

# Polyphyly of the spring-parsleys (*Cymopterus*): molecular and morphological evidence suggests complex relationships among the perennial endemic genera of western North American Apiaceae

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**Abstract:** Cladistic analyses of DNA sequences from the nuclear rDNA internal transcribed spacer region and cpDNA *rps16* intron and, for a subset of taxa, the cpDNA *trnF-trnL-trnT* locus were carried out to evaluate the monophyly of *Cymopterus* and to ascertain its phylogenetic placement among the other perennial genera of Apiaceae (Umbelliferae) subfamily Apioideae endemic to western North America. To elucidate patterns in the evolution of specific fruit characters and to evaluate their utility in circumscribing genera unambiguously, additional evidence was procured from cross-sections of mature fruits and the results of cladistic analysis of 25 morphological characters. Analyses of the partitioned data sets resulted in weakly supported and largely unresolved phylogenetic hypotheses, possibly due to the rapid radiation of the group, whereas the combined analysis of all molecular evidence resulted in a well-resolved phylogeny with higher bootstrap support. The traditionally used fruit characters of wing shape and composition and orientation of mericarp compression are highly variable. The results of these analyses reveal that *Cymopterus* and *Lomatium*, the two largest genera of western North American Apiaceae, are polyphyletic, and that their species are inextricably linked with those of other endemic perennial genera of the region (such as *Aletes*, *Musineon*, *Oreoxis*, *Pseudocymopterus*, *Pteryxia*, and *Tauschia*), many of which are also not monophyletic. Prior emphasis on characters of the fruit in all systems of classification of the group has led to highly artificial assemblages of species. A complete reassessment of generic limits of all western endemic Apiaceae is required, as is further systematic study of this intractable group.

**Key words:** Apiaceae, *Cymopterus*, phylogeny, ITS, *rps16* intron, morphology.

**Résumé :** Pour évaluer la monophylie du genre *Cymopterus* et pour s'assurer de sa position phylogénétique parmi les autres genres pérennes des Apiaceae (Umbelliferae) sous famille Apioideae endémiques à l'ouest nord-américain, les auteurs ont conduit des analyses cladistiques en utilisant des séquences d'ADN provenant de la région de l'espaceur interne transcrit du rADN nucléaire et de l'intron cpADN *rps16*, ainsi que du lieu cpADN *trnF-trnL-trnT* pour un sous ensemble de taxons. Afin d'élucider les patrons dans l'évolution de caractères spécifiques du fruit et d'évaluer leur utilité pour circonscrire les genres de façon non ambiguë, ils ont obtenu des preuves supplémentaires à partir de sections transverses de fruits matures et de résultats d'analyses cladistiques portant sur 25 caractères morphologiques. L'analyse des ensembles de données réparties conduit à des hypothèses phylogénétiques faiblement supportées et largement irrésolues, possiblement dû à la rapide radiation de ce groupe, alors que les analyses combinées de toute la preuve moléculaire conduit à une phylogénie bien définie avec un fort support en lacet. Les caractères traditionnellement utilisés du fruit tel que la forme de l'aile et la composition ainsi que l'orientation de la compression du méricarpe sont fortement variables. Les résultats de ces analyses révèlent que les genres *Cymopterus* et *Lomatium*, les deux plus grands genres d'Apiaceae nord-américaines, sont polyphylétiques, et que leurs espèces sont inextricablement liées avec celles de d'autres genres endémiques et pérennes de la région (tels que *Aletes*, *Musineon*, *Oreoxis*, *Pseudocymopterus*, *Pteryxia* et *Tauschia*) dont plusieurs ne sont également pas monophylétiques. L'emphase placées jusqu'ici sur les caractères du fruit dans tous les systèmes de classification du groupe à conduit à des assemblages très artificiels d'espèces. On doit revoir complètement les limites génériques de toutes les Apiaceae nord-américaines endémiques afin de poursuivre l'étude systématique de ce groupe récalcitrant.

**Mots clés :** Apiaceae, *Cymopterus*, phylogénie, ITS, *rps16* intron, morphologie.

[Traduit par la Rédaction]

Received 23 July 2002. Published on the NRC Research Press Web site at <http://canjbot.nrc.ca> on 24 January 2003.

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## Introduction

Considerable confusion exists with regard to the proper delimitation of and relationships among the perennial endemic genera of western North American Apiaceae (Umbelliferae) subfamily Apioideae. This confusion is particularly evident in those taxa surrounding *Cymopterus* Raf. (the spring-parsleys). Historical treatments range from the recognition of many small, generically distinct elements (such as *Aulospermum* J.M. Coult. & Rose, *Glehnia* F. Schmidt ex Miq., *Oreoxis* Raf., *Phellopterus* (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose, *Pseudocymopterus* J.M. Coult. & Rose, *Pteryxia* (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose, and *Rhysopterus* J.M. Coult. & Rose; Coulter and Rose 1900; Mathias 1930; Mathias and Constance 1944–1945) to different sections and subgroups within the highly variable and expanded genus *Cymopterus* (Jones 1908). Contemporary treatments recognize *Oreoxis*, *Pseudocymopterus*, and *Pteryxia* as distinct genera (e.g., Kartesz 1994), or include them within a broadly circumscribed *Cymopterus* (Cronquist 1997; Table 1). Putatively related to *Cymopterus* sensu lato are the genera *Aletes* J.M. Coult. & Rose, *Harbouria* J.M. Coult. & Rose, *Lomatium* Raf., *Musineon* Raf., *Neoparrya* Mathias, *Oreonana* Jeps., *Orogenia* S. Watson, *Podistera* S. Watson, *Shoshonea* Evert & Constance, and *Tauschia* Schltld. (Mathias 1930; Evert and Constance 1982; Sun et al. 2000). Many of these genera have a xerophytic or semixerophytic habit. They occur practically without exception in the dry, sandy, or alkaline regions of western North America (NA) and usually in montane or alpine habitats (Mathias 1930). Many species are narrowly distributed and have strict edaphic requirements. They are all herbaceous perennials and are frequently low-growing and acaulescent.

Traditionally, classification of Apiaceae has been based on anatomical and morphological features of the mature fruit, sometimes to the exclusion of all other characters. Many of these features are apparent only after detailed examination and sectioning. In most umbellifers, the dry schizocarp splits down a broad commissure into two one-seeded mericarps that are typically joined by a central stalk (carpophore). In some species, the carpophore may be obsolete by adnation of its halves to the commissural faces of the mericarps. The fruit may be compressed laterally, at right angles to the commissural plane, or dorsally, parallel to the commissural plane, if it is compressed at all. Each mericarp commonly bears five primary, longitudinal ribs or ridges that contain the vascular bundles: three dorsal and two marginal (or lateral), with the ribs filiform to broadly winged. Oil canals (vittae) are commonly present in the intervals between the primary ridges, with additional vittae occurring on the commissural face. In the absence of mature fruits, many perennial species of Apiaceae endemic to western NA are essentially indistinguishable. Indeed, when considered collectively, these plants present such a confusing integration of characters that generic delimitation is made exceedingly difficult.

The genus *Cymopterus*, as currently treated, consists of some 35–45 species, with Utah, Nevada, Idaho, and California holding the greatest diversity (Kartesz 1994; Cronquist 1997; Table 1). Its name is derived from the Greek *kyma*, a wave, and *pteron*, a wing, referring to the often undulate

wings of the fruit, for the marginal and usually one or more of the dorsal ribs are conspicuously winged. However, these ribs and wings vary greatly in shape and composition, as does the orientation of fruit compression. The ribs may appear as inconspicuous lines or be highly prominent. The shape of the wings in cross section may be short or extended into linear projections of various forms, and their composition may vary from thin and scarious to thick and corky. Loss of the carpophore occurs in nearly half of the species, presumed to have happened several times independently during the evolution of the genus (Hartman and Constance 1985; Cronquist 1997; Hartman 2000). The number of vittae in the intervals varies from 3 to 5, but in some species there may be only one. Most species are caespitose, with the taproot surmounted by a branching, surficial caudex, while others have pseudoscapes arising from the subterranean crown of the taproot (Cronquist 1997). *Cymopterus* occurs in a wide variety of, and often very restricted, habitat types, and its concomitant variation in growth forms and fruit types makes any taxonomic definition of the genus difficult and precludes inferences of infrageneric relationships.

