs or small trees, but the petals are only connate at the base and have fringed appendages on the inner surfaces near the base (corolline ligules; Eyde 1966; Gustafsson 1995; Kårehed 2007b). Peculiar for Argophyllaceae, and giving *Argophyllum* its name, are the T-shaped hairs found on most parts of the plants (Al-Shammary and Gornall 1994), and especially on the lower surface of the leaves where they can give a silvery or whitish impression. Phellinaceae (Fig. 10.2F) are also small trees or shrubs with the leaves sometimes densely arranged in pseudo-whorls, but with free petals without any appendages (Barriera et al. 2007). It is possible that other synapomorphies will be discovered when more is known about the distribution of anatomical, embryological, phytochemical and karyological characters as well as the reproductive systems. The fruits in the APA clade are berries (most Alseuosmiaceae), drupes (Phellinaceae, *Corokia* in Argophyllaceae) or capsules (*Platyspermation* and Argophyllaceae except *Corokia*).

PENTAPHRAGMATACEAE

Although the support for Core Asterales is high, its sister group is still not known with any certainty. The most recently published phylogeny suggests Pentaphragmataceae as sister to Core Asterales, followed by a clade with Campanulaceae and Rousseaceae as sister to all remaining Asterales (Fig. 10.1). This relationship was obtained in the Bayesian analysis of Winkworth et al. (2008), but their sampling was made with the phylogeny of the entire campanulids in mind, and not to resolve relationships within the orders. The most likely alternatives to this hypothesis are either a clade with Pentaphragmataceae together with Campanulaceae as the sister group to Core Asterales followed by Rousseaceae as sister to all other Asterales (Kårehed et al. 1999; B. Bremer et al. 2002, but with *Stylidium* as the closest sister to Campanulaceae!), or a clade with Pentaphragmataceae as sister to Campanulaceae followed by Rousseaceae as sister to these two families only (Lundberg and Bremer 2003). *Pentaphragma* (with ca. 30 herbaceous species of southeastern Asia, the Malay Archipelago, and New Guinea) is the sole genus in Pentaphragmataceae (Fig. 10.2I; Lammers 2007b), and was for a long time closely associated with Campanulaceae, by some authors even included in this family. It differs from Campanulaceae in many respects, most markedly in its asymmetrical leaf bases (somewhat reminiscent of *Begonia*) and the flowers in helicoid cymes, but also in wood anatomy, lack of secondary pollen presentation and associated syndromes, pollen morphology, embryology (endosperm with single-celled micropylar

haustoria only), and floral structures (the hypanthium is adnate to the ovary only by five longitudinal septa, perhaps of filamental origin, thus creating five nectariferous pits; Vogel 1998). In *Pentaphragma*, the fruit is a berry with numerous seeds. Unfortunately, almost nothing is known about the phytochemistry or reproductive systems, including dispersal, of this genus.

