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Asterids

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Abstract

Asterids (over 80,000 species) are grouped into 10 orders and about 100 families. Molecular phylogenetic analyses have supported a phylogeny with a core of euasterids consisting of two main clades: lamiids and campanulids. The order Cornales is the most basal clade in the asterids followed by Ericales as the closest relative of the euasterids. The asterid timetree shows that divergences among the 10 orders occurred in the early Cretaceous, 128–106 million years ago (Ma). A majority of the asterid families evolved before the Cretaceous–Paleogene boundary (66 Ma). These results suggest that continental breakup during the Cretaceous may have influenced the early diversification of asterids.

Asterids constitute one of the major clades of the flowering plants (Fig. 1). It comprises more than 80,000 species or nearly one-third of all flowering plants. They are grouped in 10 orders and about 100 families (1, 2). Two of the five most species-rich flowering plant families are asterids, the sunflower Family Asteraceae with 23,000 species and the coffee or madder Family Rubiaceae with about 13,000 species. There are hundreds of economically important species within the asterids, and some families are particularly important sources for foods, spices, flavorings, or drugs. Active chemical substances (e.g., alkaloids) are common in many species. The most important are coffee (*Coffea arabica* in Rubiaceae) and tea (*Camellia sinensis* in Theaceae), which both contain caffeine and similar alkaloids. Tobacco (*Nicotiana tabacum*) with its active substance nicotine is a member of Solanaceae, a family that contains several other poisonous and hallucinogenic plants. Periwinkles (*Catharanthus roseus*) of the Apocynaceae yield potent alkaloid drugs, which have drastically lowered mortality in leukemia.

A few asterid species have oil-rich fruits and are important sources of vegetable fatty acids; oil from olives (*Olea europaea* in Oleaceae) and sunflower (*Helianthus*

annuus in Asteraceae). Two important staple crops belong to the order Solanales, sweet potatoes (*Ipomoea batatas* in Convolvulaceae) and potatoes (*Solanum tuberosum* in Solanaceae). Two cosmopolitan although mainly Mediterranean families, Lamiaceae and Apiaceae, are well known as sources of spices or vegetables; Apiaceae include dill (*Anethum graveolens*), celery (*Apium graveolens*), coriander (*Coriandrum sativum*), carrot (*Daucus carota*), fennel (*Foeniculum vulgare*), and parsley (*Petroselinum crispum*), and Lamiaceae include lavender (*Lavendula*), mint (*Mentha*), basil (*Ocimum*), oregano and marjoram (*Origanum*), rosemary (*Rosmarinus officinalis*), and thyme (*Thymus*). Other families also include important vegetables; for example, lettuce (*Lactuca sativa*) and artichokes (*Cynara cardunculus*) from Asteraceae, and tomatoes (*Solanum lycopersicum*), and chillies, and red and green pepper (*Capsicum annuum*) from Solanaceae. Asterids comprise numerous horticulturally important genera or species; only a few examples can be mentioned here, for example heath (*Erica* in Ericaceae) and lilacs (*Syringa* in Oleaceae); and forget-me-not (*Myosotis* in Boraginaceae) and in Asteraceae there are several hundred commonly cultivated species of *Ageratum*,



Fig. 1 Asterid representatives (clockwise, from upper left). *Cornus* sp., Cornaceae, Cornales; *Campanula glomerata*, Campanulaceae, campanulids; *Lamium maculatum*, Lamiaceae, lamiids; *Erica vestita*, Ericaceae, Ericales. Credits: B. Bremer, K. Bremer, and T. Eriksson (*Lamium*).

