

A PHYLOGENETIC STUDY OF THE ORDER ASTERALES USING ONE MORPHOLOGICAL AND THREE MOLECULAR DATA SETS

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We obtained two most parsimonious cladograms using a data set of 100 characters derived from morphology, anatomy, embryology, chemistry, and karyology, combined with three nucleotide sequence data sets (the chloroplast genes *atpB*, *ndhF*, and *rbcL*) in a phylogenetic analysis of all 12 currently recognized families in the angiosperm order Asterales, represented by 40 genera. Most clades were supported by a jackknife value of at least 50% and a Bremer support of 5 or more. Rouseaceae *sensu lato* (including Carpodetaceae), together with Pentaphragmataceae and Campanulaceae s.l., is the sister group to the rest of the Asterales. A sister group relationship between *Donatia* and Stylidiaceae is well supported both morphologically and by molecular data, and we suggest that *Donatia* should again be treated as a subfamily in Stylidiaceae. The sister group relationship between Calyceraceae and Asteraceae is well supported.

Keywords: Asteraceae, Asterales, *atpB*, Calyceraceae, Campanulaceae, combined analysis, *Donatia*, *ndhF*, phylogeny, *rbcL*, Stylidiaceae.

Introduction

The order Asterales comprises more than 10%, or 26,000 species, of the angiosperm species diversity. The vast majority of them, or ca. 23,000 species (Bremer 1994a), are classified in one single family, the easily characterized Asteraceae. Thus, it is not surprising that in the Asterales often only this family is included (Thorne 1968; Dahlgren 1975; Cronquist 1981; Takhtajan 1997). The presumably closely related Campanulaceae and their relatives were sometimes also included, but more often they have been treated as a separate order, Campanulales (Takhtajan 1997). Campanulales have usually included Campanulaceae, with the subfamilies Campanuloideae, Lobelioideae, Cyphioideae, and the recently erected Nemacladoideae and Cyphocarpoideae and their supposed relatives Pentaphragmataceae and Sphenocleaceae (Thorne 1968, 1992; Dahlgren 1975; Takhtajan 1997), and sometimes also Goodeniaceae, Brunoniaceae, Calyceraceae, Stylidiaceae, and Donatiaceae in various combinations (Takhtajan 1966, 1983; Cronquist 1981; Thorne 1992). Today, Sphenocleaceae have been transferred to Solanales (Cosner et al. 1994), and Brunoniaceae are included in Goodeniaceae (Carolin 1977; Gustafsson 1996; Gustafsson et al. 1996).

Furthermore, many taxa have been moved from various positions in the angiosperm system to a more inclusive Asterales: (1) Menyanthaceae, formerly included in Gentianales either as a family of its own or as a subfamily in Gentianaceae, are now included in a clade that also consists of Asteraceae, Calyceraceae (Downie and Palmer 1992; Olmstead et al. 1992), and

Goodeniaceae; (2) *Argophyllum* of Argophyllaceae has often been placed in Saxifragaceae-Escallonioidae (Engler 1890, 1928), while the second genus of Argophyllaceae, *Corokia*, often has been included in Cornaceae (Hooker 1867; Harms 1897; Wangerin 1910; Allan 1961; Melchior 1964; and others), although some authors noted that the two genera seemed to be closely related (Engler 1928; Eyde 1966). Today, they are recognized as members of the same family in Asterales on the basis of embryological (Kapil and Bhatnagar 1992) and molecular (Gustafsson et al. 1996; Kårehed et al. 1999; Olmstead et al. 2000) evidence; (3) Rouseaceae (including Carpodetaceae; Lundberg 2001), with four genera formerly included in different subfamilies in the Englerian Saxifragaceae (Engler 1928), are now recognized as a member of Asterales (Gustafsson and Bremer 1997; Koontz and Soltis 1999; Lundberg 2001); (4) Phellinaceae, a monogeneric family treated as a member of Aquifoliaceae (Aquifoliales) by Baillon (1892) and Loesner (1901, 1942), are now regarded as sister group to Argophyllaceae (Backlund and Bremer 1997; Gustafsson and Bremer 1997; Kårehed et al. 1999); and (5) Alseuosmiaceae, a diverse family with its four genera earlier variously placed in Caprifoliaceae (Hooker 1873 and Fritsch 1891, among others), Ericaceae (Bentham 1869; Drude 1889; Stevens 1971), or close to a heterogeneous Escalloniaceae (Airy Shaw 1965; Thorne 1992) or an even more heterogeneous Grossulariaceae (including Escalloniaceae; Cronquist 1981), are now considered the sister group to a Phellinaceae-Argophyllaceae clade (Backlund and Bremer 1997; Gustafsson and Bremer 1997; Kårehed et al. 1999). Thus, the number of families included in Asterales has increased from just one (or at most eight) to 12 in only 10 yr.

Even if we now have a much better understanding of what taxa should be included in Asterales, there are still uncertainties about the exact placement of several of them. The basal branching order has at best received low support values, and

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only few, limited analyses have included all taxa currently recognized at the family level in Asterales (Savolainen et al. 2000b; Lundberg 2001), none of them with focus on the order. In this article, we present a reliable phylogeny of Asterales as currently circumscribed (Angiosperm Phylogeny Group [APG] 1998), and we use this phylogeny to discuss the morphological evolution within the order and perhaps also arrive at a stable family-level classification of Asterales.

Material and Methods

Taxon Sampling

The data matrix consists of 40 genera representing all 12 currently recognized families of Asterales (APG 1998; Lundberg 2001). Several families have all or most of their genera sampled by us (table 1). The two largest families, Asteraceae and Campanulaceae, are represented by only a few genera, but an attempt to include most of the currently recognized subfamilies (sometimes treated as families; Takhtajan 1997) has been made. In Campanulaceae, the monogeneric subfamily Cyphocarpoideae has not been included in the analysis because of lack of material, but in the phylogenetic analysis by Ayers (1999), this subfamily has been found to be closely associated with subfamily Lobelioideae, and its exclusion from our analysis is, thus, not expected to affect any interfamilial relationships. A newly identified member of Asterales, *Platyspermatum* (previously placed in Escalloniaceae but shown to be a member of Asterales by R. Schmid and J. Lundberg [unpublished manuscript]), was also included despite very little published information and the absence of any good herbarium material.

Five genera (*Griselinia* and *Melanophylla* of Apiales, *Viburnum* and *Symphoricarpos* of Dipsacales, and *Ilex* of Aquifoliales) that represent the three other orders currently recognized in the Euasterids II (*sensu* APG 1998) as well as three representatives for Escalloniaceae (considered *incertae sedis* in Euasterids II; *Quintinia*, *Escallonia*, and *Anopterus*) were chosen as outgroups. Previous analyses (Chase et al. 1993; Cosner et al. 1994; Olmstead et al. 2000; Soltis et al. 2000) have indicated that Aquifoliales are sister to all other Euasterids II,

and, hence, the root was placed between *Ilex* and the other taxa.

Morphological, Anatomical, Embryological, Palynological, Karyological, and Chemical Data

A data matrix was constructed (fig. 1) for 100 characters used to code morphological, anatomical, embryological, palynological, karyological, and chemical data collected from standard literature (Metcalfe and Chalk 1950, 1979, 1983; Hegnauer 1964, 1966, 1969a, 1969b, 1973, 1989, 1990; Davis 1966; Gibbs 1974; Corner 1976; Cutler and Gregory 1998) as well as more specific literature (referred to in app. B). Morphological data have been checked on herbarium specimens (table 2) as well as living plants.

Characters variable within taxa were coded as polymorphic, and no attempts to determine the plesiomorphic (ancestral) state within the genus were made. Characters with inapplicable states were coded using the reductive coding strategy (as recommended by Strong and Lipscomb 1999). Multistate characters were treated as unordered to avoid false statements on character polarity.

Molecular Data

For this study, 24 new *atpB* gene nucleotide sequences, six new *ndhF* sequences, and three new *rbcL* sequences were obtained, and they are reported here for the first time (table 3; including information on the EMBL/GenBank accession numbers and vouchers). The DNA sequenced were usually extracted from herbarium material, according to the methods of Saghai-Marooof et al. (1984), modified by Doyle and Doyle (1987); a few specimens were sequenced from DNA extracted from silica-dried or fresh material. The DNA were purified with QIAquick PCR kit (Qiagen) according to the instructions provided by the manufacturer. Amplification was done using the polymerase chain reaction (PCR) with *atpB* primers described by Hoot et al. (1995), *ndhF* primers described by Oxelman et al. (1999), or *rbcL* primers described by Olmstead et al. (1992). The PCR products were sequenced with auto-

Table 1
Taxon Sampling

Family	Number of genera	Genera sampled	Level of sampled genera (%)
Alseuosmiaceae	4	<i>Alseuosmia</i> , <i>Crispiloba</i> , <i>Wittsteinia</i>	75
Argophyllaceae	2	<i>Argophyllum</i> , <i>Corokia</i>	100
Asteraceae	Ca. 1535	<i>Barnadesia</i> , <i>Cichorium</i> , <i>Echinops</i> , <i>Gerbera</i> , <i>Helianthus</i> , <i>Tagetes</i> , <i>Tragopogon</i>	0.5
Calyceraceae	6	<i>Acicarpha</i> , <i>Boopis</i> , <i>Moschopsis</i>	50
Campanulaceae	Ca. 90	<i>Campanula</i> , <i>Codonopsis</i> , <i>Dialypetalum</i> , <i>Lobelia</i> , <i>Pseudonemacladus</i>	6
Donatiaceae	1	<i>Donatia</i>	100
Goodeniaceae	12	<i>Brunonia</i> , <i>Dampiera</i> , <i>Goodenia</i> , <i>Scaevola</i>	33
Menyanthaceae	5	<i>Fauria</i> , <i>Menyanthes</i> , <i>Nymphoides</i> , <i>Villarsia</i>	80
Pentaphragmataceae	1	<i>Pentaphragma</i>	100
Phellinaceae	1	<i>Phelline</i>	100
Rousseaceae	4	<i>Abrophyllum</i> , <i>Carpodetus</i> , <i>Cuttsia</i> , <i>Roussea</i>	100
Stylidiaceae	4	<i>Forstera</i> , <i>Levenhookia</i> , <i>Phyllachne</i> , <i>Stylidium</i>	100
Asterales unplaced as to family		<i>Platyspermatum</i>	

Note. The numbers of genera for each family are collected from Bremer (1994a), Mabberley (1997), Takhtajan (1997), Kårehed et al. (1999), Laurent et al. (1999), and Lundberg (2001). The levels of sampled genera are percentages of the total number of genera of the family.