Phylogenetic studies of these endemic and largely cordilleran genera are few, and have focused almost exclusively upon *Lomatium* (Schlessman 1984; Simmons 1985; Mastrogiuseppe et al. 1985; Gilmartin and Simmons 1987; Soltis and Kuzoff 1993; Soltis and Novak 1997; Soltis et al. 1995; Hardig and Soltis 1999). To ascertain what genera might be most closely related to *Lomatium*, Gilmartin and Simmons (1987) carried out phenetic analyses and, for one of the phenetic groups they delimited, a cladistic analysis was conducted using morphological data. Their examination of 88 NA genera using combinations of character states for three binary characters revealed 7 phenetic alliances, with one group (the “*Lomatium* alliance”) comprising *Lomatium*, *Cymopterus*, *Glehnia*, *Polytaenia* DC., *Prinosciadium* S. Watson, *Pseudocymopterus*, and *Pteryxia*. This group was the closest phenetically to two other alliances, represented by such genera as *Aletes*, *Donnellsmithia* J.M. Coult. & Rose, *Harbouria*, *Musineon*, *Neoparrya*, *Orogenia*, *Taenidia* (Torr. & A. Gray) Drude, *Tauschia*, *Thaspium* Nutt., and *Zizia* W.D.J. Koch. The results of their cladistic analyses were equivocal in suggesting a clear sister group to *Lomatium*, but did highlight the possible paraphyletic nature of *Cymopterus* (and *Pteryxia*). Monophyly of all remaining taxa was tacitly assumed.

Herein, we present results of a phylogenetic study of *Cymopterus* and its allies based on molecular and morphological evidence. Our first objective is to evaluate the monophyly of *Cymopterus*. However, given the complex and overlapping patterns of morphological character variation observed, both within the genus and among its putative allies, we hypothesize a priori that the genus is not monophyletic. Thus, our second objective is to determine the phylogenetic relationships of the elements that currently comprise *Cymopterus* with other perennial, endemic umbellifers of western NA. Patterns in the evolution of individual morphological characters and their usefulness in clade determination will be assessed, as will the comparative utility of DNA sequence data for several chloroplast and nuclear loci in their ability to resolve relationships among these taxa. The results obtained will eventually enable us to

**Table 1.** A comparison of taxonomic treatments for *Cymopterus* sensu lato and selected allies.

Mathias (1930)	Mathias and Constance (1944–1945)	Weber (1984, 1991); Weber and Wittmann (1992)	Kartesz (1994)	Cronquist (1997)
<i>Musineon divaricatum</i> (Pursh) Nutt. ex Torr. & A. Gray	<i>Musineon divaricatum</i>		<i>Musineon divaricatum</i>	<i>Musineon divaricatum</i>
<i>Musineon divaricatum</i> var. <i>hookeri</i> (Torr. & A. Gray) Mathias	<i>Musineon divaricatum</i> var. <i>hookeri</i>		<i>Musineon divaricatum</i> var. <i>hookeri</i>	<i>Musineon divaricatum</i>
<i>Musineon vaginatum</i> Rydb.	<i>Musineon vaginatum</i>		<i>Musineon vaginatum</i>	<i>Musineon vaginatum</i>
<i>Musineon lineare</i> (Rydb.) Mathias	<i>Musineon lineare</i>		<i>Musineon lineare</i>	<i>Musineon lineare</i>
<i>Musineon tenuifolium</i> Nutt. ex Torr. & A. Gray	<i>Musineon tenuifolium</i>	<i>Aletes tenuifolius</i> (Nutt. ex Torr. & A. Gray) W.A. Weber	<i>Musineon tenuifolium</i>	
<i>Rhysopterus plurijugus</i> J.M. Coult. & Rose	<i>Rhysopterus plurijugus</i>		<i>Cymopterus corrugatus</i>	<i>Cymopterus corrugatus</i>
<i>Neoparrya lithophila</i> Mathias	<i>Neoparrya lithophila</i>	<i>Aletes lithophilus</i> (Mathias) W.A. Weber	<i>Neoparrya lithophila</i>	
<i>Aletes acaulis</i> (Torr.) J.M. Coult. & Rose	<i>Aletes acaulis</i>	<i>Aletes acaulis</i>	<i>Aletes acaulis</i>	
<i>Aletes humilis</i> J.M. Coult. & Rose	<i>Aletes humilis</i>	<i>Aletes humilis</i>	<i>Aletes humilis</i>	
		<i>Aletes sessiliflorus</i> W.L. Theob. & C.C. Tseng	<i>Aletes sessiliflorus</i>	
		<i>Aletes eastwoodiae</i> (J.M. Coult. & Rose) W.A. Weber		
		<i>Aletes juncea</i> (Barneby & N.H. Holmgren) W.A. Weber		
		<i>Aletes latilobus</i> (Rydb.) W.A. Weber		
		<i>Aletes minima</i> (Mathias) W.A. Weber		
		<i>Aletes nuttallii</i> (A. Gray) W.A. Weber		
		<i>Aletes parryi</i> (S. Watson) W.A. Weber		
		<i>Aletes scabra</i> (J.M. Coult. & Rose) W.A. Weber		
			<i>Aletes filifolius</i> Mathias, Constance & W.L. Theob.	
<i>Oreoxis alpina</i> (A. Gray) J.M. Coult. & Rose	<i>Oreoxis alpina</i>		<i>Oreoxis alpina</i>	<i>Cymopterus alpinus</i> A. Gray
			<i>Oreoxis alpina</i> subsp. <i>puberulenta</i> W.A. Weber	
<i>Oreoxis humilis</i> Raf.	<i>Oreoxis humilis</i>		<i>Oreoxis humilis</i>	
<i>Oreoxis bakeri</i> J.M. Coult. & Rose	<i>Oreoxis bakeri</i>		<i>Oreoxis bakeri</i>	<i>Cymopterus bakeri</i> (J.M. Coult. & Rose) M.E. Jones

Table 1 (continued).