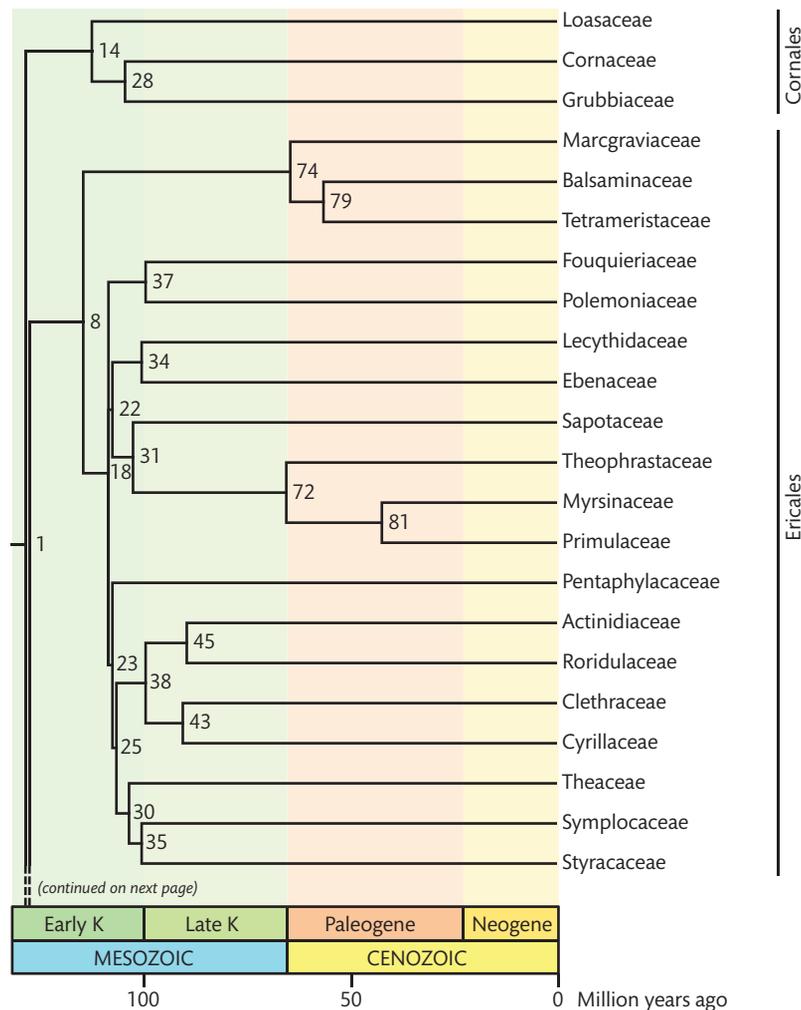


Fig. 2 Continues

Aster, *Dahlia*, *Doronicum*, *Gerbera*, *Helichrysum*, and *Rudbeckia*, for example. Asterids are often characterized morphologically as herbaceous plants with bisexual, insect-pollinated flowers, stamens in one circle, and sympetalous corollas; many contain iridoids. In the following paragraphs, I review the relationships (see also under asterids in a review of tricolpates; 3) and divergence times of the 10 orders and families of the asterids.

When molecular data became available about 15 years ago, it became evident that the asterids are a much larger group of plants than earlier assumed (4–6). Later analyses of more plants and genes corroborated the first molecular analyses and generated more detailed knowledge of the group (7–17). The most comprehensive molecular study of the asterids with over 100 families investigated for six different chloroplast markers (*rbcl*, *ndhF*, *matK*, *trnT-trnF* including *trnL*, *trnV-*atpE**, *rps16* intron) was

published in 2002 by Bremer *et al.* (1). In that study the basal interrelationships were supported for the first time, with Cornales as the first clade to branch off and being closest to a clade of Ericales and the euasterids. The euasterids are split in two main clades, the lamiids and the campanulids, both with strong support. The lamiids contain the order Garryales, Gentianales, Solanales, and Lamiales, and the campanulids contain the Aquifoliales, Apiales, Dipsacales, and Asterales. Family interrelationships within orders are in most cases not fully resolved. In a later, but more taxon-restricted study based on the nuclear gene RPB2, a gene with two paralogues (18), the same general phylogeny was supported but with a few unexpected exceptions. Holly (*Ilex*—Aquifoliales) and the genus *Escallonia* usually assigned to the campanulids (e.g., 1, 15) instead belong to the lamiids. However, these results remain to be corroborated by other studies.