Table 2

Material Examined for Morphological Part of the Matrix

- Adoxaceae. *Viburnum foetens* Decn.: Polunin, Sykes & Williams 2036 (UPS). *Viburnum foetidum* Wall.: Smith 10047 (UPS). *Viburnum formosanum* Hayata: Ohwi 1869 (UPS). *Viburnum grandiflorum* Wall.: Ludlow, Sherriff & Hicks 16002 (UPS).
- Alseuosmiaceae. *Alseuosmia banksii* A. Cunn. var. *linariifolia* (A. Cunn.) R.O. Gardner: Colenso 326 (K). *Alseuosmia macrophylla* A. Cunn.: Ambler s.n. (S); Chapman s.n. (K). *Crispiloba disperma* (S. Moore) C.G.G.J. van Steenis: Telford 10906 (CBG). *Wittsteinia vacciniacea* F. Muell.: Stauffer, Willis, and Muir 5454 (CANB).
- Aquifoliaceae. *Ilex glabra* A. Gray: Sargent 8174 (UPS). *Ilex integra* C.P. Thunberg ex A. Murray: Matsumura s.n. (UPS).
- Argophyllaceae. *Argophyllum ellipticum* Labill.: Arembro 944 (P). *Argophyllum montanum* Schlechter: Hurlimann 749 (P); Skottsberg 117 (S). *Argophyllum* sp.nov.: Telford 6964 (CBG 7800149, at CANB). *Corokia carpodetoides* (F. Muell.) L.S. Smith: Hutton 98 (CBG 8317801, at CANB); McComish 147 (K). *Corokia cotoneaster* Raoul: Taylor 2623 (CBG 8805000, at CANB). *Corokia macrocarpa* T. Kirk: Travers s.n. (W).
- Asteraceae. *Barnadesia laurifolia* (Poir.) O. Ktze: Asplund 16595 (UPS). *Barnadesia parviflora* Spruce ex Benth. & Hook.f.: Asplund 17121 (UPS). *Barnadesia rosea* Lindl.: Malme 1648 (UPS). *Echinops dahuricus* Fisch.: Rosenius 457a (UPS). *Gerbera ambigua* (Cass.) Sch. Bip.: Mogg 17005 (UPS). *Gerbera anandria* (L.) Sch. Bip.: Ching s.n. (UPS). *Helianthus decapetalus* L.: Schumacher s.n. (UPS). *Helianthus divaricatus* L.: Blomberg s.n. (UPS). *Tagetes lucida* Cav.: Pringle 760 (UPS). *Tagetes minuta* L.: Malme 788 (UPS). *Tragopogon orientale* L.: Brown s.n. (UPS).
- Calyceae. *Acicarpa pinnatifida* Miers: Lorentz s.n. (UPS). *Acicarpa procumbens* Less.: Lorentz 1178 (UPS). *Acicarpa spathulata* R. Br.: Mosén 3425 (UPS). *Acicarpa tribuloides* Juss.: Malme 326 (UPS). *Boopis anthemoides* Juss.: Lorentz s.n. (UPS). *Boopis australis* Decne.: Skottsberg 863 (UPS). *Moschopsis rosulata* (N.E. Br.) Dusén: Skottsberg 685 (UPS).
- Campanulaceae. *Campanula cochlearifolia* Lam.: Alm s.n. (UPS). *Campanula erinus* L.: Alm s.n. (UPS). *Campanula latifolia* L.: Ludlow & Sherriff 7728 (UPS). *Campanula ramosissima* Sibth. & Sm.: Bigo s.n. (UPS); Julin s.n. (UPS). *Campanula runcunculoides* L.: Hylander s.n. (UPS). *Codonopsis ovata* Benth.: Fuller s.n. (UPS). *Codonopsis viridis* Wall.: Ludlow, Sherriff & Hicks 21478 (UPS). *Dialypetalum floribundum* Benth.: Rakoto 165 (UPS). *Dialypetalum* sp.: Gustafsson 244 (UPS). *Lobelia dortmanna* L.: Rolland-Germain 6062 (UPS). *Lobelia erinus* L.: Bremer 433 (UPS); Phillipson, Clement & Rafamanantsoa 3881 (UPS).
- Caprifoliaceae. *Symphoricarpos albus* (L.) S.F. Blake: Turesson & Alm 378 (UPS). *Symphoricarpos longiflorus* A. Gray: Porter 3667 (UPS). *Symphoricarpos occidentalis* Hook.: Brenckie s.n. (UPS); Cronquist 6785 (UPS).
- Escalloniaceae. *Anopterus glandulosus* Labill.: Vitt 29180 (UPS). *Escallonia pendula* (R. & P.) Pers.: Woytkowski 34334 (UPS). *Escallonia pulverulenta* (R. & P.) Pers.: Günther & Buchtien s.n. (UPS). *Escallonia resinosa* (R. & P.) Pers.: Hawkes, Hjerting, Cribb & Huaman 5125 (UPS). *Quintinia verdonii* F. Muell.: Vitt 27650 (UPS).
- Goodeniaceae. *Brunonia australis* Sm.: Gustafsson & Bremer 81 (UPS); Muir 254 (UPS). *Dampiera angulata* Rajput & Carolin: Gustafsson & Bremer 140 (UPS). *Dampiera krauseana* Rajput & Carolin: Gustafsson & Bremer 67 (UPS). *Dampiera spicigera* Benth.: Gustafsson & Bremer 52 (UPS). *Goodenia berardiana* (Gaudich.) Carolin: Gustafsson & Bremer 50 (UPS). *Goodenia mimuloides* S. Moore: Gustafsson & Bremer 74 (UPS). *Goodenia ovata* Sm.: Aston 804 (UPS). *Goodenia pterigosperma* R. Br.: Gustafsson & Bremer 148 (UPS). *Scaevola crassifolia* Labill.: Copley 2921 (UPS). *Scaevola lanceolata* Benth.: Gustafsson & Bremer 32 (UPS). *Scaevola mollis* Hook. & Arn.: Fagerlind 7165 (UPS). *Scaevola porocarya* F. Muell.: Gustafsson & Bremer 41 (UPS).
- Griselinaceae. *Griselinia littoralis* Raoul: Nilsson NZ4 (S); Selling s.n. (S). *Griselinia lucida* Forst.f.: Berggren s.n. (S).
- Melanophyllaceae. *Melanophylla madagascariensis* Keraudren: Humblot 437 (S).
- Menyanthaceae. *Fauria crista-galli* Makino: Gustafsson s.n. (UPS, flowers in alcohol). *Menyanthes trifoliata* L.: Holm BC254 (UPS); Turesson & Alm 166 (UPS). *Nymphoides aquaticum* Fernald: Godfrey 49191 (UPS). *Villarsia parnassifolia* (Labill.) R. Br.: Gustafsson & Bremer 165 (UPS), Gustafsson & Bremer 167 (UPS).
- Phellinaceae. *Phelline billardieri* Panch. ex Loes.: Franc 816 (K). *Phelline comosa* Labill.: Mackee 2503 (P).
- Rousseaceae. *Abrophyllum ornans* Hook.f.: Caley s.n. (UPS); Gray 1063 (K). *Carpodetus arboreus* Schlechter: Millar NGF 23675 (K). *Carpodetus serratus* J.R. Forst. & G. Forst.: Oswald s.n. (UPS); Womersley NGF 9438 (K). *Cuttisia viburnea* F. Muell.: Coveny 9875 (K); Hoogland & Hayes 8609 (K). *Roussea simplex* Sm.: Barday 2853 (K); Bernardi 14713 (K); Boivin s.n. (P); Bosser 22.630 (P); Coode 4120 (K); D'Urville s.n. (P); Lorence 2149 (P).
- Stylidiaceae. *Donatia fascicularis* J.R. Forst. & G. Forst.: Swenson & Martinsson 301 (UPS). *Forstera bidwillii* Hook.f.: Hamlin 794 (UPS). *Forstera tenella* Hook.f.: Berggren s.n. (UPS). *Levenhookia leptantha* Benth.: Bremer & Gustafsson 38 (UPS), Bremer & Gustafsson 75 (UPS). *Phyllachne uliginosa* J.R. Forst. & G. Forst.: Swenson & Martinsson 305 (UPS), Moore 2727 (UPS).

Note. Abbreviations of the herbaria follow Holmgren et al. (1990).

ment was straightforward and without any indels. The aligned part of the *atpB* gene corresponds to positions 25–1497, and that of the *rbcL* gene corresponds to positions 31–1428.

Also, the *ndhF* gene was unproblematic to align, although it was necessary to introduce several in-frame indels in the alignment (table 4 gives more detailed information for each of the indels). Eight of the indels are parsimony informative and coded as additional binary characters. The aligned part of the *ndhF* gene corresponds to positions 1–2223. The

aligned matrix can be received from the first author (lundberg@sys.bot.kyoto-u.ac.jp) on request.

Cladistic Analysis

The parsimony analysis was done with PAUP* 4.0b10 (Swofford 2001), using heuristic searches with random addition sequences (with 100 addition sequence replicates; when the morphological data set was analyzed separately, 1000 ad-

Table 3

Species Used in Nucleotide Sequence Data Matrix

Family and species	<i>atpB</i>	<i>ndhF</i>	<i>rbcL</i>
Adoxaceae:			
<i>Viburnum opulus</i> L.	AJ235640 (Savolainen et al. 2000a)
<i>Viburnum rhytidophyllum</i> Hemsl.	...	AF027273 (Oxelman et al. 1999)	X87398 (Gustafsson et al. 1996)
Alseuosmiaceae:			
<i>Alseuosmia macrophylla</i> A. Cunn.	AJ236198 (Albach et al. 2001)	AJ238334 (Kårehed et al. 1999)	X87377 (Gustafsson et al. 1996)
<i>Crispiloba disperma</i> (S. Moore) Steenis	AJ318968; for this study; Telford 10654 (CBG)	AJ238338 (Kårehed et al. 1999)	X87382 (Gustafsson et al. 1996)
<i>Wittsteinia vacciniacea</i> F. Muell.	AJ318985, AJ318986; for this study; Carroll 452 (CBG)	AJ238345 (Kårehed et al. 1999)	X87399 (Gustafsson et al. 1996)
Aquifoliaceae:			
<i>Ilex crenata</i> Thunb.	AJ235502 (Savolainen et al. 2000a)	AF130206 (Olmstead et al. 2000)	L01928 (Albert et al. 1992)
Argophyllaceae:			
<i>Argophyllum</i> sp.	AJ318965; for this study; Telford 3762 (CBG)	AJ238335 (Kårehed et al. 1999)	X87379 (Gustafsson et al. 1996)
<i>Corokia cotoneaster</i> Raoul	AJ235445 (Savolainen et al. 2000a)	AJ238337 (Kårehed et al. 1999)	L11221 (Xiang et al. 1993)
Asteraceae:			
<i>Barnadesia caryophylla</i> (Vell.) S.F. Blake	AF209537 (Soltis et al. 2000)	L39394 (Kim and Jansen 1995)	L01887 (Albert et al. 1992; Olmstead et al. 1992)
<i>Cichorium intybus</i> L.	AJ235433 (Savolainen et al. 2000a)	L39390 (Kim and Jansen 1995)	L13152 (Kim et al. 1992)
<i>Echinops bannaticus</i> Rochel ex Schrad.	AJ318973; for this study; Bremer s.n. (UPS)
<i>Echinops exaltatus</i> Schrad.	...	L39411 (Kim and Jansen 1995)	L13650 (Kim et al. 1992)
<i>Gerbera jamesonii</i> Bolus	AJ236200 (Albach et al. 2001)	L39403 (Kim and Jansen 1995)	L13643 (Kim et al. 1992)
<i>Helianthus annuus</i> L.	AJ236205 (Albach et al. 2001)	L39383 (Kim and Jansen 1995)	L13929 (Michaels et al. 1993)
<i>Tagetes erecta</i> L.	...	L39466 (Kim and Jansen 1995)	L13637 (Kim et al. 1992)
<i>Tagetes</i> sp.	AJ236206 (Albach et al. 2001)
<i>Tragopogon dubius</i> Scop.	AJ236197 (Albach et al. 2001)
<i>Tragopogon porrifolius</i> L.	...	L39391 (Kim and Jansen 1995)	L13647 (Kim et al. 1992)
Calyceraceae:			
<i>Acicarpa tribuloides</i> Juss.	AJ318963; for this study; Gustafsson 207 (UPS)	AJ318987; for this study; Gustafsson 207 (UPS)	X87376 (Gustafsson et al. 1996)
<i>Boopis anthemoides</i> Juss.	...	L39384 (Kim and Jansen 1995)	L13860 (Michaels et al. 1993)
<i>Boopis graminea</i> Phil.	AJ236199 (Albach et al. 2001)
<i>Moschopsis rosulata</i> (N.E. Br.) Dusén	AJ318979; for this study; Swenson & Martinsson 303 (UPS)	AJ318988; for this study; Swenson & Martinsson 303 (UPS)	X87390 (Gustafsson et al. 1996)
Campanulaceae:			
<i>Campanula ramosissima</i> Sibth. and Sm.	...	L39387 (Kim and Jansen 1995)	L13861 (Michaels et al. 1993)
<i>Campanula trachelium</i> Brot.	AJ235423 (Savolainen et al. 2000a)
<i>Codonopsis lanceolata</i> Trautv.	...	AF130185 (Olmstead et al. 2000)	...
<i>Codonopsis ovata</i> Benth.	L18797 (Cosner et al. 1994)
<i>Codonopsis pilosula</i> (Franch.) Nannf.	AJ236202 (Albach et al. 2001)
<i>Cyphia rogersii</i> S. Moore	AJ318970; for this study; Bremer 3813 (UPS)	AJ238339 (Kårehed et al. 1999)	AJ419698; for this study; Bremer 3813 (UPS)
<i>Dialypetalum</i> sp.	AJ318972; for this study; Gustafsson 244 (UPS)	AJ318989; for this study; Gustafsson 244 (UPS)	AJ318991; for this study; Gustafsson 244 (UPS)
<i>Lobelia angulata</i> Forst.	AJ235524 (Savolainen et al. 2000a)

Table 3
(Continued)

Family and species	<i>atpB</i>	<i>ndhF</i>	<i>rbcL</i>
<i>Lobelia cardinalis</i> L.	...	AF130187 (Olmstead et al. 2000)	AF042659 (T. J. Givnish et al., unpublished manuscript) ^a
<i>Pseudonemacladus oppositifolius</i> (B.L. Rob.) McVaugh	AJ318982; for this study; Robinson 3300 (UPS)	AJ292983; for this study; Robinson 3300 (UPS)	AJ318992; for this study; Robinson 3300 (UPS)
Caprifoliaceae:			
<i>Symphoricarpos albus</i> (L.) S.F. Blake	AJ236208 (Albach et al. 2001)	...	L11682 (Olmstead et al. 1992)
<i>Symphoricarpos orbiculatus</i> Moench	...	AF130195 (Olmstead et al. 2000)	...
Donatiaceae:			
<i>Donatia fascicularis</i> J.R. Forst. and G. Forst.	...	AJ225074 (Laurent et al. 1999)	X87385 (Gustafsson et al. 1996)
<i>Donatia</i> sp.	AJ236203 (Albach et al. 2001)
Escalloniaceae:			
<i>Anopterus macleyanus</i> F. Meull.	AJ318964; for this study; Telford s.n. (EBG)	AJ292984; for this study; Telford s.n. (EBG)	Y10673 (Backlund and Bremer 1997)
<i>Escallonia coquimbensis</i> J. Rémy	L11183 (Morgan and Soltis 1993)
<i>Escallonia rubra</i> (Ruiz and Pav.) Pers.	AJ318974; for this study; Backlund s.n. (UPS)	AJ277383 (Lundberg 2001)	...
<i>Platyspermatium crassifolium</i> Guillaumin	AJ419689 (R. Schmid and J. Lundberg, unpublished manuscript)	AJ496220 (R. Schmid and J. Lundberg, unpublished manuscript)	AJ419700 (R. Schmid and J. Lundberg, unpublished manuscript)
<i>Quintinia quatrefagesii</i> F. Muell.	AJ318983; for this study; Lundberg 37 (UPS)
<i>Quintinia verdonii</i> F. Muell.	...	AJ238344 (Kårehed et al. 1999)	X87394 (Gustafsson et al. 1996)
Goodeniaceae:			
<i>Brunonia australis</i> Sm. ex R. Br.	AJ318966; for this study; Gustafsson & Bremer 81 (UPS)	...	X87380 (Gustafsson et al. 1996)
<i>Dampiera spicigera</i> Benth.	AJ318971; for this study; Gustafsson & Bremer 52 (UPS)	...	X87383 (Gustafsson et al. 1996)
<i>Dampiera diversifolia</i> de Vriese	...	L39386 (Kim and Jansen 1995)	...
<i>Goodenia ovata</i> Sm.	AJ318977; for this study; Gustafsson 208 (UPS)	AJ318990; for this study; Gustafsson 208 (UPS)	X87386 (Gustafsson et al. 1996)
<i>Scaevola aemula</i> R. Br.	AF209670 (Soltis et al. 2000)
<i>Scaevola frutescens</i> Krause	...	L39385 (Kim and Jansen 1995)	L13932 (Michaels et al. 1993)
Griselinaceae:			
<i>Griselinia littoralis</i> (Raoul) Raoul	AJ236213 (Albach et al. 2001)
<i>Griselinia lucida</i> G. Forst.	...	AF130205 (Olmstead et al. 2000)	L11225 (Xiang et al. 1993)
Melanophyllaceae:			
<i>Melanophylla alnifolia</i> Baker	AJ236212 (Albach et al. 2001)	AJ236244 (Albach et al. 2001)	U50254 (Plunkett et al. 1996)
Menyanthaceae:			
<i>Fauria crista-galli</i> Makino	AJ318975; for this study; Chase 3501 (K)	AJ238340 (Kårehed et al. 1999)	X87391 (Gustafsson et al. 1996)
<i>Menyanthes trifoliata</i> L.	AJ235533 (Savolainen et al. 2000a)	L39388 (Kim and Jansen 1995)	L14006 (Olmstead et al. 1993a)
<i>Nymphoides geminata</i> (R. Br.) Kuntze	AJ236204 (Albach et al. 2001)
<i>Nymphoides indica</i> (L.) Kuntze	...	AF130181 (Olmstead et al. 2000)	...
<i>Nymphoides peltata</i> Kuntze	X87392 (Gustafsson 1996)
<i>Villarsia calthifolia</i> F. Muell.	...	AF130180 (Olmstead et al. 2000)	L11685 (Olmstead et al. 1992)

