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Phylogeny of the *Asterales* sensu lato based on *rbc*L sequences with particular reference to the *Goodeniaceae*

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Abstract: The *rbc*L gene of 25 taxa was sequenced and analyzed cladistically in order to define more precisely the order *Asterales* s.l. and to reconstruct the phylogeny of *Goodeniaceae.* The cladistic analyses show that the *Asterales* comprise the families *Abrophyllaceae, Alseuosmiaceae, Argophyllaceae, Asteraceae, Calyceraceae, Campanulaceae* s.l., *Donatiaceae, Goodeniaceae* (including *Brunoniaceae*), *Menyanthaceae, Pentaphragmataceae,* and *Stylidiaceae. Abrophyllaceae, Alseuosmiaceae, Brunoniaceae,* and *Donatiaceae* have previously not been studied in this respect. Within the *Goodeniaceae,* four groups supported by the *rbc*L data can be distinguished: the genus *Lechenaultia,* the *Anthotium-Dampiera*-group, the genus *Brunonia,* and a group formed by the remaining genera, the *Scaevola-Goodenia*-group.

The relationships of the largest family of angiosperms, the *Asteraceae,* have been debated for a long time, and several different families have been suggested to be the closest relatives, such as *Campanulaceae* s.l., *Lobeliaceae, Calyceraceae, Apiaceae,* and *Rubiaceae.* The old idea of a close relationship between *Asteraceae* and *Campanulaceae/Lobeliaceae* has remained popular, and is manifest in many of the more recent systems of the angiosperms (TAKHTAJAN 1987, DAHLGREN 1989, THORNE 1992), where the *Asteraceae* are associated with the *Campanulaceae* s.l. and in some cases also with the *Brunoniaceae, Calyceraceae, Goodeniaceae, Donatiaceae, Pentaphragmataceae, Sphenocleaceae,* and *Stylidiaceae.* Sometimes all these families are united in one order (WAGENITZ 1964) or a subclass (TAKHTAJAN 1987). The varying systematic treatment of this group has recently been reviewed by LAMMERS (1992), COSNER & al. (1994), and GUSTAFSSON & BREMER (1995).

Recent cladistic analyses of molecular data confirm that most of the aforementioned families form a well-supported, monophyletic group, the "*Asterales-Campanulales*" (OLMSTEAD & al. 1992, CHASE & al. 1993, MICHAELS & al. 1993, COSNER & al. 1994). Some of the results of the molecular studies are, however, clearly in conflict with earlier classifications. One family of those traditionally associated with *Campanulaceae,* the *Sphenocleaceae,* was found to belong in a different part of the *Asteridae,* the *Solanales-Boraginales* alliance (COSNER & al. 1994). Two taxa previously not placed in the vicinity of the *Asteraceae* or *Campanulaceae* were found to belong there: the genus *Corokia* (traditionally placed in *Cornaceae*) and the *Menyanthaceae* (previously placed near or in the *Gentianaceae* but moved to *Solanales* by CRONQUIST 1981). The morphological analysis by GUSTAFSSON & BREMER (1995) support a position for *Menyanthaceae* within the *Asterales-Campanulales,* while *Argophyllaceae* (comprising *Corokia* and *Argophyllum*) occupy the sister group (or most basal) branch of the clade. Both the analysis by GUSTAFSSON & BREMER and the molecular study by COSNER & al. (1994) indicate that the order consists roughly of two major clades, one comprising *Asteraceae, Calyceraceae, Goodeniaceae,* and *Menyanthaceae,* the other the *Campanulaceae* s.l. and *Stylidiaceae.* The positions of the other families in the group are less certain; they either differ in the two studies (*Argophyllaceae, Pentaphragmataceae,* and *Sphenocleaceae*) or are not included in the molecular studies (*Brunoniaceae* and *Donatiaceae*).

The *Asterales-Campanulales*-clade will, in accordance with GUSTAFSSON & BREMER (1995), in the following be referred to as the *Asterales.* This is a clade in the large group of mostly sympetalous angiosperms with unitegmic and tenuinucellar ovules, a group nowadays usually referred to as the *Asteridae* (WAGENITZ 1992).

Variation in the chloroplast gene *rbc*L has been the subject of intensive study in the last few years, and sequences of this particular gene are now available for a very large number of angiosperms, which makes wide-range comparisons possible. Recently, however, attention has been drawn to functional constraints of DNA sequence data, to be considered particularly at higher taxonomic levels (ALBERT & al. 1994 a, b). Notwithstanding these problems, *rbc*L variation has contributed to the resolution of systematic problems at or below the familial, ordinal, and superordinal levels in angiosperms, as demonstrated by numerous recent studies (e.g., CHASE & al. 1993, OLMSTEAD & al. 1993, COSNER & al. 1994, BREMER & al. 1995). As a step towards a more precise delimitation and understanding of the phylogeny within the order *Asterales,* the *rbc*L-gene of 25 taxa, indicated by earlier classification and morphological similarity to belong within or to have affinities with the order, were sequenced in the present study.

The unexpected position of the genus *Corokia* in the *rbc*L trees published, i.e., within the *Asterales,* called for inclusion of likely relatives of that genus in the present analysis. Selecting candidates is problematic, as *Corokia* has had very different systematic placements. The traditional association with *Cornaceae* is strongly contradicted by morphology (EYDE 1966) and *rbc*L data; the latter indicate that other members of that family are only distantly related to the *Asterales* (CHASE & al. 1993, XIANG & al. 1993). The other group in which *Corokia* has been included, the *Saxifragaceae-Escallonioideae,* is known to be highly heterogeneous morphologically (BENSEL & PALSER 1975, HIDEUX & FERGUSON 1976), and has been shown by molecular studies to be grossly paraphyletic (MORGAN & SOLTIS 1993). HALLIER (1908), however, recognized the strong morphological similarity between *Corokia* and the genus *Argophyllum* (in, e.g., indumentum and petal structure), and TAKHTAJAN (1987) described a new family *Argophyllaceae* comprising these two genera. *Argophyllum* was included here to test the idea of a close relationship between these genera. Another genus, *Cuttsia,* like *Corokia* and *Argophyllum* placed in *Saxifragaceae-Escallonioideae* by ENGLER (1930), was considered by HALLIER (1908) to be the closest relative of *Argophyllum* and *Corokia.* In the system of ENGLER (1930), *Cuttsia* is placed together with *Abrophyllum* in the tribe *Cuttsieae.* No material of *Cuttsia* was available for study, but *Abrophyllum,* which appears to be its closest relative, was included. Another genus in the *Saxifragaceae-Escallonioideae* that seems to be of interest for understanding the relationships of *Asterales* is the genus *Escallonia* itself. According to *rbc*L-data (e.g., CHASE & al. 1993), it belongs in the same major branch of *Asteridae* ("Asterid II" in the sense of CHASE & al. 1993) as the *Asterales.* Here belong also the orders *Dipsacales* and *Araliales.* In the present study the genus *Quintinia,* one of three genera in the tribe *Escallonieae* (*Saxifragaceae-Escallonioideae,* ENGLER 1930), was included to investigate its relationship to the *Asterales.*

Representatives of all three genera of the *Alseuosmiaceae* (in the wide sense of VAN STEENIS 1984) were sequenced, as their floral morphology has some rare features (e.g., presence of petal wings and basal petal appendages) in common with families of the *Asterales* such as *Goodeniaceae, Menyanthaceae,* and *Argophyllaceae.* The *Alseuosmiaceae* have not been suggested to be related to the *Asterales,* but to the *Caprifoliaceae* (the genus *Alseuosmia*; FRITSCH 1891), *Escalloniaceae* or the *Pittosporaceae* (AIRY SHAW 1965, CRONQUIST 1981).

The present study contributes an *rbc*L sequence for the previously not sequenced *Donatiaceae.* This monotypic family is usually placed in the *Asterales-Campanulales,* but sometimes elsewhere, as in the *Ericanae-Stylidiales* (DAHLGREN 1989) or as a tribe of its own in *Saxifragaceae* (ENGLER 1890). It is generally believed to be close to the *Stylidiaceae,* among which it has sometimes been included, sharing with them the position and reduced number of stamens. *Donatia* differs, however, from *Stylidiaceae* in several ways, e.g., in having free petals and styles.

Although both morphological and molecular studies support inclusion of *Menyanthaceae* in the *Asterales,* according to the results of some of the molecular studies (DOWNIE & PALMER 1992, CHASE & al. 1993, MICHAELS & al. 1993) the family appears to be paraphyletic. The studies based on *rbc*L (those by CHASE & al. 1993 and MICHAELS & al. 1993) include two taxa only, but these represent two alliances in the family with radically different pollen morphology (NILSSON 1973). The present study contributes *rbc*L sequences for one more genus in each group, to illuminate further the problem of possible paraphyly in this family.

Molecular studies (e.g., MICHAELS & al. 1993, COSNER & al. 1994) and the morphological analysis by GUSTAFSSON & BREMER (1995) agree in that they identify a monophyletic group comprising the *Asteraceae, Calyceraceae,* and *Goodeniaceae.* In the molecular studies cited, based on *rbc*L sequences, the sister group of *Asteraceae* is the *Calyceraceae* and *Goodeniaceae* combined. In an analysis based on *ndh*F sequences (R. K. JANSEN & K.-J. KIM, presented at the *Compositae* conference, Kew 1994), the *Calyceraceae* alone are the sister group of *Asteraceae.* In this context, the previously not sequenced genus *Brunonia* is also interesting. It is sometimes included in the *Goodeniaceae* (e.g., by BESSEY 1915), but usually treated in a monotypic family although generally regarded to be close to the *Goodeniaceae,* possessing the peculiar stylar indusium characteristic of that family. In the tree resulting from Gustafsson & Bremer's (1995) cladistic analysis, *Brunoniaceae* and *Goodeniaceae* are sister groups. Some of the features of *Brunonia* approach the *Asteraceae,* e.g., uniovulate ovary with basal placentation and the pappus-like calyx modifications. It has therefore been put forward as a possible closest relative of *Asteraceae,* e.g., by Jeffrey (1977). In the present study, the *rbc*L-gene was sequenced for 9 of the 11 genera of *Goodeniaceae* (a sequence of *Scaevola* has already been published), as well as for two representatives of *Calyceraceae,* of which only one has previously been sequenced. This was done in order to establish the sister group relationship of the *Asteraceae,* to determine the systematic position of *Brunonia,* and to obtain a preliminary phylogenetic model of the *Goodeniaceae,* a model which may serve as a foundation for further morphological and biogeographical studies of that family.