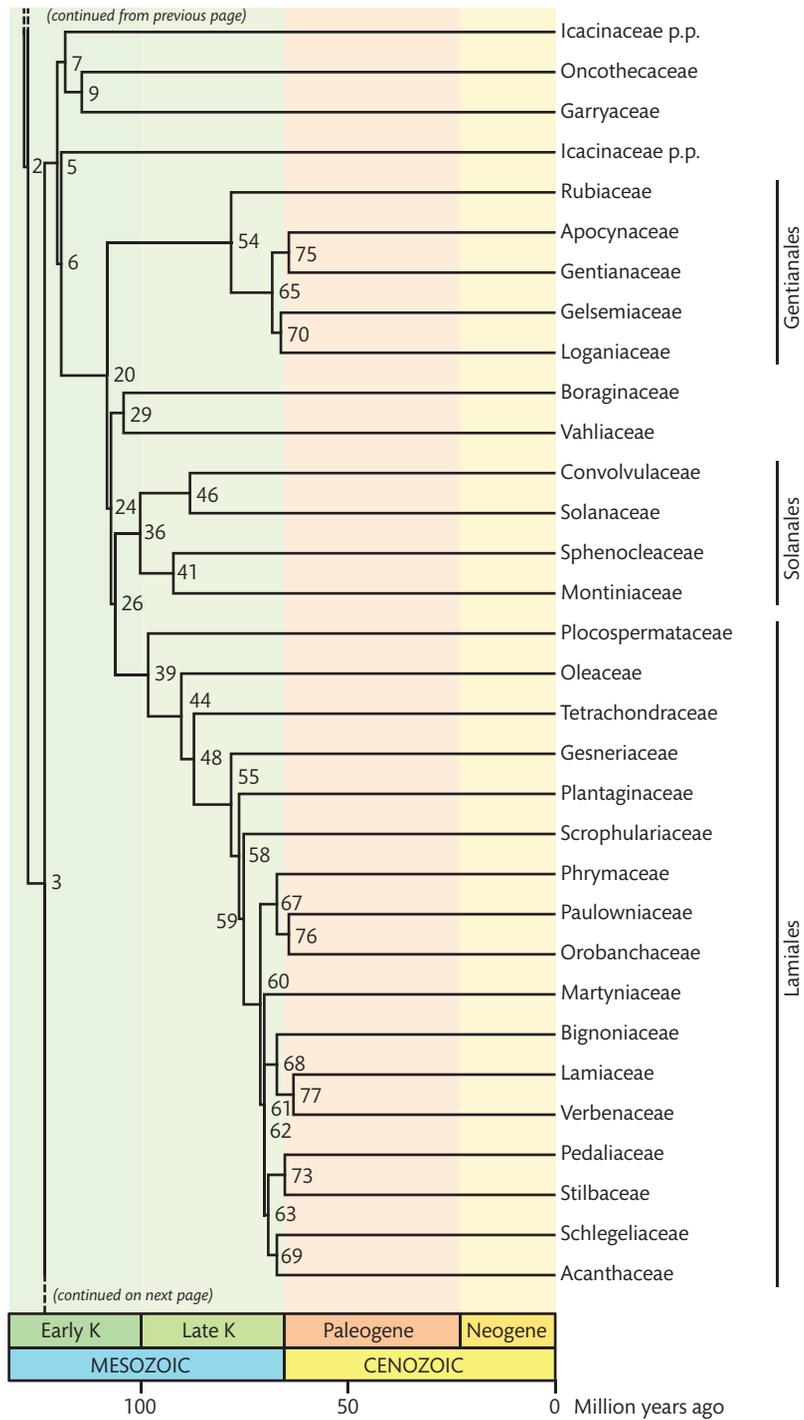


Fig. 2 Continues

Cornales is difficult to characterize but many members have small flowers with free petals and few stamens. The position of Cornales as closest to the other asterids, that is Ericales and euasterids, seems to be settled (1,

15, 17), even if a single gene analysis (of *matK*), without support, contradicts these results (19). Relationships of the six to eight families are still not fully understood despite several studies (1, 20–22). In the latest study of

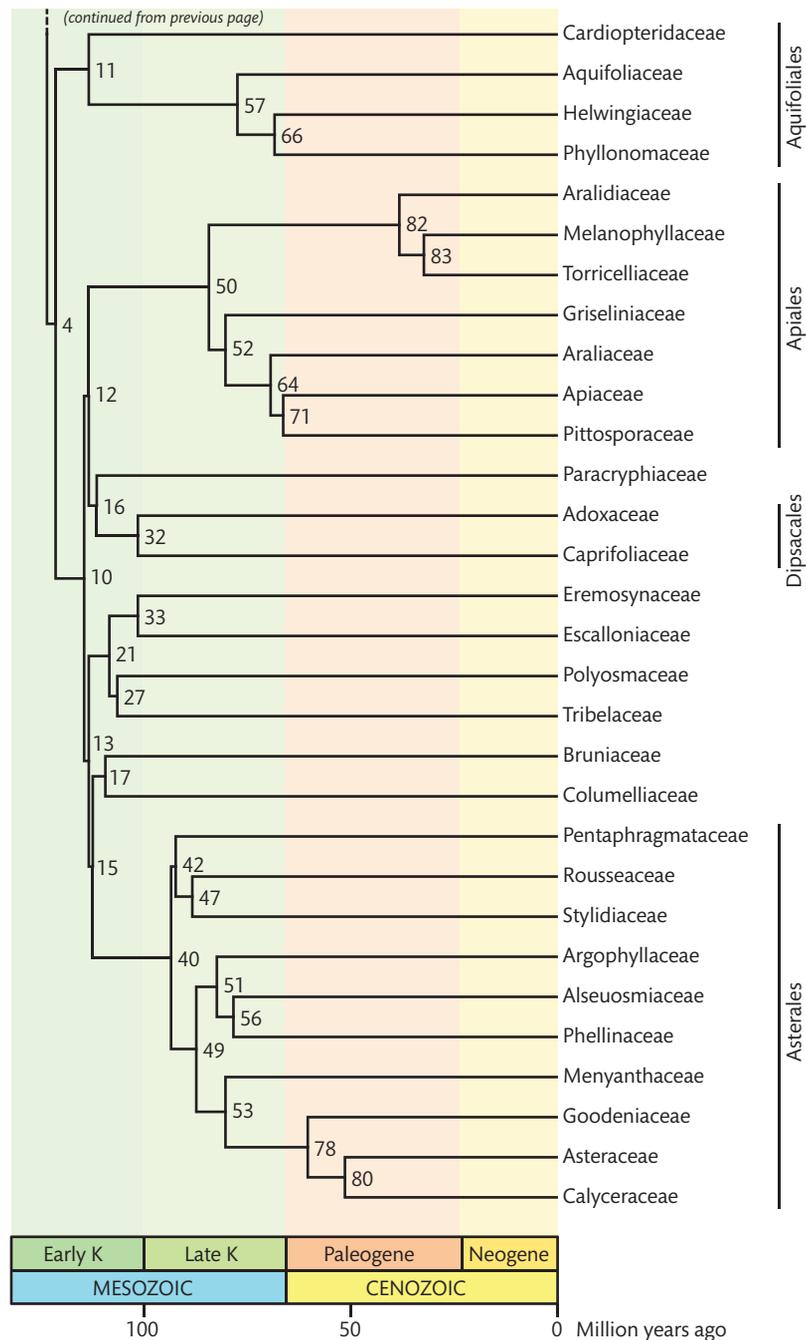


Fig. 2 A timetree of asterids. Divergence times are shown in Table 1. *Abbreviation:* K (Cretaceous).