Table 3
(Continued)

Family and species	<i>atpB</i>	<i>ndhF</i>	<i>rbcL</i>
<i>Villarsia capitata</i> Nees	AJ318984; for this study; Fagerlind 3479 (S)
Pentaphragmataceae:			
<i>Pentaphragma ellipticum</i> Poulsen	AJ318980; for this study; Singapore Botanical Garden (UPS)	AF130183 (Olmstead et al. 2000)	L18794 (Cosner et al. 1994)
Phellinaceae:			
<i>Phelline comosa</i> Labill.	AJ235557 (Savolainen et al. 2000a)	AJ238342 (Kårehed et al. 1999)	X69748 (Savolainen et al. 1994)
Rousseaceae:			
<i>Abrophyllum ornans</i> Hook.f.	AJ318962; for this study; Gustafsson 248 (UPS)	AJ238333 (Kårehed et al. 1999)	X87375 (Gustafsson et al. 1996)
<i>Carpodetus serratus</i> J.R. Forst. and G. Forst.	AJ318967; for this study; Cameron s.n. (UPS)	AJ238336 (Kårehed et al. 1999)	Y08461 (Bremer and Gustafsson 1997)
<i>Cuttsia viburnea</i> F. Muell.	AJ318969; for this study; Cejie & Williams s.n. (UPS)	AJ277382 (Lundberg 2001)	Y08462 (Bremer and Gustafsson 1997)
<i>Roussea simplex</i> Sm.	AJ235586 (Savolainen et al. 2000a)	AJ277384 (Lundberg 2001)	AF084477 (Koontz and Soltis 1999)
Stylidiaceae:			
<i>Forstera bellidifolia</i> Hook.f.	AJ318976; for this study; Walsh 3491 (MEL)	AJ225092 (Laurent et al. 1999)	AJ225056 (Laurent et al. 1999)
<i>Levenhookia pauciflora</i> Benth.	AJ318978; for this study; Bremer & Gustafsson 122 (UPS)	AJ225080 (Laurent et al. 1999)	AJ225050 (Laurent et al. 1999)
<i>Phyllachne uliginosa</i> J.R. Forst. & G. Forst.	AJ318981; for this study; Swenson & Martinsson 305 (UPS)	AJ225075 (Laurent et al. 1999)	AF307929 (Wardle et al. 2001)
<i>Stylidium emarginatum</i> Sond.	...	AJ225078 (Laurent et al. 1999)	AJ225052 (Laurent et al. 1999)
<i>Stylidium graminifolium</i> Sw.	AJ236201 (Albach et al. 2001)

Note. Species are listed according to family (APG 1998; Lundberg 2001). Accession numbers and references to previously published sequences extracted from the European Molecular Biology Laboratory (EMBL) and GenBank are given. In addition to the accession numbers, voucher information is given for the species sequenced for this study. The herbarium abbreviations are according to Holmgren et al. (1990).

* T. J. Givnish, T. B. Patterson, J. R. Hapeman, H. L. Corliss, J. F. Smith, W. J. Hahn, and K. J. Sytsma, unpublished manuscript.

dition sequence replicates were used), the MULTREES command on and using the tree-bisection-reconnection (TBR) branch swapping algorithm. Internal support for the clades was measured by Bremer support analysis (Bremer 1988, 1994b; Källersjö et al. 1992; using the reverse constraints approach) and jackknife analysis (Farris et al. 1996) using PAUP* (with an average proportion of 36.8% of the characters deleted [Farris et al. 1996] and 5000 replicates, using the heuristic search option, one random addition sequence, and TBR branch swapping). Six analyses were conducted: the four data sets analyzed separately, the three nucleotide data sets combined, as well as all combined.

The character state changes for the morphological part of the matrix were optimized with MacClade 3.08 (Maddison and Maddison 1992), tracing only unambiguous changes.

Clades receiving a jackknife (JK) support of 50%–74% and/or a Bremer support (BS) value of 1–2 are regarded as having low support, and clades receiving a JK support of 75%–94% and/or a BS of 3–5 are moderately supported, while highly supported clades are those receiving JK values of 95% or higher and a BS of at least 6.

Results

The separate analyses (fig. 2) gave no well-supported clades that contradicted the results from the combined analysis. This was taken as evidence that the data sets were congruent, and the discussion in the remaining part of the article will deal only with the results from the combined analysis.

Two most parsimonious trees (5879 steps, parsimoniously uninformative characters excluded, consistency index [CI] = 0.436, retention index [RI] = 0.608; fig. 3) were obtained by the parsimony analysis of the combined data set. Of the 100 morphological characters, 86 are homoplastic (fig. 4). All but three ingroup clades received JK support of more than 50%, and all but seven received a BS value of more than 4. Of the 39 ingroup clades, 29 are supported by a JK value of at least 95% and a BS value of at least 6 and can thus be regarded as strongly supported. Of the 10 remaining clades, six are supported by a JK value of at least 75% and/or a BS value of at least 3 and are thus moderately supported. All clades traditionally recognized on family level are well supported, including the recently suggested Rousseaceae *sensu lato* (including

Table 4
Insertions or Deletions (Indels) Introduced to the *ndhF* Sequence during Alignment Procedure

Indel	Character number	Location	Size	Taxa
1		1405–1407	3	<i>Pentaphragma</i>
2	1	1431/1432	6	<i>Forstera</i> , <i>Levenhookia</i> , <i>Phyllachne</i>
3a		1443/1444	21	Insertion relative to <i>Nicotiana</i> present in all taxa
3b	2	1443/1444	6	Six extra bp in <i>Donatia</i> and <i>Scaevola</i>
4	3	1446/1447	3	<i>Symphoricarpos</i> , <i>Viburnum</i>
5		1450–1452	3	<i>Symphoricarpos</i>
6		1453–1461	9	<i>Roussea</i>
7		1468–1476	9	<i>Griselinia</i>
8		1480–1485	6	<i>Lobelia</i>
9		1485/1486	6	<i>Viburnum</i>
10		1489–1491	3	<i>Ilex</i>
11		1501–1503	3	<i>Ilex</i>
12		1503/1504	3	<i>Ilex</i>
13		1504–1512	9	<i>Viburnum</i>
14a		1513–1515	3	Deletion relative to <i>Nicotiana</i> present in all taxa
14b		1513–1518	6	Three extra bp deleted in <i>Pseudonemacladus</i>
14c		1513–1524	12	Nine extra bp deleted in <i>Boopis</i>
15		1561–1566	6	<i>Corokia</i>
16		1572/1573	3	<i>Forstera</i>
17	4	1693–1698	6	<i>Campanula</i> , <i>Codonopsis</i> , <i>Dialypetalum</i> , <i>Lobelia</i> , <i>Pseudonemacladus</i>
18	5	1702–1710	9	<i>Cichorium</i> , <i>Helianthus</i> , <i>Tagetes</i> , <i>Tragopogon</i>
19		1746/1747	6	<i>Levenhookia</i>
20		1747–1770	24	<i>Pentaphragma</i>
21	6	1755/1756	6	<i>Levenhookia</i> , <i>Phyllachne</i>
22		1773/1774	6	<i>Stylidium</i>
23	7	1911/1912	3	<i>Forstera</i> , <i>Levenhookia</i>
24	8	1911/1912	6	Six extra bp in <i>Forstera</i> , <i>Levenhookia</i> , <i>Moschopsis</i>

Note. The location is relative to the *ndhF*-sequence of *Nicotiana tabacum* (Shinozaki et al. 1986, as corrected by Olmstead et al. 1993b), with the first nucleotide in the *ndhF* start codon as position 1. An en dash indicates the range of nucleotides deleted, and a slash indicates the location of an insertion relative to the *N. tabacum* sequence. The sizes of the indels are in number of base pairs. Indels 3 and 14 are of different sizes in different taxa and are then given the same numbers but with different alphabetic separators for each size class. The deletions 3a and 14a (relative to *Nicotiana*) present in all sampled taxa were excluded from the alignment.

Carpodetaceae; JK = 97%, BS = 11, node 3 in fig. 3), Campanulaceae *sensu lato* (JK = 100%, BS = 96, node 7), and Stylidiaceae *sensu lato* (including *Donatia*; JK = 100%, BS = 16, node 31). The monophyly of a clade with *Pentaphragma* and Campanulaceae s.l. receives only moderate support (JK = 62%, BS = 3, node 6), while the monophyly of a clade with Rousseeaceae s.l., Campanulaceae s.l., and *Pentaphragma* receives only low support (JK < 50%, BS = 1, node 2). Within the well-supported MGCA clade (Menyanthaceae, Goodeniaceae, Calyceraceae, and Asteraceae; JK = 98%, BS = 11, node 14), a clade with Calyceraceae and Asteraceae is well supported (JK = 100%, BS = 23, node 22), with a monophyletic Goodeniaceae (JK = 100%, BS = 18, node 19) as their sister group (JK = 100%, BS = 49, node 18). Menyanthaceae are a member of the MGCA clade as sister to the remaining families (Asteraceae, Calyceraceae, and Goodeniaceae). Stylidiaceae and the MGCA clade form a low-supported clade (JK < 50%, BS = 2, node 13). Sister to this Stylidiaceae-MGCA clade is a low-supported clade (JK = 50%, BS = 2, node 35) with Alseuosmiaceae, Argophyllaceae, Phellinaceae, and *Platyspermation*. Within this clade, *Platyspermation* and Alseuosmiaceae form a well-supported clade (JK = 100%, BS = 58, node 36), while the monophyly of a

clade with Phellinaceae and Argophyllaceae receives only moderate support (JK = 87%, BS = 5, node 39).

The morphological data matrix (fig. 1) consists of 100 characters, of which 92 are parsimony informative and eight are variable but uninformative. The proportion of polymorphic character states in the matrix is about 7%. The proportion of missing data in the morphological data matrix is fairly high, around 18%. As could be expected, the missing data are not equally distributed among the taxa, and 13 taxa (in decreasing order: *Platyspermation*, *Dialypetalum*, *Pseudonemacladus*, *Crispiloba*, *Villarsia*, *Moschopsis*, *Fauria*, *Wittsteinia*, *Melanophylla*, *Roussea*, *Brunonia*, *Abrophyllum*, and *Cuttsia*) account for more than 50% of the missing data. The missing data are also not equally distributed among characters, with embryological and phytochemical characters contributing most to the missing data.

The aligned and analyzed part of the *atpB* sequence had an aligned length of 1473 positions. Of these, 976 were invariant among the taxa, 188 were variable but uninformative for parsimony analysis, and 309 were parsimony informative. The analyzed part of the *rbcL* nucleotide sequence had a length of 1395 positions. Of these, 952 positions were invariant among the taxa, 142 were variable but parsimony uninformative, and

301 were informative. The aligned and analyzed part of the *ndhF* sequence had a total aligned length of 2264 positions, of which 1065 were invariant, 399 were variable but uninformative, and 800 were parsimony informative. The binary indel coding of the aligned *ndhF* sequence resulted in eight parsimony informative characters (table 4). The total number of parsimony informative characters from the nucleotide sequence data set (excluding the *ndhF* indels) was 1410 characters and for the complete data set was 1512 characters.

Discussion

The combined analysis gave two most parsimonious trees, with 29 of the 39 ingroup clades strongly supported (i.e., with JK values of 95% or more and BS values at least 6). Some of the only moderately supported groups concern intrafamily relationships (i.e., within Campanulaceae, Calyceraceae, and Stylidiaceae), while others identify clades also found in previous phylogenetic analyses. These include a clade consisting of Alseuosmiaceae, Phellinaceae, and Argophyllaceae (Gustafsson et al. 1996 [*Phelline* was not included in their analyses]; Backlund and Bremer 1997; Bremer and Gustafsson 1997; Gustafsson and Bremer 1997; Källersjö et al. 1998; Kårehed et al. 1999; Lundberg 2001). These results, with most of the intrafamilial clades in Asterales receiving high or moderate support, are promising because they give us a detailed phylogeny that can be used to discuss the morphological evolution, biogeography, and age of Asterales. In this article, we will concentrate on the morphology of the order, and particularly the well-supported clades are discussed with emphasis on morphological synapomorphies (summarized in table 5) and their evolution.

