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Evolution of the Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae

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ABSTRACT. Based on results from cladistic analyses of morphology and DNA sequences (the two chloroplast genes *rbcL* and *ndhF*), the three Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae are each monophyletic, belong within Asterales, and together form a monophyletic group. Two new *rbcL* sequences and thirteen new *ndhF* sequences were obtained. Congruence tests did not reveal any significant incongruence between the two molecular data sets or between the molecular and morphological data. The character evolution of the Alseuosmiaceae-Argophyllaceae-Phellinaceae group is discussed. The Australasian ancestor of this group was probably a woody plant with simple, alternate, serrate leaves and regular, choripetalous, epigynous flowers borne in panicles. All three families should be retained in line with the "principle of ease of identification."

Among the asterids, a subclass comprising more than one fourth of all species of flowering plants, there are several well-known orders, for example, Apiales and Asterales (cf., e.g., APG 1998). There are also additional taxa with uncertain positions, which may belong in any of these. This study deals with three families comprising seven genera, which in the past have been difficult to place with any certainty.

The three woody families Alseuosmiaceae, Argophyllaceae, and Phellinaceae (Figs. 1–3) all have a similar, Australasian distribution. The genera had previously been placed in families with rather different relationships (Table 1), but now it is clear that they all belong within Asterales (Gustafsson et al. 1996; Backlund and Bremer 1997; Gustafsson and Bremer 1997; Källersjö et al. 1998). These recent studies were based on information from DNA sequences of the chloroplast *rbcL* gene. Apart from placing the three families in Asterales, the *rbcL* data indicate that the three families form a monophyletic group.

Part of this study is to investigate the monophyly of the families as a group, the monophyly of each family, and to clarify their relationships. Both molecular and morphological data were employed. In addition to *rbcL* sequences, sequences from another chloroplast gene, *ndhF*, were used. The *ndhF* gene has a higher substitution rate than *rbcL* (Olmstead and Palmer 1994), and has been useful in solving phylogenetic problems at both family and lower levels (e.g., recent studies by Neyland and Urbatsch 1996; Bohs and Olmstead 1997; Smith et al. 1997a;

Smith et al. 1997b; Terry et al. 1997). Morphological studies, mainly of herbarium material, and thorough studies of the literature have provided additional data. The morphological characters were optimized on the phylogeny in order to explore how character states evolve.

Taxonomic Background and Distribution. ALSEUOSMIACEAE. Included in Alseuosmiaceae are four genera, *Alseuosmia* (four species; Gardner 1978b; recent studies suggest the recognition of a fifth species; M. Merrett, pers. comm.), *Wittsteinia* (two species; Tirel 1996), *Periomphale* and *Crispiloba* (both monotypic; Tirel and Jérémie 1996 and van Steenis 1984, respectively). When Cunningham (1839a) described the New Zealand genus *Alseuosmia,* he suggested that it was strongly allied with Cornaceae, Caprifoliaceae, and Loranthaceae. Considering the differences between *Alseuosmia* and these families he proposed *Alseuosmia* as a distinct family. The genus was, however, placed in Caprifoliaceae by many workers (e.g., Hooker 1873; Fritsch 1891; Schlechter 1906). Airy Shaw (1965) provided the first formal description of Alseuosmiaceae. He excluded *Alseuosmia* and the New Caledonian genera *Periomphale* and *Memecylanthus* from Caprifoliaceae based on alternate leaves, valvate corolla lobes, and (as noticed by Erdtman 1952) pollen morphology and geographic isolation. *Memecylanthus* is now sunk into *Periomphale* (see below). Airy Shaw (1965) suggested that Alseuosmiaceae are best placed between Escalloniaceae and Loganiaceae. The placement of Alseuosmiaceae near Escalloniaceae (or Saxifragaceae-Escallonioideae) was accepted by
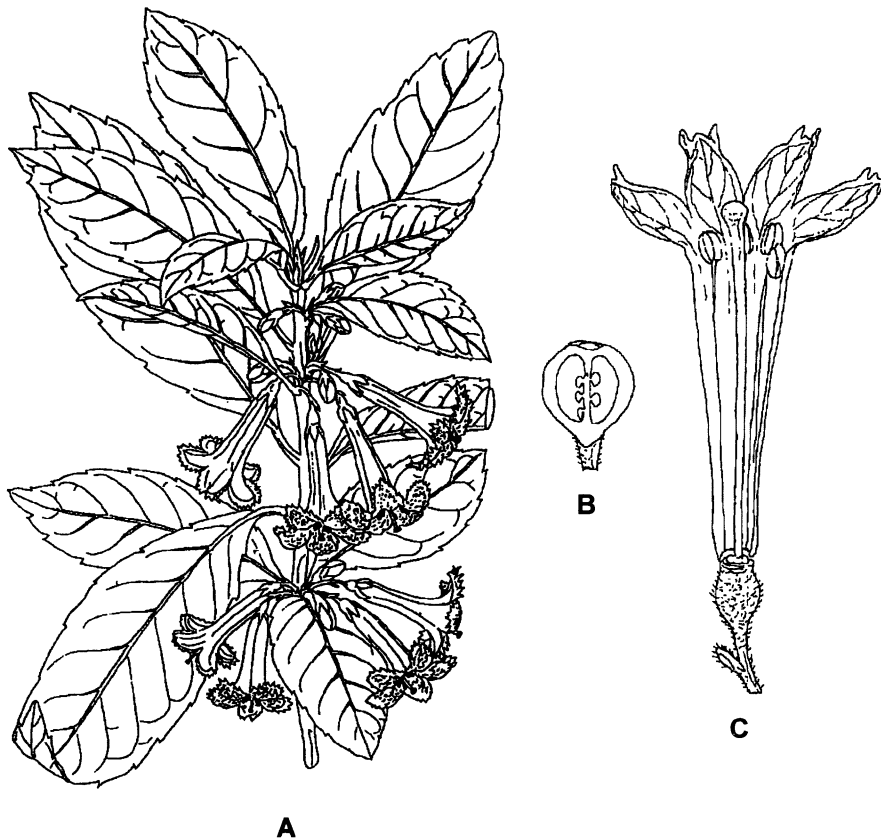
FIG. 1.   Alseuosmiaceae. A. *Alseuosmia macrophylla* A. Cunn., habit (×1/2). B, C. *A. banksii* A. Cunn. B. Longitudinal section of ovary (ca. ×2). C. Flower with corolla laid open (×4). Modified after Hooker (1853–55; B, C; 1887; A).

Gardner (1978b), Dickison (1986), Thorne (1992), and others. Cronquist (1981) placed the family near Grossulariaceae (including Escalloniaceae) and Pittosporaceae. Takhtajan (1997) treated it as a member of Hydrangeales, an order comprising Escalloniaceae and several other taxa formerly assigned to that family.

Wittsteinia was long thought to be a monotypic genus from Victoria, Australia, consisting only of *W. vacciniacea*. Now it is clear that the genus *Wittsteinia* is a member of Alseuosmiaceae, and also that it includes an additional species, *W. papuana*, an epiphytic shrublet from New Guinea (van Steenis 1978, 1984, 1986). *Wittsteinia* has been placed in Ericaceae (e.g., Bentham 1869 and Drude 1889), but, based mainly on stamen characters, Burtt (1949) maintained that its position is within Epacridaceae. Stevens (1971) noticed that *Wittsteinia* is different from other Ericaceae and he consequently established a new subfamily, Wittsteinioideae.

Van Steenis (1978) reduced *Memecylanthus* and *Pachydiscus* (cf. Airy Shaw 1965 and Hutchinson 1967) from New Caledonia to *Periomphale*, and later he sunk *Periomphale* itself into *Wittsteinia*, since both genera included species with fleshy dentate leaves and cleistogamous flowers (van Steenis 1984). However, in Flore de la Nouvelle-Calédonie (Tirel and Jérémie 1996) *Periomphale* is maintained as a separate genus (see also Tirel 1996).

The fourth genus of Alseuosmiaceae, *Crispiloba*, was earlier included erroneously as a synonym of *Randia* (Rubiaceae). Van Steenis (1984) realized that the correct position for this monotypic genus from Queensland, Australia, is within Alseuosmiaceae. All four genera within Alseuosmiaceae share features such as heavily scented flowers with petal wings (Fig. 1A, C) and the presence of hairs in the leaf axils (van Steenis 1984).

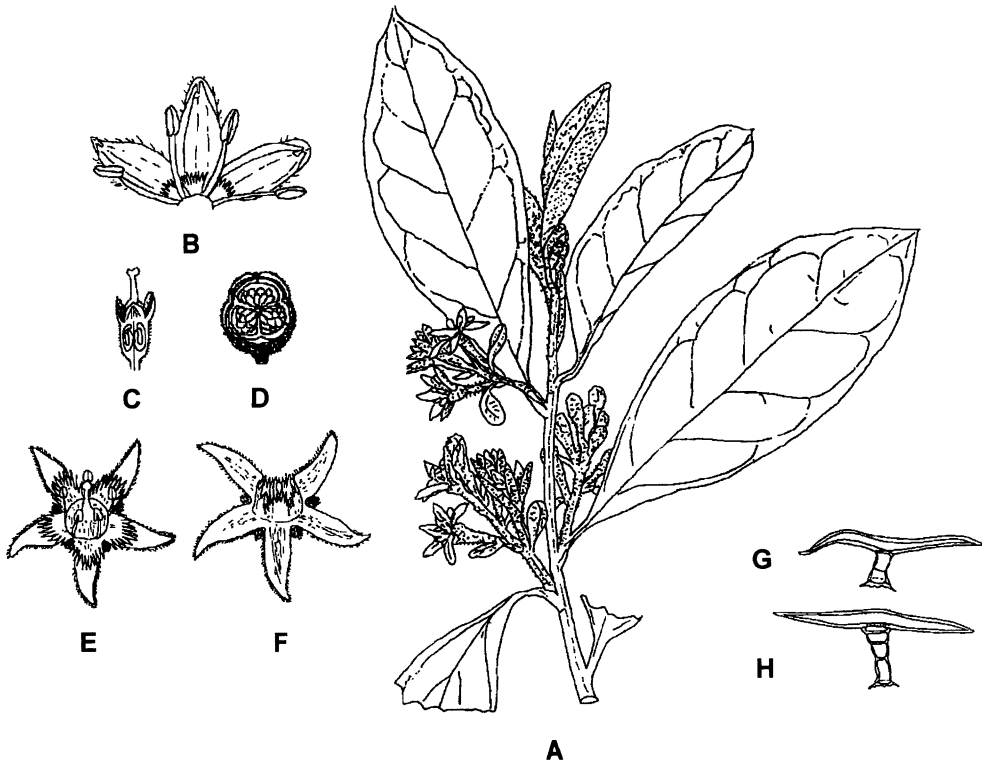ARGOPHYLLACEAE.   Argophyllaceae consist of two genera, *Argophyllum* (ca. 15 species; Zemann

FIG. 2. Argophyllaceae. A. *Corokia macrocarpa* Kirk, habit (×1). B, C. *C. buddleioides* A. Cunn. B. Flower opened out (ca. ×2). C. vertical section of gynoecium (ca. ×2). D-F. *Argophyllum ellipticum* Labill. D. Transverse section of capsule (×2). E. Flower opened out (×2). F. Flower (×2). G. *A. lejourdani* F. Muell., T-hair (×100). H. *C. macrocarpa* Kirk, T-hair (×100). Modified after Wangerin (1909; A), Wilkinson (1993; B, C), Labillardière (1824; D-F), and Al-Shammary and Gornall (1994; G, H).