the order (22) which is the most comprehensive and is based on three molecular markers (26S rDNA, *matK*, *rbcl*), the authors recognize eight families of which three are monogeneric: Cornaceae, Alangiaceae, and Hydrostachyaceae. The other families are supported as monophyletic with high to moderate bootstrap support,

Nyssaceae (79%), Mastixiaceae (93%), Grubbiaceae (97% including Curtisiaceae), Loasaceae (98%), and Hydrangeaceae (67%). There are no or very low support for the interrelationships of the families in the study. The highest support is for the close relatives Nyssaceae and Mastixiaceae (72%) and it should be noted that

Table 1. Divergence times (Ma) among asterids.

Timetree		Estimates		Timetree		Estimates	
Node (Fig. 2)	Time (Ma)	Ref. (54) Time	Ref. (59) Time	Node (Fig. 2)	Time (Ma)	Ref. (54) Time	Ref. (59) Time
1	128.0	-	128	43	90.0	54-43	90
2	127.0	-	127	44	90.0	64-55	90
3	123.0	112-102	123	45	89.0	-	89
4	121.0	107-99	121	46	88.0	66-65	88
5	120.0	-	120	47	88.0	-	88
6	119.0	-	119	48	87.0	-	87
7	118.0	-	118	49	87.0	77-70	87
8	114.0	-	114	50	84.0	-	84
9	114.0	-	114	51	82.0	-	82
10	114.0	101-94	114	52	80.0	-	80
11	113.0	-	113	53	80.0	69-65	80
12	113.0	-	113	54	78.0	64-61	78
13	113.0	-	113	55	78.0	-	78
14	112.0	-	112	56	78.0	-	78
15	112.0	-	112	57	77.0	-	77
16	111.0	-	111	58	76.0	57-45	76
17	109.0	-	109	59	75.0	-	75
18	108.0	-	108	60	71.0	-	71
19	108.0	-	108	61	70.0	-	70
20	108.0	89-83	108	62	70.0	-	70
21	108.0	-	108	63	69.0	-	69
22	107.0	-	107	64	69.0	-	69
23	107.0	-	107	65	68.0	-	68
24	107.0	-	107	66	68.0	-	68
25	106.0	-	106	67	67.0	-	67
26	106.0	-	106	68	67.0	-	67
27	106.0	-	106	69	67.0	-	67
28	104.0	-	104	70	66.0	-	66
29	104.0	-	104	71	66.0	-	66
30	103.0	-	103	72	65.0	42-40	65
31	102.0	-	102	73	65.0	-	65
32	101.0	81-78	101	74	64.0	-	64
33	101.0	80-72	101	75	64.0	-	64
34	100.0	-	100	76	64.0	-	64
35	100.0	63-61	100	77	63.0	-	63
36	100.0	78-76	100	78	60.0	-	60
37	99.0	-	99	79	56.0	-	56
38	99.0	-	99	80	51.0	-	51
39	98.0	-	98	81	42.0	33-26	42
40	93.0	-	93	82	38.0	-	38
41	92.0	-	92	83	32.0	-	32
42	92.0	-	92				

Note: Node times in the timetree represent the mean of time estimates from different studies. In ref. (59), semiparametric rate smoothing was employed in the analysis of six molecular markers and six fossil calibrations were used within the asterids. Ref. (54) involved an analysis using a nonparametric rate smoothing of a three molecular marker and calibrated with one fossil outside the asterids. Note that not all clades are congruent between the two studies.

these together with Alangiaceae and Cornaceae were all included in the last family in APG II (2). The phylogenetic position of *Hydrostachys* (Hydrostachyaceae) is probably the most problematic one. It is a morphologically much reduced water plant and many of its chloroplast genes show a great number of substitutions that might mislead the analyses (15). Possibly, *Hydrostachys* may belong in or together with Hydrangeaceae (23).

Ericales comprise mostly woody plants with alternate, simple leaves; most members contain ellagic acid. Variation in floral characters is great. A choripetalous corolla, one-whorled androecium, two integuments, and cellular endosperm seem to be plesiomorphic conditions in the order, but all characters are to some extent homoplastic (24). The close relationship between Ericales and the euasterids is now strongly supported (1) and in recent years major progress has been achieved in resolving the phylogeny of the large order Ericales comprising over 10,000 species (e.g., 4–6, 25–27). Representatives of all of the approximately 23 families have been included in three recent comprehensive molecular studies (1, 24, 28) based on 6, 11, and 5 molecular markers, respectively. The closest relatives to most families are now well understood, with sequence data of up to 20 kb. The order comprises two strongly supported closest relatives, one comprising Marcgraviaceae, Tetrameristaceae, and Balsaminaceae, and another comprising the rest of the order (1, 24, 28). Of the 20 families in this group, all except three (Lecythidaceae, Pentaphragmaceae, Theaceae) are included in one of five well-supported family groups: the *balsaminoid* group (Marcgraviaceae, Tetrameristaceae, and Balsaminaceae), the *polemonoid* group (Fouquieriaceae and Polemoniaceae), the *ericoid* group (Ericaceae, Cyrillaceae, Clethraceae, Sarracenaceae, Actinidiaceae, and Roridulaceae), the Diapensiaceae group (Diapensiaceae, Styracaceae, and Symplocaceae); and the *primuloid/ebenoid* group (Myrsinaceae, Primulaceae, Theophrastaceae, Maesaceae, Ebenaceae, and Sapotaceae).