Asterales sensu lato

Despite the very high support values for this clade (JK = 100%, BS = 32, node 1 in fig. 3), only two morphological synapomorphies could be identified, the absence of apotracheal wood parenchyma and the valvate corolla aestivation. None of these is exclusive for Asterales; furthermore, both show other states within the order. Apotracheal wood parenchyma is present in Goodeniaceae (Carlquist 1969a), some Alseuosmiaceae (Dickson 1986; Carlquist 1992), and Rouseaceae subfamily Carpodetoideae (Hils 1985). The valvate corolla aestivation reverses to an imbricate aestivation in the *Donatia*-Stylidiaceae clade and occurs in parallel in several taxa outside of Asterales (among the Euasterids II, valvate petals are also known from, e.g., Apiaceae and from *Forgesia* and *Valdivia* of Escalloniaceae). Thus, it is possible that the choice of another outgroup would change the optimization of these characters. Other previously suggested synapomorphies for Asterales in the present circumscription either are synapomorphies for less inclusive clades (e.g., the secondary pollen presentation, possibly also the presence of the oligosaccharide inulin that replaces starch as the carbohydrate storage in many members of Asterales) or may be plesiomorphies (e.g., a basic chromosome number of nine as suggested by Bremer et al. [2001], which can also be found in the outgroup taxa).

Rouseaceae sensu lato

A clade consisting of the four genera *Roussea*, *Carpodetus*, *Cuttsia*, and *Abrophyllum* (node 3) was first recognized by Savolainen et al. (2000b) and Lundberg (2001), and it has recently been suggested that it should be recognized at family level (Lundberg 2001). The monophyly of the family is well supported (JK = 97%, BS = 11) by molecular data and by an increase in the number of carpels and ovary locules from two to five or more. The family has a peculiar distribution, with *Roussea* endemic to the mountain forests of the young volcanic island of Mauritius and the other three genera growing some 7700 km farther east, in eastern Australia, New Guinea, and New Zealand.

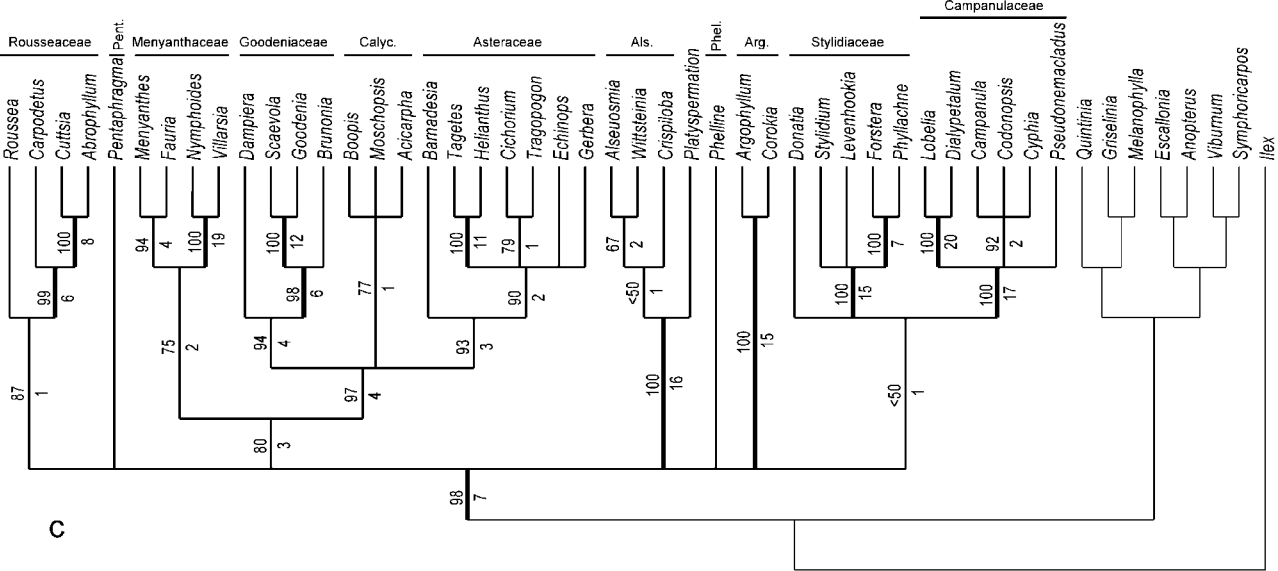
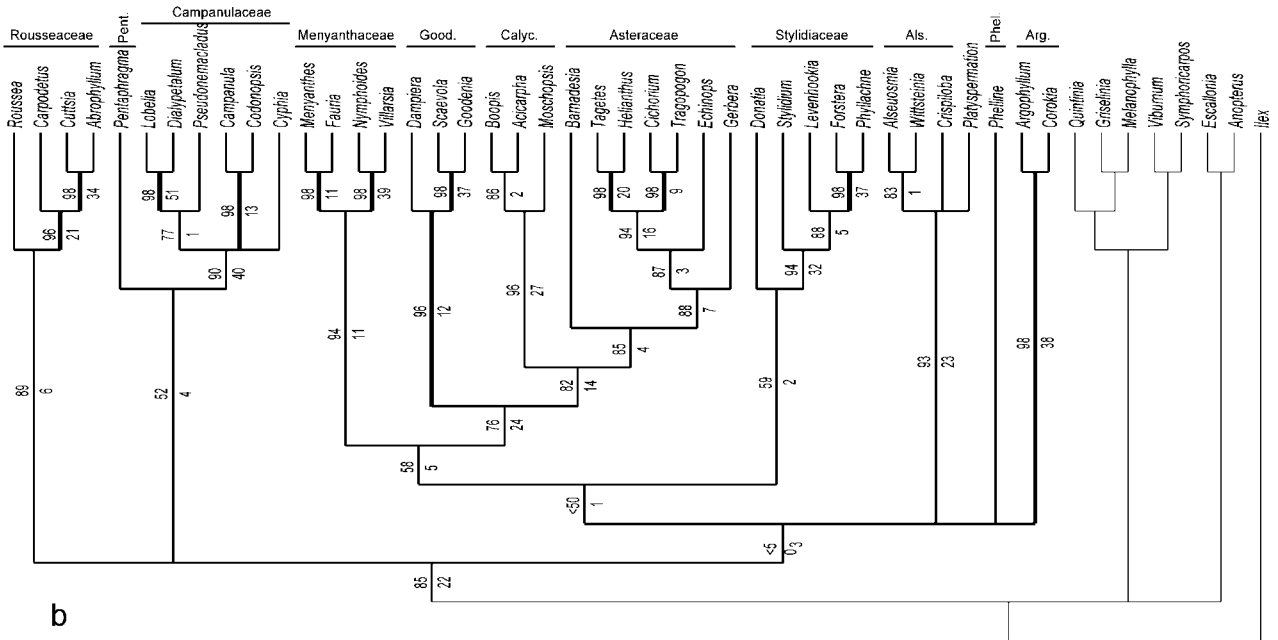
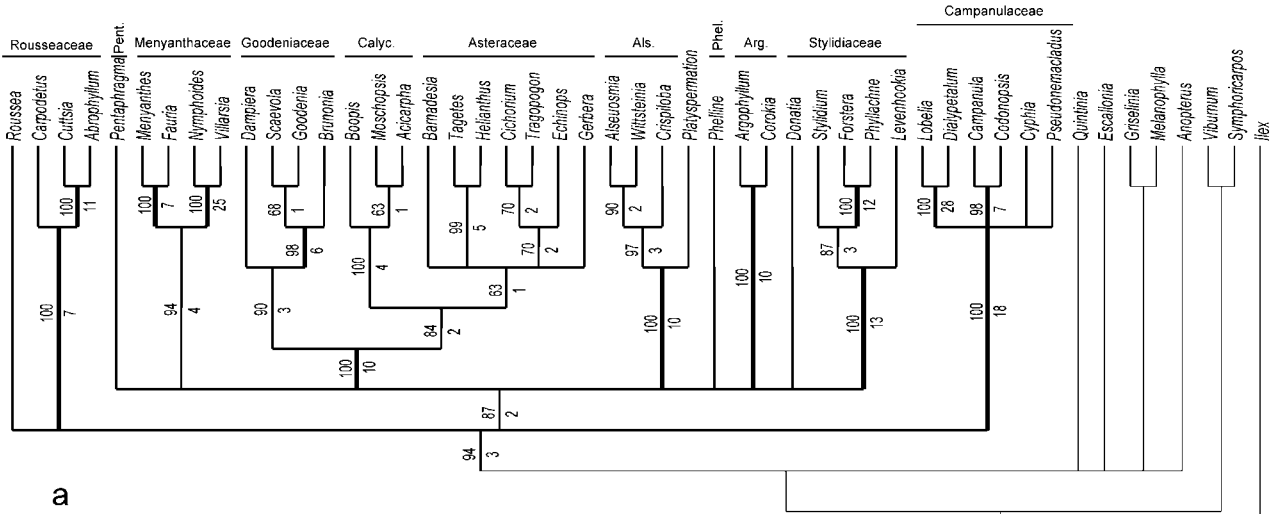
The Pentaphragma-Campanulaceae Clade

The *Pentaphragma*-Campanulaceae relationship (Schönland 1889) has been questioned by several earlier phylogenetic analyses on the basis of *rbcL* sequences (Cosner et al. 1994; Backlund and Bremer 1997; Savolainen et al. 2000b) or on *ndhF* sequence data (Jansen and Kim 1996; Olmstead et al. 2000). Other researchers have emphasized the dissimilarities between Campanulaceae and *Pentaphragma*; some wood anatomy features are supposed to be inconsistent with a close relationship between *Pentaphragma* and Campanulaceae (Carlquist 1997), as are pollen morphology (Dunbar 1978) and the arrangement and morphology of the nectaries (Vogel 1998). This analysis, however, gives moderate support (JK = 62%, BS = 3, node 6) for the monophyly of a clade with *Pentaphragma* and Campanulaceae s.l. Synapomorphies for this clade are the presence of a free hypanthium and the petal venation, where the secondary veins form a dense reticulum (Gustafsson 1995).

Campanulaceae sensu lato

A widely circumscribed Campanulaceae (node 7) that includes Lobeliaceae (here represented by *Lobelia* and *Dialypetalum*), Nemacladaceae (e.g., *Pseudonemacladus*), and Cyphiaceae (*Cyphia*) is strongly supported (JK = 100%, BS = 96). Cyphocarpaceae (*Cyphocarpus*), which have not been included in the analysis because of lack of material, are probably also best accommodated in Campanulaceae (Ayers 1999). Synapomorphies for the Campanulaceae s.l. clade include the latex cell ducts (paralleled in the tribe Lactucae of Asteraceae) and an *ndhF* deletion at position 1693–1698. The zygomorphic flowers, which characterize all subfamilies except for Campanuloideae, are probably a synapomorphy for a Cyphioideae-Nemacladioideae-Lobelioideae clade (Demker 1998).

In an early version of this article, the published *rbcL* sequence for *Cyphia elata* (L18796; Cosner et al. 1994) was included and aligned with the other *rbcL* sequences. In order to align this sequence, four single nucleotide gaps would be necessary to introduce in the sequence, which was taken as indications that this *rbcL* sequence might represent a pseudogene. A new *rbcL* sequence was obtained for *Cyphia rogersii* and replaced the suspected pseudogene. With the new *rbcL* sequence, together with a previously published *ndhF* sequence for the same species and a new *atpB* sequence, *Cyphia* moved from a position as the sister to the rest of the Campanulaceae (obtained in previously published analyses that have included