Material and methods

Total DNA was extracted from fresh or silica gel dried leaves (Chase & Hillis 1991), according to the methods by Saghai-Maroof & al. (1984) and Doyle & Doyle (1987). Double-stranded DNA of the *rbc*L gene was amplified by the polymerase chain reaction (PCR) using two synthetic primers (Olmstead & al. 1992). The 5′-end primer was identical to the first 26 nucleotides of *rbc*L of tobacco, *Nicotiana tabacum* L., and the 3′-end primer corresponds to a region approximately 100 nucleotides outside the coding region. For 12 of the 25 taxa studied, PCR amplification with this primer combination was unsuccessful, in spite of repeated attempts. For these taxa the 3′-primer was replaced by internal primers attaching near the end of the gene. A second run with asymmetric amplification was performed to obtain single-stranded DNA (Kaltenboeck & al. 1992). The single-stranded DNA was sequenced using internal primers designed by G. Zurawski at the DNAX Research Institute. The 25 new sequences (Table 1) have been submitted to the EMBL (European Molecular Biology Laboratory) archives.

To investigate the systematic position of the taxa putatively related to the *Asterales,* 12 of the previously unpublished sequences were analysed together with 70 sequences already published. The latter were obtained from the NCBI (National Center for Biotechnology Information) archives, and are listed in Table 2. The previously published sequences were sampled with the aim to represent all major lineages within the "Asterid" and "Rosid" groups sensu Chase & al. (1993). As many of the taxa under study had previously been placed in the *Saxifragaceae* s.l., members of this diverse group are particularly well represented in the sample. The resulting tree was oriented with *Caltha* (*Ranunculaceae*) at the base, in agreement with the trees obtained by Chase & al. (1993).

In the first analysis, a monophyletic group containing the *Asterales* was identified. All taxa within this group were analyzed in a second cladistic analysis, together with another 13 sequences new to the present study. In addition, 13 sequences from GenBank/EMBL that were not included in the first analysis were added. All 26 taxa added in the second analysis have accepted taxonomic positions within families represented in the first analysis. The sampling strategy was to include all available sequences of *Asterales* in the second analysis, with the exception of *Asteraceae* and *Campanulaceae* s.l., where a selection was made based on previously published studies. *Nicotiana* was included as outgroup, resulting in a total of 57 taxa in the second analysis.

The data matrices for the two phylogenetic analyses comprise characters corresponding to nucleotide positions 27 to 1428 of the *rbc*L sequence. For taxa amplified with internal primers, a number (224 or 52) of the positions at the end of the gene are missing. In the first, larger analysis, partial uncertainties (IUPAC symbols other than A, C, G, T, or N)

Table 1. Specimens investigated. Family classification according to Takhtajan (1987)

Species	Family	Voucher	EMBL nr.
Abrophyllum ornans Hook. f.	*Escalloniaceae*	Gustafsson 211 (UPS)	X87375
Acicarpha tribuloides Juss.	*Calyceraceae*	Gustafsson 207 (UPS)	X87376
Alseuosmia macrophylla A. Cunn.	*Alseuosmiaceae*	V. Mackinder s.n. (UPS)	X87377
Anthotium rubriflorum F. Muell. ex Benth.	*Goodeniaceae*	Gustafsson & Bremer 139 (UPS)	X87378
Argophyllum spec.	*Argophyllaceae*	Telford 5462 (CBF)	X87379
Brunonia australis Sm. ex R. Br.	*Brunoniaceae*	Gustafsson & Bremer (UPS)	X87380
Coopernookia strophiolata (F. Muell.) Carolin	*Goodeniaceae*	Gustafsson & Bremer 138 (UPS)	X87381
Crispiloba disperma (S. Moore) Steenis	*Alseuosmiaceae*	Telford 10654 (CBG)	X87382
Dampiera spicigera Benth.	*Goodeniaceae*	Gustafsson & Bremer 52 (UPS)	X87383
Diaspasis filifolia R. Br.	*Goodeniaceae*	Gustafsson & Bremer 168 (UPS)	X87384
Donatia fascicularis J. R. Forst. & G. Forst.	*Donatiaceae*	Swenson & Martinsson 301 (UPS)	X87385
Goodenia ovata Sm.	*Goodeniaceae*	Gustafsson 208 (UPS)	X87386
Goodenia scapigera R. Br.	*Goodeniaceae*	Gustafsson & Bremer 143 (UPS)	X87387
Lechenaultia heteromera Benth.	*Goodeniaceae*	Gustafsson & Bremer 150 (UPS)	X87388
Lonicera orientalis Lam.	*Caprifoliaceae*	Backlund 267 (UPS)	X87389
Moschopsis rosulata (N. E. Br.) Dusén	*Calyceraceae*	Swenson & Martinsson 303 (UPS)	X87390
Nephrophyllidium crista-galli Gilg	*Menyanthaceae*	Gustafsson 209 (UPS)	X87391
Nymphoides peltata (S. G. Gmel.) Kuntze	*Menyanthaceae*	Gustafsson 212 (UPS)	X87392
Phyllachne uliginosa J. R. Forst. & G. Forst.	*Stylidiaceae*	Swenson & Martinsson 305 (UPS)	X87393
Quintinia verdonii F. Muell.	*Escalloniaceae*	Telford 3244 (CBG)	X87394
Selliera radicans Cav.	*Goodeniaceae*	Gustafsson 210 (UPS)	X87395
Velleia paradoxa R. Br.	*Goodeniaceae*	Gustafsson 206 (UPS)	X87396
Verreauxia reinwardtii (de Vriese) Benth.	*Goodeniaceae*	Gustafsson & Bremer 59 (UPS)	X87397
Viburnum rhytidophyllum Hemsl. ex Forb. & Hemsl.	*Viburnaceae*	Backlund 271 (UPS)	X87398
Wittsteinia vacciniacea F. Muell.	*Alseuosmiaceae*	Carroll 452 (CBG)	X87399

Table 2. Enumeration of previously published sequences extracted from NCBI archives that were used in the analyses. Species are listed alphabetically, with family classification according to the system of Takhtajan (1987)

Species	Family	NCBI access no.	Year	Reference
Acer saccharum L.	*Aceraceae*	L13181	1993	Chase, M. W. & al.
Anagallis arvensis L.	*Primulaceae*	M88343	1992	Manhart, J. R. & Rettig, J. H.
Antirrhinum majus L.	*Scrophulariaceae*	L11688	1993	Olmstead, R. G. & al.
Aralia spinosa L.	*Araliaceae*	L11166	1993	Chase, M. W. & al.
Aucuba japonica Thunb.	*Aucubaceae*	L11210	1993	Xiang, Q.-Y. & al.
Barnadesia caryophylla (Veil.) S. F. Blake	*Asteraceae*	L13859	1993	Michaels, H. J.
Berzelia lanuginosa (L.) Brongn.	*Bruniaceae*	L14391	1994	Olmstead, R. G. & al.
Boopis anthemoides Juss.	*Calyceraceae*	L13860	1993	Michaels, H. J.
Brassica oleracea L.	*Brassicaceae*	M88342	1992	Manhart, J. R.
Brexia madagascarensis Thouars ex Ker Gawl.	*Brexiaceae*	L11176	1993	Morgan, D. R. & Soltis, D. E.
Byrsonima crassifolia (L.) Kunth	*Malphigiaceae*	L01892	1993	Albert, V. A. & al.
Caltha palustris L.	*Ranunculaceae*	L02431	1993	Albert, V. A. & al.
Campanula ramosa Wall.	*Campanulaceae*	L13861	1993	Michaels, H. J.
Carthamnus tinctorius L.	*Asteraceae*	L13862	1993	Michaels, H. J.
Cercidiphyllum japonicum Siebold & Zucc.	*Cercidiphyllaceae*	L11673	1994	Olmstead, R. G. & al.
Chiococca alba (L.) A. Hitch.	*Rubiaceae*	L14394	1994	Olmstead, R. G. & al.
Clermontia kakeana Meyen	*Lobeliaceae*	L18789	1993	Cosner, M. E. & al.
Clethra alnifolia L.	*Clethraceae*	L12609	1993	Kron, K. A. & Chase, M. W.
Codonopsis ovata Benth.	*Campanulaceae*	L18797	1993	Cosner, M. E. & al.
Cornus mas L.	*Cornaceae*	L11216	1993	Xiang, Q.-Y. & al.
Corokia cotoneaster Raoul	*Argophyllaceae*	L11221	1993	Xiang, Q.-Y. & al.
Cucurbita pepo L.	*Cucurbitaceae*	L21938	1994	Swensen, S. M.
Cyphia elata Harv.	*Cyphiaceae*	L18796	1993	Cosner, M. E. & al.
Cyphocarpus rigescens Miers	*Cyphiaceae*	L18792	1993	Cosner, M. E. & al.
Dasyphyllum diacanthoides (Less.) Cabrera	*Asteraceae*	L13863	1993	Michaels, H. J.
Davidia involucrata Baill.	*Davidiaceae*	L11223	1993	Xiang, Q.-Y. & al.
Desfontainia spinosa Ruiz & Pav.	*Desfontainiaceae*	Z29670	1994	Bremer, B. & al.
Dianthus caryophyllus L.	*Caryophyllaceae*	M77699	1991	Giannasi, D. E. & al.
Dillenia indica L.	*Dilleniaceae*	L01903	1993	Albert, V. A. & al.