THE BASAL DIVISION: CAMPANULACEAE AND ROUSSEACEAE

As noted above, the sister to all other Asterales might be a clade with Campanulaceae and Rousseaceae (Winkworth et al. 2008; Fig. 10.1). Campanulaceae (Fig. 10.2L), the bellflowers and lobelias, hardly need any lengthy introduction (see Lammers 2007a, for more information). Its 84 genera (and nearly 2400 species) are shared among five subfamilies of markedly unequal size. Unfortunately, neither the relationships between the subfamilies, nor among the genera within the subfamilies, are particularly well known even if some recent progress has been made (e.g., Eddie et al. 2003; Antonelli 2007). Two of the subfamilies, Cyphioideae with *Cyphia* (64 species in Africa) and Cyphocarpoideae with *Cyphocarpus* (three species in Chile), are monogeneric, Nemacladoideae have three genera and fifteen species endemic to southwestern United States and adjacent parts of Mexico, while the two cosmopolitan subfamilies Lobelioideae (with 29 genera and almost 1200 species, most of them in South America) and Campanuloideae (with 50 genera and about 1050 species, most of them in Africa, Asia, and Europe), share the greater part of the species diversity. Most Campanulaceae are herbs (although there are some woody species forming trees up to 15 m tall) with alternate, spirally arranged leaves (rarely opposite or whorled). A network of articulated laticifers is associated with the phloem, and the latex produced is milky and white (or sometimes colored), and in Lobelioideae rich in pyridine alkaloids (replaced by polysterols in Campanuloideae). Neither iridoids nor sesquiterpene lactones are produced in Campanulaceae. The flowers of the subfamilies are quite different in symmetry, but are often showy and larger than those found in many other families of Asterales. The ovary is often inferior with the hypanthium adnate to it, and the fruits are often capsular, dehiscing by valves, slits or pores, but also indehiscent dry, papery fruits or berries are present. Various forms of secondary pollen presentations are found in Campanulaceae (Leins and Erbar 2006). In Campanuloideae, with mostly actinomorphic corollas of various shapes, the pollen is released from the introrse anthers and collected by hairs on the growing style. These hairs are commonly invaginating, thus facilitating the transfer of the pollen to the visiting pollinator. In Lobelioideae, with more or less zygomorphic flowers and coherent anthers forming an anther tube, a pump mechanism is present. The pollen is collected by a ring of stylar hairs just below the stigmatic lobes, and is then pushed up through the anther tube by the growing style. Species of *Cyphia* (the sole genus of Cyphioideae) lack stylar elongation, but collect the pollen in a "pollen box" formed by the emptied anthers as the walls and the stylar tip furnished with a ring of rigid hairs at the bottom. The pollination biology of Nemacladoideae and Cyphocarpoideae is much less studied. The pump mechanism of Lobelioideae, together with the presence of inulin as storage compound (present in the whole family), has inspired hypotheses about a close relationship between Asteraceae and Lobelioideae, but it seems fairly certain that the secondary pollen presentation of both clades are parallelisms, and that the presence of inulin is a plesiomorphy shared with many other (perhaps all?) members of Asterales.

The sister of Campanulaceae might be the small woody family Rousseaceae (Fig. 10.2J, K; Winkworth et al. 2008; but see the discussion above). Rousseaceae s.l. (Lundberg 2001; but see Koontz et al. 2007, and Gustafsson 2007) consists of two subfamilies, Rousseoideae with the genus *Roussea* (one species endemic to Mauritius) and Carpodetoideae with three genera (and five species in eastern Australia, New Guinea, New Zealand, and the Solomon Islands). They are shrubs or trees (to 20 m tall) or climbers (*Roussea*) with alternate or opposite (*Roussea*) and gland-toothed leaves. The petals are clearly connate in *Roussea*, but becoming free early in the development in the other genera. The flowers are also much larger in *Roussea* than in the other genera. In *Roussea* the petals are thick and fleshy, revolute at the apex, and the flowers produce copious amounts of nectar. It seems that the flowers are pollinated by geckos that also aid in dispersing the seeds by eating the berries (D. Hansen, pers. comm.). In Carpodetoideae the fruits are either berries (fleshy in *Abrophyllum* and leathery in *Carpodetus*) or loculicidal capsules (*Cuttsia*). The ovaries are superior in *Roussea*, *Abrophyllum* and *Cuttsia*, but more or less inferior in *Carpodetus*, and in all genera commonly 5(–7)-locular with numerous ovules. In Asterales, multilocular ovaries are otherwise almost only restricted to some Campanuloideae.

With the dichotomy between the Campanulaceae-Rousseaceae clade on one side, and the Pentaphragmataceae–Core Asterales clade on the other, we have reached the basal node of Asterales. Only some few uncertain synapomorphies for Asterales have so far been suggested (K. Bremer et al. 2001; Lundberg and Bremer 2003), including valvate aestivation (also frequently found outside Asterales and thus perhaps a plesiomorphy), presence of inulin (not investigated for several important clades,

most notably the Rousseaceae and the APA clade), a base chromosome number of $x = 9$ (only a few chromosome counts are available for Rousseaceae and the APA clade), and secondary pollen presentation (probably better interpreted as of two apparently independent origins within Asterales, one for Campanulaceae and one for the Goodeniaceae-Asteraceae-Calyceraceae clade, respectively). It is, however, possible that there are other synapomorphies to be identified when the embryology, palynology and phytochemistry of the badly known clades in Asterales and its immediate relatives among the campanulids are more studied.

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