1907; Däniker 1931; Guillaumin and Virot 1953; Forster 1990) from eastern Australia and New Caledonia, and *Corokia*. *Corokia* has a south Pacific distribution that extends over 6,000 km (Smith 1958). Of the six species of *Corokia* one is endemic to northern New South Wales, one to Lord Howe Island, two to New Zealand, one to the Chatham Islands, and yet another to Rapa Island (e.g., Eyde 1966).

The two genera have not always been placed together. *Argophyllum* was mostly placed in Saxifragaceae-Escallonioideae (e.g., Engler 1890; Schlechter 1906; Engler 1928; Thorne 1992), or, if this subfamily was recognized as a family of its own, in Escalloniaceae (Willis 1966; Takhtajan 1983). *Corokia*, on the other hand, was often included in Cornaceae (Hooker 1867; Harms 1897; Wangerin 1909; Cheeseman 1925; Allan 1961; Melchior 1964; Hutchinson 1967; Cronquist 1981). Cunningham (1839b), the author of the genus, initially suggested that *Corokia*

is related to Rhamnaceae, but Raoul (1844, 1846) argued that it is better placed in Cornaceae. Dahlgren (1980) included *Corokia* as a separate family in Cornales. Serological investigations indicate that *Corokia* is misplaced in Cornaceae (Brunner and Fairbrothers 1978; Lee 1985), and *rbcL* sequence data suggest affinities, not with Cornaceae, but with Asteraceae (Xiang et al. 1993).

It was Hallier (1908) who first suggested a close relationship between the two genera, based on the presence of T-shaped hairs (Fig. 2G, H) and the resemblance of the corolline ligules in both genera (Fig. 2B, E, F); he consequently considered *Corokia* to be nothing more than a reduced *Argophyllum*. Evidence from floral anatomy (Eyde 1966), pollen morphology (Hideux and Ferguson 1976; Ferguson and Hideux 1978), and molecular data (Gustafsson et al. 1996; Backlund and Bremer 1997; Gustafsson and Bremer 1997; Källersjö et al. 1998; this study) further indicates a relationship between the two
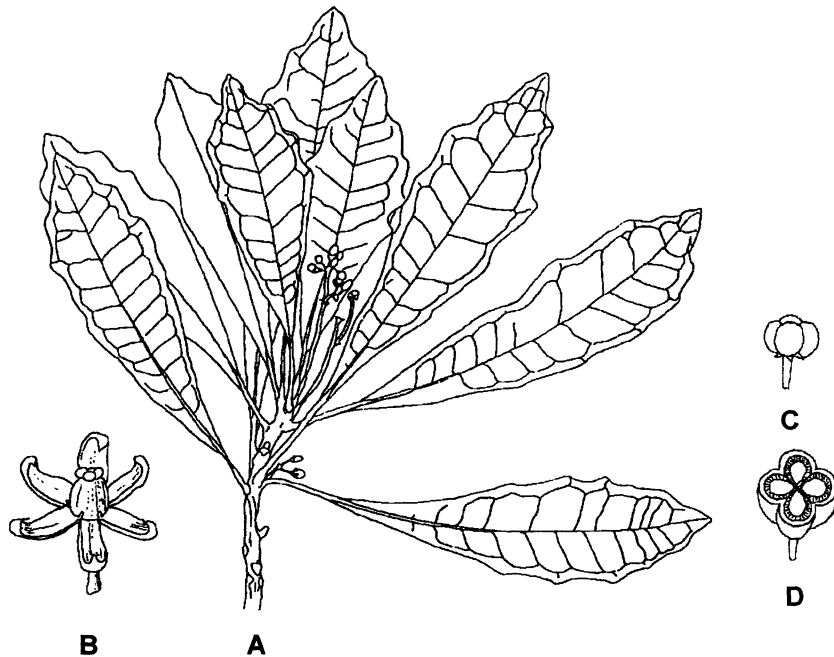
FIG. 3.   Phellinaceae. A. *Phelline lucida* Vieill. ex Baill., habit (x2/5). B. *P. erubescens* Baill., female flower with reduced staminodes (x4). C, D. *P. comosa* Labill. C. Fruit (x3/2). D. Transverse section of fruit (ca. x2). Modified after Loesener (1942; A, B) and Labillardière (1824; C, D).

genera. Several authors have noted that *Argophyllum* and *Corokia* should be placed together, for example, Engler (1928), Erdtman (1952), Swamy (1954), Smith (1958), Takhtajan (1983), and Thorne (1983, 1992).

After studying the floral anatomy of *Corokia*, Eyde (1966) concluded that it does not belong in Cornaceae but is close to *Argophyllum*, and that neither of the two genera has an indisputable position within Saxifragaceae sensu Engler. Takhtajan (1987) was the first to suggest that the two genera are so similar that they deserve to be arranged in the same family, Argophyllaceae. Based on embryological studies, Kapil and Bhatnagar (1992) thought that *Corokia* was best treated as a distinct family, more closely related to Stylidiaceae (in Asterales sensu APG 1998) than to Cornaceae or to Escalloniaceae. Most recently, Takhtajan (1997) described Corokiaceae as a new family, also noting the differences in "placentation, the number of ovules, and the structure of fruits and seeds" (Takhtajan 1997). He placed this new family together with Argophyllaceae, Alseuosmiaceae, and eleven other families in his Hydrangeales-Cornidae.

PHELLINACEAE.   This family comprises one genus of about ten species, all endemic to New Cal-

edonia (cf., e.g., Loesener 1901; Mabberley 1997; Takhtajan 1997). *Phelline* was regarded as a member of Rutaceae (Hooker 1862) before Baillon's (1892) placement of the genus in Aquifoliaceae. Loesener (1901) treated it as a separate tribe of Aquifoliaceae, mainly because of the valvate petals with inflexed apicula (Fig. 3B). Affinities with Araliaceae have also been suggested (Willis 1966). *Phelline* was given familial rank by Takhtajan (1966), because it differs from Aquifoliaceae in having "valvate petals, by the character of the inflorescence, the hemitropous or weakly campylotropous ovules, the wood anatomy, the quite different sporoderm morphology and the leaf venation" (Takhtajan 1969). However, he considered the family closely related to Aquifoliaceae in Icacinales–Rosidae (Takhtajan 1997). Other characters that make *Phelline* distinct from Aquifoliaceae are leaf anatomy, anatomy of the petiole (Baas 1975), and pollen morphology (Lobreau-Callen 1977). In the system of Cronquist (1981), *Phelline* was retained in Aquifoliaceae (Cronquist 1981).

MATERIALS AND METHODS

Taxon Sampling.   Molecular Studies. To investigate the position and the monophyly of Alseuos-

TABLE 1. List of genera under study, families associated with each genus by past studies, and authors who first suggested a new family placement.

Genus	Family	Author
Alseuosmiaceae		
Alseuosmia:	Cornaceae	Cunningham 1839a
	Caprifoliaceae	Hooker 1853–55
	Alseuosmiaceae	Airy Shaw 1965
Crispiloba:	Rubiaceae	Moore 1917 (as Randia)
	Alseuosmiaceae	Airy Shaw 1965
Periomphale:	Gesneriaceae	Baillon 1888
(incl. *Memecylanthus*	Caprifoliaceae	Schlechter 1906
and *Pachydiscus*)	Alseuosmiaceae	Airy Shaw 1965
Wittsteinia:	Ericaceae	von Mueller 1861
	Epacridaceae	Burtt 1949
	Alseuosmiaceae	Airy Shaw 1965
Argophyllaceae		
Argophyllum:	Saxifragaceae	Endlicher 1839
	Escalloniaceae	Willis 1966
	Argophyllaceae	Takhtajan 1987
Corokia:	Rhamnaceae	Cunningham 1839b
	Cornaceae	Raoul 1844
	Saxifragaceae	Engler 1928
	Escalloniaceae	Willis 1966
	Corokiaceae	Dahlgren 1980
	Argophyllaceae	Takhtajan 1987
Phellinaceae		
Phelline:	close to Pouteria (Sapotaceae)	Labillardire 1824
	Rutaceae	Hooker 1862
	Aquifoliaceae	Baillon 1891
	Phellinaceae	Takhtajan 1966

miaceae, Argophyllaceae, and Phellinaceae, 27 *rbcL* and *ndhF* sequences representing all families of Asterales were analyzed together with two additional sequences (*Quintinia verdonii* and *Viburnum rhytidophyllum*) from the euasterids II (sensu APG 1998; cf. asterid II sensu Chase et al. 1993), the latter used as outgroup for the rooting of the trees (Table 2). The sampling is based on the results of earlier extensive *rbcL* analyses including many rosid and asterid taxa (Gustafsson et al. 1996; Backlund and Bremer 1997; Gustafsson and Bremer 1997) and the analysis by Källersjö et al. (1998) including taxa from cyanobacteria to flowering plants. In a few instances (*Cyphia, Dampiera, Dasyphyllum, Lobelia,* and *Pentaphragma*), *rbcL* and *ndhF* sequences were not available from the same species. Since these genera are well supported as monophyletic (e.g., Wimmer 1953; Cabrera 1959; Kapil and Vijayaraghavan 1965; Wimmer 1968; Dunbar 1978; Thulin 1978; Rajput and Carolin 1988), sequences from different species of the same genus were pooled.