Dipsacus sativus (L.) Honck.	*Dipsacaceae*	L13864	1993	Michaels, H. J.
Escallonia coquimbensis Remy	*Escalloniaceae*	L11183	1993	Morgan, D. R. & Soltis, D. E.
Eucommia ulmoides Oliv.	*Eucommiaceae*	L01917	1993	Albert, V. A. & al.
Fagus sylvatica L.	*Fagaceae*	L13340	1994	Martin, P. G. & Dowd, J. M.
Fouquieria splendens Engelm.	*Foquieriaceae*	L11675	1993	Olmstead, R. G. & al.
Francoa sonchifolia Cav.	*Frankoaceae*	L11184	1993	Morgan, D. R. & Soltis, D. E.
Garrya elliptica Douglas ex Lindl.	*Garryaceae*	L01919	1993	Soltis, D. E. & al.
Gentiana procera Holm	*Gentianaceae*	L14398	1994	Olmstead, R. G. & al.
Geranium grandiflorum Gilib.	*Geraniaceae*	L01920	1993	Albert, V. A. & al.
Gossypium hirsutum L.	*Malvaceae*	X15886	1993	Ulmasov, T. N. & al.
Griselinia lucida G. Forst.	*Griseliniaceae*	L11225	1993	Xiang, Q.-Y. & al.
Heliotropium arborescens L.	*Boraginaceae*	L14399	1994	Olmstead, R. G. & al.
Helwingia japonica (Thunb.) F. Dietr.	*Helwingiaceae*	L11226	1993	Xiang, Q.-Y. & al.
Humulus lupulus L.	*Cannabaceae*	U02729	1993	Chase, M. W.
Hydrangea macrophylla Torr.	*Hydrangeaceae*	L11187	1993	Morgan, D. R. & Soltis, D. E.
Ilex crenata Thunb.	*Aquifoliaceae*	L01928	1993	Albert, V. A. & al.
Itea virginica L.	*Iteaceae*	L11188	1993	Morgan, D. R. & Soltis, D. E.
Lactuca sativa L.	*Asteraceae*	L14073	1993	Michaels, H. J.
Ligustrum vulgare L.	*Oleaceae*	L11686	1993	Olmstead, R. G. & al.
Lobelia erinus L.	*Lobeliaceae*	L13930	1993	Michaels, H. J.
Ludwigia peruviana (L.) Hara	*Onagraceae*	L10221	1993	Conti, E. & al.
Manilkara zapota (L.) Royen	*Sapotaceae*	L01932	1993	Albert, V. A. & al.
Medicago sativa L.	*Fabaceae*	X04975	1993	Aldrich, J. & al.
Menyanthes trifoliata L.	*Menyanthaceae*	L14006	1994	Olmstead, R. G.
Montinia caryophyllacea Thunb.	*Montiniaceae*	L11194	1993	Morgan, D. R. & Soltis, D. E.
Nemacladus ramosissmus Nutt.	*Nemacladaceae*	L18791	1993	Cosner, M. E. & al.
Nicotiana otophora Griseb.	*Solanaceae*	M16867	1989	Lin, C. M. & al.
Osyris lanceolata Hochst. & Steud.	*Santalaceae*	L11196	1993	Morgan, D. R. & Soltis, D. E.
Oxalis dillenii Jacq.	*Oxalidaceae*	L01938	1993	Albert, V. A. & al.
Parnassia fimbriata Banks	*Parnassiaceae*	L01939	1993	Albert, V. A. & al.
Pentaphragma ellipticum Poulsen	*Pentaphragmataceae*	L18794	1993	Cosner, M. E.
Phyllonoma laticuspis (Turcz.) Engl.	*Dulongiaceae*	L11201	1993	Morgan, D. R. & Soltis, D. E.
Pittosporum japonicum Hort. ex C. Presl.	*Pittosporaceae*	L11202	1993	Morgan, D. R. & Soltis, D. E.
Polemonium reptans L.	*Polemoniaceae*	L11687	1993	Olmstead, R. G. & al.
Prunus laurocerasus L.	*Rosaceae*	U06809	1994	Soltis, D. E. & al.

Table 2 (continued)

Species	Family	NCBI access no.	Year	Reference
Rhamnus catharticus L.	*Rhamnaceae*	L13189	1993	Chase, M. W. & al.
Rhododendron hippophaeoides Balf. f. & Forrest	*Ericaceae*	L01949	1993	Albert, V. A. & al.
Ribes aureum Pursh	*Grossulariaceae*	L11204	1993	Morgan, D. R. & Soltis, D. E.
Sambucus racemosa L.	*Sambucaceae*	L14066	1993	Donoghue, M. J. & al.
Sarracenia flava L.	*Sarraceniaceae*	L01952	1993	Albert, V. A. & al.
Saxifraga integrifolia Hook.	*Saxifragaceae*	L01953	1993	Albert, V. A. & al.
Scaevola frutescens Krause	*Goodeniaceae*	L13932	1993	Michaels, H. J.
Sedum rubrotinctum Clausen	*Crassulaceae*	L01956	1993	Albert, V. A. & al.
Sphenoclea zeylanica Gaertn.	*Sphenocleaceae*	L18798	1993	Cosner, M. E. & al.
Streptocarpus holstii Engl.	*Gesneriaceae*	L14409	1994	Olmstead, R. G.
Stylidium graminifolium Sw.	*Stylidiaceae*	L18790	1993	Cosner, M. E. & al.
Tetracarpaea tasmanica Hook. f.	*Tetracarpaeaceae*	L11207	1993	Morgan, D. R. & Soltis, D. E.
Vahlia capensis Thunb.	*Vahliaceae*	L11208	1993	Morgan, D. R. & Soltis, D. E.
Valeriana officinalis L.	*Valerianaceae*	L13934	1993	Michaels, H. J.
Verbena bonariensis L.	*Verbenaceae*	L14412	1994	Olmstead, R. G.
Vernonia mespilifolia Less.	*Asteraceae*	L13646	1993	Kim, K.-J. & al.
Villarsia calthifolia F. Muell.	*Menynthaceae*	L1168	1993	Olmstead, R. G. & al.
Viola soraria Willd.	*Violaceae*	L11674	1993	Olmstead, R. G. & al.
Vitis aestivalis Michx.	*Vitaceae*	L01960	1993	Albert, V. A. & al.

were all treated as uncertainty in order to avoid application of the very time-consuming equate-macro in the program used.

Phylogenetically uninformative characters were ignored during analysis. Parsimony analyses were conducted using PAUP version 3.1.1 (Swofford 1993), under the assumptions of Fitch parsimony (Fitch 1971). The analyses were performed using the heuristic search algorithm with 100 random addition sequence replicates using the TBR (Tree Bisection-Reconnection) branch swapper, holding 5 trees at each step. The smaller matrix was also analysed using Farris's (1969) successive approximations approach to character weighting. To evaluate the stability of the branches, a Bremer support analysis (Bremer 1988, 1994; Källersjö & al. 1992) was performed on the results obtained from the second analysis, using the "Autodecay" HyperCard stack (T. Eriksson, pers. comm.). Furthermore, a bootstrap analysis with 1000 replicates (Felsenstein 1985) was pursued on the same matrix.

Results

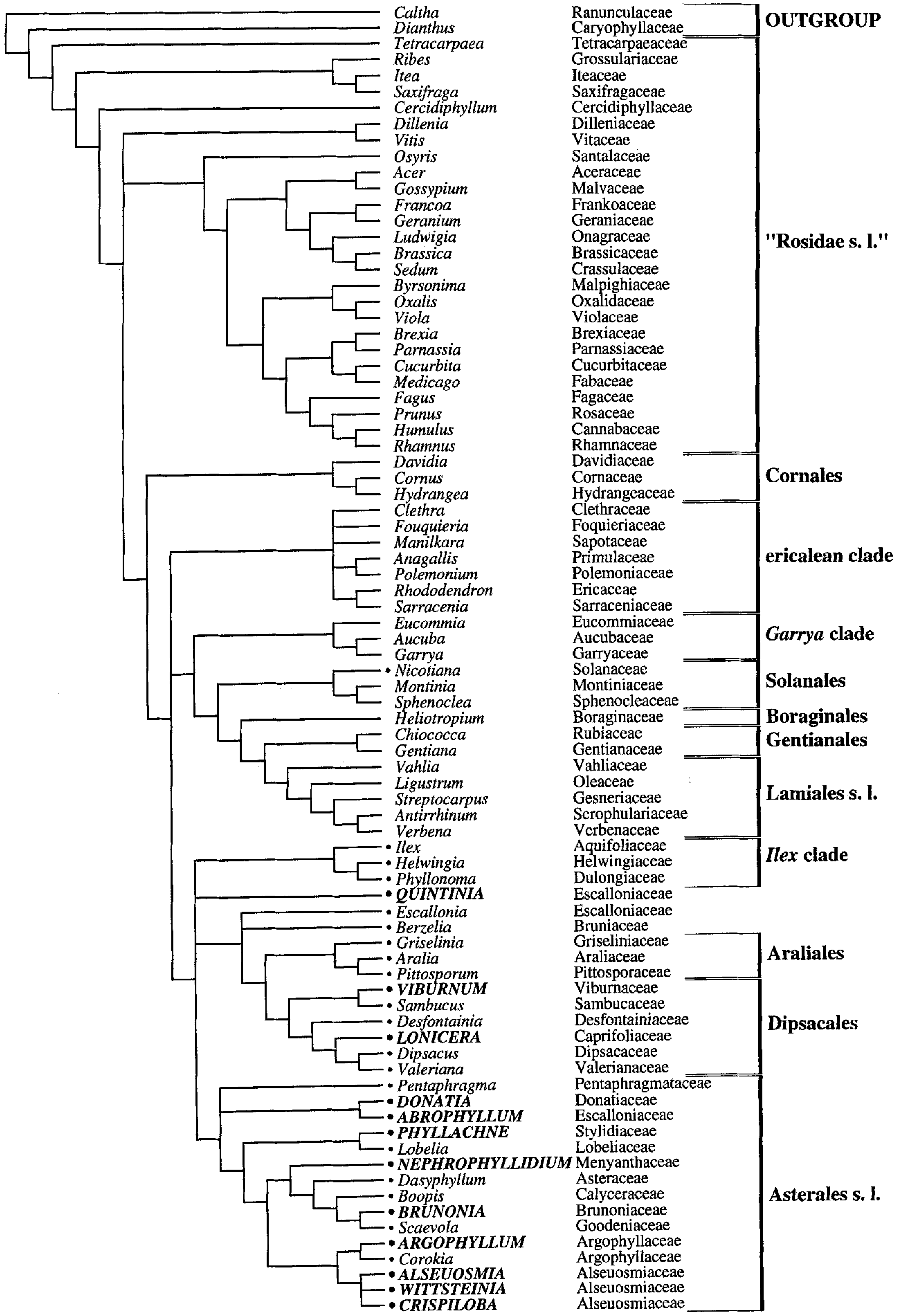
The first parsimony analysis yielded 88 equally parsimonious trees of a length of 3069 steps, a consistency index of 0.243 and a retention index of 0.402. The strict consensus tree is shown in Fig. 1. The taxa tested for affinity with *Asterales* proved to belong within the group, with the exception of *Quintinia,* which has an uncertain position somewhere within the major clade containing the *Asterales, Dipsacales,* and *Araliales,* corresponding to the "Asterid II" sensu Chase & al. (1983). *Abrophyllum, Argophyllum, Brunonia, Donatia,* and the three genera of *Alseuosmiaceae* apparently belong in the *Asterales.*