Mathias (1930)	Mathias and Constance (1944–1945)	Weber (1984, 1991); Weber and Wittmann (1992)	Kartesz (1994)	Cronquist (1997)
<i>Oreoxis macdougalii</i> (J.M. Coult. & Rose) Rydb.	<i>Aletes macdougalii</i> J.M. Coult. & Rose	<i>Aletes macdougalii</i>	<i>Aletes macdougalii</i>	<i>Cymopterus macdougalii</i> (J.M. Coult. & Rose) Tidestr.
		<i>Aletes macdougalii</i> subsp. <i>breviradiatus</i> W.L. Theob. & C.C. Tseng	<i>Aletes macdougalii</i> subsp. <i>breviradiatus</i>	<i>Cymopterus macdougalii</i>
			<i>Oreoxis trotteri</i> S.L. Welsh & S. Goodrich	<i>Cymopterus trotteri</i> (S.L. Welsh & S. Goodrich) Cronquist
<i>Pseudocymopterus montanus</i> (A. Gray) J.M. Coult. & Rose	<i>Pseudocymopterus montanus</i>		<i>Pseudocymopterus montanus</i>	<i>Cymopterus lemmonii</i> (J.M. Coult. & Rose) Dorn
<i>Pseudocymopterus davidsonii</i> (J.M. Coult. & Rose) Mathias	<i>Pteryxia davidsonii</i> (J.M. Coult. & Rose) Mathias & Constance		<i>Pteryxia davidsonii</i>	<i>Pseudocymopterus davidsonii</i>
<i>Pseudocymopterus anisatus</i> (A. Gray) J.M. Coult. & Rose	<i>Pteryxia anisata</i> (A. Gray) Mathias & Constance	<i>Aletes anisatus</i> (A. Gray) W.L. Theob. & C.C. Tseng	<i>Aletes anisatus</i>	
<i>Pseudocymopterus humboldtensis</i> (M.E. Jones) Mathias	<i>Cymopterus humboldtensis</i> M.E. Jones		<i>Cymopterus nivalis</i>	<i>Cymopterus nivalis</i>
<i>Pseudocymopterus bipinnatus</i> (S. Watson) J.M. Coult. & Rose	<i>Cymopterus bipinnatus</i> S. Watson	<i>Aletes bipinnata</i> (S. Watson) W.A. Weber	<i>Cymopterus nivalis</i>	<i>Cymopterus nivalis</i>
<i>Pseudocymopterus nivalis</i> (S. Watson) Mathias	<i>Cymopterus nivalis</i> S. Watson	<i>Aletes nivalis</i> (S. Watson) W.A. Weber	<i>Cymopterus nivalis</i>	<i>Cymopterus nivalis</i>
<i>Pseudocymopterus hendersonii</i> J.M. Coult. & Rose	<i>Pteryxia hendersonii</i> (J.M. Coult. & Rose) Mathias & Constance	<i>Aletes hendersonii</i> (J.M. Coult. & Rose) W.A. Weber	<i>Pteryxia hendersonii</i>	<i>Cymopterus hendersonii</i> (J.M. Coult. & Rose) Cronquist
		<i>Aletes longiloba</i> (Rydb.) W.A. Weber	<i>Pteryxia hendersonii</i>	<i>Cymopterus hendersonii</i>
			<i>Pseudocymopterus longiradiatus</i> Mathias, Constance & W.L. Theob.	
<i>Pteryxia terebinthina</i> (Hook.) J.M. Coult. & Rose	<i>Pteryxia terebinthina</i>		<i>Pteryxia terebinthina</i>	<i>Cymopterus terebinthinus</i> (Hook.) Torr. & A. Gray
<i>Pteryxia terebinthina</i> var. <i>foeniculacea</i> (Nutt. ex Torr. & A. Gray) Mathias	<i>Pteryxia terebinthina</i> var. <i>foeniculacea</i>		<i>Pteryxia terebinthina</i> var. <i>foeniculacea</i>	<i>Cymopterus terebinthinus</i> var. <i>foeniculaceus</i> (Nutt. ex Torr. & A. Gray) Cronquist
<i>Pteryxia terebinthina</i> var. <i>calcareo</i> (M.E. Jones) Mathias	<i>Pteryxia terebinthina</i> var. <i>calcareo</i>		<i>Pteryxia terebinthina</i> var. <i>albiflora</i>	<i>Cymopterus terebinthinus</i> var. <i>albiflorus</i> (Nutt. ex Torr. & A. Gray) M.E. Jones

**Table 1** (continued).

Mathias (1930)	Mathias and Constance (1944–1945)	Weber (1984, 1991); Weber and Wittmann (1992)	Kartesz (1994)	Cronquist (1997)
<i>Pteryxia terebinthina</i> var. <i>californica</i> (J.M. Coult. & Rose) Mathias	<i>Pteryxia terebinthina</i> var. <i>californica</i>		<i>Pteryxia terebinthina</i> var. <i>californica</i>	<i>Cymopterus terebinthinus</i> var. <i>albiflorus</i>
<i>Pteryxia terebinthina</i> var. <i>albiflora</i> (Nutt. ex Torr. & A. Gray) Mathias	<i>Pteryxia terebinthina</i> var. <i>albiflora</i>		<i>Pteryxia terebinthina</i> var. <i>albiflora</i>	<i>Cymopterus terebinthinus</i> var. <i>albiflorus</i>
<i>Pteryxia petraea</i> (M.E. Jones) J.M. Coult. & Rose	<i>Pteryxia petraea</i>	<i>Aletes petraeus</i> (M.E. Jones) W.A. Weber	<i>Pteryxia petraea</i>	<i>Cymopterus petraeus</i> M.E. Jones
<i>Aulospermum longipes</i> (S. Watson) J.M. Coult. & Rose	<i>Cymopterus longipes</i> S. Watson		<i>Cymopterus longipes</i>	<i>Cymopterus longipes</i>
<i>Aulospermum planosum</i> Osterh.	<i>Cymopterus planosus</i> (Osterh.) Mathias		<i>Cymopterus lapidosus</i> (M.E. Jones) M.E. Jones <i>Cymopterus planosus</i>	<i>Cymopterus longipes</i>
<i>Aulospermum ibapense</i> (M.E. Jones) J.M. Coult. & Rose	<i>Cymopterus ibapensis</i> M.E. Jones		<i>Cymopterus ibapensis</i>	<i>Cymopterus longipes</i> var. <i>ibapensis</i> (M.E. Jones) Cronquist
<i>Aulospermum glaucum</i> (Nutt.) J.M. Coult. & Rose	<i>Cymopterus glaucus</i> Nutt.		<i>Cymopterus glaucus</i>	
<i>Aulospermum watsonii</i> J.M. Coult. & Rose	<i>Cymopterus watsonii</i> (J.M. Coult. & Rose) M.E. Jones		<i>Cymopterus ibapensis</i>	<i>Cymopterus longipes</i> var. <i>ibapensis</i>
<i>Aulospermum aboriginum</i> (M.E. Jones) Mathias	<i>Cymopterus aboriginum</i> M.E. Jones		<i>Cymopterus aboriginum</i>	<i>Cymopterus aboriginum</i>
<i>Aulospermum minimum</i> Mathias	<i>Cymopterus minimus</i> (Mathias) Mathias		<i>Cymopterus minimus</i>	<i>Cymopterus minimus</i>
<i>Aulospermum basalticum</i> (M.E. Jones) Tidestr.	<i>Cymopterus basalticum</i> M.E. Jones		<i>Cymopterus basalticum</i>	<i>Cymopterus basalticum</i>
<i>Aulospermum rosei</i> M.E. Jones ex J.M. Coult. & Rose	<i>Cymopterus rosei</i> (M.E. Jones ex J.M. Coult. & Rose) M.E. Jones		<i>Cymopterus rosei</i>	<i>Cymopterus rosei</i>
<i>Aulospermum duchesnense</i> (M.E. Jones) Tidestr.	<i>Cymopterus duchesnensis</i> M.E. Jones		<i>Cymopterus duchesnensis</i>	<i>Cymopterus duchesnensis</i>
<i>Aulospermum purpureum</i> (S. Watson) J.M. Coult. & Rose	<i>Cymopterus purpureum</i> S. Watson		<i>Cymopterus purpureum</i>	<i>Cymopterus purpureum</i>
<i>Aulospermum jonesii</i> (J.M. Coult. & Rose) J.M. Coult. & Rose	<i>Cymopterus jonesii</i> J.M. Coult. & Rose		<i>Cymopterus jonesii</i>	<i>Cymopterus jonesii</i>
<i>Aulospermum panamintense</i> (J.M. Coult. & Rose) J.M. Coult. & Rose	<i>Cymopterus panamintensis</i> J.M. Coult. & Rose		<i>Cymopterus panamintensis</i>	
<i>Aulospermum panamintense</i> var. <i>acutifolium</i> J.M. Coult. & Rose	<i>Cymopterus panamintensis</i> var. <i>acutifolius</i> (J.M. Coult. & Rose) Munz		<i>Cymopterus panamintensis</i> var. <i>acutifolius</i>	

Table 1 (continued).