MORPHOLOGICAL AND COMBINED STUDIES. Morphological characters for representatives of all genera (except *Periomphale*) of the three families under study were examined. The position of the three families within Asterales is well supported (e.g., Backlund and Bremer 1997; Gustafsson and Bremer 1997; Källersjö et al. 1998; this study), but their precise sister group relationships within the order are not known, making the choice of outgroup difficult. On the other hand, a patristically closer outgroup (with a smaller number of steps along the connecting branches) may be more reliable for rooting the ingroup than the sister group, minimizing the risk of long branch attraction and false rooting (cf. Nixon and Carpenter 1993 and Lyons-Weiler et al. 1998). The families patristically closest to the Alseuosmiaceae-Argophyllaceae-Phellinaceae group in the molecular analyses are Carpodetaceae, Donatiaceae, and Menyanthaceae. Rooting the ingroup with any of these families, separate or in combination, does not affect tree topology. For the mor-

phological and combined analyses the family Carpodetaceae was chosen as outgroup because it shares many more morphological characters with the three ingroup families than either Donatiaceae, Menyanthaceae or any other family of Asterales.

Twenty-three species were scored for the morphological data set. Since some of the species would have been coded identically, or almost so, in the morphological data matrix (see below), we excluded six species (*Argophyllum grunowii, A. montanum, A. nitidum, Corokia buddleioides, Phelline confertifolia,* and *P. erubescens*) from the analyses in order to reduce the number of terminals, and hence the number of equally parsimonious trees.

In the combined analysis, the DNA sequences were included with the morphological characters for those eleven species where sequences were available (for *Cuttsia* only *rbcL* data). Those species that lacked sequences were coded with 'missing data' for all positions. An analysis of only those species with complete data sets resulted in exactly the same overall topology as did the analysis of the entire combined data matrix. Thus, including species with missing data (sequences) does not appear to affect the topology.

Molecular Data. The *rbcL* and *ndhF* genes were sequenced either from DNA extracted for this study (*Corokia cotoneaster, Cyphia rogersii, Phelline billardieri,* and *P. lucida*), or from the same total DNA used by Gustafsson et al. (1996; *Abrophyllum ornans, Alseuosmia macrophylla, Argophyllum* sp., *Crispiloba disperma, Fauria crista-galli, Quintinia verdonii,* and *Wittsteinia vacciniacea*) and Gustafsson and Bremer (1997; *Carpodetus serratus*). These extractions were made from fresh or herbarium material or from silica gel dried leaves (Chase and Hills 1991) according to the methods of Saghai-Maroof et al. (1984) and Doyle and Doyle (1987). The DNAs were purified with Qiaquick PCR kit (Qiagen) according to the instructions provided by the manufacturer. With the use of primers kindly shared by Robert K. Jansen and Richard G. Olmstead, the two genes were amplified using the Polymerase Chain Reaction (PCR). The amplifications were performed with Taq DNA Polymerase (Promega) according to the manufacturer's protocol. The thermal cycles consisted of an initial denaturation step for 7 min at 94°C followed by 30 cycles consisting of 1 min of denaturation at 94°C, 1 min of annealing at 60°C, and 2 min of extension at 72°C. PCR was terminated with a final step of 7 min at 72°C. For the *ndhF* gene two overlapping double stranded fragments, one for each end of the gene, were amplified. The double stranded product

was either sequenced with automated sequencing (*Abrophyllum ornans, Corokia cotoneaster, Cyphia rogersii, Fauria crista-galli, Phelline billardieri, P. comosa, P. lucida,* and *Quintinia verdonii*) after purification with the Qiaquick PCR kit (Qiagen) according to the instructions from the manufacturer (using ddH$_2$O as eluting agent), or used as a template for a second run with asymmetric amplification to obtain single stranded DNA for manual sequencing (Sanger et al. 1977; Kaltenboeck et al. 1992). The automated sequencing was done through cycle-sequencing with AmpliTaq® DNA Polymerase, FS (Perkin Elmer) using the manufacturer's protocol. The reactions were run on a GeneAmp PCR System 9600 (Perkin Elmer) and analyzed on an ABI 377 Sequencer (Perkin Elmer). The single-stranded DNAs were sequenced manually using Sequenace (Version 2.0 (United States Biosystems) with ^{35}S-labeled dATP following the protocol outlined by the manufacturer. In the analyses nucleotide positions 27 to 1,428 of the *rbcL* gene and positions 1 to 2,214 of the *ndhF* gene were used. The sequences were aligned manually using the reading frame of the corresponding amino acid sequence. Seven potentially phylogenetic informative insertion/deletion events (only present in the *ndhF* sequences) were included in the data set as additional characters and coded as absent or present.

Morphological Data. The specimens studied are listed in Table 3 and the pollen slides investigated are listed in Table 4. Floral parts investigated under the microscope were first rehydrated in boiling water with a few drops of aerosol as detergent, subsequently fixed in Copenhagen mixture (70 parts 95% ethanol, 29 parts distilled water and 1 part glycerol), and finally mounted on slides in Hoyer's solution (Anderson 1954). The drupes of *Corokia* and *Phelline* were softened in concentrated hydrochloric acid for two to three days before they were sectioned and fixed in Copenhagen mixture. Leaf parts were bleached in sodium hydroxide (5%) for one to seven days before they were washed in distilled water and mounted as described above.

Sections of buds from *Argophyllum ellipticum* (*Schlechter 15431,* S), *A. lejourdani* (*Blake 2173,* K), *Phelline billardieri* (*Bonati 316,* K), and *P. lucida* (*Franc s.n.,* K) were made following the protocol outlined by Gustafsson (1996). The buds were first rehydrated in boiling water and then dehydrated in an alcohol series (from ethanol to butanol) before they were embedded in paraffin. Transverse 20 μm sections were cut with a microtome, fixed on slides,

TABLE 2. Species used in the molecular analyses listed according to family. The family classification follows APG (1998). Accession numbers and references to already published sequences extracted from the European Molecular Biology Laboratory (EMBL) and GenBank archives are given. For the 15 sequences made for this study references are also given to voucher specimens. [1]In the EMBL/GenBank archives and in Michaels et al. (1993) this species is listed as *Campanula ramosa* Sibth. & Smith. Here we refer to it as *C. ramosissima* Sibth. & Smith, assuming that this name is intended since the former does not exist in Index Kewensis (Hooker and Jackson 1895; O. Demker, pers. comm.). [2]Sequenced by Kim & Jansen (unpublished study), and used by their permission. [3]Listed as *Nephrophyllidium crista-galli* Gilg in the EMBL/GenBank archives. [4]DNA from *Phelline comosa* was supplied by M. Chase, Royal Botanic Gardens, Kew.

Family Species	rbcL	ndhF EMBL/GenBank no.; reference; voucher information
Adoxaceae		
Viburnum rhytidophyllum Hemsl. ex Forb. & Hemsl.	X87398; Gustafsson et al. 1996	AF027273; Oxelman et al. 1999
Alseuosmiaceae		
Alseuosmia macrophylla A. Cunn.	X87377; Gustafsson et al. 1996	AJ238334; this study; Mackinder s.n. (UPS)
Crispiloba disperma (S. Moore) Steen.	X87382; Gustafsson et al. 1996	AJ238338; this study; Telford 10654 (CBG)
Wittsteinia vacciniacea F. Muell.	X87399; Gustafsson et al. 1996	AJ238345; this study; Carroll 452 (CBG)
Argophyllaceae		
Argophyllum sp.	X87379; Gustafsson et al. 1996	AJ238335; this study; Telford 5462 (CBG)
Corokia cotoneaster Raoul	L11221; Xiang et al. 1993	AJ238337; Taylor 2623 (CBG 8805000, at CANB); this study
Asteraceae		
Barnadesia caryophylla (Veil.) S. F. Blake	L13859; Michaels et al. 1993	L39394; Kim and Jansen 1995
Carthamus tinctorius L.	L13862; Michaels et al. 1993	L39417; Kim and Jansen 1995
Dasyphyllum argenteum Kunth	—	L39392; Kim and Jansen 1995
D. diacanthoides (Less.) Cabrera	L13863; Michaels et al. 1993	—
Vernonia mespilifolia Less.	L13646; Kim et al. 1992	L39427; Kim and Jansen 1995
Calyceraceae		
Boopis anthemoides Juss.	L13860; Michaels et al. 1993	L39384; Kim and Jansen 1995
Campanulaceae		
Campanula ramosissima Sibth. & Smith[1]	L13861; Michaels et al. 1993	L39387; Kim and Jansen 1995
Cyphia elata Harv.	L18796; Cosner et al. 1994	—
C. rogersii S. Moore	—	AJ238339; this study; Bremer 3813 (UPS)
Lobelia erinus L.	L13930; Michaels et al. 1993	—
L. sp.	—	[2]
Carpodetaceae		
Abrophyllum ornans Hook. f. ex Benth.	X87375; Gustafsson et al. 1996	AJ238333; this study; Gustafsson 211 (UPS)
Carpodetus serratus J. R. Forst. & G. Forst.	Y08461; Gustafsson and Bremer 1997	AJ238336; this study; Cameron s.n. (UPS)
Cuttsia viburnea F. Muell.	Y08462; Bremer and Gustafsson 1997	—
Donatiaceae		
Donatia fascicularis J. R. Forst. & G. Forst.	X87385; Gustafsson et al. 1996	AJ225074; Laurent et al. (in press)

TABLE 2.   Continued.