In the second analysis, where taxa of the "Asterid II"-clade in the first analysis (*Ilex* through *Crispiloba* in Fig. 1) were analyzed together with additional taxa, the search gave 6672 trees with a length of 1359 steps, a consistency index of 0.377 and a retention index of 0.591. The strict consensus tree from this search is shown in Fig. 2. Implications from this tree are, e.g., the following: *Alseuosmiaceae* and *Argophyllaceae* are sister groups, and so are *Asteraceae* and *Goodeniaceae; Brunonia* is nested within the *Goodeniaceae;* and *Asteraceae, Goodeniaceae,* and *Calyceraceae* together constitute a monophyletic group, the sister group of which are the *Menyanthaceae.*

Successive approximations weighting resulted in a single tree with a topology identical to one of the most parsimonious trees. This single tree is shown in Fig. 3, which also displays branch lengths as well as support and bootstrap values for individual branches. In this tree *Donatia* has an unexpected position (in view of its former systematic placement), being the sister group of *Abrophyllum,* but among the most parsimonious trees there are also topologies where *Donatia* is sister group to the *Stylidiaceae.* Notable are the high bootstrap and Bremer support values for the monophyly of each of the families *Alseuosmiaceae* and *Argophyllaceae,* and for the "*Scaevola-Goodenia*-group" (*Diaspasis* through *Verreauxia* in Fig. 3) within the *Goodeniaceae.* The three families *Asteraceae, Calyceraceae,* and *Goodeniaceae* form a group with relatively high Bremer support. The order *Asterales* as a whole has low support and bootstrap values.

Discussion

The taxa under study all belong in a monophyletic group comprising the *Araliales, Dipsacales,* and *Asterales* (Fig. 1). This group corresponds to the "Asterid II" of


Caltha Ranunculaceae
Dianthus Caryophyllaceae
OUTGROUP
Tetracarpaea Tetracarpaeaceae
Ribes Grossulariaceae
Itea Iteaceae
Saxifraga Saxifragaceae
Cercidiphyllum Cercidiphyllaceae
Dillenia Dilleniaceae
Vitis Vitaceae
Osyris Santalaceae
Acer Aceraceae
Gossypium Malvaceae
Francoa Frankoaceae
Geranium Geraniaceae
Ludwigia Onagraceae
Brassica Brassicaceae
Sedum Crassulaceae
Byrsonima Malpighiaceae
Oxalis Oxalidaceae
Viola Violaceae
Brexia Brexiaceae
Parnassia Parnassiaceae
Cucurbita Cucurbitaceae
Medicago Fabaceae
Fagus Fagaceae
Prunus Rosaceae
Humulus Cannabaceae
Rhamnus Rhamnaceae
"Rosidae s. l."
Davidia Davidiaceae
Cornus Cornaceae
Hydrangea Hydrangeaceae
Cornales
Clethra Clethraceae
Fouquieria Foquieriaceae
Manilkara Sapotaceae
Anagallis Primulaceae
Polemonium Polemoniaceae
Rhododendron Ericaceae
Sarracenia Sarraceniaceae
ericalean clade
Eucommia Eucommiaceae
Aucuba Aucubaceae
Garrya Garryaceae
Garrya clade
• Nicotiana Solanaceae
Montinia Montiniaceae
Sphenoclea Sphenocleaceae
Solanales
Heliotropium Boraginaceae
Boraginales
Chiococca Rubiaceae
Gentiana Gentianaceae
Gentianales
Vahlia Vahliaceae
Ligustrum Oleaceae
Streptocarpus Gesneriaceae
Antirrhinum Scrophulariaceae
Verbena Verbenaceae
Lamiales s. l.
• Ilex Aquifoliaceae
• Helwingia Helwingiaceae
• Phyllonoma Dulongiaceae
Ilex clade
• QUINTINIA Escalloniaceae
• Escallonia Escalloniaceae
• Berzelia Bruniaceae
• Griselinia Griseliniaceae
• Aralia Araliaceae
• Pittosporum Pittosporaceae
Araliales
• VIBURNUM Viburnaceae
• Sambucus Sambucaceae
• Desfontainia Desfontainiaceae
• LONICERA Caprifoliaceae
• Dipsacus Dipsacaceae
• Valeriana Valerianaceae
Dipsacales
• Pentaphragma Pentaphragmataceae
• DONATIA Donatiaceae
• ABROPHYLLUM Escalloniaceae
• PHYLLACHNE Stylidiaceae
• Lobelia Lobeliaceae
• NEPHROPHYLLIDIUM Menyanthaceae
• Dasyphyllum Asteraceae
• Boopis Calyceraceae
• BRUNONIA Brunoniaceae
• Scaevola Goodeniaceae
• ARGOPHYLLUM Argophyllaceae
• Corokia Argophyllaceae
• ALSEUOSMIA Alseuosmiaceae
• WITTSTEINIA Alseuosmiaceae
• CRISPILOBA Alseuosmiaceae
Asterales s. l.

Chase & al. (1993; *rbc*L gene sequences of the whole angiosperm system studied). Olmstead & al. (1993) specifically studied the interrelationships of *Asteridae* based on *rbc*L sequences, and among the most parsimonious trees resulting from their cladistic analyses, there are trees where the "Asterid II" are paraphyletic. It should be noted that the analysis of Olmstead & al. (1993), as opposed to the much larger one by Chase & al. (1995), was run to completion. The present study was not designed to investigate the interrelationships of *Asteridae,* and the results, regarding the higher taxonomic levels in *Asteridae* and *Rosidae,* should be considered with caution, as they partly disagree with those of more inclusive analyses already published.

***Saxifragaceae-Escallonioideae* and the *Asterales*.** In the consensus trees (Figs. 1, 2), *Quintinia* is at the unresolved base of the "Asterid II". Nothing can be said with certainty about its position other than it belongs in this main branch of Asteridae. In the tree resulting from successive weighting (Fig. 3), *Quintinia* is not sister group to *Escallonia,* with which it was grouped by Engler (1930), nor to any other included member of the *Saxifragaceae-Escallonioideae* sensu Engler, but it occupies a branch of its own in the grade basal to the *Asterales.* The *Saxifragaceae-Escallonioideae*, often given family rank, have very different circumscriptions in different systems; two extremes are those of Engler (1930) and Takhtajan (1987). In the former system, the group is large and very heterogenous, in the latter, numerous segregates are elevated to family rank, leaving a small core family with seven genera. Even the restricted *Escalloniaceae* sensu Takhtajan (here represented by *Escallonia, Quintinia,* and *Abrophyllum*) are a heterogenous group morphologically, as is well documented for their floral morphology (Bensel & Palser 1975), palynology (Hideux & Ferguson 1976), and indumentum (Al-Shammary & Gornall 1994). The pronounced paraphyly of the *Saxifragaceae* s.l. revealed by studies of *rbc*L sequences has already been extensively discussed by Morgan & Soltis (1993); many of the members of *Saxifragaceae* s.l. included in their study were shown to be quite distantly related to each other and to the *Saxifragaceae* s.str. The position of *Quintinia* in the present analysis is just another example of the artificiality of the group. It is interesting to note that, as opposed to *Escallonia,* the *Asterales,* and in fact all *Asteridae, Quintinia* has bitegmic ovules, the plesiomorphic condition in angiosperms (Philipson 1974).

Quintinia excepted, all taxa investigated hold positions within a monophyletic group corresponding to the *Asterales.* This group, although less densely sampled, appears also in other cladistic studies of the *Asteridae,* based on *rbc*L (Olmstead & al. 1992, 1993; Chase & al. 1993; Cosner & al. 1994). Within the *Asterales,* the