Interrelationships of these five family groups are not resolved. Within the *primuloid/ebenoid* group the first three families (Myrsinaceae, Primulaceae, and Theophrastaceae) form a clade. In the latest study of the Ericales (28), a Bayesian analysis supports two new groups. One of these includes all families except the *balsaminoid* family group and *polemonoid* group, the other includes the *ericoid* family group and the Diapensiaceae family group together with Theaceae. However, these two new groups (with Bayesian support) were not supported in a corresponding parsimony analysis.

Euasterids are characterized by a sympetalous corolla with epipetalous stamens. There is convincing molecular support for a monophyletic euasterid group (100% in 1, 19) and also strong support for the two subgroups of lamiids (100% in 1) and campanulids (99% in 1), respectively. This relationship has been shown before but with lower support (e.g., 17, 19, 29).

Lamiids are well supported by molecular data (1, 17, 19) but difficult to characterize morphologically. The basal relationships of the lamiids are still partly obscure, despite analysis of six markers (1). The problems involve taxa of the Icacinaceae and Oncothecaceae which are not placed to order. Further, Icacinaceae has in recent studies been demonstrated to be at least biphyletic (29, 30, 31). All four orders of the lamiids are supported as monophyletic (1) Garryales (100%), Gentianales (100%), Solanales (90%), and Lamiales (100%).

Garryales comprise dioecious shrubs or trees. The order forms a strongly supported clade with two families only, Garryaceae (including Aucubaceae; 2) and Eucommiaceae (1, 19). Interrelationships among Garryales, Icacinaceae, Oncothecaceae, and remaining lamiid orders are still unresolved.

There is a strongly supported (100%) and taxon-rich group of core lamiids. Here belong the three orders Gentianales, Lamiales, and Solanales, each strongly supported as monophyletic (1), and also Boraginaceae (including Ehretiaceae and Hydrophyllaceae) and Vahliaceae. Ever since the first molecular cladistic analyses of a comprehensive asterid set of taxa (5, 6), it has been clear that these core lamiid taxa are closely related (1, 15, 17, 29, 30) but their interrelationships remain an open question.

Gentianales are characterized by stipules with specific glands (colleters; secondarily absent in some, e.g., Gentianaceae), unique within the asterids. Rubiaceae, the second largest asterid family, is the closest relative of the other families and these are characterized by internal phloem. Alkaloids are very common in the order and also in several other asterids. The present circumscription of Gentianales was established when molecular data became available. The order comprises five monophyletic and strongly supported families: Apocynaceae, Gelsemiaceae, Gentianaceae, Loganiaceae, and Rubiaceae (1). The six-gene analysis (1) showed Apocynaceae and Gentianaceae as closest relatives, and these two together as closest to the pair of Gelsemiaceae and Loganiaceae. However, the taxon sampling was very small in the six-gene analysis and in a study with more taxa but only two gene interrelationships were unresolved (32).

Solanales is an order with few if any unique morphological characters. Alternate leaves are present in all five families. There are a few unique characters for Convolvulaceae and Solanaceae, for example, wood characters and occurrence of similar alkaloids. The order, including five families, was supported as monophyletic by the six-gene analysis (1). Earlier analyses have not included all families or the order has not been resolved as monophyletic (13, 29, 30). There is a close relationship between Solanaceae and Convolvulaceae (1, 13), and between Hydroleaceae and Sphenocleaceae (1), but interrelationships of these two family pairs and the Family Montiniaceae are uncertain. The position of Montiniaceae in Solanales has been disputed and ontogenetic and anatomical data point more to an affinity to Escalloniaceae (33).

Lamiales in general (but not basal groups Plocospermataceae, Oleaceae, and Tetrachondraceae) have zygomorphic flowers where the five corolla lobes are arranged in a bilabiate flower with reductions in stamen numbers. Most Lamiales have four or two stamens. The order is known as a highly supported clade of asterid families (13, 17, 29, 34, 35, 36). Lamiales currently contain more than 20 families (1, 2) but many are difficult to circumscribe (16, 38, 39). Within the order the basal branches are strongly supported. Plocospermataceae is closest relative to the rest of the Lamiales followed by Oleaceae as closest to the rest (17, 34, 37), then Tetrachondraceae as closest to the rest (37), and subsequently Gesneriaceae as closest to the rest of the order (including also *Peltanthera* and *Sanango*; 17, 15, 37). There is strong support for the monophyly of Plantaginaceae (including Globulariaceae) and Scrophulariaceae (including Myoporaceae and Buddlejaceae; 1, 16, 17, 36) in their new circumscriptions. There is one well-supported group of families comprising Phrymaceae, Paulowniaceae, and Orobanchaceae (including Cyclocheilaceae). Interrelationships of the remaining families, viz. Acanthaceae (including Avicenniaceae), Bignoniaceae, Byblidaceae, Lamiaceae, Lentibulariaceae, Martyniaceae, Pedaliaceae, Schlegeliaceae, Stilbaceae, and Verbenaceae, are unclear.