Family Species	rbcL	ndhF
		EMBL/GenBank no.; reference; voucher information
Escalloniaceae		
Quintinia verdonii F. Muell.	X87394; Gustafsson et al. 1996	AJ238344; this study; Telford 3244 (CBG)
Goodeniaceae		
Dampiera diversifolia Vriese	—	L39386; Kim and Jansen 1995
D. spicigera Benth.	X87383; Gustafsson et al. 1996	—
Scaevola frutescens Krause	L13932; Michaels et al. 1993	L39385; Kim and Jansen 1995
Menyanthaceae		
Fauria crista-galli Makino[3]	X87391; Gustafsson et al. 1996	AJ238340; this study; Chase 3501 (K)
Menyanthes trifoliata L.	L14006; Olmstead et al. 1993	L39388; Kim and Jansen 1995
Pentaphragmataceae		
Pentaphragma ellipticum Poulsen	L18794; Cosner et al. 1994	—
P. sp.	—	[2]
Phellinaceae		
Phelline billardieri Panch. ex Loes.	AJ238346; this study; van Balgooy 7013 (L)	AJ238341; this study; van Balgooy 7013 (L)
P. comosa Labill.	X69748; Savolainen et al. 1994	AJ238342; this study; Ziesing 289 (CBG)[4]
P. lucida Vieill. ex Baill.	AJ238347; this study; van Balgooy 7034 (L)	AJ238343; this study; van Balgooy 7034 (L)
Stylidiaceae		
Forstera bellidifolia Hook. f.	AJ225056; Laurent et al. (in press)	AJ225082; Laurent et al. (in press)
Phyllachne uliginosa J. R. Forst. & G. Forst.	X87393; Gustafsson et al. 1996	AJ225075; Laurent et al. (in press)
Stylidium graminifolium Sw.	L18790; Cosner et al. 1994	AJ225076; Laurent et al. (in press)

and after the paraffin had been removed, stained with safranin and light green.

For most characters, we have tried to confirm data from the literature, but for some characters (mainly anatomical and palynological) we have relied on earlier work (literature cited). In some cases data were unavailable and, consequently, the morphological data matrix used in the analyses has 12% of the cells scored with unknown states.

The characters studied (Table 5) are chosen to reveal the relationships between the genera of the families under study. Autapomorphies for single species are excluded. The character states for each species are given in the data matrix (Table 6). Because we do not consider evolutionary trends for any of the characters well enough understood to propose transformation series, all multistate characters were treated as unordered.

Cladistic Analyses. Cladistic analyses were performed using PAUP 3.1.1 (Swofford 1993). During all analyses each character was equally weighted. When analyzing the molecular matrix for most parsimonious trees, the heuristic search method, with 100 random addition sequences, the tree-bisection-reconnection (TBR) algorithm, and the MULPARS option in effect, were used. The most parsimonious trees for the morphological and combined matrices were found using branch-and-bound. Strict consensus trees were computed together with tree length, consistency (CI; Kluge and Farris 1969) and retention indices (RI; Farris 1989) for all analyses.

Bremer support values (Bremer 1988; Källersjö et al. 1992; Bremer 1994) were calculated by using the computer program AutoDecay 2.9.10 (Eriksson 1997). Jackknifing, with a deletion frequency of 37% (a generally used fraction since it approaches the fraction of replaced characters in bootstrap analy-

TABLE 3. Specimens examined for the morphological work. If other material than herbarium sheets have been investigated a note is given in the list. Abbreviations of the herbaria follow Holmgren, Keuken and Schofield (1990).

Alseuosmiaceae

Alseuosmia banksii var. *linariifolia* A. Cunn. (syn. *A. linariifolia* A. Cunn.): *Allan 7823* (CHR); *Carse s.n* (CHR 289141); *Carse 1414/6* (CHR 289147); *Colenso 326* (K)

Alseuosmia macrophylla A. Cunn.: *Ambler s.n.* (S); *Chapman s.n.* (CHR 258560); *Chapman s.n.* (K); *Colenso 240* (K); *Cooper s.n.* (CHR 213439); *Druce s.n.* (CHR 325957); *Mackinder s.n.*; leaves in alcohol (UPS)

Crispiloba disperma (S. Moore) Steen.: *Brass 18335* (CANB 186088); *Brass 20311* (CANB 192275); *Gray 945* (CANB 463302); *Gray 1904* (K); *Telford 10654* (CBG 8801844, at CANB); *Telford 10906* (CBG 9003469, at CANB)

Wittsteinia vacciniacea F. Muell.: *Carrol 452*; silica gel dried leaves (CBG); *Carroll s.n. 9847* (CBG 9847, at CANB); *Gunn s.n.* (CANB 251590); *Muir 2905* (K); *Palser 84-103* (CANB 391817); *Stauffer, Willis, and Muir 5454* (CANB 182140); *von Mueller 49773* (CANB 230429); *collector unknown s.n.* (S)

Argophyllaceae

Argophyllum ellipticum Labill.: *Cribs 994* (P); *McKee 9895* (K); *Schlechter 15431* (S); *Vieillard 885* (S)

Argophyllum grunowii Zahlbr.: *Balansa 3510* (P); *Grunow s.n.* (W)

Argophyllum lejourdani F. Muell.: *Blake 9751* (CANB 359089); *Blake 21773* (K); *Byrnes 3924* (CANB 293153); *Jones s.n.* (CANB 189318); *Telford 8772* (CBG 8203359, at CANB)

Argophyllum montanum Schltr. (syn. *Argophyllum schlechterianum* Bonati & Petitm.): *Franc 641* (P); *Franc 641* (W); *Hürlimann 749* (P); *Skottsberg 117* (S)

Argophyllum nitidum J. R. Forst. & G. Forst.: *Vieillard 886* (P); *Vieillard 886* (S)

Argophyllum nullumense R. T. Baker: *Kårehed 184* (UPS)

Argophyllum sp. nov.: *Telford 5462* (CBG 7702543, at CANB); *Telford 6964* (CBG 7800149, at CANB)

Corokia buddleioides A. Cunn: *Allen s.n.* (K); *Bergler s.n.* (W); *Gardner 247* (CBG 7807005, at CANB); *Macmillan 69/83* (CANB; 197123); *Sinclair s.n.* (S)

Corokia carpodetoides (F. Muell.) L. S. Smith: *Crisp 4544 and Telford* (topotype: CBG 7809955, at CANB); *Hutton 98* (CBG 8317801, at CANB); *Hutton 107* (CBG 8413999, at CANB); *McComish 147* (K)

Corokia cotoneaster Raoul: *Douglass s.n.* (CANB 476001); *Melville 5054* (K); *Strid 22137* (S); *Taylor 2623* (CBG 8805000, at CANB); *Travers s.n.* (S); fruits from Göteborg Botanical Garden, 1995.

Corokia macrocarpa Kirk: *Courtney s.n.* (CHR 436625); *Given 12834 and Williams* (CHR 403159); *Gustafsson s.n.* (UPS); *Sykes 369/93* (CHR 496663A); *Travers s.n.* (W); fruits from Christchurch Botanic Gardens, 1994.

Carpodetaceae

Abrophyllum ornans Hook. f. ex Benth.: *Gray 1063* (K); *Kårehed 182* (UPS); *L. J. W. & G. T. 5557* (K)

Carpodetus serratus J. R. Forst. & G. Forst.: *Oswald s.n.* (UPS)

Cuttsia viburnea F. Muell.: *Coveni 9875 and Haegi* (K); *Hoogland and Hayes 8609* (K)

Phellinaceae

Phelline billardieri Panch. ex Loes.: *Bonati 316* (K); *Jaffré 180* (P); *Vieillard 350, 351* (K)

Phelline comosa Labill.: *MacKee 2503* (P); *McKee 9852* (K); *Schmid 2504* (P); *Skottsberg 147* (S); *Skottsberg 182* (S)

Phelline confertifolia Baill.: *McPherson 5230* (P); *Schlechter 15215* (S)

Phelline erubescens Baill.: *Balansa 1831* (isotype: P); *Schlechter 15469* (S)

Phelline lucida Vieill. ex Baill.: *Baumann-Bodenheim 5647* (P); *Franc s.n.* (K); *McKee 9805* (K); *Schlechter 15340* (S)

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ses; Farris et al. 1996), was performed with the program Xac (used by permission of James S. Farris) with a replicate number of 1,000 (branch swapping, 5 random restarts).

To test the congruence of the two molecular data sets and the morphological and the molecular data sets, respectively, we used the program Xarn (with permission of James S. Farris), which is a development of Arn (Farris et al. 1995; branch swapping is included in Xarn). From the original data Xarn generates random matrices of the same sizes as the original matrices. The null hypothesis of incongruence is rejected if the sum of the tree lengths of the partitioned original data is less than that of the matrices resulting from the random partitions in 95% of the replicates. We used branch swapping on 10,000 replicates (5 random restarts).

RESULTS

The Molecular Study. The molecular matrix yielded one most parsimonious tree of 2,365 steps

TABLE 4.   Pollen slides investigated. The following pollen slides from the collection of the Palynological laboratory, Swedish Museum of Natural History, Stockholm, were investigated. Slide numbers refering to this collection are given within square brackets.

Alseuosmiaceae

Alseuosmia banksii var. *linariifolia* A. Cunn. (syn. *A. linariifolia* A. Cunn.): *Carse s.n.* (AK)[18524]
Alseuosmia macrophylla A. Cunn.: *Fenton s.n.* [5819]; *Steele s.n.* (WELTU)[20768]

Argophyllaceae

Argophyllum cryptophlebum Zemann: *White 1489* (S)[17794]
Argophyllum nitidum J. R. Forst. & G. Forst.: *Selling s.n.* (S)[17793]
Corokia cotoneaster Raoul: *Melville and Godley s.n.* (CHR)[100]; *Nilsson et al. NZ 57* (S)[22.619]

Carpodetaceae

Carpodetus serratus J. R. Forst. & G. Forst.: *Nilsson NZ 75* (S)[22.527]; *Wassilieff s.n.* (WELTU)[20854]

(excluding phylogenetic uninformative characters; Fig. 4). The consistency and the retention indices are 0.53 and 0.60, respectively. Alseuosmiaceae, Argophyllaceae, and Phellinaceae, each monophyletic, form a monophyletic group (Bremer support = 3, jackknife value = 58), in which Alseuosmiaceae are sister to Argophyllaceae and Phellinaceae.