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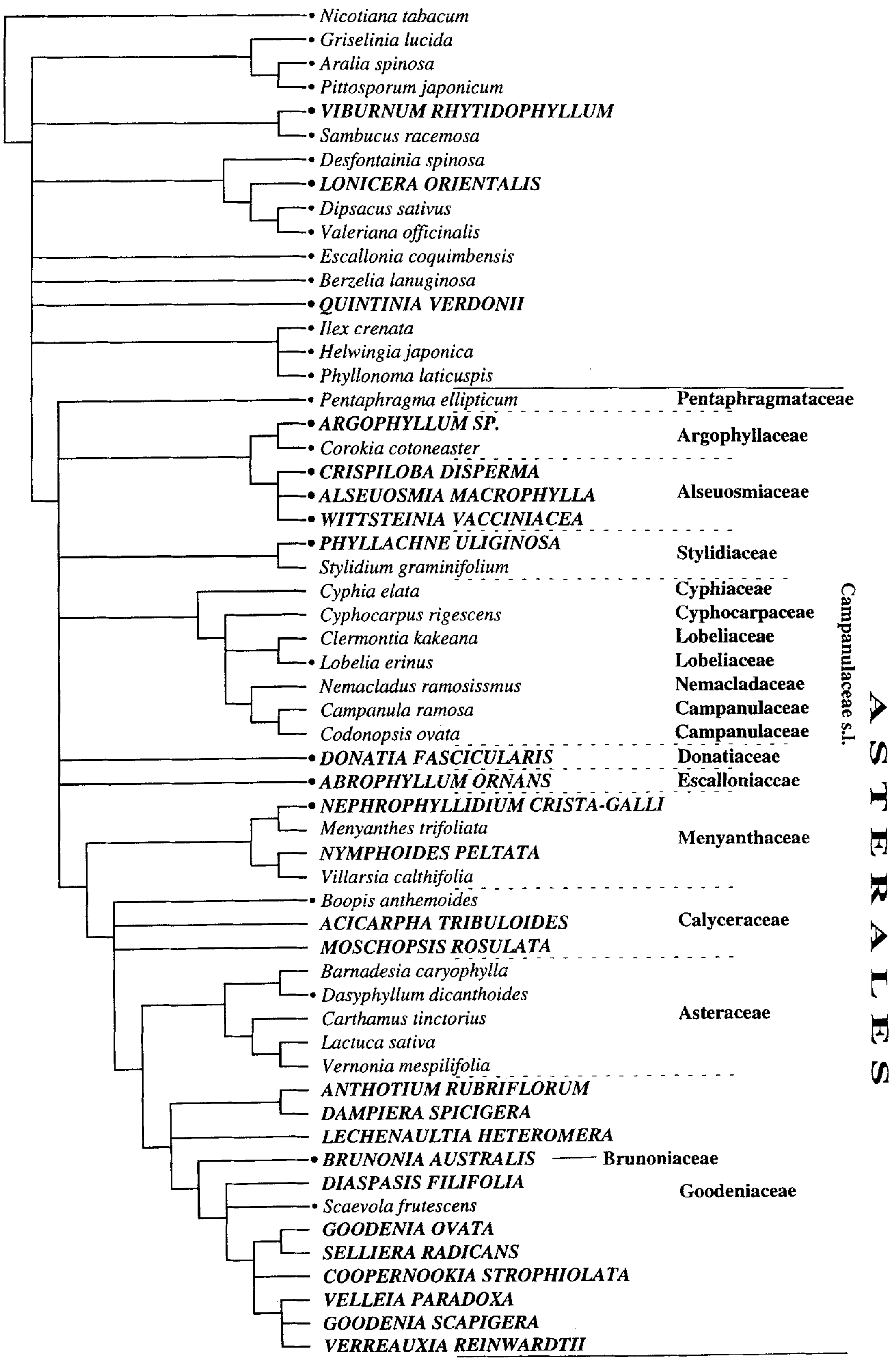
Fig. 1. Strict consensus tree of 88 equally parsimonious trees resulting from cladistic analysis of *rbc*L sequence data. Taxa in capital letters have been sequenced for this study. Full taxon names and vouchers for these are given in Table 1. Sequences from the other taxa were previously published and are listed in Table 2. Dots denote taxa also analysed in the second analysis (Fig. 2). Family names follow Takhtajan (1987). Ordinal names and other names of higher taxonomic rank are applied in accordance with Olmstead & al. (1993), unless denoted by citation marks


Nicotiana tabacum
Griselinia lucida
Aralia spinosa
Pittosporum japonicum
VIBURNUM RHYTIDOPHYLLUM
Sambucus racemosa
Desfontainia spinosa
LONICERA ORIENTALIS
Dipsacus sativus
Valeriana officinalis
Escallonia coquimbensis
Berzelia lanuginosa
QUINTINIA VERDONII
Ilex crenata
Helwingia japonica
Phyllonoma laticuspis
Pentaphragma ellipticum
Pentaphragmataceae
ARGOPHYLLUM SP.
Corokia cotoneaster
Argophyllaceae
CRISPILOBA DISPERMA
ALSEUOSMIA MACROPHYLLA
WITTSTEINIA VACCINIACEA
Alseuosmiaceae
PHYLLACHNE ULIGINOSA
Stylidium graminifolium
Stylidiaceae
Cyphia elata
Cyphiaceae
Cyphocarpus rigescens
Cyphocarpaceae
Clermontia kakeana
Lobeliaceae
Lobelia erinus
Lobeliaceae
Nemacladus ramosissmus
Nemacladaceae
Campanula ramosa
Campanulaceae
Codonopsis ovata
Campanulaceae
Campanulaceae s.l.
DONATIA FASCICULARIS
Donatiaceae
ABROPHYLLUM ORNANS
Escalloniaceae
NEPHROPHYLLIDIUM CRISTA-GALLI
Menyanthes trifoliata
NYMPHOIDES PELTATA
Villarsia calthifolia
Menyanthaceae
Boopis anthemoides
ACICARPHA TRIBULOIDES
MOSCHOPSIS ROSULATA
Calyceraceae
Barnadesia caryophylla
Dasyphyllum dicanthoides
Carthamus tinctorius
Lactuca sativa
Vernonia mespilifolia
Asteraceae
ANTHOTIUM RUBRIFLORUM
DAMPIERA SPICIGERA
LECHENAULTIA HETEROMERA
BRUNONIA AUSTRALIS
Brunoniaceae
DIASPASIS FILIFOLIA
Scaevola frutescens
GOODENIA OVATA
SELLIERA RADICANS
COOPERNOOKIA STROPHIOLATA
VELLEIA PARADOXA
GOODENIA SCAPIGERA
VERREAUXIA REINWARDTII
Goodeniaceae
ASTERALES

basal relationships differ between the numerous most parsimonious trees, and in the consensus tree from the second analysis (Fig. 3), there is a polytomy with seven branches at the base of the order.

Apart from *Corokia,* another two genera of the *Saxifragaceae-Escallonioideae, Abrophyllum* and *Argophyllum,* belong in the *Asterales.* A position for *Argophyllum* in the *Asterales* was expected, given the previously suggested position of *Corokia* in the order, and the many morphological similarities between *Argophyllum* and that genus. *Abrophyllum,* on the other hand, has not been specifically discussed in connection with any *Asterales,* and it was retained by Takhtajan (1987) in his restricted *Escalloniaceae.* However, it can be said to be indirectly involved, as *Cuttsia,* apparently its closest relative, was suggested by Hallier (1908) to be closely related to *Corokia* and *Argophyllum.* He proposed that the three genera should be treated in a taxon of their own. Krach (1976) found strong similarities in seed morphology between *Cuttsia, Abrophyllum* and *Argophyllum.* The two small eastern Australian genera *Abrophyllum* and *Cuttsia* were placed in their own tribe, *Cuttsieae,* in the *Saxifragaceae-Escallonioideae* by Engler (followed by Takhtajan 1987), and they obviously largely agree in floral structure (Engler 1930). The genera are strikingly similar in trichome anatomy (Al-Shammary & Gornall 1994) and in petal venation (Gustafsson 1995). Nakai (1943) distinguished the monotypic family *Abrophyllaceae,* but *Cuttsia* was obviously meant to remain in *Escalloniaceae.* The name *Abrophyllaceae* has seemingly not been applied in classification schemes since its publication.

The idea that the *Asterales* have their closest relatives or ancestors in the *Saxifragaceae* and particularly the *Escallonioideae* had actually been put forward before the era of molecular studies. Carolin (1978) stated: "There is nothing in the hypothetical ancestral flower of the *Campanulales* which discounts the *Saxifragaceae* (s.l.) as a possible ancestor, and they also have the required suite of trichomes, particularly in the *Escallonioideae.*" According to Takhtajan (1987), the order *Campanulales* (in a restricted sense) is connected through the *Pentaphragmataceae* to a hypothetical ancestor similar to present-day *Escalloniaceae* (in his system embracing *Abrophyllum, Cuttsia, Escallonia,* and *Quintinia,* of the genera discussed here).

Argophyllaceae. The close relationship between *Corokia* and *Argophyllum* suggested first by Hallier (1908) is confirmed by the present results. Morphologically there are also many striking similarities. Apart from an overall similarity of the flowers, both genera have similar fringed petal appendages near the base of the adaxial side of the petals. In addition, they both have a rare type of T-shaped hairs covering much of the plant (Weiss 1890, Eyde 1966, Al-Shammary & Gornall 1994). The fruits, however, are different; *Argophyllum* has a many-seeded capsular fruit and *Corokia* a drupe. Hallier (1908) considered *Corokia* to be simply a specialized *Argophyllum.* Even though a close association between the two gene-