Mathias (1930)	Mathias and Constance (1944–1945)	Weber (1984, 1991); Weber and Wittmann (1992)	Kartesz (1994)	Cronquist (1997)
<i>Phellopterus montanus</i> Nutt. ex. Torr. & A. Gray	<i>Cymopterus montanus</i> Nutt. ex Torr. & A. Gray		<i>Cymopterus montanus</i>	
<i>Phellopterus macrorhizus</i> (Buckley) J.M. Coult. & Rose	<i>Cymopterus</i> <i>macrorhizus</i> Buckley		<i>Cymopterus macrorhizus</i>	
<i>Phellopterus bulbosus</i> (A. Nelson) J.M. Coult. & Rose	<i>Cymopterus bulbosus</i> A. Nelson		<i>Cymopterus bulbosus</i>	<i>Cymopterus bulbosus</i>
<i>Phellopterus purpurascens</i> (A. Gray) J.M. Coult. & Rose	<i>Cymopterus</i> <i>purpurascens</i> (A. Gray) M.E. Jones		<i>Cymopterus</i> <i>purpurascens</i>	<i>Cymopterus</i> <i>purpurascens</i>
<i>Phellopterus multinervatus</i> J.M. Coult. & Rose	<i>Cymopterus</i> <i>multinervatus</i> (J.M. Coult. & Rose) Tidestr.		<i>Cymopterus</i> <i>multinervatus</i>	<i>Cymopterus</i> <i>multinervatus</i>
<i>Cymopterus cinerarius</i> A. Gray	<i>Cymopterus cinerarius</i>		<i>Cymopterus cinerarius</i>	<i>Cymopterus</i> <i>cinerarius</i>
<i>Cymopterus megacephalus</i> M.E. Jones	<i>Cymopterus</i> <i>megacephalus</i>		<i>Cymopterus</i> <i>megacephalus</i>	<i>Cymopterus</i> <i>megacephalus</i>
<i>Cymopterus deserticola</i> Brandegee	<i>Cymopterus deserticola</i>		<i>Cymopterus deserticola</i>	
<i>Cymopterus globosus</i> (S. Watson) S. Watson	<i>Cymopterus globosus</i>		<i>Cymopterus globosus</i>	<i>Cymopterus globosus</i>
<i>Cymopterus coulteri</i> (M.E. Jones) Mathias	<i>Cymopterus coulteri</i>		<i>Cymopterus coulteri</i>	<i>Cymopterus coulteri</i>
<i>Cymopterus corrugatus</i> M.E. Jones	<i>Cymopterus corrugatus</i>		<i>Cymopterus corrugatus</i>	<i>Cymopterus</i> <i>corrugatus</i>
<i>Cymopterus acaulis</i> (Pursh) Raf.	<i>Cymopterus acaulis</i>		<i>Cymopterus acaulis</i>	<i>Cymopterus acaulis</i>
<i>Cymopterus fendleri</i> A. Gray	<i>Cymopterus fendleri</i>		<i>Cymopterus acaulis</i> var. <i>fendleri</i> (A. Gray) S. Goodrich	<i>Cymopterus acaulis</i> var. <i>fendleri</i>
			<i>Cymopterus acaulis</i> var. <i>greeleyorum</i> J.W. Grimes & P.L. Packard	<i>Cymopterus acaulis</i> var. <i>greeleyorum</i>
			<i>Cymopterus acaulis</i> var. <i>higginsii</i> (S.L. Welsh) S. Goodrich	<i>Cymopterus acaulis</i> var. <i>fendleri</i>
			<i>Cymopterus acaulis</i> var. <i>parvus</i> S. Goodrich	<i>Cymopterus acaulis</i> var. <i>greeleyorum</i>
<i>Cymopterus newberryi</i> (S. Watson) M.E. Jones	<i>Cymopterus newberryi</i>		<i>Cymopterus newberryi</i>	<i>Cymopterus</i> <i>newberryi</i>
	<i>Cymopterus ripleyi</i> Barneby		<i>Cymopterus ripleyi</i>	<i>Cymopterus ripleyi</i>
	<i>Cymopterus gilmanii</i> C. Morton		<i>Cymopterus gilmanii</i>	
			<i>Cymopterus beckii</i> S.L. Welsh & S. Goodrich	<i>Cymopterus beckii</i>
			<i>Cymopterus davisii</i> R.L. Hartm.	<i>Cymopterus davisii</i>
			<i>Cymopterus evertii</i> R.L. Hartm. & R.S. Kirkp.	<i>Cymopterus evertii</i>

**Table 1** (concluded).

Mathias (1930)	Mathias and Constance (1944–1945)	Weber (1984, 1991); Weber and Wittmann (1992)	Kartesz (1994)	Cronquist (1997)
			<i>Cymopterus goodrichii</i> S.L. Welsh & Neese	<i>Cymopterus goodrichii</i>
			<i>Cymopterus douglassii</i> R.L. Hartm. & Constance	
			<i>Cymopterus williamsii</i> R.L. Hartm. & Constance	

**Note:** Authors of plant names are standardized according to Brummitt and Powell (1992).

achieve our broader goals, which are to define and delimit the various generic elements that have been confused with *Cymopterus* and to produce a modern classification of the group that reflects its evolutionary history.

## Materials and methods

### Molecular tools

For phylogenetic inference, we have exploited variation in the two nuclear ribosomal DNA (rDNA) internal transcribed spacers (ITS) and the chloroplast DNA (cpDNA) *rps16* intron. Previous studies have demonstrated the utility of these loci for estimating infrafamilial relationships in other Apiaceae (Downie and Katz-Downie 1996, 1999; Downie et al. 1998, 2000a, 2000c; Lee and Downie 1999, 2000), as well as in angiosperms in general (Baldwin et al. 1995; Lidén et al. 1997; Oxelman et al. 1997). For a subset of taxa, we also examined variation from the cpDNA *trnF-trnL-trnT* (*trnF-L-T*) locus. This region, comprising two intergenic spacers and the *trnL* intron, has not been used for phylogenetic study of Apiaceae, although it has been used successfully in other groups at comparable taxonomic levels (Taberlet et al. 1991; Gielly and Taberlet 1994). Congruence of relationships derived from independent lines of evidence is necessary to examine the robustness of the phylogenetic hypothesis and to identify discrepant organismal and gene phylogenies.

### Accessions examined

One hundred and fifty accessions representing 148 species in 73 genera of Apiaceae subfamily Apioideae were examined for ITS, *rps16* intron, and (or) *trnF-L-T* sequence variation (Table 2). Complete ITS sequences for 66 taxa are reported here for the first time; combining these with 82 previously published or available ITS sequences yielded a matrix of 148 taxa for a global analysis. For two *Lomatium* species, data for only ITS-1 were available (Soltis and Kuzoff 1993). Fifty-six complete *rps16* intron sequences (plus a portion of its flanking 3' exon region) were procured as part of this study and combined with 29 previously published sequences for a matrix of 85 taxa. Twenty-seven complete *trnF-L-T* sequences were also obtained, representing the *trnF-trnL* and *trnL-trnT* intergenic spacer regions, gene *trnL* with its intron, and portions of genes *trnF* and *trnT*. Eighty-three accessions were included in both the ITS and *rps16* intron analyses; 27 species were common to all three

molecular data sets, including the analysis of morphological data.