According to the Xarn analysis the *rbcL* and the *ndhF* data are not significantly incongruent (alfa = 0.057). We will therefore limit our discussion to the results of the combined molecular data, since we believe that using all available data gives the best indication of the true phylogeny (the theory behind combining different data sets and the justification for relying more on the results of combined than on single analyses are discussed by, for example, Kluge and Wolf 1993, de Queiroz et al. 1995, Bremer 1996, Nixon and Carpenter 1996, and Kluge 1998, and will not be repeated here).

The Morphological and Combined Studies. The morphological and molecular data are congruent (alfa = 0.80). In the consensus tree of the 42 most parsimonious trees from the combined analysis (Fig. 5; 537 steps long, CI = 0.81, RI = 0.85) each of the three families is monophyletic. Alseuosmiaceae are sister to Argophyllaceae and Phellinaceae, just as in the analysis of the combined molecular data. If the morphological data are analyzed separately, Phellinaceae are sister to the other two families and *Corokia carpodetoides* is basal within *Corokia*. The morphological characters are optimized on one of the most parsimonious trees from the combined study in Fig. 6.

DISCUSSION

The monophyly of the clade consisting of Alseuosmiaceae, Argophyllaceae, and Phellinaceae,

suggested by the *rbcL* studies of Backlund and Bremer (1997) and Gustafsson and Bremer (1997), albeit with low bootstrap/jackknife values, is further corroborated by this study. The inclusion of *ndhF* data again confirms that Alseuosmiaceae, Argophyllaceae, and Phellinaceae form a monophyletic group, and that the position of this group is within Asterales (Fig. 4).

The following discussion on character evolution and family circumscriptions within the group under study will mostly concern the results of the analysis derived from the combined morphological and molecular data sets.

Evolution of the Alseuosmiaceae-Argophyllaceae-Phellinaceae Group.   In addition to their similar distribution, Alseuosmiaceae, Argophyllaceae, and Phellinaceae are characterized by the following features: They are all woody, have vessels with many-barred, scalariform perforation plates, and trilacunar nodes with three traces. Their leaves are simple, alternate, exstipulate (according to Loesener 1901, *Phelline* sometimes has inconspicuous stipules and Takthajan 1997 mentioned that the leaves are "mostly estipulate"; stipules in *Phelline* are not mentioned in the works by Loesener 1942, Guillauman 1948, Baas 1975, and we have not observed any) and have a poorly differentiated mesophyll and anomocytic stomata. They have regular, mostly pentamerous flowers. The haploid chromosome number appears to be nine (Phellinaceae have not been investigated; see Gardner 1976 for Alseuosmiaceae and Wanscher 1933, Hamel 1953, and Hair and Beuzenberg 1959 for Argophyllaceae), not rare in the euasterids but different from that of, for example, *Carpodetus* (n = 14, 15; Hair and Beuzenberg 1960; Borgmann 1964), another of the few woody members of Asterales.

As detailed above, many morphological characters are shared by Alseuosmiaceae, Argophyllaceae, and Phellinaceae, but it is hard to find morphological support for the group, since several of these characters are present in other taxa as well, for example, in Carpodetaceae. They are therefore interpreted as symplesiomorphies within a larger group, and consequently of no value in delimiting the group of the three families.

The common ancestor of the group that consists of the three families Alseuosmiaceae, Argophyllaceae, and Phellinaceae, probably had all the characters mentioned above. Its distribution may have been Australasian, judging from the present distribution of the group and the discussion by Bremer and Gustafsson (1997) which suggested an Australasian origin for Asterales as a whole.

A more complete picture of the ancestor may be obtained by examining the character states assigned to the branch connecting the ingroup with Carpodetaceae on the cladogram in Fig. 6. We suggest that the leaves of the ancestor were serrate (character 1), had short and square palisade cells (character 3) and a lacunose spongy mesophyll (character 4). The flowers of the common ancestor of Alseuosmiaceae, Argophyllaceae, and Phellinaceae were borne in panicles, choripetalous, bisexual, and had an inferior ovary (characters 14, 15, 18, and 27, respectively). The pollen grains of the ancestor probably lacked supratectal elements (character 22) and had well developed columellae (character 23). The pollen grains of *Carpodetus* are different from this type; they are, for example, united in tetrahedral tetrads. The only members of Asteridae that have their pollen united in such a way are found in Ericales (Praglowski and Grafström 1985). However, the other genera of Carpodetaceae (*Abrophyllum* and *Cuttsia*), have pollen similar to that of *Argophyllum* and *Corokia* (character 24; Ferguson and Hideux 1978), even though pollen of the former has a striate-rugulate tectum like that of *Carpodetus.*

The ancestor of Alseuosmiaceae, Argophyllaceae, and Phellinaceae furthermore presumably had wood with helical thickenings in the vessels (character 32), septate fibers or fiber-tracheids (character 34), and heterogenous rays (character 35). The presence of septa in the fibers/fiber-tracheids, regarded as a substitution for axial parenchyma (Carlquist 1975), suggests wood with very sparse or no axial parenchyma, as is found in the wood of Alseuosmiaceae and Argophyllaceae.

ALSEUOSMIACEAE. Van Steenis's (1984) inclusion of *Wittsteinia* (including *Periomphale*) and *Crispiloba*

in Alseuosmiaceae is supported by our results. In all the analyses, this monophyletic family has very high support (Figs. 4, 5). In the lineage leading from the hypothetical ancestor described above to Alseuosmiaceae a number of characters evolved. The flowers have become sympetalous (character 15) and have developed conspicuous petal wings (character 16) and epipetalous stamens (character 19; inserted only at the base of the corolla in *Periomphale* and *Wittsteinia*; Stevens 1971; Tirel 1996; Tirel and Jérémie 1996). These features are also encountered elsewhere in Asterales and among eusterids II. Outside Alseuosmiaceae, pronounced petal wings are found in Goodeniaceae and Menyanthaceae, and very delicate petal wings may also be present in Argophyllaceae (Gustafsson 1995). Most eusterids II, predominantly sympetalous species, have their corolla initiated by a ring-shaped primordium, that is, in an early ontogenetic stage they are sympetalous even if the petals later become free (e.g., as in the Apiaceae; Leins and Erbar 1987; Erbar 1991; Alseuosmiaceae were not investigated). Taking this into consideration, it seems likely that the clearly sympetalous flowers of Alseuosmiaceae have developed from a choripetalous ancestor, as suggested above, with a ring-shaped corolla primordium. This is supported also by the observations that in *Argophyllum* there is a basal fusion of the petals (Zemann 1907; Hallier 1908; Engler 1928) and in *Corokia* two adjacent corolla lobes may be united for most of their length (Eyde 1966).

The inflorescences (character 14) in the Alseuosmiaceae lineage have been reduced from panicles to fascicles in the leaf axils or to terminal, umbel-like inflorescences (*Crispiloba*).

Wood anatomy synapomorphies for Alseuosmiaceae are the stem endodermis with prominent Casparian banding (character 31; unusual among woody dicotyledons; Dickison 1989) and living fibers which store starch at maturity (character 33; Dickison 1986). Furthermore, the family, except for *Crispiloba* and *Periomphale*, has become rayless (character 35; Dickison 1986). From Dickison's investigations of the wood of Alseuosmiaceae "it seems very likely that the family evolved from a small, shrubby ancestor, subsequently became semiherbaceous, followed by the development of a secondarily woody body in some taxa" (Dickison 1989). The leaf veins of Alseuosmiaceae are surrounded by endodermoid cells (character 7); exceptions to this are *Periomphale* and *Wittsteinia vacciniacea* (see discussion by Dickison 1989).

One character shared by Alseuosmiaceae and

TABLE 5. The morphological characters.

Leaves and Petiole

1. Leaves more or less entire (0), serrate (1).
     All the genera have 'hydathodal swellings', either in association with the teeth or, as in the species with entire leaves, along the margin and/or at the apex (cf. Hils 1985). For characters concerning leaf anatomy (characters 2–7) see the works of Zemann (1907), Baas (1975), Hils (1985), and Dickison (1989).
2. Mesophyll poorly differentiated (0), with well differentiated palisade layer (1).
3. Palisade cells as seen in transection short and square (0), (at least uppermost) palisade cells columnar-elongate (1).
4. Spongy mesophyll compact (0), lacunose (1).
5. Cells surrounding leaf veins/veinlets non-sclerenchymatous (0), sclerenchymatous with pitted walls (1), endodermoid (cf. Dickison 1989) (2).
6. Guard cells level with epidermis cells (0), raised above epidermis (1).
7. Guard cells with outer stomatal ledges (0), with both outer and inner stomatal ledges (1).
     The outer stomatal ledges in *Wittsteinia* are double (Dickison 1989).
8. Petiolar vascular bundles remain separated throughout petiole (0), fuse to result in a shallow arc at about medial level of the petiole (1), split secondarily into more bundles from basal part of petiole and upwards (2).
     How the petiolar vascular bundles behave on their way up the petiole is discussed in Watari (1939), Swamy (1954), Stevens (1971), Baas (1975), Hils (1985), and Dickison (1989). All the genera studied are trilacunar. Exceptions to this are *Argophyllum laxum* and *Corokia virgata*, which are pentalacunar and unilacunar, respectively. In *Phelline billardieri* splitting of the traces takes place before entering the petiole (Baas 1975). For Carpodetaceae various conditions intermediate between character state '1' and '2' occur, and, consequently, Carpodetaceae are coded as polymorphic.
9. Centric bundles throughout petiole absent (0), present (1).