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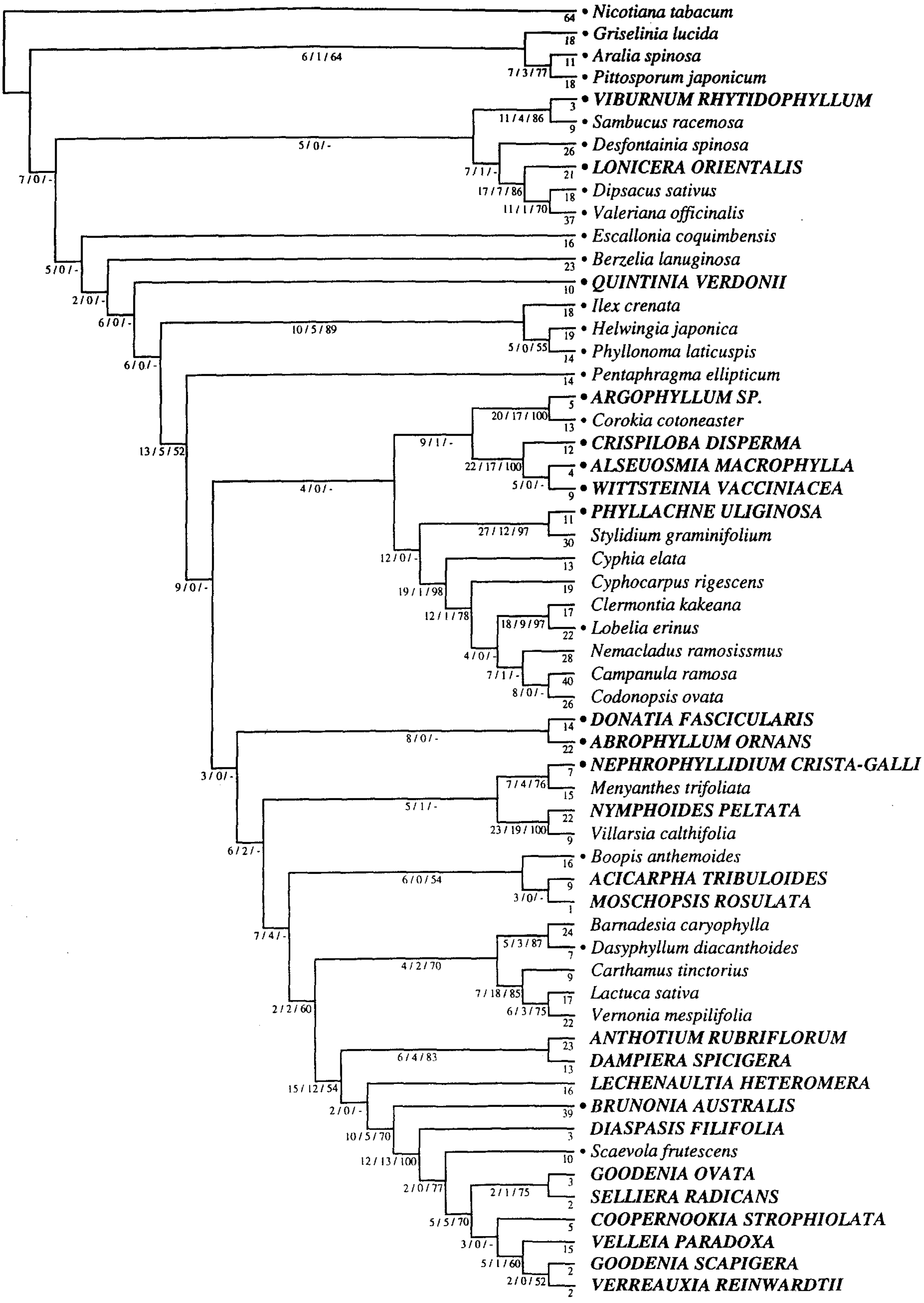
Fig. 2. Strict consensus tree of 6672 equally parsimonious trees based on *rbc*L sequences. Taxa in capital letters have been sequenced for this study Full taxon names and vouchers for these are given in Table 1. Sequences from the other taxa are previously published and listed in Table 2. Dots denote taxa also analysed in the first, tentative analysis (Fig. 1). Family names follow Takhtajan (1987)


64 • Nicotiana tabacum
18 • Griselinia lucida
6/1/64
11 • Aralia spinosa
7/3/77
18 • Pittosporum japonicum
3 • VIBURNUM RHYTIDOPHYLLUM
11/4/86
9 • Sambucus racemosa
5/0/-
26 • Desfontainia spinosa
7/0/-
7/1/-
21 • LONICERA ORIENTALIS
17/7/86
18 • Dipsacus sativus
11/1/70
37 • Valeriana officinalis
16 • Escallonia coquimbensis
5/0/-
23 • Berzelia lanuginosa
2/0/-
10 • QUINTINIA VERDONII
6/0/-
18 • Ilex crenata
10/5/89
19 • Helwingia japonica
5/0/55
14 • Phyllonoma laticuspis
6/0/-
14 • Pentaphragma ellipticum
5 • ARGOPHYLLUM SP.
20/17/100
13 • Corokia cotoneaster
9/1/-
13/5/52
12 • CRISPILOBA DISPERMA
22/17/100
4 • ALSEUOSMIA MACROPHYLLA
4/0/-
5/0/-
9 • WITTSTEINIA VACCINIACEA
11 • PHYLLACHNE ULIGINOSA
27/12/97
30 Stylidium graminifolium
12/0/-
13 Cyphia elata
19 Cyphocarpus rigescens
19/1/98
9/0/-
17 Clermontia kakeana
12/1/78
18/9/97
22 • Lobelia erinus
28 Nemacladus ramosissmus
4/0/-
7/1/-
40 Campanula ramosa
8/0/-
26 Codonopsis ovata
14 • DONATIA FASCICULARIS
8/0/-
22 • ABROPHYLLUM ORNANS
3/0/-
7 • NEPHROPHYLLIDIUM CRISTA-GALLI
7/4/76
15 Menyanthes trifoliata
5/1/-
22 NYMPHOIDES PELTATA
23/19/100
9 Villarsia calthifolia
6/2/-
16 • Boopis anthemoides
6/0/54
9 ACICARPHA TRIBULOIDES
3/0/-
1 MOSCHOPSIS ROSULATA
24 Barnadesia caryophylla
7/4/-
5/3/87
7 • Dasyphyllum diacanthoides
4/2/70
9 Carthamus tinctorius
7/18/85
17 Lactuca sativa
6/3/75
2/2/60
22 Vernonia mespilifolia
23 ANTHOTIUM RUBRIFLORUM
6/4/83
13 DAMPIERA SPICIGERA
15/12/54
16 LECHENAULTIA HETEROMERA
2/0/-
39 • BRUNONIA AUSTRALIS
10/5/70
3 DIASPASIS FILIFOLIA
12/13/100
10 • Scaevola frutescens
GOODENIA OVATA
2/0/77
3
2/1/75
SELLIERA RADICANS
2
5/5/70
5 COOPERNOOKIA STROPHIOLATA
3/0/-
15 VELLEIA PARADOXA
5/1/60
2 GOODENIA SCAPIGERA
2/0/52
2 VERREAUXIA REINWARDTII

ra of *Argophyllaceae* (Takhtajan 1987) is easy to accept, it is difficult to find substantial morphological and chemical support for their placement in the *Asterales.*

Alseuosmiaceae. The genera *Alseuosmia, Wittsteinia,* and *Crispiloba* form a particularly strongly supported group (Fig. 3). The three genera together make up the *Alseuosmiaceae* sensu van Steenis (1984), but the taxonomic history of this group is complicated, and the constituent genera have had very different placements, in a number of disparate families. The genus *Alseuosmia* itself has been placed in the *Caprifoliaceae* (Fritsch 1891), where it is clearly out of place morphologically, e.g., by way of its alternate leaves, induplicate-valvate corolla lobes, and features of wood anatomy (Dickison 1986). The *Alseuosmiaceae* were recognized as a family of their own by Airy Shaw (1965), and since then, other taxa have been added gradually, most recently by van Steenis (1984), whose treatment was accepted by Takhtajan (1987) and Thorne (1992). Van Steenis (1984) included the genus *Wittsteinia,* into which he sunk the genus *Periomphale,* which Gardner (1978) had previously included. *Wittsteinia,* in the original, monotypic sense, has previously been placed in *Ericaceae* (e.g., by Drude 1889) or *Epacridaceae* (originally suggested by Burtt 1949), but would certainly be an aberrant member of both families. The third genus in the family, *Crispiloba,* was erected (by van Steenis 1984) to accomodate a species previously assigned to *Randia* (*Rubiaceae*). The extension of *Alseuosmiaceae* implemented by van Steenis (1984) is clearly supported by the present analysis.

The sister group of the *Alseuosmiaceae* are the *Argophyllaceae.* There are obviously many differences between these families; the *Alseuosmiaceae* have fairly large sympetalous flowers with long stamen-corolla tubes, whereas most *Argophyllaceae* have inconspicuous, choripetalous flowers (sometimes the petals are fused at the very base; Zemann 1907). Some unusual floral features, however, are found in both families. Fringed petal appendages are present on the adaxial side of the petals in most *Argophyllaceae* (Eyde 1966). *Crispiloba* has a similar structure at the presumably homologous position, the base of the corolla lobes (van Steenis 1984), while *Wittsteinia* has a ring-shaped outgrowth just below the corolla sinuses (Gardner 1978). Petal wings (thin, lateral appendages, induplicate in bud) similar to those of *Goodeniaceae* and *Menyanthaceae* are present in *Corokia buddleioides* A. Cunn (*Argophyllaceae*) and most *Alseuosmiaceae* (M. Gustafsson, original obs.). If the wood anatomy of *Corokia* (Patel 1973) and *Alseuosmiaceae* (Dickison 1986) are compared, no important differences are revealed, apart from the raylessness in *Alseuosmia* and *Wittsteinia vacciniacea* F. Muell., which was interpreted as derived by Dickison (1986). He concluded that the features of wood anatomy combined with other evidence indicate a relationship between *Alseuosmiaceae* and the woody *Saxifragaceae.* Such a relationship, particularly with the *Escallonioideae,* had previously been suggested by, e.g., Airy Shaw (1965). The trichomes

Fig. 3. One of 6672 equally parsimonious trees based on *rbc*L sequences. The topology is identical to that obtained when applying the successive approximations weighting procedure to the same data. Below branches are given as follows: branch lengths/Bremer support values/bootstrap values. Dashes represent bootstrap values of 50% or lower

of *Alseuosmiaceae* are pluricellular and uniseriate, and structurally and developmentally similar to the peculiar T-shaped hairs of *Pittosporaceae,* which are in turn very similar to those of *Corokia* and *Argophyllum* (Gardner 1978, Dickison 1986). Like the *Argophyllaceae, Alseuosmiaceae* are poorly known in such important aspects as embryology and chemistry. Comparative studies in these fields are imperative to illuminate further the relationship between these families and their relatives in the *Asterales.* A notable fact, finally, is that the two families are very similar in their geographical distribution, as they are both virtually confined to eastern Australia, New Zealand, and New Caledonia.

***Campanulaceae* sensu lato.** The *rbc*L variation in the *Campanulaceae* s.l. was specifically studied by Cosner & al. (1994), and no new sequences from this group are added here. An important finding of Cosner & al. (1994) is the position of the genus *Sphenoclea* outside the *Asterales.* Traditionally it is placed near or in the *Campanulaceae,* in spite of important morphological differences. In the widely sampled cladistic analysis by Cosner & al. (1994), *Sphenoclea* does not appear in or even near the *Asterales,* but rather in another major branch of *Asteridae, Solanales-Boraginales,* with the genus *Hydrolea* (*Hydrophyllaceae* or *Hydroleaceae*) as sister group. The first author of the present paper has independently sequenced the *rbc*L-gene of *Sphenoclea,* using material of different origin but obtaining the same result as regards systematic position after cladistic analysis (M. Gustafsson, unpubl.).