Kartesz (1994), whose checklist of Apiaceae was influenced by the work of Lincoln Constance, recognized 78 genera of subfamily Apioideae in NA (north of Mexico). Of these, we have sampled 61 plus nine meso-American genera (*Arracacia* Bancr., *Coaxana* J.M. Coult. & Rose, *Coulterophytum* B.L. Rob., *Dahliaphyllum* Constance & Breedlove, *Enantiophylla* J.M. Coult. & Rose, *Mathiasella* Constance & C.L. Hitchc., *Myrrhidendron* J.M. Coult. & Rose, *Prionosciadium*, and *Rhodosciadium* S. Watson). These meso-American genera (plus *Donnellsmithia*) are endemic to the highlands of Mexico and neighboring Central America (Mathias 1965), exhibit a large number of paleopolyploid members (Bell and Constance 1966; Moore 1971), and have been provisionally recognized as the *Arracacia* clade (Downie et al. 2000b, 2001). A previous study had suggested a possible affinity of *Prionosciadium* and *Donnellsmithia* with *Cymopterus* (Gilmartin and Simmons 1987); the fruits of many of these meso-American taxa are morphologically similar to those of *Angelica* and some *Lomatium*. In this paper, we follow the nomenclature of Kartesz (1994) with one exception — the name *Helosciadium nodiflorum* (L.) W.D.J. Koch replaces *Apium nodiflorum* (L.) Lag. (Downie et al. 2000b, 2000c). Emphasis was placed on sampling the perennial endemic members of western NA Apioideae, with the selection of species influenced primarily by material availability. We examined 17 of the 35 species of *Cymopterus* recognized by Kartesz (1994). Also examined were five of six species of *Aletes*, 28 of 78 species of *Lomatium*, three of four species of *Musineon*, three of four species of *Oreoxis*, and two of four species of *Pteryxia*. The Eurasian genera *Physospermum* Cusson and *Pleurospermum* Hoffm. were used to root all trees in the global analyses; their selection as outgroups is based on previous higher-level studies (summarized in Downie et al. 2001).

### Experimental strategy

Leaf material for DNA extraction was obtained either directly from the field, from plants cultivated from seed in the greenhouse, from herbarium specimens, or from the personal collections of Lincoln Constance (University of California Botanical Garden, Berkeley, Calif.). Vouchers and their depositions are indicated in Table 2. Details of DNA extraction, polymerase chain reaction (PCR) primer construction

**Table 2.** Species of Apiaceae subfamily Apioideae examined for nuclear rDNA ITS (148 taxa), cpDNA *rps16* intron (85 taxa), and (or) *trnF-L-T* (27 species) sequence variation.

Species	Source and voucher	GenBank accession No.		
		ITS-1, ITS-2	<i>rps16</i> intron	<i>trnF-L-T</i>
<i>Aegopodium podagraria</i> L.	Downie et al. 1998	U30536, U30537		
<i>Aethusa cynapium</i> L.	Downie et al. 1998	U30582, U30583	AF110539	
<i>Aletes acaulis</i> (Torr.) J.M. Coult. & Rose	U.S.A., Colorado, Larimer Co., Canyon of the Big Thompson, 15 July 1989, <i>Hartman 24386</i> (RM)	AF358461, AF358528	AF358595	
<i>Aletes anisatus</i> (A. Gray) W.L. Theob. & C.C. Tseng	U.S.A., Colorado, Park Co., Corral Creek, 6 August 1995, <i>Chumley 2807</i> (RM)	AF358462, AF358529	AF358596	AF444008
<i>Aletes humilis</i> J.M. Coult. & Rose	Downie et al. 1998	U78401, U78461		
<i>Aletes macdougalii</i> J.M. Coult. & Rose subsp. <i>breviradiatus</i> W.L. Theob. & C.C. Tseng	U.S.A., New Mexico, San Juan Co., Blanco, 2 May 1982, <i>Hartman 13963</i> (RM)	AF358463, AF358530	AF358597	
<i>Aletes sessiliflorus</i> W.L. Theob. & C.C. Tseng	U.S.A., New Mexico, Rio Arriba Co., NW of Embudo, 1 May 1992, <i>Hartman 13954</i> (RM)	AF358464, AF358531		
<i>Ammi majus</i> L.	Downie et al. 1998	U78386, U78446	AF164814	
<i>Anethum graveolens</i> L.	Downie et al. 1998	U30550, U30551	AF110542	
<i>Angelica ampla</i> A. Nelson	Downie et al. 1998	U79597, U79598	AF358598	
<i>Angelica archangelica</i> L. subsp. <i>archangelica</i>	Downie et al. 1998	U30576, U30577	AF110536	AF444007
<i>Angelica arguta</i> Nutt. ex Torr. & A. Gray	Downie et al. 1998	U79599, U79600		
<i>Angelica breweri</i> A. Gray	Downie et al. 1998	U78396, U78456	AF358599	
<i>Angelica pinnata</i> S. Watson	U.S.A., Wyoming, Lincoln Co., Commissary Ridge, 22 July 1993, <i>Hartman 41500</i> (RM)	AF358465, AF358532	AF358600	
<i>Angelica roseana</i> L.F. Hend.	U.S.A., Wyoming, Teton Co., Blue Miner Lake, 25 August 1994, <i>Hartman 50090</i> (RM)	AF358466, AF358533		
<i>Angelica sylvestris</i> L.	Downie et al. 1998	U78414, U78474		
<i>Anthriscus caucalis</i> M. Bieb.	Downie et al. 1998	U79601, U79602	AF110549	
<i>Apium graveolens</i> L.	Downie et al. 1998	U30552, U30553	AF110545	
<i>Arracacia aegopodioides</i> (Kunth) J.M. Coult. & Rose	Cult. UC Berkeley; Mexico, Oaxaca, <i>Breedlove 72231</i> (CAS), L. Constance pers. coll. C-2408	AF358467, AF358534		
<i>Arracacia bracteata</i> J.M. Coult. & Rose	Cult. UC Berkeley; Mexico, Oaxaca, <i>Breedlove 72536</i> (CAS), L. Constance pers. coll. C-2412	AF358468, AF358535		
<i>Arracacia brandegei</i> J.M. Coult. & Rose	Downie et al. 1998	U30570, U30571		
<i>Arracacia nelsonii</i> J.M. Coult. & Rose	Downie et al. 1998	U30556, U30557		
<i>Arracacia tolucensis</i> (Kunth) Hemsl. var. <i>tolucensis</i>	Cult. UC Berkeley; Mexico, Querétaro, Cerro Zamorano, 16 December 1978, <i>Ornduff 8560</i> (UC), L. Constance pers. coll. C-2124	AF358469, AF358536		
<i>Arracacia tolucensis</i> var. <i>multifida</i> (S. Watson) Mathias & Constance	Cult. UC Berkeley; Mexico, UNAM 88, L. Constance pers. coll. C-2355	AF358470, AF358537		
<i>Berula erecta</i> (Huds.) Coville	Downie et al. 1998	U79605, U79606	AF164819	
<i>Bifora radians</i> M. Bieb.	Downie et al. 1998	U78408, U78468	AF164809	
<i>Carum carvi</i> L.	Downie et al. 1998	U78377, U78437		
<i>Caucalis platycarpus</i> L.	Downie et al. 1998	U78364, U78424	AF123745	
<i>Chaerophyllum tainturieri</i> Hook.	Downie et al. 2000a	AF073647, AF073648		