Trichomes

10. Erect unicellular hairs absent (0), present (1).
     Unicellular hairs are described for *Alseuosmia* by Gardner (1976) and Dickison (1989). Stevens (1971) noticed the presence of an indumentum of unicellular hairs in *Wittsteinia*, a condition also mentioned by Dickison (1989).
11. Strongly curved unicellular hairs absent (0), present (1).
     These hairs are found in Carpodetaceae and look rather different from the unicellular hairs that are present in Alseuosmiaceae. The former have a warty cuticle and their base embedded in the epidermis (Bensel and Palser 1975; Al-Shammary and Gornall 1994). The two hair types are therefore not regarded as homologous.
12. Multicellular uniseriate hairs absent (0), present (1).
     These hairs are confined to the leaf axils both in Alseuosmiaceae (Stevens 1971; Gardner 1976; van Steenis 1984; Dickison 1989) and in Phellinaceae (Baas 1975). The hairs in Alseuosmiaceae are rusty brown and have an elongated, pointed, top cell, whereas those of Phellinaceae are paler with a subglobular top cell. The cellular organization is identical in the two families, however, and consequently we consider these hairs homologous.
13. T-hairs absent (0), present (1).
     The T-hairs of Argophyllaceae consist of a multicellular stalk and a two-armed, T-shaped, apical cell (Fig. 2G, H). Descriptions of the hairs and their distribution on the plants are found, for instance, in the works of Weiss (1890), Zemann (1907), Eyde (1966), and Al-Shammary and Gornall (1994). Even though there are minor differences in the appearance of the T-hairs between *Argophyllum* and *Corokia*, we do not hesitate to interpret them as homologous; they are "remarkably similar . . . in all their species and clearly support a close relationship between the genera" (Al-Shammary and Gornall 1994).

Inflorescences

14. Flowers in panicles (0), in racemes (1), fasciculate in the leaf axils (2), in few-flowered, umbel-like inflorescences (3).
     The species with character state '2' or '3' may occasionally have only solitary flowers. To interpret the inflorescences for Alseuosmiaceae we have followed Stevens (1971), Gardner (1976), and van Steenis (1984). Unlike other authors (Bentham 1869 and Drude 1889), who only reported solitary flowers in *Wittsteinia vacciniacea*, Stevens (1971) mentioned one to two-flowered inflorescences in this species, a condition we can confirm. The inflorescences of Argophyllaceae are treated, albeit briefly, by a number of authors (Forster and Forster 1776; Schlechter 1906; Zemann 1907; Engler 1928; Guillaumin 1948; Allan 1961; Hutchins 1994). Data on Phellinaceae are found, for example, in the works of Loesener (1901, 1908), and Guillaumin (1948).

TABLE 5.   Continued.

Corolla

15. Flowers choripetalous or with petals fused at the very base (0), sympetalous (1).

The petals of *Argophyllum* are fused at the very base (Zemann 1907; Hallier 1908; Engler 1928). They are, however, not clearly sympetalous as the flowers of Alseuosmiaceae; the corolla tube is only poorly developed, and we therefore code them as choripetalous.

16. Petal wings delicate, without veins, or absent (0) conspicuous, lobed, and vascularized (1).

17. Corolline ligules absent (0), present (1).

At the base of the petals in *Argophyllum* and *Corokia*, there are fringed appendages (Fig 2B, E, F; Forster and Forster 1776; Zemann 1907; Hallier 1908; Engler 1928; Eyde 1966). We have chosen to call these corolline ligules in concordance with Eyde (1966). The corolline ligules are missing in *C. macrocarpa* (Eyde 1966) and in some specimens of *C. carpodetoides* (Smith 1958).

Sexual system

18. All flowers hermaphroditic (0), hermaphroditic and female flowers on separate plants (1), flowers unisexual (2).

The gynodioecism in *Carpodetus* is described by Shore (1969).

Androecium

19. Stamens free (0), epipetalous (1).

20. Anthers less than twice as long as wide (0), at least twice as long as wide (1).

In the taxa with character state '0' the anthers are clearly less than twice as long as wide. Therefore, more accurate length:width ratios are not given.

Pollen

Data on pollen morphology (characters 21–25) are taken from Erdtman (1952), Hideux and Ferguson (1976), Lobreau-Callen (1977), Ferguson and Hideux (1978), and Praglowski and Grafström (1985). Some pollen were also studied by light microscopy (see Table 5).

21. Sexine thinner than nexine (0), as thick as or thicker than nexine (1).

22. Tectum without supratectal elements (0), rugulate/striate-rugulate (1), with spinules (2).

We have chosen to call the supratectal elements in *Phelline* and *Corokia* spinules. Spinules are defined as spines shorter than 3 μm (Erdtman 1952). The recommended term microspines (Punt et al. 1994) are shorter than 1 μm, while the spines of some species of *Phelline* are 1.3 μm long (Lobreau-Callen 1977). Therefore, we find it unjustified to divide this character state further.

23. Columellae well developed (0), poorly developed (not visible in LM), less than 1.5 times as long as wide (1).

The pollen grains of *Alseuosmia* are here, as by Hufford (1992), regarded as having well developed columellae, visible in the light microscope, even though they were described as baculate by Erdtman (1952).

24. Pollen with a prominent H-shaped endoaperture absent (0), present (1).

25. Pollen with lamellation and thinning of the endexine absent (0), present (1).

Gynoecium

Information about the gynoecium and embryology (characters 26–29) is found in the works of Bentham (1869), von Mueller (1885), Engler (1890), Loesener (1901), Zemann (1907), Engler (1928), Mauritzon (1933), Allan (1961), Baas (1975), Gardner (1976, 1978a), van Steenis (1984), Kapil and Bhatnagar (1992), and Gustafsson and Bremer (1997).

26. Stigma on style (0), sessile (1).

27. Ovary inferior (0), semi-inferior (1), superior (2).

28. Ovules per locule few-many (0), one (1).

Embryology

29. Embryo minute (0), elongate (1).

All the genera have fleshy endosperm.

Fruit

30. Endocarp dry (0), fleshy (1), stony (2).

We decided to look only at the endocarp in order to be sure to compare homologous structures. Since the ovary position varies among the genera studied, the outer fruit layers are probably not derived from the same structures. The taxa with dry or fleshy endocarps correspond to taxa with capsules or berries, respectively. *Corokia* and *Phelline* have drupes, i.e., stony endocarps.

TABLE 5. Continued.

Wood Anatomy

The wood anatomy of the genera under study are described by Cox (1948), Stern et al. (1969), Patel (1973a, 1973b), Baas (1975), Hils (1985), and Dickison (1986, 1989).

31. Stem endodermis with prominent Casparian banding absent (0), present (1).

32. Helical thickenings in vessels absent (0), present (1).

The helical thickenings in the vessels are, when present, very fine (Patel 1973a, 1973b; Hils 1985; Dickison 1986). Baas (1975) mentioned no helices in the vessels of *Phelline*. Cox (1948) and Dickison (1986) were not able to demonstrate any helices for *Wittsteinia*.

33. Living fibers with stored starch at maturity absent (0), present (1).

Living fibres with stored starch at maturity are reported from Alseuosmiaceae (Dickison 1986). Since we have not seen any other reports on such fibres, and since it is very likely that they should have been reported if present, those species investigated outside Alseuosmiaceae are given the character state '0' for this character.

34. Septate fibers/fiber-tracheids absent (0), present (1).

35. Rays in secondary wood absent (0), heterogeneous (1).

Phellinaceae is the multicellular, uniseriate hairs in the leaf axils (character 12). The hairs in Alseuosmiaceae are rusty brown (likely due to tannin deposits; Gardner 1976) with a long, pointed top-cell (Stevens 1971; Gardner 1976; Gardner 1978a; van Steenis 1984; Dickison 1989) unlike those of Phellinaceae, which are paler and have a subglobular top-cell (Baas 1975). Because of the different appearance of the hairs in the two families, we prefer to interpret hairy leaf axils as a parallelism resulting from the development of different, homologous hair types instead of the equally parsimonious interpretation involving a reversal for Argophyllaceae (cf. Fig. 6).

Crispiloba has several autapomorphies not included in the data matrix. These include the colleter-like appendages in the corolla throat, leaves arranged in pseudowhorls (van Steenis 1984; according to Loesener 1901, the leaves towards the apex of the branches in one species of *Phelline* are also arranged in pseudowhorls, and in other species these leaves are crowded so as to look almost opposite or whorled), and the presence of "numerous elongate filiform or fibrosclereids distributed in the stem, petiole, and leaf mesophyll" (Dickison 1989).

ARGOPHYLLACEAE. The monophyly of Argophyllaceae is supported by the following morphological characters: guard cells that are raised above the surrounding epidermal cells (character 6; Hils 1985), T-hairs (character 13; Weiss 1890; Zemann 1907; Hallier 1908; Eyde 1966; Bensel and Palser 1975; Al-Shammary and Gornall 1994), corolline ligules (character 17; Zemann 1907; Hallier 1908; Engler 1928; Smith 1958; Eyde 1966), and pollen with an H-shaped endoaperture and lamellation of the endexine (characters 24 and 25; Hideux and Ferguson 1976; Ferguson and Hideux 1978). The pollen of Argophyllaceae is quite distinct from that of the other two families. However, in *Abrophyllum* and *Cuttsia*, pollen similar to this type is found (character 24; Hideux and Ferguson 1976; Ferguson and Hideux 1978). This suggests that the Argophyllaceae may in fact have pollen more reminiscent of the ancestor to the Alseuosmiaceae-Argophyllaceae-Phellinaceae group.

The T-hairs and the corolline ligules are the characters most often emphasized when grouping *Argophyllum* and *Corokia* together. There are also different kinds of corolline appendages in *Crispiloba* (colleter-like, at the throat of the corolla; van Steenis 1984), *Periomphale*, and *Wittsteinia* (carunculate corolla lobes; van Steenis 1978; van Steenis 1986; Tirel 1996; Tirel and Jérémie 1996). Eyde (1966) reported darkly staining cells, which he called tannin-containing cells, in flowers of *Corokia*. The sections of buds from *Argophyllum* show darkly staining cells, possibly similar to those of *Corokia*. Floral tannin is also shown to be present in Alseuosmiaceae (Gardner 1976).