Campanulids are divided by a basal split into two main groups, as demonstrated with strong support in several molecular studies, Aquifoliales and the rest of the campanulids, respectively (1, 5, 17, 29, 31).

Aquifoliales have stipules and they provide a possible character, otherwise rare in asterids (occur also in Gentianales and Garryales). Another unique character may be the unisexual flowers found in most members (occurs also in Garryales). Fleshy fruits may

be another feature for Aquifoliales, although fleshy fruits occur also within all the other orders and have evolved independently several times. Helwingiaceae and Phyllonomaceae both have epiphyllous inflorescences. It has been shown that Aquifoliales contains not only Aquifoliaceae, Helwingiaceae, and Phyllonomaceae (2) but also some former Icacinaceae genera (2, 29). It has been proposed (31) that many former Icacinaceae genera belong in Cardiopteridaceae or Stemonuraceae, families formerly of uncertain position but now shown to belong in Aquifoliales. The relationships between the families of Aquifoliales seem to be fully resolved and strongly supported (31). Cardiopteridaceae is closest to Stemonuraceae and these two are closest to the rest with Aquifoliaceae as closest to the pair of Phyllonomaceae and Helwingiaceae.

The core campanulids, the closest relative to Aquifoliales, contain the three well-defined and strongly supported orders, Apiales, Dipsacales, and Asterales, as well as a number of families without order (1, 2, 40), viz. Bruniaceae, Columelliaceae, Eremosynaceae, Escalloniaceae, Paracryphiaceae, Polyosmaceae, Sphenostemonaceae, and Tribelaceae. The relationships among these families and the three orders are in most parts still unclear. One clade with high to medium support (1, 40) includes Eremosynaceae, Escalloniaceae, Polyosmaceae, and Tribelaceae. Earlier studies including some of these taxa have also failed to give a clear indication of where they belong within the campanulids (29, 30). Another supported group is that between Paracryphiaceae, *Quintinia* and Sphenostemonaceae (40). The relationship between *Paracryphia* and *Sphenostemon* has also been demonstrated in another study (30).

Apiales members generally have an enlarged sheath of the petiole, a unique character for this group. They have free petals with alternate stamens differing from most other asterids but this feature occurs also in various other groups of the asterids, for example, Cornales. Apiales is a strongly supported order (1, 17, 19, 29, 41). The order contains 10 families (2, 41), with Pennantiaceae as closest to the rest of the families. The next clade contains one branch with Aralidiaceae, Melanophyllaceae, and Torricelliaceae (1, 41) and another branch with Griselinaceae as closest to Pittosporaceae, Myodocarpaceae, Mackinlayaceae, Apiaceae, and Araliaceae. Circumscriptions and delimitations of particularly Apiaceae, Araliaceae, and Pittosporaceae are problematic (e.g., 42, 43).

Dipsacales have many taxa with zygomorphic flowers, although there are several exceptions with regular

flowers, for example in Valerianaceae. The monophyletic order (1, 15, 17, 29, 44–46) now contains two or alternatively seven families (2). If seven families are accepted, Adoxaceae is the closest relative of the rest of the families (= Caprifoliaceae s. l.). Valerianaceae and Dipsacaceae are well supported as closest relatives (1, 46), so is a clade of these two families together with Morinaceae and Linnaeaceae (46, 47). The interrelationships of this clade, Diervilleaceae and Caprifoliaceae, *sensu stricto* are not resolved with any strong support.

Asterales includes 12 or 13 families (1, 2). Most species have valvate corolla aestivation in contrast to the more common imbricate condition in the asterids. The storage compound is the carbohydrate inulin in many Asterales and it is another probable character. Rouseaceae (40) is closest to the rest of the order, however only with low support. An early recognized (48–50) and strongly supported group contains Asteraceae, Calyceraceae, Goodeniaceae, and Menyanthaceae. There is strong support for Menyanthaceae as closest to the other three families (1). The interrelationships among Asteraceae, Calyceraceae, and Goodeniaceae differ in different studies (1, 17, 29, 30, 50–52). Another supported group of families comprises Argophyllaceae, Alseuosmiaceae, and Phellinaceae (51). The interrelationships among these three families remain somewhat unclear. The exact positions of the Families Pentaphragmataceae, Campanulaceae, Stylidaceae, and Donatiaceae differ in different studies and are so far not convincingly demonstrated.