Another genus placed near or in the *Campanulaceae* is *Pentaphragma.* This morphologically isolated taxon obviously belongs in the *Asterales,* in the successive weighting tree as the most basal branch, as sister group to the rest of the order (Fig. 3). In the cladistic analysis by Cosner & al. (1994) it is basal in one of the two major clades in the *Asterales* (the clade comprising *Asteraceae, Calyceraceae, Menyanthaceae,* and in that case also *Corokia*) while in the analysis by Gustafsson & Bremer (1995), it is basal in the other main branch (comprising the *Campanulaceae* s.l., the *Stylidiaceae* and, in that case, also the *Donatiaceae* and *Sphenocleaceae*).

As established by Cosner & al. (1994), the remaining *Campanulaceae* form a monophyletic group, as is the case in the analysis of Gustafsson & Bremer (1995), where they are represented by the five segregate families, *Campanulaceae, Lobeliaceae, Cyphiaceae, Nemcladaceae,* and *Cyphocarpaceae.* This group will here be referred to as the *Campanulaceae* s.l. The relationship between the segregate families differs between the morphological and the *rbc*L-studies, and to clarify the interrelationships of the *Campanulaceae* s.l., further study is needed, involving extended sampling for molecular study and a morphological analysis including several representative genera of each family.

***Stylidiaceae* and *Donatiaceae*.** In the *rbc*L-tree published by Cosner & al. (1994), the *Stylidiaceae,* represented by *Stylidium,* are the sister group to *Campanulaceae* s.l. Such a relationship is also seen in the present results, in the tree resulting from successive weighting (Fig. 3). The two genera included, *Phyllachne* and *Stylidium,* share a very long branch. Morphologically too, this family is very apomorphic (i.e., it has a large number of apomorphies), one unique feature being the floral column consisting of two anthers fused with the style.

In the first analysis, with a restricted sampling in the *Asterales,* the genus

Donatia is sister group to *Abrophyllum*. The same relationship is found in many of the most parsimonious trees resulting from the second analysis, where *Asterales* were more densely sampled, as well as in the tree resulting from successive weighting (Fig. 3). An association between *Donatia* and *Abrophyllum* has not been suggested before, and the two genera share no characters in outer morphology (apart from features widespread in *Asteridae* and *Rosidae*). It should be noted, however, that *Abrophyllum* is poorly known chemically and embryologically, and there is of course a possibility that investigations in these fields may reveal similarities. The most common position for *Donatia* in more recent systems is close to the *Stylidiaceae* in the *Asterales,* and in some of the most parsimonious trees of the second cladistic analysis, *Donatia* is sister group to the *Stylidiaceae.* It is sometimes included in *Stylidiaceae,* as by MILDBREAD (1908) and DAHLGREN (1983). In the morphological analysis by GUSTAFSSON & BREMER (1995), *Stylidiaceae* and *Donatiaceae* are sister taxa. Characters shared by these two genera are reductions in stamen number (2–3 in *Donatia,* 2 in *Stylidiaceae*), extrorse anthers (unique in the order), and extrastaminal nectary. Embryologically, they are similar too, e.g., in ovule development and configuration of megagametophyte and endosperm haustoria (PHILIPSON & PHILIPSON 1973). The similarity in habit, ecology, and distribution has probably also contributed to the association of the two taxa. *Donatia* is, however, different from *Stylidiaceae* in many ways. It has free styles and free petals, and the pollen is tricolporate, while the *Stylidiaceae* have 2–8-colpate pollen with a granular colpus membrane (ERDTMAN 1952, ERICKSON 1981), somewhat similar to the pollen of some *Campanulaceae* (e.g., *Codonopsis* and *Cyanathus*).

Systematic positions outside the *Asterales* have been suggested for *Donatia* as well as for the *Stylidiaceae. Donatia* is in a tribe of its own within the *Saxifragaceae-Saxifragoideae* in the treatment of that family by ENGLER (1890). HUTCHINSON (1973) included *Donatiaceae* (monotypic) in his *Saxifragales, Stylidiaceae,* including *Donatia,* were placed in *Ericanae-Stylidiales* by DAHLGREN (1989). The fact that *Donatia* does belong in the *Asterales* is clear from the present results. This is also supported by the presence of inulin in *Donatia* (GIBBS 1974), a polysaccharide otherwise rare in angiosperms. The position relative to other taxa within the order, however, remains ambiguous. If the available morphological evidence is considered, a position near the *Stylidiaceae* seems to be the most plausible. A cladistic analysis combining morphological and molecular data, and/or inclusion of further taxa likely to be related to *Abrophyllum, Donatia,* and *Stylidiaceae* could help to solve the problem. One interesting genus in this context is the South American *Tribeles,* which was suggested to be the ancestor of *Donatia* by HALLIER (1908). It was placed in the *Saxifragaceae-Escallonioideae* in ENGLER's (1930) system, transferred to a family of its own by AIRY SHAW (1965), who was followed by TAKHTAJAN (1987). This interesting genus appears to be different from *Donatia* in many aspects of floral morphology; the corolla aestivation is contorted (AIRY SHAW 1965; not known from *Asterales*), a disc is absent, and the carpels are apparently entirely fused, as opposed to *Donatia.* The anthers are, however, extrorse as in *Donatia* and *Stylidiaceae,* and the carpel number is three, as in the South American *Donatia fascicularis* J. R. FORST. & G. FORST.

The *Asteraceae-Calyceraceae-Goodeniaceae-Menyanthaceae*-clade. One of the major clades in the *Asterales* is that consisting of the families *Menyanthaceae,* *Calyceraceae, Goodeniaceae,* and *Asteraceae.* Though poorly supported by the present data, it forms a monophyletic group also in other molecular studies, such as those by Cosner & al. (1994; *rbc*L sequences) and R. Jansen & K.-J. Kim (unpubl.; *ndh*F sequences). The monophyly of the group of four families has also support from morphology (Lammers 1992, Gustafsson & Bremer 1995). Embryologically it is characterized by the absence of endosperm haustoria and multinucleate tapetal cells. The four families also share unique features of floral venation (Gustafsson 1995 a). Petal morphology is particularly similar in *Menyanthaceae* and *Goodeniaceae,* taxa that are also characterized by the frequent occurrence of sclerenchymatous idioblasts.

Menyanthaceae. The *Menyanthaceae* are basal to a clade comprising *Asteraceae, Calyceraceae,* and *Goodeniaceae.* The family has the same position as in the morphology tree obtained by Gustafsson & Bremer (1995; after successive weighting). In the strict consensus tree (Fig. 2), the family is monophyletic. The paraphyly indicated by some of the *rbc*L studies (e.g., Michaels 1993) is probably an artefact, perhaps explained by the relatively large difference between the two representatives included in these studies, *Menyanthes* and *Villarsia* (cf. branch lengths in Fig. 3), and the restricted sampling of related taxa. The pronounced distinction between the *Menyanthes-Nephrophyllidium* group and the *Villarsia-Nymphoides* group indicated by the molecular data is strongly supported by palynological data (Nilsson 1973) and floral venation (Lindsey 1938). The unity of the *Menyanthes-Nephrophyllidium* clade is also supported by seed morphology (Chuang & Ornduff 1992). Indeed, *Nephrophyllidium* was included in *Menyanthes* by Bentham (1876). Flavonoid data (Bohm & al. 1986) indicate a close relationship between *Nymphoides* and *Villarsia,* but do not support a close affinity between *Nephrophyllidium* and *Menyanthes.* The fifth genus, *Liparophyllum,* which was not available for the present study, has affinities with the *Villarsia-Nymphoides* group, palynologically as well as in its seed morphology (Nilsson 1973, Chuang & Ornduff 1992), whereas its flavonoid pattern is isolated in the family (Bohm & al. 1986). In conclusion, there seem to be two fairly distinct and well-defined groups in this family.

Asteraceae relationships. The present results suggest a sister group relationship between the *Asteraceae* and the *Goodeniaceae* (Fig. 2); the support value, however, is low. The sister group of these two families are the *Calyceraceae* (paraphyletic in some of the most parsimonious trees, cf. Fig. 2). The group formed by these three families has relatively high support-values (Fig. 3). The *Goodeniaceae* have previously been identified as a good sister group candidate of *Asteraceae* based on floral ontogeny (Harris 1991). The two families share "the greatest amount of derived ontogenetic characters" as compared to *Calyceraceae* and *Lobeliaceae.* Other morphological comparisons, particularly of pollen, have in many cases (Turner 1977, Skvarla & al. 1977, Hansen 1992) rather identified the *Calyceraceae* as the closest relatives of *Asteraceae,* although the *Goodeniaceae* too are very similar palynologically, sharing with the other families, e.g., a highly differentiated columella layer. A sister group relationship between *Asteraceae* and *Calyceraceae* was also found by Jansen & Kim (presented at the *Compositae* conference, Kew 1994), using *ndh*F sequences. Jansen & Kim's analysis, however, included only one species of *Calyceraceae* and two of *Goodeniaceae.* In earlier *rbc*L-studies (e.g., Michaels & al. 1993, Cosner & al. 1994), *Calyceraceae* and *Goodeniaceae* are sister groups, but these families had only one representative each. All three relationships possible between these families have thus been suggested at one time or the other. A study of petal venation (Gustafsson 1995) documented the same pattern in the *Goodeniaceae* as in a group of basal *Asteraceae* (the *Stenopadus*-group). This pattern, being more complex and characterized by less fusion of veins, was hypothesized by Carlquist (1961) to be primitive in the *Asteraceae*. To complicate the picture, the *Calyceraceae* have a more "advanced" petal venation, also present in the majority of *Asteraceae*. In the cladogram of Gustafsson & Bremer (1995), based on morphology, these three families form a monophyletic group, but the relationship between them is unresolved. All three have, apart from the palynological similarities, several features in common, such as secondary pollen presentation, more or less connate anthers (apparently plesiomorphic in the variable *Goodeniaceae*) and frequent occurrence of a specialized filamental collar (or more accurately, connective base; Pesacreta & al. 1994, Gustafsson & Bremer 1995). In conclusion, the association of the three families *Asteraceae, Calyceraceae,* and *Goodeniaceae* appears to be very well founded, whereas the relationship between them is much less certain. In order to resolve with confidence the relationship between the three families, a more thorough cladistic analysis of the group is required. Such an analysis should combine morphological and molecular data and include several genera of each family.