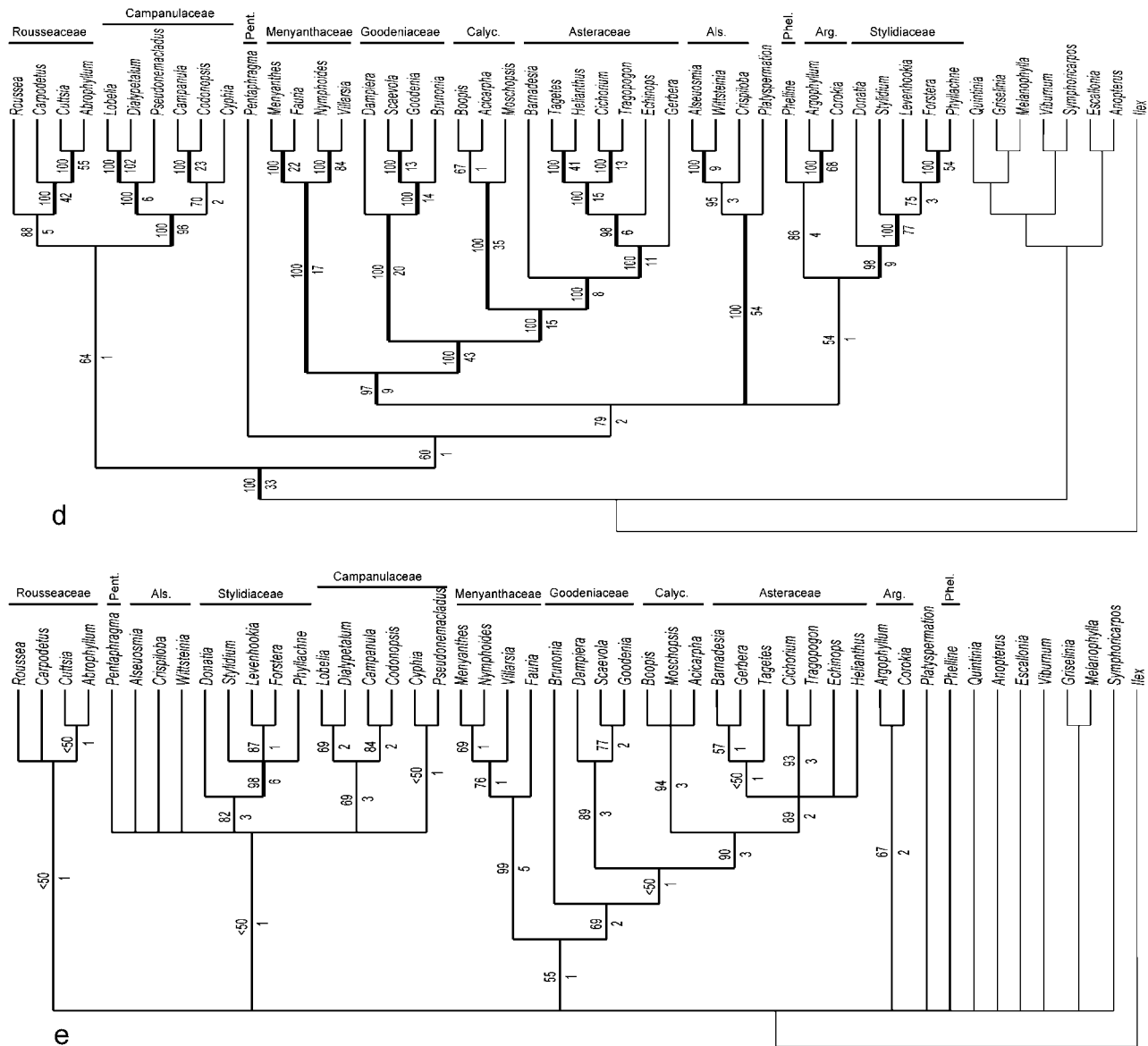


Fig. 2 Strict consensus cladograms summarizing the results of the separate analyses as well as the analysis of the nucleotide sequence data. The ingroup (Asterales) branch supports are indicated for each branch, with the jackknife support values (%) above the branches and the Bremer support values below. Well-supported branches (i.e., with jackknife values >94% and Bremer support >5) are thicker than the less well-supported branches. Tree length, consistency index (CI), and retention index (RI) values are given for each analysis and are given with the parsimoniously uninformative characters excluded. Als. = Alseuosmiaceae; Arg. = Argophyllaceae; Calyc. = Calyceraceae; Pent. = Pentaphragmataceae; Phel. = Phellinaceae. *a*, *atpB*: 616 most parsimonious cladograms (from 17 tree islands), each 1007 steps long and with CI = 0.47 and RI = 0.65. *b*, *ndhF*: 60 most parsimonious cladograms (from one island), each 3287 steps, CI = 0.45, RI = 0.60. *c*, *rbcL*: 183 most parsimonious cladograms (from two islands), each 1066 steps, CI = 0.41, RI = 0.60. *d*, Nucleotide sequence data (*atpB*, *ndhF*, and *rbcL*): three most parsimonious cladograms (from one island), 5386 steps, CI = 0.45, RI = 0.60. *e*, morphology: 3038 most parsimonious cladograms (from 38 islands), each 457 steps, CI = 0.35, RI = 0.67.

the *rbcL* sequence of *Cyphia*; Cosner et al. 1994; Gustafsson et al. 1996; Backlund and Bremer 1997; Bremer and Gustafsson 1997; Gustafsson and Bremer 1997; Kårehed et al. 1999; Savolainen et al. 2000b; Lundberg 2001) to a position within Campanulaceae as the sister taxon to Campanuloideae.

The Core Asterales

The Core Asterales consists of Menyanthaceae, Goodeniaceae, Calyceraceae, Asteraceae, Alseuosmiaceae, Phellinaceae, Argophyllaceae, Styliidiaceae, and the genus *Pla-*

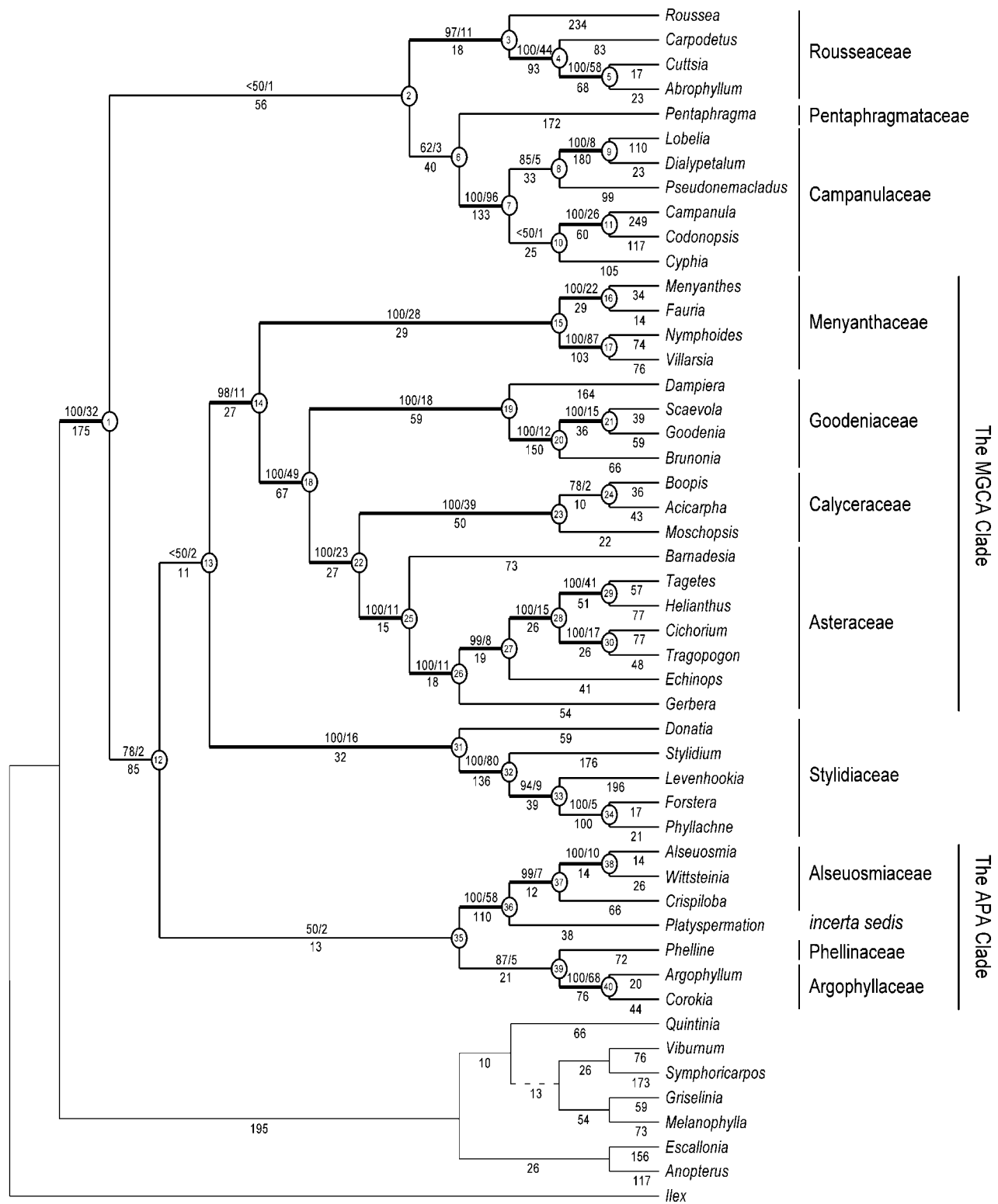


Fig. 3 One of the two most parsimonious cladograms resulting from the combined analysis (morphological and *atpB*, *ndhF*, and *rbcL* nucleotide sequence data). The trees are 5879 steps long (excluding uninformative characters) and are from the same tree island, with a consistency index of 0.44 and a retention index of 0.61. The ingroup (Asterales) branch supports are indicated above each branch, given as jackknife support values (%) / Bremer support values. Well-supported branches (jackknife support >94% and Bremer support >5) are thicker than the less well-supported branches, and the single branch not common to the two most parsimonious cladograms is dotted. Branch lengths as given by PAUP* (assigned branch lengths, under DELTRAN) are given below each branch.

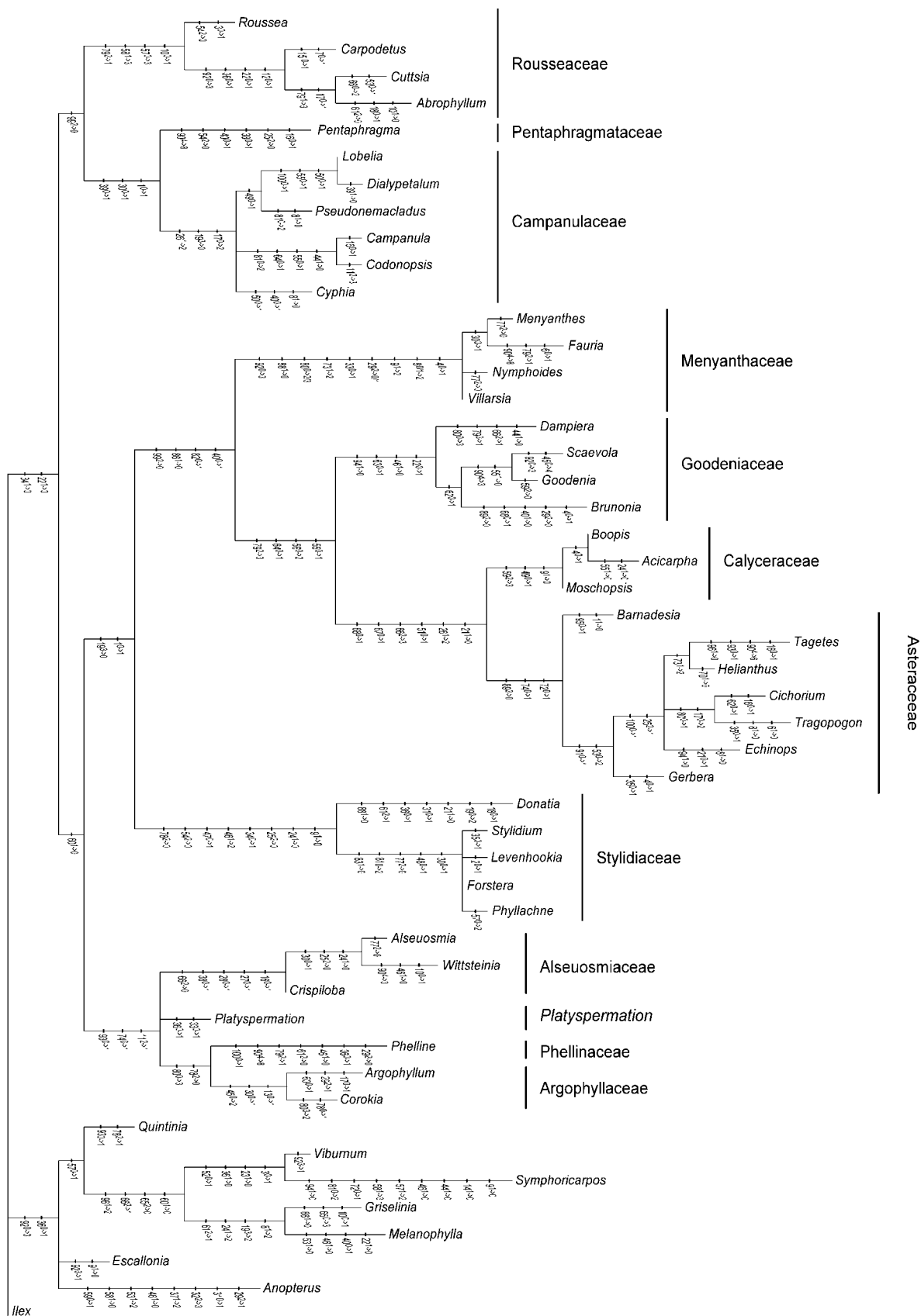


Fig. 4 The morphological characters optimized on one of the most parsimonious trees. Only unambiguous changes are shown. Nodes not supported by morphological characters are collapsed.

tyspermatation. The monophyly of this clade receives only moderate support (JK = 78%, BS = 2, node 12), but a placenta that is not intrusive supports the clade. The other members of Asterales all have an intrusive placenta, which also seems to be the plesiomorphic state for Asterales. Within the Core Asterales is one large and very well-supported clade, the MGCA clade, and three smaller but still more or less well-supported clades (the *Platyspermatation*-Alseuosmiaceae clade, the Stylidiaceae s.l., and the Argophyllaceae-Phellinaceae clade). The relationships between the latter three clades are less well supported.