The divergence time of angiosperms in general have been estimated in a number of studies based on differences in DNA sequences and the age of relevant fossils (e.g., 53, 54). Wikström *et al.* (54) included many asterid taxa. There are a few studies addressing questions about specific orders, families, or genera of asterids (55–58). One paper of Bremer *et al.* (59) has the focus on dating the asterid plants in particular. These authors investigated 111 taxa representing 82 of the 102 asterid families. As most families were represented by a single taxon, only interfamily divergence times were estimated, but for most other clades within-family estimates were made, between the earliest-diverging lineages. Wikström *et al.* (54) investigated a three-gene data set using non-parametric rate smoothing and one calibration point from one rosoid fossil, a species distant from the asterids. They estimated the split of asterids from their closest relatives to be at least 122–112 Ma, and the earliest split among living asterids to be 117–107 Ma. Bremer *et al.* (59) used six molecular markers (three coding and three noncoding) with focus on the asterid families and they

used six asterid fossils as calibration points. Their main dating method was a semiparametric rate smoothing by penalized likelihood. They also used alternative dating methods and subsets of data to explore the effects for various sources of error. Only asterid taxa were included so the divergence time for the asterids as a group was not estimated, but the earliest split among living asterids was estimated to be at least 128 Ma (mean value for the six fossils). They found that analyses with one fossil at a time gave different results and found no way to tell which calibration point was “wrong”; so they considered the mean value as the best estimate (as in Table 1). Wikström *et al.* (54) obtained consistently younger age estimates, mostly 10 to 20 million years younger for most major groups and orders. The reason is probably that the asterids are in a phylogenetically derived position in their tree (54) and comparison with fossils—not used as constraints in their analysis—shows that the age of such derived groups is underestimated in their results (54). It should be noted that there are many more uncertain, weakly supported clades (<50% jackknife support) in their analysis (54) compared to the six fossil–six gene analysis of Bremer *et al.* (59). In the latter study all orders, except for the Garryales, are well supported (>85% jackknife support). Estimated divergence times for the different clades, presented below and in Table 1 (Fig. 2), are generally based on the study by Bremer *et al.* (59), unless otherwise stated.

The fossil record of asterids is extensive particularly from younger strata, but many older asterid fossils of well-preserved floral structures are also known from the Lower Cretaceous. However, despite the increasing number of Cretaceous fossils, few can be assigned to modern taxa at the level below the order. Whole plant preservation is rare, and most fossils are typically detached organs such as leaves, fruits, seeds, flowers, or dispersed pollen. This could explain some of the problems in placing fossils in modern taxa. The six reference fossils chosen from within the asterids and used as calibration points (59) are all described based on reproductive structures and can be attached unequivocally to the phylogenetic tree. The fossils are all from strata that are considered relatively well dated. Each fossil here is mentioned in connection to its phylogenetic position (59). All divergence time estimates in the following discussion are minimum estimated ages and the errors associated with these estimates are left out in the interest of simplifying the discussion. For details of the accuracy of the estimates, readers are referred to the original publication (59).

Cornales was the first order to split off when the asterids diversified in the early Cretaceous, 128 Ma (59), and earliest split among living asterids is estimated as 112 Ma. Divergence times were not estimated for all included families due to uncertainty of relationships and also as few representatives were included (59). In other studies, Cornaceae has been estimated to have diverged from Alangiaceae 58 Ma (57) or 73–64 Ma (54). In the latter study, all investigated families (Cornaceae, Alangiaceae, Hydrangeaceae, Hydrostachyaceae, Loasaceae, Nyssaceae) were estimated to have divergence dates before various ages from 92 to 61 Ma. The oldest fossil that could be related to Cornales and Cornaceae is *Hironoia fusiformis*, an extinct taxon collected from the Futaba Group sediments at Kamitikaba, Japan (60). Synapomorphies of the fruits of the fossil occur also in extant Cornaceae. The age of the sediments is established as early Coniacian to early Santonian, giving a minimum age for the Nyssaceae–Mastixiaceae branch as early coniacian about 88 Ma (60).

Soon after the Cornales split off, Ericales diverged from the remaining stock of the asterids, the euasterids, at 127 Ma (59). Most included families are estimated to be of early Cretaceous age, only Balsaminaceae, Tetrameristaceae, Myrsinaceae, and Primulaceae are distinctly younger. Four of the ~20 families (Pentaphragmaceae, Styracaceae, Tetrameristaceae, and Theaceae) are estimated to have a divergence time of 107, 100, 56, and 103 Ma, respectively (59). Fossils with synapomorphies indicating affinity to Ericales and Pentaphragmaceae are common in the Lower Cretaceous. The oldest fossils of this group are characteristic seeds clearly assignable to the modern genus *Eurya* and included in an extinct species, *Eurya crassitesta*. *Eurya* is known from several core samples and localities in Central Europe ranging in age from the Santonian about 86 Ma and onward (61). There are also fossils assignable to Actinidiaceae. The oldest are from late Turonian (about 89 Ma) of Central Europe and include characteristic seed synapomorphies shared with those of the modern genus *Saurauia*. Two extinct species were established, *Saurauia alenae* and *Saurauia antique*, both recorded from several assemblages in Central Europe and ranging in age from the late Turonian to the Maastrichtian (61).