**Table 2** (continued).

Species	Source and voucher	GenBank accession No.			
		ITS-1, ITS-2	<i>rps16</i> intron	<i>trnF-L-T</i>	
<i>Ciclospermum leptophyllum</i> (Pers.) Sprague ex Britton & E.H. Wilson	U.S.A., Oklahoma, Pittsburg Co., 9 May 1991, <i>Seigler et al. 13245</i> (ILL)	AF358471, AF358538			
<i>Cicuta maculata</i> L. var. <i>angustifolia</i> Hook.	U.S.A., Wyoming, Goshen Co., Bear Creek, 4 August 1994, <i>Nelson et al. 33517</i> (RM)	AF358472, AF358539	AF358601		
<i>Coaxana purpurea</i> J.M. Coult. & Rose	Downie et al. 1998	U30572, U30573			
<i>Conioselinum chinense</i> (L.) Britton, Stern & Poggenb.	Downie et al. 1998	U78374, U78434			
<i>Conioselinum scopulorum</i> (A. Gray) J.M. Coult. & Rose	Katz-Downie et al. 1999	AF008634, AF009113			
<i>Conium maculatum</i> L.	Downie et al. 1998	U30588, U30589	AF110546		
<i>Coriandrum sativum</i> L.	Downie et al. 1998	U30586, U30587			
<i>Coulterophytum jaliscense</i> McVaugh	Cult. UC Berkeley; Mexico, Jalisco, Zarzamora (Las Joyas), Sierra de Manantlán, <i>Iltis et al. 1299</i> (UC), L. Constance pers. coll. C-2236	AF358473, AF358540			
<i>Coulterophytum laxum</i> B.L. Rob.	Downie et al. 1998	U30560, U30561			
<i>Cryptotaenia canadensis</i> (L.) DC.	Downie et al. 1998	U79613, U79614	AF358602		
<i>Cuminum cyminum</i> L.	Downie et al. 1998	U78362, U78422			
<i>Cymopterus acaulis</i> (Pursh) Raf. var. <i>acaulis</i>	U.S.A., Colorado, Garfield Co., Grand Hogback, Burning Mtn., 27 May 1991, <i>Vanderhorst 2236</i> (RM)	AF358474, AF358541	AF358603		
<i>Cymopterus acaulis</i> var. <i>fendleri</i> (A. Gray) S. Goodrich	U.S.A., Utah, Emery Co., S of Price River, 14 May 1979, <i>Hartman 8674</i> (RM)	AF358475, AF358542	AF358604		
<i>Cymopterus basalticus</i> M.E. Jones	U.S.A., Utah, Millard Co., Desert Range Experiment Station, 22 May 1982, <i>Fonken</i> <i>1611</i> (RM)	AF358476, AF358543			
<i>Cymopterus bulbosus</i> A. Nelson	U.S.A., Utah, Uintah Co., ESE of Vernal, 18 April 1982, <i>Hartman 13951</i> (RM)	AF358477, AF358544			
<i>Cymopterus duchesnensis</i> M.E. Jones	U.S.A., Utah, Uintah Co., Tridell, 28 May 1982, <i>Hartman 13984</i> (RM)	AF358478, AF358545	AF358605		
<i>Cymopterus evertii</i> R.L. Hartm. & R.S. Kirkp.	U.S.A., Wyoming, Hot Springs Co., SE of Meeteetse, 30 May 1985, <i>Hartman 20097</i> <i>and Haines</i> (RM)	AF358479, AF358546	AF358606		
<i>Cymopterus globosus</i> (S. Watson) S. Watson	Downie et al. 1998	U78398, U78458	AF358607	AF444009	
<i>Cymopterus ibapensis</i> M.E. Jones	U.S.A., Utah, Sevier Co., UT 4, 26 May 1982, <i>Hartman 13978</i> (RM)	AF358480, AF358547			
<i>Cymopterus jonesii</i> J.M. Coult. & Rose	U.S.A., Utah, Washington Co., road to Apex Mine, 20 May 1981, <i>Fonken 1195</i> (RM)	AF358481, AF358548	AF358608		
<i>Cymopterus longipes</i> S. Watson	U.S.A., Wyoming, Lincoln Co., Grade Canyon Creek, 22 May 1993, <i>Hartman</i> <i>37464</i> (RM)	AF358483, AF358550	AF358609		
<i>Cymopterus montanus</i> Nutt. ex Torr. & A. Gray	U.S.A., Colorado, El Paso Co., Rockrimmon Road, 18 May 1982, <i>Hartman 13968</i> (RM)	AF358484, AF358551	AF110534	AF444010	
<i>Cymopterus multinervatus</i> (J.M. Coult. & Rose) Tidestr.	U.S.A., Arizona, Mohave Co., Mt. Trumbull, 31 March 1983, <i>Hartman 14098</i> (RM)	AF358485, AF358552	AF358610	AF444011	
<i>Cymopterus nivalis</i> S. Watson	U.S.A., Wyoming, Teton Co., E of Crystal Creek, 24 June 1994, <i>Hartman 46444</i> and <i>Cramer</i> (RM)	AF358486, AF358553	AF358611	AF444012	
<i>Cymopterus panamintensis</i> J.M. Coult. & Rose var. <i>panamintensis</i>	U.S.A., California, Inyo Co., Argus Range NNE of Ridgecrest, <i>Ertter 7043</i> (UC)	AF358487, AF358554			

Table 2 (continued).

Species	Source and voucher	GenBank accession No.			
		ITS-1, ITS-2	<i>rps16</i> intron	<i>trnF-L-T</i>	
<i>Cymopterus planosus</i> (Osterh.) Mathias	U.S.A., Colorado, Routt Co., base of Dunckley Flat Tops, 16 June 1991, <i>Vanderhorst 2592</i> (RM)	AF358488, AF358555	AF358612		
<i>Cymopterus purpurascens</i> (A. Gray) M.E. Jones	U.S.A., Arizona, Mohave Co., NE of Peach Springs, 30 March 1983, <i>Hartman 14096</i> (RM)	AF358489, AF358556			
<i>Cymopterus purpureus</i> S. Watson	U.S.A., Colorado, Garfield Co., Grand Hogback, 25 May 1991, <i>Vanderhorst</i> <i>2166a</i> (RM)	AF358490, AF358557	AF358613	AF444013	
<i>Cymopterus williamsii</i> R.L. Hartm. & Constance	U.S.A., Wyoming, Natrona Co., along Baker Cabin, 23 May 1994, <i>Nelson 30642</i> (RM)	AF358491, AF358558	AF358614	AF444014	
<i>Cynosciadium digitatum</i> DC.	U.S.A., Illinois, Jackson Co., Shawnee Natl. Forest, 27 May 1993, <i>Phillippe 21886</i> (ILLS)	AF358492, AF358559			
<i>Dahliaphyllum almedae</i> Constance & Breedlove	Downie et al. 1998	U78395, U78455			
<i>Daucus pusillus</i> Michx.	Lee and Downie 1999	AF077788, AF077103	AF123729		
<i>Enantiophylla heydeana</i> J.M. Coult. & Rose	Downie et al. 1998	U30558, U30559			
<i>Erigenia bulbosa</i> (Michx.) Nutt.	Katz-Downie et al. 1999	AF008636, AF009115	AF110554		
<i>Falcaria vulgaris</i> Bernh.	Downie et al. 1998	U78378, U78438			
<i>Foeniculum vulgare</i> Mill.	Downie et al. 1998	U78385, U78445	AF110543		
<i>Harbouria trachypleura</i> (A. Gray) J.M. Coult. & Rose	U.S.A., New Mexico, Colfax Co., Philmont Scout Ranch, 24 June 1991, <i>Embry 56</i> (RM)	AF358493, AF358560	AF358615	AF444015	
<i>Helosciadium nodiflorum</i> (L.) W.D.J. Koch (as <i>Apium</i> <i>nodiflorum</i> (L.) Lag.)	Downie et al. 2000c	AF164823, AF164848	AF164820		
<i>Heracleum sphondylium</i> L.	Downie et al. 1998	U30544, U30545	AF164800		
<i>Levisticum officinale</i> W.D.J. Koch	Downie et al. 1998	U78389, U78449			
<i>Ligusticum canadense</i> (L.) Britton	Katz-Downie et al. 1999	AF008635, AF009114			
<i>Ligusticum porteri</i> J.M. Coult. & Rose var. <i>porteri</i>	Downie et al. 1998	U78375, U78435			
<i>Ligusticum scoticum</i> L.	Downie et al. 1998	U78357, U78417	AF123756		
<i>Lilaeopsis carolinensis</i> J.M. Coult. & Rose	Petersen et al. 2002	AF466276			
<i>Lomatium bicolor</i> (S. Watson) J.M. Coult. & Rose var. <i>bicolor</i>	U.S.A., Wyoming, Sublette Co., Packsaddle Ridge, 21 June 1993, <i>Nelson 26111 and</i> <i>Nelson</i> (RM)	AF358494, AF358561	AF358616	AF444016	
<i>Lomatium brandegei</i> (J.M. Coult. & Rose) J.F. Macbr.	Hardig and Soltis 1999	AF011803, AF011820			
<i>Lomatium californicum</i> (Nutt.) Mathias & Constance	Downie et al. 1998	U78397, U78457	AF358617	AF444017	
<i>Lomatium concinnum</i> (Osterh.) Mathias	Hardig and Soltis 1999	AF011804, AF011821			
<i>Lomatium cous</i> (S. Watson) J.M. Coult. & Rose	U.S.A., Wyoming, Sublette Co., Palmer Peak, 5 August 1994, <i>Hartman 49374</i> (RM)	AF358495, AF358562	AF358618		
<i>Lomatium dasycarpum</i> (Torr. & A. Gray) J.M. Coult. and Rose subsp. <i>dasycarpum</i>	Downie et al. 1998	U30580, U30581	AF358619	AF444018	
<i>Lomatium dissectum</i> (Nutt.) Mathias & Constance var. <i>dissectum</i>	Hardig and Soltis 1999	AF011809, AF011826			
<i>Lomatium foeniculaceum</i> (Nutt.) J.M. Coult. & Rose subsp. <i>foeniculaceum</i>	U.S.A., Wyoming, Converse Co., Southern Powder River Basin, 12 May 1994, <i>Nelson</i> <i>30083</i> (RM)	AF358496, AF358563			