The MGCA Clade

A well-supported clade (JK = 98%, BS = 11, node 14) that consists of the four families Menyanthaceae, Goodeniaceae, Calyceraceae, and Asteraceae was first identified as late as 1992 (Downie and Palmer 1992; Lammers 1992; Olmstead et al. 1992; though none of these molecular analyses included Goodeniaceae) and since then by both molecular (Chase et al. 1993; Morgan and Soltis 1993; Cosner et al. 1994; Olmstead et al. 2000; Soltis et al. 2000; Bremer et al. 2001) and morphological (Gustafsson and Bremer 1995) studies. The clade is supported by several morphological synapomorphies: the presence of petal lateral veins (Gustafsson 1995), micropylar endosperm haustoria that have been lost (Cosner et al. 1994; the absence of chalazal haustoria might be a plesiomorphy for the group), and an integument that is thick and multilayered (Inoue and Tobe 1999). Other previously suggested synapomorphies can equally parsimoniously be interpreted as symplesiomorphies for this clade or as having several multiple origins within the MGCA clade. The simple vessel element perforation plates (Gustafsson and Bremer 1995) predominating the four-family clade are also found in other Asterales (the presence of multiperforate plates in some Asteraceae probably reflects paedomorphism; Carlquist 1966), and the apical confluent lateral veins of the petals (Gustafsson 1995; Gustafsson and Bremer 1995) cannot unequivocally be interpreted as a synapomorphy since lateral veins are absent in most (but not all) of the remaining taxa of Asterales. The multinucleate tapetal cells suggested as a synapomorphy for the four-family clade by Albach et al. (2001) are present in Menyanthaceae,

Calyceraceae, and subfamily Asteroideae in Asteraceae, while the tapetum cells are binucleate in Goodeniaceae and several Asteraceae as well as in most other members of Asterales. It thus seems best to interpret the origin of the multinucleate tapetum from a binucleate as three independent events, with the binucleate state as a symplesiomorphy for the MGCA clade.

Within the MGCA clade, the monophyletic Menyanthaceae (JK = 100%, BS = 28, node 15) are the sister group to a well-supported (JK = 100%, BS = 49, node 18) Goodeniaceae-Calyceraceae-Asteraceae clade. Synapomorphies for this latter clade are the presence of a prominent and branched columella layer in the pollen grains and a secondary pollen presentation syndrome including fused anthers.

The Calyceraceae-Asteraceae clade

The long-standing controversy about the closest relative to Asteraceae has now more or less coalesced into three alternatives: Calyceraceae (Gustafsson and Bremer 1995; Kim and Jansen 1995; Downie et al. 1996; Jansen and Kim 1996; Bremer and Gustafsson 1997; Carlquist and DeVore 1998; Olmstead et al. 2000; Bremer et al. 2001), Goodeniaceae (Gustafsson and Bremer 1995; Gustafsson et al. 1996), or a clade with Calyceraceae and Goodeniaceae (Chase et al. 1993; Michaels et al. 1993; Cosner et al. 1994; Savolainen et al. 2000b; Soltis et al. 2000). This study gives very strong support (JK = 100%, BS = 23, node 22) for a clade with Asteraceae and Calyceraceae, while Goodeniaceae are their sister group. There are several potential synapomorphies shared by Calyceraceae and Asteraceae, some of which were reviewed by Hansen (1992). The pollen of most Calyceraceae (Skvarla et al. 1977; Hansen 1992) and some Barnadesioideae (Skvarla et al. 1977; Hansen 1991; Zhao et al. 2000) has similar rounded intercolpar concavities, although the homology of this character has recently been questioned (Zhao et al. 2000; it is, however, unclear how they reached their conclusion; furthermore, one of the cladograms they showed as support for an independent origin of the intercolpar concavities in Calyceraceae and Barnadesioideae does not support this assumption). There are also similarities in the internal morphology of the pollen grains (Hansen 1992). The flowers of both families

Table 5

Some Important Clades Found in Combined Analysis

Clade (node number)	Support	Selected synapomorphies
Asterales s.l. (1)	JK: 100%/BS: 32	Petal buds valvate; apotracheal parenchyma absent
Calyceraceae-Asteraceae (22)	JK: 100%/BS: 23	Imperforate tracheary element pits simple; filament collar present; fused seed coat and endocarp; fruits dispersed by a modified calyx
Campanulaceae s.l. (7)	JK: 100%/BS: 96	Latex cell ducts present; only libriform fibers present; <i>ndhF</i> deletion at positions 1693–1698
Goodeniaceae-Calyceraceae-Asteraceae (18)	JK: 100%/BS: 49	Anthers fused with each other; active pollen presentation; pollen with a branched, prominent columella layer
The MGCA Clade (14)	JK: 98%/BS: 11	Integument thick; micropylar endosperm haustoria absent
Phellinaceae-Argophyllaceae (39)	JK: 87%/BS: 5	Pollen with rugulose sexine
Rousseaceae s.l. (3)	JK: 97%/BS: 11	Carpels and ovary locules numerous
Stylidiaceae s.l. (31)	JK: 100%/BS: 16	Nodes unilacunar; wood-rays absent; petals imbricate; extrastaminal floral nectar disk present; stamens 2–3; anthers extrorse

Note. Support values are given as jackknife support (JK) and Bremer support (BS). Only some selected synapomorphies are included. The node numbers refer to the strict consensus tree (fig. 1).

are usually aggregated into compact heads surrounded by involucre bracts, and the calyx is modified into a fruit dispersal apparatus (scaly and persistent in many Calyceraceae, pappus of various shapes in Asteraceae). There are also similarities in wood anatomy (Carlquist and DeVore 1998), e.g., the libriform fibers with simple pits found in Asteraceae (all tribes) and many Calyceraceae but not in Goodeniaceae; in petal venation, where the lateral veins are not anastomosing with the midvein (Hansen 1992; Gustafsson 1995; anastomosing in Menyanthaceae and Goodeniaceae); and in fruit morphology and anatomy. The distribution of the two families is also similar. Calyceraceae is a Central and South American family, while one of the oldest lineages of Asteraceae, subfamily Barnadesioideae, is entirely South American. This is also the region where the majority of the next-oldest Asteraceae lineages, i.e., the paraphyletic tribe Mutisieae, is found (Bremer 1994a). Conversely, Goodeniaceae is almost entirely Australian, with a few widely dispersed tropical shore plants as the exceptions. Differences in placentation (the single ovule of Calyceraceae is pendulous from the top of the locule, while in Asteraceae it is basal and erect) and chemistry (Calyceraceae, and also Goodeniaceae and Menyanthaceae, produce iridoids, while those substances are absent in Asteraceae where sesquiterpene lactones prevail) are often used as arguments against a very close relationship between Calyceraceae and Asteraceae. None of these dissimilarities, however, would be any better explained with Goodeniaceae or a combined Goodeniaceae-Calyceraceae clade as sister to Asteraceae than with Calyceraceae.

The *Donatia*-Stylidiaceae Clade

The genus *Donatia*, with its two species, was first placed in Saxifragaceae (Lindley 1853; Agardh 1858; Baillon 1872; Engler 1890) but later was transferred to Stylidiaceae as a monogeneric subfamily (Mildbraed 1908). This inclusion in Stylidiaceae was soon questioned (Chandler 1911; Skottsberg 1915; Rapson 1953), and a new monogeneric family for *Donatia* was suggested. The reasons for the exclusion of *Donatia* from Stylidiaceae were mainly differences in flower morphology; *Donatia* has actinomorphic flowers with free petals and free stamens, while Stylidiaceae have zygomorphic, sympetalous flowers where the stamens are united with the style into a column. However, further studies of embryology (Philipson and Philipson 1973), floral anatomy (Carolin 1960), and palynology (Erdtman 1952) have shown many similarities between *Donatia* and Stylidiaceae (e.g., the extrastaminal position of the nectaries, few stamens either inserted at the base of the style as in *Donatia* or completely fused with it as in Stylidiaceae, and the presence of both micropylar and chalazal haustoria), which suggests a position of *Donatia* either within Stylidiaceae or at least very close to this family. It was thus hardly surprising when we found that *Donatia* and Stylidiaceae form a strongly supported clade (JK = 100%, BS = 16, node 31). Several morphological synapomorphies support this clade, including a reversal to an imbricate petal bud aestivation in the otherwise valvate Asterales, a reduction in the number of stamens to only two or three, and the extrorse anthers. We also found that some of the earlier suggested embryological similarities between *Donatia* and Stylidiaceae are merely symplesiomorphies (e.g., the presence of endosperm haustoria). A

merging of *Donatia* with Stylidiaceae as a monogeneric subfamily (Donatioideae), as done by Mildbraed (1908), would reflect the close phylogenetic relationship of the taxa while it still would emphasize the many synapomorphies supporting Stylidiaceae *sensu stricto* (i.e., subfamily Stylidioideae), and this is supported by us.

The APA Clade

This analysis identified a clade with low support consisting of Alseuosmiaceae, Argophyllaceae, Phellinaceae, and *Platyspermation* (the APA clade; JK = 50%, BS = 2, node 35). Previous analyses have also identified this clade, with the exception of *Platyspermation*, which has not been included, but with only low support at best (*rbcL* sequence data: Gustafsson et al. 1996; Backlund and Bremer 1997; Gustafsson and Bremer 1997; Källersjö et al. 1998; Savolainen et al. 2000b; *ndbF* and *rbcL* sequence data: Kärehed et al. 1999; Lundberg 2001). The morphological synapomorphies for the clade are few and only poorly known. The male gametophyte is three celled at pollen dispersal (with a parallelism in Asteraceae), and ellagic acid is present in at least *Alseuosmia* and *Corokia*, while the other taxa in the APA clade are not investigated.

Within this clade, the Argophyllaceae-Phellinaceae clade receives moderate support (JK = 87%, BS = 5, node 39). This analysis also strongly supports a clade with Alseuosmiaceae and *Platyspermation* (JK = 100%, BS = 58, node 36), a very poorly known genus previously placed in Myrtaceae, Rutaceae, or, more recently, Escalloniaceae (Schmid 1980; van Steenis 1982). Another recent analysis also supports a position of *Platyspermation* within Asterales as the sister taxon to Alseuosmiaceae (R. Schmid and J. Lundberg, unpublished manuscript).

Conclusions

With the combination of three molecular data sets and one morphological data set, we have been able to reconstruct a fairly reliable and detailed phylogeny of the order Asterales. With a well-corroborated phylogeny, detailed questions regarding character evolution (both molecular and morphological), biogeography, and dating might be answered with confidence. It will also be possible to reach a stable classification that reflects the relationships between the taxa. There are, however, still some major clades with low support values, e.g., the basal split between the Rouseaceae-*Pentaphragma*-Campanulaceae clade and the rest of the Asterales. These less well-supported clades can probably receive higher support with more data collected, e.g., through sequencing of other genes and through detailed embryological and phytochemical investigations.

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Appendix A

A Synopsis of Classification

The number of genera and species are given for each family and subfamily. They are mainly compiled from Bremer (1994a), Mabberley (1997), and Takhtajan (1997).

Asterales Lindl. (11 families/1671 genera/26,000 species)
Rousseaceae DC. (4 genera/6 species)
Rousseoideae Horan. (1/1)
Carpodetoideae (Fenzl) J. Lundberg (3/5)
Campanulaceae Juss. (ca. 95/2230)
Campanuloideae Burnett (ca. 60/950)
Cyphioideae (DC.) Schönland (1/60)
Cyphocarpioideae (Miers) M.H.G. Gustafsson (1/2)
Lobelioideae (Juss.) Schönland (29/1200)
Nemacladioideae (Nutt.) M.H.G. Gustafsson (3/15)
Pentaphragmataceae J. Agardh (1/ca. 25)
The Core Asterales
Alseuosmiaceae Airy Shaw (4/ca. 9)
Argophyllaceae (Engl.) Takht. (2/ca. 22)
Phellinaceae (Loes.) Takht. (1/ca. 10)
<i>Platyspermation</i> Guillaumin
Stylidiaceae R. Br. (5/170)
Donatioideae (Engl.) Mildbr. (1/2)
Stylidioideae (R. Br.) Kitt. (4/170)
The MGCA Clade
Menyanthaceae (Dumort.) Dumort. (5/60)
Goodeniaceae R. Br. (including Brunoniaceae) (12/420)
Calyceraceae R. Br. ex Rich. (6/50)
Asteraceae Dumort. (ca. 1535/23,000)
Barnadesioideae (Benth. and Hook.f.) K. Bremer and R.K. Jansen (9/92)
"Mutisieae" Cass. (76/970)
Carduoideae Kitam. (83/2500)
Cichorioideae Kitam. (232/3230)
Asteroideae (Cass.) Lindl. (1135/16,200)

Appendix B

Characters Used in the Morphological, Anatomical, Embryological, Palynological, Karyological, and Chemical Data Matrix

Morphology and Leaf Anatomy

Data have been collected from literature (Baillon 1872, 1880, 1886; Baker 1877; Höck 1889; Schönland 1889; Thouvenin 1890; Fritsch 1891; Kronfeld 1892; Gilg 1895; Harms 1897; Reiche 1900; Loesner 1901, 1942; Mildbraed 1908; Wangerin 1910; Krause 1912a, 1912b; Sinnott 1914; Engler 1928; Watari 1939; Airy Shaw 1941, 1954, 1965; Wimmer 1943, 1953, 1968; Metcalfe and Chalk 1950; Rapson 1953; Swamy 1954; van Slooten 1954; Allan 1961; Eyde 1966; Philipson 1967; Sleumer 1968; Carlquist 1969a; Stern et al. 1969; Stevens 1971; Patel 1973a, 1973b; Stern 1974; Baas 1975; Gardner 1976, 1978; Cullen 1978; Ramamonjjarisoa 1980; Schmid 1980; Böcher 1981; Aston 1982; van Steenis 1982,

1984; Hils 1985; Rosatti 1986; Dickison 1989; Forster 1990; Al-Shammary 1991; Hufford 1992; Dillon and Muñoz-Schik 1993; Al-Shammary and Gornall 1994; Bremer 1994a; Hutchins 1994; Judd et al. 1994; Gustafsson 1996; Gustafsson et al. 1996; Hansen 1997; Scott 1997; Takhtajan 1997; Carlquist and DeVore 1998; Gornall et al. 1998; Gregory 1998; Schatz et al. 1998; Kårehed et al. 1999; Laurent et al. 1999) and from our own observations of herbarium material. Some additional literature is mentioned below.