Two fruit types are present in Argophyllaceae (character 30). *Argophyllum* has loculicidal capsules (Fig. 2D) and *Corokia* has drupes. There are several known cases where fleshy fruits have evolved from dry fruits as an adaption to attract animals to help disperse the seeds (see, e.g., Cronquist 1988). It seems unlikely that, as in the shortest optimization in the cladogram of Fig. 6, a drupaceous fruit once it has evolved would reverse to a capsule. We suggest instead that the loculicidal capsule of *Argophyllum* is a plesiomorphic state that has been re-

TABLE 6. The morphological data matrix. Unknown character states are denoted with question marks and polymorphisms are coded with 'a' (=0/1), 'b' (=1/2), or 'c' (=1/3).

	Character number						
	00000 12345	00001 67890	11111 12345	11112 67890	22222 12345	22223 67890	33333 12345
Abrophyllum ornans	11110	00b00	10000	00000	11010	12001	00001
Carpodetus serratus	11100	00b00	10000	00100	?1100	00001	01001
Cuttsia viburnea	11110	00b00	10000	00000	11010	02000	00001
Alseuosmia banksii	a0012	00101	01021	10011	10000	000?1	1??1?
Alseuosmia macrophylla	10012	00101	01021	10011	10000	000?1	11110
Crispiloba disperma	00012	00000	01031	1001?	?????	000?1	11111
Wittsteinia vacciniacea	10110	00001	01021	10010	?????	00001	10110
Argophyllum ellipticum	000?0	??200	00100	01000	?????	01000	01011
Argophyllum lejourdani	100?0	????0	00100	01000	10011	01000	?????
Argophyllum nullumense	10100	10100	00100	01000	10011	01000	01011
Argophyllum sp.	1???0	????0	00100	01000	?????	01000	?????
Corokia carpodetoides	10110	00100	00100	0a001	12011	00112	?????
Corokia cotoneaster	0???0	??100	00120	01001	12011	00112	01011
Corokia macrocarpa	00110	10100	00110	00001	12011	00112	01011
Phelline billardieri	00011	01210	01000	00200	02100	12102	?????
Phelline comosa	00011	01??0	01000	00200	02100	12102	?????
Phelline lucida	00011	01210	010c0	00200	01100	12102	00001

tained (the fruits in *Cuttsia* are also capsular; Gustafsson and Bremer 1997), and that the drupes in *Corokia* and *Phelline* have evolved independently. This interpretation is supported by the fact that the drupes in *Phelline* have separate pyrenes and, in addition, an integument with radially elongated, horseshoe-shaped cells (Fig. 3C, D; Thevénard 1906), not seen in *Corokia*. If the plesiomorphic nature of the capsule in *Argophyllum* is to be sustained there has to be an independent origin of baccate fruits in the Alseuosmiaceae lineage.

The position of the monophyletic *Argophyllum* and *Corokia* within the classification has not been clear. This study supports that a position within Asterales is more appropriate than other positions proposed earlier (see the introduction).

Corokia was erected to family level by Takhtajan (1997; see the introduction). We see no reason for such a treatment. Elevating a small genus such as *Corokia* to a monotypic family would only lead to nomenclatural redundancy and consequently loss of phylogenetic information (cf. Backlund and Bremer 1998). *Argophyllum* and *Corokia* are closely related and share the presence of such easily recognized characters as T-hairs and corolline ligules; this relationship should be evident in the classification.

PHELLINACEAE. This study shows that the correct position of the Phellinaceae is within Asterales (Fig. 4). The monophyly of the family has very high support values in both the molecular and combined analyses. The lineage leading to Phellinaceae has gone through considerable morphological evolution. In fact, this family has become so distinct from Argophyllaceae that it is hard to find morphological support for their relationship as sister groups suggested by the molecular data. Synapomorphies for Phellinaceae include: pitted sclerenchymatous cells that surround the leaf veinlets (character 5), guard cells with both outer and inner stomatal ledges (character 7), centric petiolar bundles (character 9), unisexual flowers (character 18), pollen with a sexine which is thinner than the nexine (character 21), sessile stigma (character 26), and superior ovary (character 27). The petals of *Phelline* are easily recognized by having an inflexed apiculus. This feature can also be seen, at least in young flowers, in the other genera studied (cf. Webb 1994). A number of homoerythrina alkaloids have been detected in *Phelline* (e.g., Debourges and Langlois 1982; Pusset et al. 1989; Langlois 1990; Aladsesanmi et al. 1991), compounds not encountered elsewhere in the studied group.

Some of the synapomorphies listed above deserve comment. Surrounding the veinlets in *Periomphale* there are cells possibly similar to those found in association with the veins in *Phelline* (Dickison 1989). The centric petiolar bundles throughout the petiole is a condition almost unmatched in other dicotyledons (Baas 1975). Baas concluded after
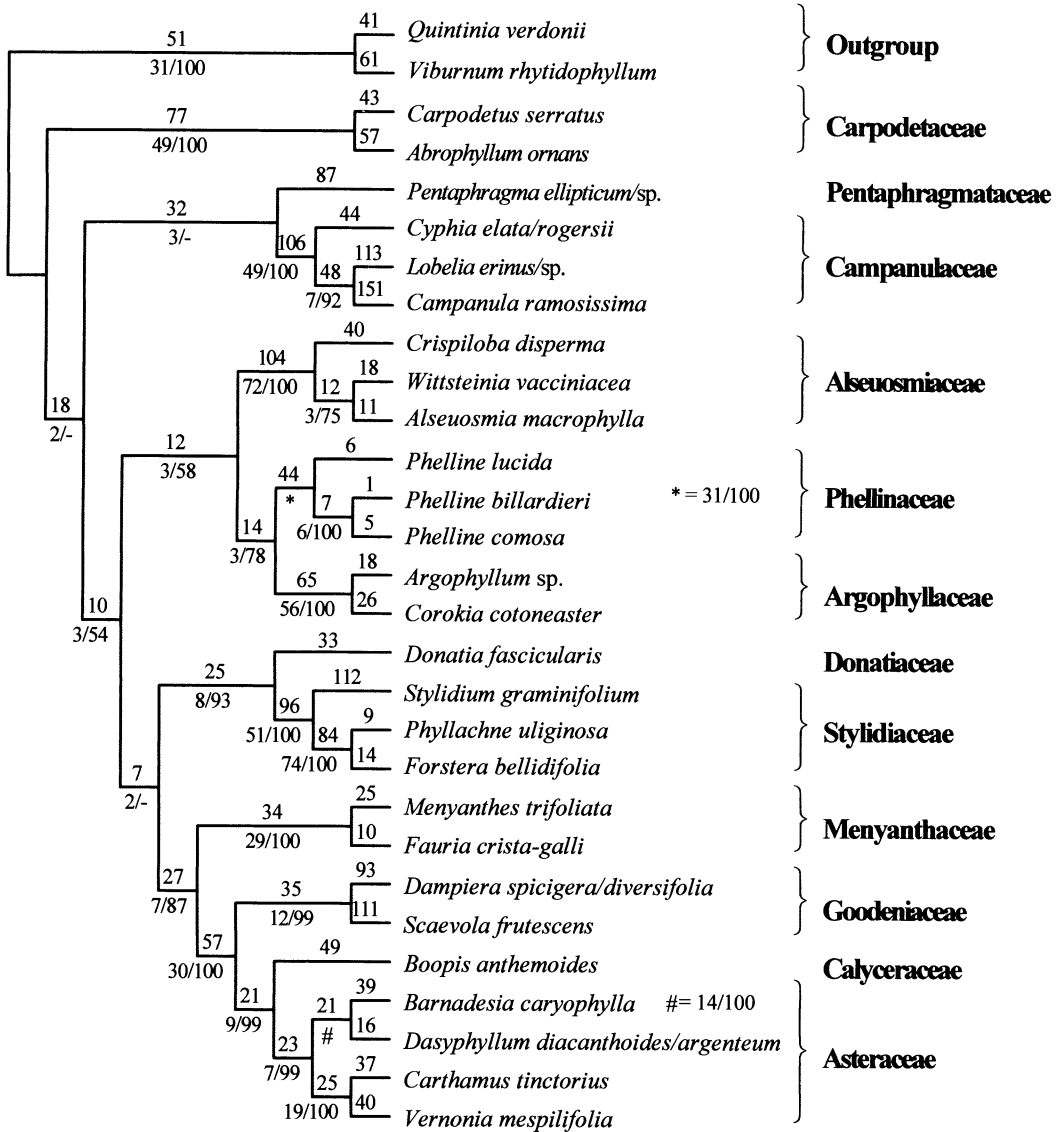
FIG. 4. The single most parsimonious tree from the cladistic analysis of the *rbcL* and *ndhF* data combined. Branch lengths are indicated above the branches and Bremer support and jackknife values are indicated below the branches in that order. Jackknife values lower than 50% are not given. The family classification follows APG (1998).

studying wood anatomy that *Phelline* has among the most primitive wood of any dicotyledon with vessels. A sessile stigma (character 26) is found outside this group in, for example, *Abrophyllum*. In Asterales most taxa have inferior ovaries, but the presence of a superior ovary (character 27) in *Phelline* is by no means unique in the order. This character may even vary within a single family, as in Carpodetaceae (superior ovary in *Abrophyllum*, almost

so in *Cuttsia*, and inferior in *Carpodetus*; Gustafsson and Bremer 1997). In the cladogram in Fig. 6, drupaceous fruits (character 31) appear in the ancestral lineage common to Argophyllaceae and Phellinaceae. In both *Phelline* and *Corokia* there is only one apically attached ovule in each locule (character 28). The drupes of *Phelline* differ, however, from the ones in *Corokia* as mentioned above.