**Table 2** (continued).

Species	Source and voucher	GenBank accession No.			
		ITS-1, ITS-2	<i>rps16</i> intron	<i>trnF-L-T</i>	
<i>Lomatium graveolens</i> (S. Watson) Dorn & R.L. Hartm. var. <i>graveolens</i>	U.S.A., Wyoming, Sublette Co., Packsaddle Ridge, 21 June 1993, <i>Nelson 26101 and Nelson</i> (RM)	AF358497, AF358564	AF358620	AF444019	
<i>Lomatium grayi</i> (J.M. Coult. & Rose) J.M. Coult. & Rose	Soltis and Kuzoff 1993 (ITS-1 only)	(not in GenBank)			
<i>Lomatium greenmanii</i> Mathias	Hardig and Soltis 1999	AF011805, AF011822			
<i>Lomatium howellii</i> (S. Watson) Jeps.	Hardig and Soltis 1999	AF011800, AF011817			
<i>Lomatium idahoense</i> Mathias & Constance	Hardig and Soltis 1999	AF011806, AF011823			
<i>Lomatium junceum</i> Barneby & N.H. Holmgren	U.S.A., Utah, Emery Co., NE of Emery, 18 June 1982, <i>Fonken 1962</i> (RM)	AF358498, AF358565	AF358621	AF444020	
<i>Lomatium juniperinum</i> (M.E. Jones) J.M. Coult. & Rose	U.S.A., Utah, Cache Co., Bear River Range, 12 August 1980, <i>Hartman 11885</i> (RM)	AF358499, AF358566	AF358622	AF444021	
<i>Lomatium laevigatum</i> (Nutt.) J.M. Coult. & Rose	Soltis and Kuzoff 1993 (ITS-1 only)	(not in GenBank)			
<i>Lomatium latilobum</i> (Rydb.) Mathias	U.S.A., Utah, Grand Co., SE of Moab, 13 April 1995, <i>Tuby 3772</i> (RM)	AF358500, AF358567	AF358623		
<i>Lomatium lucidum</i> (Nutt. ex. Torr. & A. Gray) Jeps.	Hardig and Soltis 1999	AF011799, AF011816			
<i>Lomatium macrocarpum</i> (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose	U.S.A., Wyoming, Lincoln Co., Dempsey Ridge, 25 June 1993, <i>Nelson 26537 and Nelson</i> (RM)	AF358501, AF358568	AF358624	AF444022	
<i>Lomatium nudicaule</i> (Pursh) J.M. Coult. & Rose	U.S.A., Nevada, Elko Co., S. of Hot Creek, 16 May 1979, <i>Hartman 8736</i> (RM)	AF358502, AF358569	AF358625	AF444023	
<i>Lomatium nuttallii</i> (A. Gray) J.F. Macbr.	Hardig and Soltis 1999	AF011811, AF011828			
<i>Lomatium orientale</i> J.M. Coult. & Rose	U.S.A., Wyoming, Natrona Co., along Notches, 23 May 1994, <i>Nelson 30536</i> (RM)	AF358503, AF358570			
<i>Lomatium parvifolium</i> (Hook. & Arn.) Jeps.	Hardig and Soltis 1999	AF011801, AF011818			
<i>Lomatium repostum</i> (Jeps.) Mathias	Hardig and Soltis 1999	AF011802, AF011819			
<i>Lomatium rigidum</i> (M.E. Jones) Jeps.	Hardig and Soltis 1999	AF011797, AF011814			
<i>Lomatium scabrum</i> (J.M. Coult. & Rose) Mathias var. <i>scabrum</i>	U.S.A., Utah, Millard Co., S. of Ganison, 16 May 1981, <i>Fonken 1168</i> (RM)	AF358504, AF358571	AF358626		
<i>Lomatium shevockii</i> R.L. Hartm. & Constance	Hardig and Soltis 1999	AF011798, AF011815			
<i>Lomatium triternatum</i> (Pursh) J.M. Coult. & Rose subsp. <i>platycarpum</i> (Torr.) Cronquist	U.S.A., Wyoming, Lincoln Co., Boulder Ridge, 22 May 1993, <i>Hartman 37526</i> (RM)	AF358505, AF358572	AF358627		
<i>Mathiasella bupleuroides</i> Constance & C.L. Hitchc.	Downie et al. 1998	U78394, U78454			
<i>Musineon divaricatum</i> (Pursh) Nutt. ex Torr. & A. Gray var. <i>divaricatum</i>	U.S.A., Wyoming, Platte Co., NW of Chugwater, 26 May 1994, <i>Nelson 30905</i> (RM)	AF358506, AF358573	AF358628	AF444024	
<i>Musineon tenuifolium</i> Nutt. ex Torr. & A. Gray	U.S.A., Wyoming, Niobrara Co., Hat Creek Breaks, 17 May 1994, <i>Nelson 30335</i> (RM)	AF358507, AF358574	AF358629	AF444025	
<i>Musineon vaginatum</i> Rydb.	U.S.A., Wyoming, Sheridan Co., Big Horn Mtns., 18 June 1979, <i>Hartman 9020</i> (RM)	AF358508, AF358575	AF358630		
<i>Myrrhidendron donnell-smithii</i> J.M. Coult. & Rose	Downie et al. 1998 ( <i>Grantham and Parsons 0433-90</i> )	U30554, U30555			
<i>Myrrhis odorata</i> (L.) Scop.	Downie et al. 1998	U30530, U30531	AF123755		
<i>Neoparrya lithophila</i> Mathias	U.S.A., Colorado, Saguache Co., Upper Saguache Forest Service Station, 18 September 1983, <i>Hartman 17360</i> (RM)	AF358509, AF358576	AF358631	AF444026	