001 *Habit*: 0 = woody, 1 = herbaceous

002 *Duration*: 0 = perennial, 1 = annual

003 *Phyllotaxy*: 0 = alternate, 1 = opposite

004 *Leaf arrangement*: 0 = rosulate leaves absent, 1 = basal rosulate leaves present

005 *Leaf morphology*: 0 = simple, 1 = palmate lobed, 2 = pinnate lobed, 3 = palmate compound

006 *Leaf margins*: 0 = entire, 1 = serrate to dentate, 2 = spiny

007 *Domatia*: 0 = absent, 1 = present

008 *Petiole*: 0 = absent, 1 = present, bases not sheathing, 2 = present, bases sheathing

009 *Nodes*: 0 = unilacunar, 1 = trilacunar, 2 = penta- to multilacunar

010 *Leaf hypodermis*: 0 = absent, 1 = present

011 *Leaf vernation in bud*: 0 = involute, 1 = conduplicate, 2 = suprevolute, 3 = flat/curved

012 *Unicellular trichomes with imbedded bases*: 0 = absent, 1 = present

Eglandular, unicellular, and strongly curved trichomes with their bases imbedded in the epidermis have been described from *Abrophyllum* (Thouvenin 1890; Holle 1893), *Cuttsia*, and *Carpodetus*. For further details, see Al-Shammary and Gornall (1994).

013 *T-shaped pluricellular and uniseriate trichomes*: 0 = absent, 1 = present

The peculiar trichomes of *Argophyllum* and *Corokia*, with a multicellular stalk, a unicellular T-piece, and small slits at the junction between the T-piece and its stalk, have been noted by authors since Weiss (1890). For further details, see Al-Shammary and Gornall (1994).

Stem Anatomy

Data are entirely collected from literature (Thouvenin 1890; Fritsch 1891; Kronfeld 1892; Holle 1893; Solereder 1908; Krause 1912a; Engler 1928; Cox 1948; Adams 1949; Metcalfe and Chalk 1950, 1979, 1983; Rapson 1953; Li and Chao 1954; Carlquist 1957, 1958, 1959, 1965, 1966, 1969a, 1969b, 1981, 1992, 1997; Philipson 1967; Paliwal and Srivastava 1969; Stern et al. 1969; Patel 1973a, 1973b; Gibbs 1974; Stern 1974; Baas 1975; Gardner 1976; Carolin 1977; Thulin 1978; Ramamonjariisoa 1980; Schmid 1980; Cronquist 1981; Hils 1985; Dickison 1986, 1989; Hufford 1992; Karis et al. 1992; Lammers 1992; Judd et al. 1994; Takhtajan 1997; Carlquist and DeVore 1998; Gornall et al. 1998; Gregory 1998; Noshiro and Baas 1998).

014 *Cork origin*: 0 = pericyclic, 1 = superficial

015 *Ca-oxalate crystals in wood*: 0 = absent, 1 = druses, 2 = solitary

016 *Casparian thickenings*: 0 = absent, 1 = present

017 *Latex cells*: 0 = absent, 1 = single, 2 = ducts

018 *Resin cells*: 0 = absent, 1 = single

019 *Vessel element perforation plates*: 0 = simple, 1 = scalariform, <10 bars per plate, 2 = scalariform, 10–30 bars per plate, 3 = scalariform, 31–50 bars per plate, 4 = scalariform, >50 bars per plate

020 *Intervascular pits*: 0 = scalariform, 1 = transitional, 2 = alternate, 3 = opposite

021 *Imperforate tracheary element pits*: 0 = simple, 1 = bordered

022 *Parenchyma, apotracheal*: 0 = absent, 1 = present

023 *Parenchyma, paratracheal*: 0 = absent, 1 = present

024 *Wood-rays, uniseriate*: 0 = absent, 1 = homocellular, 2 = heterocellular

025 *Wood-rays, multiseriate*: 0 = absent, 1 = homocellular, 2 = heterocellular

026 *Imperforate elements*: 0 = tracheids, 1 = fiber-tracheids, 2 = libriform fibers

027 *Septate fibers*: 0 = absent, 1 = present

Septate fibers are found in *Pentaphragma*, Alseuosmiaceae, Argophyllaceae, *Lobelia*, *Ilex*, and some species of *Melanophylla* and *Griselinia*, although always together with nonseptate fibers (Adams 1949; Carlquist 1969b, 1997; Patel 1973a; Hils 1985; Dickison 1986; Takhtajan 1997; Noshiro and Baas 1998). Taxa in which the vegetative anatomy has been described but where septate fibers have not been mentioned have been coded as absent because it is assumed that septate fibers would have been mentioned if they were present.

028 *Living fibers storing starch at maturity*: 0 = absent, 1 = present

Living, starch-storing fibers are found in Alseuosmiaceae and *Pentaphragma* (Dickison 1986). Also, here, when these fibers are not mentioned in a vegetative anatomy description, this is taken as indication for their absence, and they are coded as absent.

Perianth and Floral Morphology

In addition to most of the literature cited under “Morphology and Leaf Anatomy,” data were also collected from Carolin (1960, 1977), Kapil and Vijayaraghavan (1965), Klopfer (1973), Sattler (1973), Bense and Palser (1975), Thulin (1978), van Steenis (1978), Erbar and Leins (1989), Erbar (1992, 1993, 1997), Hansen (1992), Cosner et al. (1994), Backlund and Donoghue (1996), Tirel (1996), Tirel and Jérémie (1996), Gustafsson and Bremer (1997), Lammers (1998), and Vogel (1998), and from our own observations of herbarium material. Data on corolla venation are mostly from Gustafsson (1995).

029 *Perianth position*: 0 = hypogynous, 1 = semiepigynous, 2 = epigynous

Pentaphragma has been coded as hypogynous because the septa separating the five deep nectar holders have been interpreted to be of filamentar origin (Vogel 1998). Thus, the only tissue connecting the hypanthium with the ovary is the lower parts of the partly epipetalous filaments, and the hypanthium can be interpreted to be hypogynously inserted.

030 *Free hypanthium*: 0 = absent, 1 = present

031 *Sepals*: 0 = fused, 1 = free

032 *Sepals, number of*: 0 = three, 1 = four, 2 = five, 3 = numerous

033 *Sepal size*: 0 = reduced, 1 = well developed and prominent

034 *Petals in bud*: 0 = valvate, 1 = imbricate

The petals are valvate in all ingroup taxa except *Donatia* and Styliidiaceae. In the outgroup used in this study, only imbricate petals are found, although valvate petals also occur in other members of the Euasterids II (e.g., Apiaceae, and *Forgesia* and *Valdivia* of Escalloniaceae).

035 *Corolla symmetry*: 0 = actinomorphic, 1 = zygomorphic of *Lamium*-type, 2 = zygomorphic of *Cyphia*-type

036 *Petal fusion*: 0 = fused, 1 = free

In all taxa included in this analysis that also were investigated by Erbar and Leins (1996), the petals originate from a

ring-formed primordium, irrespective of whether they are fused or free at maturity.

037 *Petals, number of*: 0 = four, 1 = five, 2 = numerous

038 *Petal wings*: 0 = absent, 1 = present

039 *Petal secondary veins*: 0 = not forming a dense distal reticulum, 1 = forming a dense distal reticulum

The petal venation (characters 019–044) of Asterales and related taxa has been described by Gustafsson (1995).

040 *Petal lateral veins*: 0 = absent, 1 = present

041 *Petal lateral veins*: 0 = ending subapically, 1 = apically confluent

042 *Petal lateral veins*: 0 = anastomosing with midvein, 1 = not anastomosing with midvein

043 *Petal lateral veins*: 0 = free, 1 = fused with adjacent laterals

044 *Petal venation*: 0 = anastomosing between petals, 1 = not anastomosing between petals

045 *Petal appendages*: 0 = appendages absent, 1 = paracorolla, 2 = corolline ligules, 3 = corona, 4 = barbulae

There are several types of petal appendages described in Asterales. Sometimes *Stylidium* has triangular, papillous appendages at the corolla tube throat (paracorolla). Corolline ligules are found in *Corokia* and *Argophyllum*, while a corona of more undetermined shape is present in Alseuosmiaceae. In some Menyanthaceae (particularly several species of *Nymphoides*; Aston 1982, 1987), barbulae either in the shape of fringed scales or as a rim of long papillae are present at the base of the corolla lobes. Similar pluriseriate emergences are also present at the margin of the corolla lobes of *Scaevola*.

046 *Floral nectaries*: 0 = absent, 1 = present, intrastaminal, 2 = present, extrastaminal

The floral nectaries of Asterales are often associated with the gynoecium, although the exact position and shape might be variable. Frequently, they are positioned inside the insertion of the stamens (naturally, so in taxa with stamens inserted epipetalous), but in *Donatia* the nectariferous tissue is extrastaminal. The same holds true for Stylidiaceae, but, there, the stamens are united with the style into a column (or absent, depending on the interpretation of the nature of the column; Erbar 1992), which forces the nectaries to be extrastaminal.

Androecium

In addition to most of the literature cited under “Morphology and Leaf Anatomy,” data were also collected from Perrot (1897), Burt (1948), Carolin (1960, 1977), Subramanyam (1970), Benschel and Palser (1975), Aston (1982), Stanley and Ross (1983), Erbar and Leins (1989), Erbar (1992, 1997), Hansen (1992), Karis et al. (1992), Ladd (1994), Gustafsson and Bremer (1995), Backlund and Donoghue (1996), and Vogel (1998), in addition to observations of herbarium material.

047 *Number of stamens*: 0 = (four-)five(-many), 1 = two to three

Only *Donatia* and Stylidiaceae have fewer than (four-)five stamens.

048 *Stamen-style column*: 0 = absent, 1 = present

In Stylidiaceae, the two stamens are united with the style into a bend, sometimes irritable, column that aids in pollination through its spring mechanism. The development of the

column has been studied in detail by Erbar (1992), who concluded that the origin of the column is obscure, although it might be interpreted as a receptacular tube with stigma and two sessile anthers at the top. The traditional interpretation that the column represents the style and the stamens fused into a gymnostemium (e.g., Mildbraed 1908; Subramanyam 1951) is thus not supported by Erbar (1992).

049 *Filaments*: 0 = free from each other, 1 = fused into a tube

050 *Filament hairs*: 0 = absent, 1 = present

051 *Filament collar*: 0 = absent, 1 = present

The filament collar, a differentiated region immediately below the anther, is present in all Asteraceae but is sometimes only indistinct (Bremer 1994a).

052 *Stamen-corolla tube*: 0 = absent, 1 = present

053 *Anther insertion*: 0 = basifixed, 1 = dorsifixed, 2 = saggitate

054 *Anthers*: 0 = extrorse, 1 = latrorse, 2 = introrse

055 *Anther fusion mechanism*: 0 = free, 1 = fused (conniventive)

056 *Pollen presentation*: 0 = primary; secondary: 1 = passive, 2 = active

Secondary pollen presentation (SPP) can be found in four families of Asterales, including the three largest families (Asteraceae, Campanulaceae, and Goodeniaceae) as well as Calyceraceae. SPP is also found outside Asterales but then mostly in a few scattered genera of about nine families, all without close relationship with Asterales (Ladd 1994). This indicates that SPP has arisen independently several times; this is also reflected in the wide array of mechanisms and morphologies relating to the SPP. Also in Asterales, SPP might have evolved several times and might have undergone some diversification. Ladd (1994) suggests two basic functional types of loading the pollen onto the pollen presenters: active and passive. In the active type, only present in Asteraceae, Goodeniaceae, and Lobelioideae, the pollen is collected by the pollen presenter when it is passing through the introrse anthers by the growth of the style. In contrast, in the passive type (present in Campanuloideae and also Cyphioideae), pollen is deposited on the pollen presenter already at the bud stage. The pollen is then presented to the pollinator either through subsequent growth of the style (Campanuloideae) or by active foraging by the pollinator (*Cyphia*).

Gynoecium

In addition to most of the literature cited under “Morphology and Leaf Anatomy,” data were also collected from Rosén (1935), Burt (1948), Adams (1949), Subramanyam (1951, 1970), Hutchinson (1959), Carolin (1960, 1977), Benschel and Palser (1975), Corner (1976), Krach (1976, 1977), van Steenis (1978), Aston (1982), Erbar and Leins (1989), Kiew (1990), Erbar (1992, 1993, 1997), Hansen (1992), Lammers (1992), Ladd (1994), Gustafsson and Bremer (1997); Hibscher-Jetter et al. (1997), and Vogel (1998), and from observations of herbarium material.

057 *Carpels, number of*: 0 = two, 1 = three, 2 = four, 3 = five, 4 = more than five

058 *Ovary locules*: 0 = unilocular, 1 = bilocular, 2 = trilocular, 3 = plurilocular

059 *Placentation*: 0 = axile, 1 = parietal/marginal, 2 = basal, 3 = apical, 4 = free-central

060 *Placenta*: 0 = not intrusive, 1 = intrusive

061 *Style*: 0 = absent, 1 = free and distinct, 2 = fused

062 *Style hairs*: 0 = glabrous, 1 = stylar hairs present

063 *Stylar indusium*: 0 = absent, 1 = present

The term “stylar indusium” applies to the cup-shaped pollen presenters of Goodeniaceae (including *Brunonia*; Carolin 1960).

064 *Stylar elongation*: 0 = late stylar elongation absent, 1 = present

In some taxa (i.e., Asteraceae, Calyceraceae, Goodeniaceae, Campanuloideae, and Lobelioideae), the style elongates after anther dehiscence. In these taxa, a portion of the style functions as (secondary) pollen presenters, and the growth of the style with the attached pollen facilitates the transfer of pollen from the presenter to the pollinator.