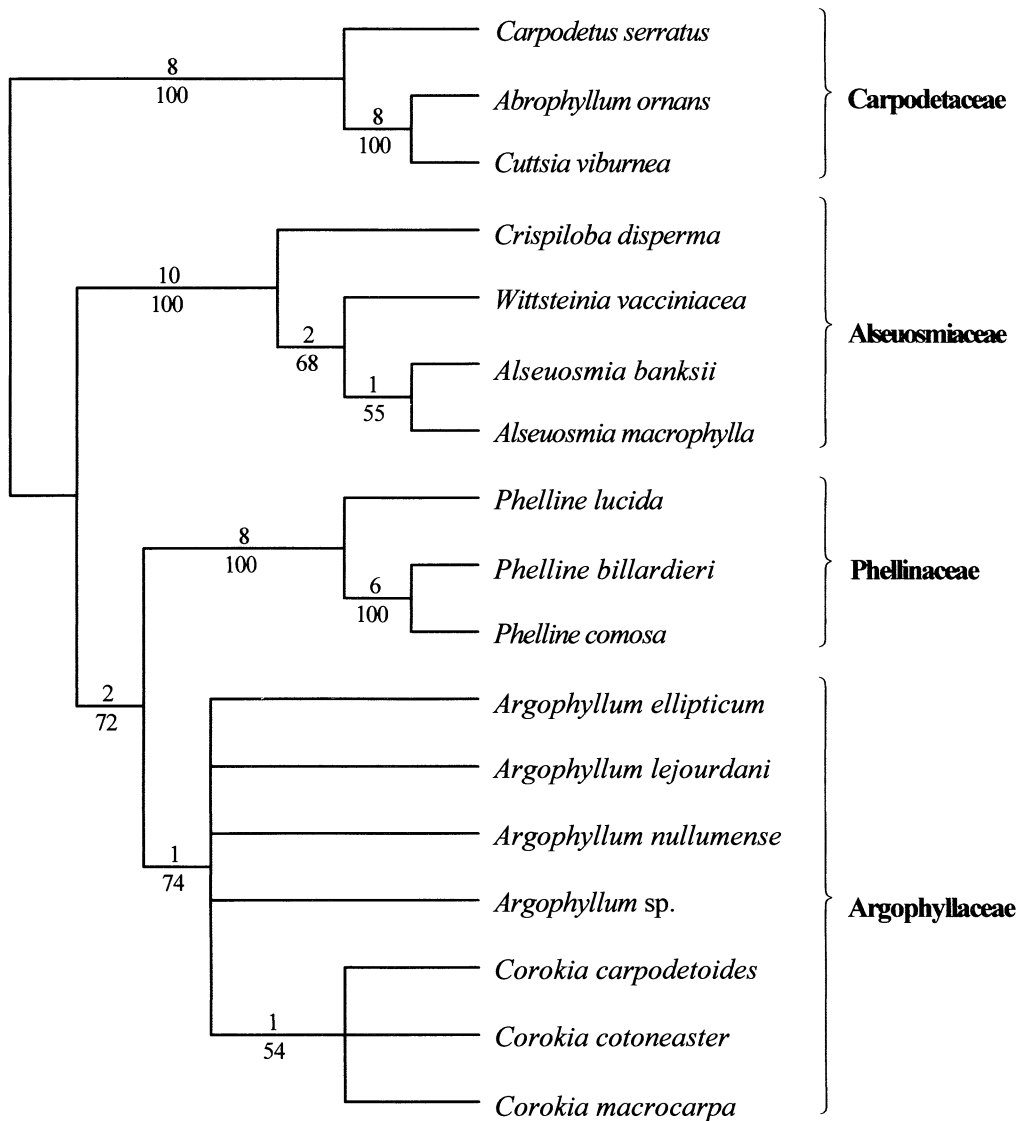Lobreau-Callen (1977) distinguished two groups

FIG. 5.   Strict consensus tree of the 42 most parsimonious trees from the cladistic analysis of the morphological data combined with molecular data. Bremer support and jackknife values are indicated above and below the branches, respectively. Jackknife values lower than 50% are not given. The family classification follows APG (1998).

of pollen in *Phelline*. One character used for the grouping was the supratectal elements (character 22). One of the groups has pollen with spinules, as does the pollen of *Corokia*, while in the other group the pollen has a rugulate tectum, also present in Carpodetaceae.

To conclude, the lineages leading to the extant Alseuosmiaceae and Phellinaceae are the lineages where most morphological evolution apparently has taken place. Consequently, the members of the

Argophyllaceae are those that have an array of characters making them most similar to the ancestor of the Alseuosmiaceae-Argophyllaceae-Phellinaceae group we have proposed.

Systematic Implications.   Each of the three families is monophyletic and well supported in all the analyses (Figs. 4, 5). Since the support (both molecular and morphological) of the three familes as a monophyletic unit is less conclusive, we see no reason to merge the families. With their present cir-

4^0 8^{12} 18^1 23^1 *Carpodetus serratus*

8^{12} 26^1 *Abrophyllum ornans* } **Carpodetaceae**

*=24^1, 27^2, 32^0

* 8^{12} 30^0 *Cuttsia viburnea*

1^0 8^0 14^3 *Crispiloba disperma*

12^1 15^1 16^1 19^1 31^1 33^1 3^1 5^0 8^0 14^3 *Wittsteinia vacciniacea*

5^2 # 14^2

#=10^1, 35^0 10^{01} *Alseuosmia banksii* } **Alseuosmiaceae**

2^0 20^1

3^0 *Alseuosmia macrophylla*

22^0

34^1

11^0 14^{13} 22^1 *Phelline lucida*

34^0 X *Phelline billardieri* } **Phellinaceae**

5^1, 7^1, 9^1, 18^2, 21^0 *Phelline comosa*

1^0, 8^2, 12^1, 22^2, 23^1, 26^1, 27^2, 28^1, 32^0

30^2 4^0, *Argophyllum ellipticum*

30^0 27^1 1^0 8^2

6^1 *Argophyllum lejourdani*

13^1

17^1 3^1 *Argophyllum nullumense*

24^1 X

25^1 *Argophyllum* sp. } **Argophyllaceae**

X 3^1

20^1 6^0 17^{01} *Corokia carpodetoides*

22^2 28^1 29^1 14^2

1^0 *Corokia cotoneaster*

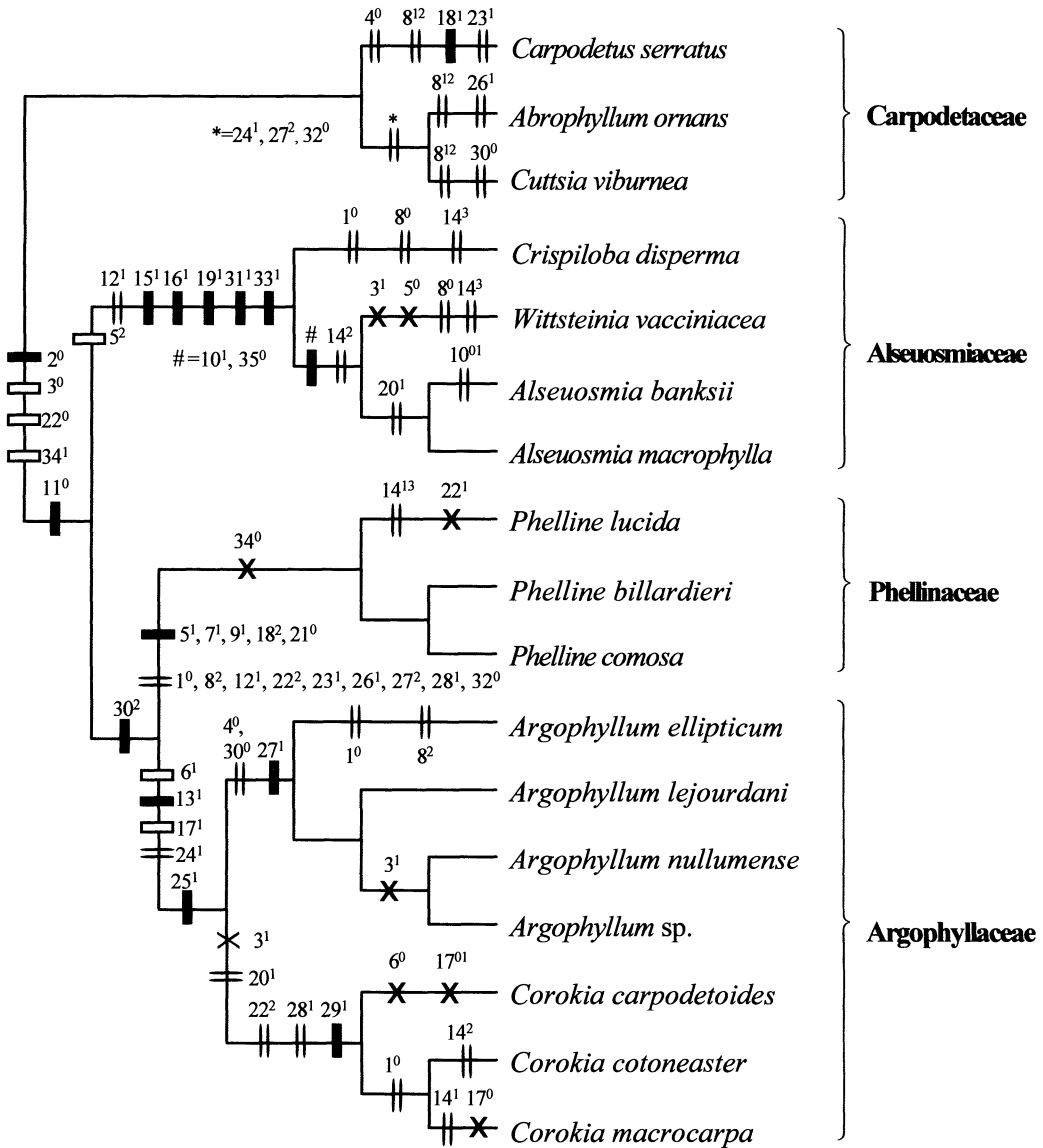14^1 17^0 X *Corokia macrocarpa*

FIG. 6. The morphological characters optimized on one of the 42 most parsimonious trees of the analysis of morphological and molecular data combined. Non-homoplastic characters are indicated with solid bars. Parallelisms are indicated with double bars. Open bars indicate synapomorphies with subsequent reversals, and crosses indicate reversals.

cumscriptions they are all easily recognized. One could argue that they should be merged, since retaining three related, small families as separate entities would obscure phylogenetic relationships and lead to the use of redundant names (cf. Backlund and Bremer 1998). We recommend that each family be retained, however, in line with the 'principle of ease of identification' (Backlund and Bremer 1998).

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