Goodeniaceae. Because of the comparatively large number of sequences of *Goodeniaceae* included in the analysis, some conclusions about the phylogeny of the family can be drawn.

Anthotium and *Dampiera* form a basal branch in the family (Figs. 2, 3). These two genera are similar in many aspects of morphology. The pollen in both genera is striate, which is otherwise unknown in the family (Skvarla & al. 1977). The two genera constitute one of four groups in a subdivision of the family based on floral venation (Carolin 1959). Furthermore, the indusial structure and pollen presentation mechanism are similar in *Anthotium* and *Dampiera* (Carolin 1960, Ladd 1994).

In the selected most parsimonious tree (Fig. 3), the genus *Lechenaultia* is the sister group to the remaining *Goodeniaceae*. The isolated position of this genus has been recognized also on the base of morphology. It has many features unmatched in the family, but most of these are seemingly apomorphic, such as the pollen tetrads and the unique fruit morphology (each seed surrounded by a separate portion of the true fruit wall; Carolin 1966). The indusial structure and the pollen presentation mechanism associated with it are basically different from other *Goodeniaceae* (Carolin 1959, Yeo 1993).

A notable feature of the cladogram (Fig. 2) is the position of *Brunonia* nested within the *Goodeniaceae*. In order to retain the monophyly of *Goodeniaceae, Brunonia* will have to be included. Amont those who have suggested inclusion in *Goodeniaceae* is Carolin (1978), the prime authority on the family, although he hypothesized that *Brunonia* has had a long history separate from other *Goodeniaceae*. *Brunonia* has a long branch in the *rbc*L tree (Fig. 3), and is also highly apomorphic in its morphology. Among features unique to *Brunonia* in the *Goodeniaceae* are actinomorphic flowers, hypogynously inserted stamens, absence of endosperm, feather-like calyx lobes, and a special type of adpressed hairs (Carolin 1971, 1978). In view of its position in the *rbc*L tree, the features mentioned as well as the condensed inflorescence and uniovulate ovary of *Brunonia,* are most easily interpreted as autapomorphies, and are thus not relevant in the discussion of interfamilial relationships, where *Brunonia* has often appeared. *Brunonia* does not form a group together with *Anthotium, Dampiera* and *Lechenaultia,* as suggested by Carolin (1978), and the similarities with these genera (connate anthers and chromosome base number x = 9) must be explained as symplesiomorphies. The sister taxon of *Brunonia* is rather the group formed by the remaining genera, the *Scaevola-Goodenia*-clade (*Diaspasis* through *Verreauxia* in Figs. 2 and 3). Palynologically, *Brunonia* is certainly very similar to members of its sister group, differing chiefly in having sexine ridges along the colpi (Duigan 1961, Skvarla & al. 1977).

There is strong support (Fig. 3; bootstrap value of 100% and a Bremer support of 13) for the *Scaevola-Goodenia*-clade, which comprises *Diapsasis, Scaevola* and the *Goodenia*-group (*Goodenia ovata* through *Verreauxia* in Figs. 2 and 3). The relationship among these three units is not evident from the consensus tree (Fig. 2), but in the tree resulting from successive weighting *Scaevola* is the sister group of the *Goodenia*-group. *Diaspasis* and *Scaevola* share some features that are rare in the *Goodenia*-group. They both have similar, bilocular, biovulate and indehiscent fruits, and subequal corolla lobes, which are arranged almost actinomorphically in *Diaspasis,* while fan-like in *Scaevola.*

The *Goodenia*-group is well-defined (the support is relatively high) and tightly knit; within it the *rbc*L variation is very limited, as is clear from the short branches (Fig. 3). The only exception is the long terminal branch of *Velleia.* The results strongly suggest that the genus *Goodenia* is paraphyletic, as the two species included (the type species of the two subgenera in the classification by Carolin & al. 1992) are not sister taxa. Support measures for relationships within the group are generally low, one exception being the sister-group relationship between *Selliera* and *Goodenia ovata* Sm. More extensive sampling is certainly required in this part of the *Goodeniaceae* in order to define generic limits and to determine relationships among genera. The *rbc*L-gene alone is probably not sufficiently variable to solve these problems. Carolin (1990), based on an unpublished analysis of the *Goodenia*-group, sunk the genera *Calogyne, Catosperma, Neogoodenia,* and *Symphyobasis* into the large and variable genus *Goodenia.* In the case of *Selliera* he left the question open whether it belongs within the genus *Goodenia,* but retained it as a separate genus pending further study. According to the *rbc*L-data, the genus *Coopernookia* (a segregate of *Goodenia;* Carolin 1968) obviously belongs within the *Goodenia*-group, and does not occupy a position basal in the family, as envisaged by Carolin (1978). This view was based largely on the chromosome base numbers in the family. *Coopernookia,* having the lowest (x = 7), was hypothesized to be most primitive (following the principles of Stebbins 1966). If the chromosome base numbers are mapped on the *rbc*L tree, it appears rather that the highest number (x = 9) is plesiomorphic (present in *Anthotium, Brunonia, Dampiera,* and *Lechenaultia*), with reduction to x = 8 in the *Scaevola-Goodenia*-group, and further reduction to x = 7 in *Coopernookia.* A base-number of x = 9 is also seen in the related *Menyanthaceae,* and is widely accepted to be the base number also in *Asteraceae* (Raven 1975). The absence of wings on the seeds of *Coopernookia* (otherwise present in the *Goodenia*-group) was also considered by Carolin (1978) to be a primitive feature, but in the light of the present results, it is more easily interpreted as a reduction associated with a highly probable switch in dispersal mechanism accompanied by the development of a strophiole in *Coopernookia*. One conclusion of the present study is that both *Coopernookia* and *Verreauxia* (and most probably the related *Pentaptilon*) should be considered when investigating the relationship between *Goodenia* and its "satellite genera".

In the above discussion of the *Goodeniaceae,* reference has been made repeatedly to the phylogenetic model of the *Goodeniaceae* constructed by Carolin (1978). Carolin's tree is basically a phenetic network based on morphological characters, and adjusted in accordance with Hennigian principles (Hennig 1966). It is in many ways similar to the topologies presented here. One difference is that *Anthotium* is linked with *Lechenaultia* rather than with *Dampiera,* and as mentioned above, *Brunonia* is associated with these three genera. The differing position of *Coopernookia,* basal in the family in Carolin's tree, is in essence the result of his polarization of characters, which in turn is based on a hypothetical ancestor rather than outgroup comparison. Such a comparison would have been difficult at the time, because neither *Asteraceae, Calyceraceae,* nor *Menyanthaceae* were discussed as close relatives of the *Goodeniaceae,* and comparisons with the more distantly related (in the light of presently available information) and morphologically highly specialized *Stylidiaceae* and *Lobeliaceae* were not fruitful (Carolin 1978).

To sum up, one could say that the *Goodeniaceae* comprise four well-defined groups: The genus *Lechenaultia,* the *Anthotium-Dampiera*-clade, the morphologically (and molecularly) highly apomorphic *Brunonia,* and a monophyletic core group, the *Scaevola-Goodenia*-clade. Cytological (Peacock 1963) and palynological data support this division, and so do features of floral venation; Carolin (1959) suggested an identical division based on such data.

Characterization of the *Asterales*. According to the present results, the order *Asterales,* defined as above, actually comprises most families placed in the orders *Campanulales* and *Asterales* s.str. in more recent systems (Cronquist 1981, Takhtajan 1987, Dahlgren 1989, Thorne 1992). These families are, apart from *Asteraceae* and *Campanulaceae,* the *Goodeniaceae* (including *Brunonia*), *Stylidiaceae, Donatiaceae,* and *Pentaphragmataceae.* Based on information from early *rbc*L studies, Thorne (1992) included also the *Menyanthaceae,* and their position in the order has been confirmed repeatedly. Apart from the families traditionally associated with *Asteraceae* and/or *Campanulaceae,* several other groups appear to belong within the *Asterales.* These are the *Argophyllaceae,* the *Alseuosmiaceae,* and *Abrophyllum* of the *Escalloniaceae.* Morphologically the order must be said to be very heterogenous. One example of this is that it comprises both choripetalous and sympetalous taxa. Today, the interest is focused more on variation in the early stages in corolla ontogeny, rather than on the sometimes problematical distinction between sympetaly and choripetaly in fully developed corollas. Those *Asterales* investigated seem to be characterized by a ring-shaped corolla primordium (Erbar 1991). This feature is not restricted to the *Asterales,* but occurs also in, e.g., *Dipsacales* (Erbar 1991), and a similar ontogeny also in the choripetalous

Apiales (Leins & Erbar 1987). Most often the flowers of *Asterales* are pentamerous with introrse anthers and valvate corolla aestivation. Secondary pollen presentation is common, but has apparently evolved twice within the group (in *Campanulaceae* s.l., and in the *Asteraceae-Calyceraceae-Goodeniaceae*-clade; Gustafsson & Bremer 1995). A tentative chemical synapomorphy for the order is the possession of higher inulins as storage carbohydrates (Pollard & Amuti 1981), although it should be noted that some of the included taxa (*Abrophyllum, Alseuosmiaceae, Argophyllaceae,* and *Pentaphragmataceae*) have apparently never been assayed for these substances.

In order to maintain the monophyly of the *Asterales,* an expansion of the order is called for, so as to accomodate also the *Argophyllaceae* (previously indicated by the position of *Corokia* in earlier molecular studies), the *Alseuosmiaceae,* and the genus *Abrophyllum* (transferred from the *Escalloniaceae* to a family of its own, *Abrophyllaceae,* possibly also encompassing the genus *Cuttsia;* Nakai 1943). Even before such an addition, the *Asterales* are very heterogenous morphologically, and the possibility of splitting the group into two or more orders has to be kept open. A prerequisite for such a division is that a small number of reasonably well supported clades can be identified within the group, clades that could be assigned ordinal rank. Due to the poorly supported relationships at the base of the order, this condition is not met, and it is proposed that the concept of *Asterales* in a wide sense should be retained for the time being.

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