065 *Ovules*: 0 = one per carpel, 1 = two per carpel, 2 = more than two per carpel, 3 = less than one per carpel

Fruit Morphology and Anatomy

In addition to most of the literature cited under “Morphology and Leaf Anatomy,” data were also collected from Burt (1948), Cox (1948), Carolin (1966), Aston (1982), Stanley and Ross (1983), Chuang and Ornduff (1992), Hansen (1992), Backlund and Donoghue (1996), and from observations of herbarium material.

066 *Fruit type*: 0 = berry, 1 = drupe, 2 = capsule, 3 = cypsel

The cypsel refers to the indehiscent, false fruits of Asteraceae and Calyceraceae that develop from an inferior ovary of two carpels and with a single seed.

067 *Fruit type*: 0 = testa and endocarp free, 1 = testa and endocarp are fused to each other

In Calyceraceae and Asteraceae, the seed coat (testa) is adnate to the endocarp.

068 *Fruit dispersal modification*: 0 = none, 1 = modified calyx

A persistent calyx modified to aid the fruit in its dispersal is termed “pappus” in Asteraceae. In this family, it has undergone extensive diversification. The pappus in Barnadesioideae is often of villous bristles, but in one of the most plesiomorphic member of Barnadesioideae, *Schlechtendahlia*, the pappus is scaly (Stuessy et al. 1996). In the other subfamilies of Asteraceae, the pappus is variously of scabrid, barbellate, or plumose bristles, of scales or awns, or of combinations or variations thereof (Bremer 1994a). Also in Calyceraceae, the calyx is persistent and scaly and aids in fruit dispersal.

Embryology, Male Gametophyte

Embryological data were collected from literature (Rosén 1938; Kapil and Vijayaraghavan 1965; Davis 1966; Brewbaker 1967; Subramanyam 1970; Vijayaraghavan and Malik 1972; Bhatnagar 1973; Gardner 1976; Kamelina 1984; Dahlgren 1991; Johri et al. 1992; Kapil and Bhatnagar 1992; Backlund and Donoghue 1996; Pacini 1996; Tobe and Morin 1996; Takhtajan 1997). The definitions of the embryological characters follow Johri et al. (1992), unless otherwise stated.

069 *Anther epidermis*: 0 = persisting, 1 = degenerating

Most anther epidermis in Asterales are persistent, although Calyceraceae are reported as having a degenerating epidermis (Watson and Dallwitz 1992).

070 *Anther wall formation*: 0 = basic, 1 = dicotyledonous

The anther wall formation is according to the dicotyledonous type in all investigated members of Asterales, with the exception of *Alseuosmia* (Gardner 1976).

071 *Number of middle layers*: 0 = one, 1 = two, 2 = three

072 *Tapetum type*: 0 = glandular, 1 = amoeboid

Most of the Asterales for which this character is known have a glandular tapetum (Tobe and Morin 1996). The exception is Asteraceae, where the tapetum is amoeboid (Davis 1966).

073 *Tapetum cells*: 0 = mononucleate, 1 = binucleate, 2 = multinucleate

074 *Male gametophytes*: 0 = two-celled, 1 = three-celled

In Asterales, the pollen grains are two celled at dispersal in *Pentaphragma* and Calyceraceae and three-celled in Asteraceae, *Alseuosmia*, and *Corokia*. There are also some polymorphic taxa, where both two- and three-celled pollen can be found, i.e., Menyanthaceae, Styliaceae, Lobelioideae, and Campanuloideae (Tobe and Morin 1996).

Pollen Morphology

Data on pollen morphology were collected from literature (Kronfeld 1892; Erdtman 1952; Stix 1960; Skvarla and Turner 1966; Stevens 1971; Bronckers and Stainier 1972; Dunbar 1973, 1975a, 1975b, 1978; Nilsson 1973; Pastre and Pons 1973; Baas 1975; Hideux and Ferguson 1976; Cabrera 1977; Ferguson 1977; Lobreau-Callen 1977; Skvarla et al. 1977; Ferguson and Hideux 1978; Thulin 1978; Takhtajan 1983, 1997; Pragłowski and Grafström 1985; Straka and Friedrich 1988; Nic Lughadha and Parnell 1989; Al-Shammary 1991; Hansen 1991, 1992; Hufford 1992; Karis et al. 1992; Judd et al. 1994; Backlund and Donoghue 1996; Gustafsson 1996; Stuessy et al. 1996; Gustafsson et al. 1997; Maciejewska 1997; Kårehed et al. 1999; Zhao et al. 2000).

075 *Intercolpar concavities*: 0 = absent, 1 = present

In some plesiomorphic Barnadesioideae, i.e., *Dasyphyllum* and *Schlechtendahlia*, each interapertural area has a large concave depression (e.g., Skvarla et al. 1977; Hansen 1991; Zhao et al. 2000). These intercolpar concavities have also been found in most species of the small family Calyceraceae (Skvarla et al. 1977; Hansen 1992), and this striking similarity in pollen morphology has been one of the strongest morphological arguments for a close relationship between Asteraceae and Calyceraceae (but see Zhao et al. 2000).

076 *Aperture number*: 0 = two, 1 = three, 2 = four, 3 = five, 4 = six, 5 = numerous

Roussea is anomalous in Asterales with its many apertures (described as penta- to hexa-aperturate by Straka and Friedrich 1988). However, there are also other taxa with a variable number of apertures. The widest range of aperture number can be found in Campanulaceae (three to 10; Takhtajan 1997) and Styliaceae (three to eight; Takhtajan 1997), while *Pentaphragma* have two to three apertures (Erdtman 1952) and *Donatia* has three to four (Takhtajan 1997).

077 *Aperture type*: 0 = colpate, 1 = porate, 2 = colporate

Colporate apertures are by far most common in Asterales. Menyanthaceae, *Alseuosmia*, *Styloidium*, and *Lobelia* are col-

pate, while *Roussea* is porate. *Campanula* is variable, with all three states present.

078 *Exine*: 0 = crassinexinous, 1 = isoexinous, 2 = crassisexinous

079 *Columella layer*: 0 = absent, 1 = reduced, 2 = prominent but unbranched, 3 = prominent and branched

080 *Sexine pattern*: 0 = without pattern (smooth), 1 = murate, 2 = striate, 3 = rugulose

081 *Supratectal processes*: 0 = without supratectal processes (smooth), 1 = verrucose, 2 = spinulose

The tectum may either be smooth or carry processes (Nilsson and Praglowski 1992). A spinulose tectum has pointed processes with a height of up to 1.5 μm , and a verrucose tectum is beset with small wartlike processes (only present in *Nymphoides*).

Embryology, Female Gametophyte

In addition to the literature cited under "Embryology, Male Gametophyte," data have also been collected from Fritsch (1891), Engler (1928), Airy Shaw (1941, 1954), Loesner (1942), Allan (1961), Philipson and Philipson (1973), Yamazaki (1974), Baas (1975), Corner (1976), Carolin (1977), van Steenis (1984), Al-Shammary (1991), Hufford (1992), Judd et al. (1994), Gustafsson and Bremer (1995), and Inoue and Tobe (1999). The definitions of the embryological characters follow Johri et al. (1992), unless otherwise stated.

082 *Integument thickness*: 0 = thin (approximately three to six cells), 1 = thick (12–25 cells)

All the ingroup taxa as well as the outgroup are unitegmic. However, the thickness of the single integument is variable and can be divided into two nonoverlapping states. Thick integuments are found in Menyanthaceae, Goodeniaceae, and Asteraceae (Tobe and Morin 1996; Inoue and Tobe 1999). In all other ingroup taxa, either the integument is thin or the thickness is unknown.

083 *Hypostase*: 0 = absent, 1 = present

084 *Embryogeny*: 0 = Solanad, 1 = Caryophyllad, 2 = Asterad, 3 = Chenopodiad

085 *Endosperm formation*: 0 = cellular, 1 = nuclear

086 *Micropylar endosperm haustoria*: 0 = absent, 1 = present

The presence or absence of micropylar and chalazal (character 087) endosperm haustoria shows an interesting pattern in Asterales (Tobe and Morin 1996). The four-family clade with Menyanthaceae, Goodeniaceae, Calyceraceae, and Asteraceae first identified by cladistic analyses of nucleotide sequence data can be characterized, inter alia, by the absence of both chalazal and micropylar endosperm haustoria, while at least a subclade of Campanulaceae *sensu lato* is characterized by the presence of both chalazal and micropylar haustoria. Unfortunately, many important taxa are unknown with respect to these characters, and this is why it is difficult to determine the plesiomorphic states in Asterales and also to answer some more specific questions, e.g., whether the presence of micropylar endosperm haustoria in *Pentaphragma* can be taken as evidence for a close relationship with Campanulaceae (Kapil and Vijayaraghavan 1965).

087 *Chalazal endosperm haustoria*: 0 = absent, 1 = present

088 *Shape of suspensor*: 0 = not filamentous, 1 = filamentous

Data on this character are entirely from Tobe and Morin (1996).

089 *Endosperm in mature seed*: 0 = absent, 1 = scanty, 2 = copious

Karyology

Data on chromosome numbers are gathered from literature (Peacock 1963; Eyde 1966; Stevens 1971; Nilsson 1973; Raven 1975; Gardner 1976; Wagenitz 1976; Carolin 1977; Tomb 1977; Goldblatt 1978; James 1979; Thulin 1983; Bohm et al. 1986; Carr and McPherson 1986; Lammers 1992; DeVore 1993; Hellmayr et al. 1994; Dawson 1995; Backlund and Donoghue 1996; Gustafsson 1996; Takhtajan 1997; Oginuma et al. 1998). The large 22-kilobase pairs chloroplast DNA inversion and its distribution have been described by Jansen and Palmer (1987a, 1987b).

090 *Chromosome base number (x)*: 0 $x = 5$, 1 $x = 6$, 2 $x = 7$, 3 $x = 8$, 4 $x = 9$, 5 $x = 10$, 6 $x = 12$, 7 $x = 15$, 8 $x > 15$

091 *22kb cpDNA inversion*: 0 = absent, 1 = present

In 1987, Jansen and Palmer (1987b) reported a large chloroplast DNA inversion from all Asteraceae except the subtribe Barnadesiinae (now subfamily Barnadesioideae) of the tribe Mutisieae. This inversion is furthermore absent from all the putatively related families that were investigated.

Chemistry

Data were collected from literature (Rapson 1953; Bate-Smith and Metcalfe 1957; Cambie et al. 1961; Bate-Smith 1962; Hegnauer 1964, 1966, 1969a, 1969b, 1973, 1989, 1990; Plouvier and Favre-Bonvin 1971; Gibbs 1974; Bate-Smith et al. 1975; Jensen et al. 1975; Gardner 1976; González 1977; Wagner 1977; Thulin 1978; Ramamonjiarisoa 1980; Pollard and Amuti 1981; Debourges and Langlois 1982; Bohm et al. 1986, 1995; Kiew et al. 1987; Pusset et al. 1989; Langlois 1990; Aladesanmi et al. 1991; Al-Shammary 1991; Hufford 1992; Lammers 1992; Tomassini et al. 1993; Bohm and Stuessy 1995; Backlund and Donoghue 1996; Seeligmann 1996; Galle 1997; Takhtajan 1997; Krebs and Ramiarantsoa 1998).

Terpenoids

092 *Iridoids*: 0 = absent; carbocyclic iridoids: 1 = Group I, 2 = Group IV; secoiridoids: 3 = Group VI, 4 = Group VII

The classification of iridoids follows Jensen et al. (1975). The primary subdivision based on the biosynthetic pathway is in carbocyclic iridoids and secoiridoids. The carbocyclic iridoids are further divided into five groups by Jensen et al. (1975), of which only one, the 10-hydroxylated compounds (Group I), is present in Asterales (as monotropein, reported from *Stylidium*; Jensen et al. 1975), while griselinoside (in Group IV, 10-carboxylated and 10-decarboxylated iridoids) is known from *Griselinia* (Jensen et al. 1975). The secoiridoids are more common in Asterales. Jensen et al. (1975) recognize four subgroups of secoiridoids, of which two are present in Asterales. The gentiopicrosides (Group VII) are reported only

from *Menyanthes* (as sweroside; Plouvier and Favre-Bonvin 1971). Simple secoiridoids (Group VI) are reported from Menyanthaceae, Goodeniaceae, Calyceraceae, and *Corokia*. Iridoids are absent from Campanulaceae, Asteraceae, *Carpodetus*, *Alseuosmia*, and *Donatia*.

Phenols

093 *Ellagic acid*: 0 = absent, 1 = present

094 *Kaempferol*: 0 = absent, 1 = present

095 *p-Coumaric acid*: 0 = absent, 1 = present

096 *Cinnamic acids*: 0 = absent; present: 1 = caffeic acid, 2 = chlorogenic acid

Other

097 *Inuline*: 0 = absent, 1 = present

Inuline-type fructans are known to be accumulated by

many members of Asterales, i.e., Menyanthaceae, Goodeniaceae, Calyceraceae, Asteraceae, Styliadiaceae, Donatiaceae, and Campanulaceae (Rapson 1953; Pollard and Amuti 1981). Outside Asterales, accumulation is known only from the distantly related Boraginaceae (Pollard and Amuti 1981) and *Sphenoclea* (Porembski and Koch 1999) in the Euasterids I. Unfortunately, the presence or absence of inulin is not known for many of the woody taxa of Asterales; thus, it is not possible to determine whether the occurrence of inulin is a synapomorphy for Asterales (with a later reversal for *Pentaphragma*) or whether it has two independent origins within Asterales.

098 *Polyacetylenes*: 0 = absent, 1 = present

099 *Proanthocyanidins*: 0 = none, 1 = delphinidin, 2 = cyanidin, 3 = pelargonidin

100 *Alkaloids*: 0 = absent or present in low amounts, 1 = present with accumulation

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