The earliest split among living euasterids, which is the same as the divergence times of the lamiids and campanulids, is estimated to be 123 Ma (59). Lamiids are estimated to have diversified 119 Ma (59) with radiation of “Icacinae” and the remaining lamiids (Garryales and the core lamiids). The oldest fossil of lamiids is a taxon of

Icacinae (59) from the Turonian (~89 Ma) of Central Europe. The record is based on fruits and is assigned to the extinct genus and species *Icacinicarya budvarensis*. The species occurs in late Turonian (89 Ma) to Santonian sediments of the Klikov sequence of the Czech Republic (61). The estimated divergence time of the order Garryales is 114 Ma, and the divergence time for the core lamiids is estimated to be 119 Ma. The relationships between the three orders Gentianales, Solanales, and Lamiales are not yet fully understood (see earlier). Gentianales is estimated to have diverged 108 Ma, and much later, 78 Ma, it diversified into two clades, one including the species-rich Family Rubiaceae (59), the other the families Apocynaceae, Gentianaceae, Gelsemiaceae, and Loganiaceae. Solanales is estimated to have diverged 106 Ma with a split off of Montiniaceae 92 Ma. Lamiales has an estimated divergence time of 106 Ma and later, 97 Ma, it is split up (59) with the earliest splits among living families estimated as Acanthaceae 54 Ma, Gesneriaceae 71 Ma, Orobanchaceae 48 Ma, Plantaginaceae 66 Ma, Scrophulariaceae 68 Ma, and Tetracondraceae 46 Ma.

In the campanulids the first deep split is between Aquifoliales and the core campanulids estimated to have taken place 121 Ma. Aquifoliales with its new expanded circumscription, including also Stemonuraceae and Cardiopteridaceae (31), is dated back to the early Cretaceous, with the earliest split among living lineages estimated as 113 Ma. The fossil record of Aquifoliales is sparse, particularly from the Cretaceous. The oldest representatives of the family are fruits from the Maastrichtian (~70 Ma) flora of Eisleben, Germany, assigned to the modern genus *Ilex* and included in the extinct species *Ilex antique* (61). The synapomorphic fruit structures are common in floras of the Tertiary. Extant species of *Ilex* are suggested to diversified during the Tertiary (62, 63).

The core campanulids contain three orders: Apiales, Dipsacales, and Asterales, and diversified in the early Cretaceous. The order Apiales is estimated to have diverged 113 Ma (59), first with a deep split at 84 Ma between the group containing Araliaceae, Melanophyllaceae, and Torricelliaceae and the group containing Griselinaceae, Pittosporaceae, Myodocarpaceae, Mackinlayaceae, Apiaceae, and Araliaceae. The earliest Apiales fossils are from the Maastrichtian (about 70 Ma) floras of Eisleben and Walbeck, Germany, and include five extinct species assigned to the modern genera *Acanthopanax* (*Acanthopanax friedrichii*, *Acanthopanax gigantocarpus*, *Acanthopanax mansfeldensis*, *Acanthopanax obliquocostatus*) and *Aralia* (*Aralia antiqua*), based on shared-derived traits in the fruits (61). Dipsacales is estimated

to have diverged 111 Ma with the first split between the Adoxaceae and the Caprifoliaceae, at 101 Ma, and with the earliest split among living lineages of Caprifoliaceae estimated as 75 Ma. An early provisional dating of the Dipsacales (64), with the fossil flower *Silvianthemum* as a reference placed among core campanulids close to *Quintinia*, estimated the earliest divergences among living members of Dipsacales to be only 70–60 Ma. Later Bell and Donoghue (58) dated the Dipsacales using many more taxa and using different methods (local clocks, nonparametric rate smoothing, penalized likelihood, Bayesian relaxed clock), coding and noncoding DNA markers, and four different Dipsacales fossils as calibration points. They found very variable age estimates for their data, dependent on the different fossils and methods, a pattern similar to that shown by Bremer *et al.* (59). Their analyses (58) imply that Dipsacales including the two main lineages Adoxaceae and Caprifoliaceae s.l. originated in the Cretaceous, 103.7 ± 6.3 Ma, whereas diversification of Adoxaceae and Caprifoliaceae mainly occurred in the Cenozoic. Asterales was estimated to have diverged 112 Ma (59). This is within the range of an earlier estimate to 96 ± 28 Ma (55) based on *rbcL* sequences and calibration with fossil Asteraceae pollen. The well-known sunflower family (Asteraceae) diverged from its closest relative much later (51 Ma) but the order also comprises several small, mainly southern hemisphere families that originated in the late Cretaceous and early Tertiary (55).

The estimation of the divergence time for the asterids, in conclusion (according to Bremer *et al.* 59), is that the asterids and its major subgroups euasterids, lamiids, campanulids, and all 10 orders diverged during the Early Cretaceous. The different orders diverged during a period from 128 to 106 Ma. Of these orders Cornales, Ericales, and Aquifoliales also diversified in the same period, Dipsacales and Solanales in the mid-Cretaceous, and the other orders of core campanulids and core lamiids in the Late Cretaceous. A majority of the 100 asterid families diverged during the Late Cretaceous. The results are not supported by the fossil record in the sense that no asterid fossil has so far been discovered from Early Cretaceous. The estimated divergence times correspond well with the continental breakup from early to mid-Cretaceous, and these events may have played a key role in diversification of the asterids.

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