**Table 2** (continued).

Species	Source and voucher	GenBank accession No.		
		ITS-1, ITS-2	<i>rps16</i> intron	<i>trnF-L-T</i>
<i>Oenanthe pimpinelloides</i> L.	Downie et al. 1998	U78371, U78431	AF110553	
<i>Oreoxis alpina</i> (A. Gray) J.M. Coult. & Rose subsp. <i>alpina</i>	U.S.A., Colorado, Rio Blanco Co., Pyramid Peak, 27 June 1991, <i>Vanderhorst 2806</i> (RM)	AF358510, AF358577		
<i>Oreoxis bakeri</i> J.M. Coult. & Rose	U.S.A., New Mexico, Santa Fe Co., Lake Peak, 19 June 1980, <i>Hartman 11725</i> (RM)	AF358511, AF358578	AF358632	
<i>Oreoxis humilis</i> Raf.	U.S.A., Colorado, Teller Co., Pikes Peak Road, 17 June 1980, <i>Hartman 11718</i> (RM)	AF358512, AF358579	AF358633	
<i>Orogenia linearifolia</i> S. Watson	U.S.A., Wyoming, Lincoln Co., Hams Fork Plateau, 23 May 1993, <i>Hartman 37557</i> (RM)	AF358513, AF358580	AF358634	
<i>Osmorhiza longistylis</i> (Torr.) DC.	Downie et al. 1998	U79617, U79618	AF123754	
<i>Oxypolis rigidior</i> (L.) Raf.	U.S.A., Illinois, Vermilion Co., Windfall Hill Prairie Nature Reserve, 17 July 1991, <i>Phillippe et al. 19411</i> (ILLS)	AF358514, AF358581		
<i>Pastinaca sativa</i> L.	Downie et al. 1998	U30546, U30547	AF110538	
<i>Perideridia kelloggii</i> (A. Gray) Mathias	Downie et al. 1998	U78373, U78433	AF358635	
<i>Petroselinum crispum</i> (Mill.) A.W. Hill	Downie et al. 1998	U78387, U78447	AF110544	
<i>Physospermum cornubiense</i> (L.) DC.	Downie et al. 1998	U78382, U78442	AF110556	
<i>Pimpinella saxifraga</i> L.	Downie et al. 1998	U30590, U30591		
<i>Pleurospermum foetens</i> Franch.	Katz-Downie et al. 1999	AF008639, AF009118	AF110559	
<i>Podistera eastwoodiae</i> (J.M. Coult. & Rose) Mathias & Constance	U.S.A., Colorado, Garfield Co., Edge Lake, 3 July 1991, <i>Vanderhorst 3016</i> (RM)	AF358515, AF358582	AF358636	AF444027
<i>Polytaenia nuttallii</i> DC.	U.S.A., Illinois, Rock Island Co., N of Cordova, 19 June 1973, <i>Evers 110464</i> (ILLS)	AF358516, AF358583	AF358637	
<i>Polytaenia texana</i> (J.M. Coult. & Rose) Mathias & Constance	U.S.A., Texas, Burnet Co., E of Briggs, 25 May 1985, <i>Barrie 1403</i> (RM)		AF358638	
<i>Prionosciadium acuminatum</i> B.L. Rob.	Cult. UC Berkeley; Mexico, Sinaloa, 3 km NE of Palmito, <i>Breedlove 36448</i> (CAS), L. Constance pers. coll. C-1871	AF358517, AF358584		
<i>Prionosciadium simplex</i> Mathias & Constance	Cult. UC Berkeley; Mexico, Tamaulipas, <i>Breedlove 63487</i> (CAS), L. Constance pers. coll. C-2341	AF358518, AF358585		
<i>Prionosciadium turneri</i> Constance & Affolter	Downie et al. 1998 (as Constance pers. coll. C-2053)	U30568, U30569		
<i>Prionosciadium watsonii</i> J.M. Coult. & Rose	Cult. UC Berkeley; Mexico, Durango, <i>Breedlove 61338</i> (CAS), L. Constance pers. coll. C-2330	AF358519, AF358586		
<i>Pseudocymopterus montanus</i> (A. Gray) J.M. Coult. & Rose	U.S.A., Colorado, Rio Blanco Co., Dunckley Flat Tops, 17 June 1991, <i>Vanderhorst 2637</i> (RM)	AF358520, AF358587	AF358639	
<i>Pteryxia hendersonii</i> (J.M. Coult. & Rose) Mathias & Constance	U.S.A., Montana, Ravalli Co., Bitterroot Wilderness, 6 August 1981, <i>Hartman 13889</i> (RM)	AF358521, AF358588	AF358640	AF444028
<i>Pteryxia terebinthina</i> (Hook.) J.M. Coult. & Rose var. <i>albiflora</i> (Nutt. ex Torr. & A. Gray) Mathias	U.S.A., Wyoming, Lincoln Co., Twin Creek, 23 May 1993, <i>Hartman 37616</i> (RM)	AF358522, AF358589	AF358641	AF444029
<i>Rhodosciadium argutum</i> (Rose) Mathias & Constance	Downie et al. 1998	U30566, U30567		
<i>Scandix pecten-veneris</i> L.	Downie et al. 1998	U30538, U30539	AF123753	
<i>Shoshonea pulvinata</i> Evert & Constance	Downie et al. 1998	U78400, U78460	AF358642	AF444030

**Table 2** (concluded).

Species	Source and voucher	GenBank accession No.			
		ITS-1, ITS-2	<i>rps16</i> intron	<i>trnF-L-T</i>	
<i>Sium suave</i> Walter	Cult. UIUC from seeds obtained from Jardin botanique de Montréal, Canada, Downie 12 (ILL)	AF358523, AF358590	AF358643		
<i>Spermolepis inermis</i> (Nutt. ex DC.) Mathias & Constance	Katz-Downie et al. 1999	AF008602, AF009081			
<i>Sphenosciadium capitellatum</i> A. Gray	Katz-Downie et al. 1999	AF008600, AF009079	AF358644		
<i>Taenidia integerrima</i> (L.) Drude	Downie et al. 1998	U78399, U78459	AF358645		
<i>Tauschia glauca</i> (J.M. Coult. & Rose) Mathias & Constance	U.S.A., California, Trinity Co., SE of Burnt Ranch, 11 July 1990, Spellenberg 10254 (RM)		AF358646		
<i>Tauschia parishii</i> (J.M. Coult. & Rose) J.F. Macbr.	U.S.A., California, San Bernardino Co., 12 April 1986, Boyd 1762 (RM)	AF358524, AF358591	AF358647		
<i>Tauschia texana</i> A. Gray	U.S.A., Texas, Gonzales Co., 22 February 1986, Barrie 1435 (RM)	AF358525, AF358592	AF358648		
<i>Thaspium barbinode</i> (Michx.) Nutt.	U.S.A., Illinois, Champaign Co., N of Tolono, 12 June 1990, Ulaszek 1484 (ILLS)	AF358526, AF358593			
<i>Thaspium pinnatifidum</i> (Buckley) A. Gray	Downie et al. 1998	U78410, U78470			
<i>Thaspium trifoliatum</i> (L.) A. Gray var. <i>trifoliatum</i>	Downie et al. 1998	U78410, U78470	AF358649	AF444031	
<i>Torilis arvensis</i> (Huds.) Link	Downie et al. 2000c	AF164844, AF164869	AF110548		
<i>Trachyspermum copticum</i> (L.) Link (as <i>T. ammi</i> (L.) Sprague in Turrill)	Downie et al. 1998	U78380, U78440			
<i>Turgenia latifolia</i> (L.) Hoffm.	Lee and Downie 1999	AF077810, AF077125	AF123743		
<i>Yabea microcarpa</i> (Hook. & Arn.) Koso-Pol.	Lee and Downie 1999	AF077806, AF077121	AF123742		
<i>Zizia aptera</i> (A. Gray) Fernald	U.S.A., Wyoming, Teton Co., road to Granite Falls, 29 May 1994, Hartman 45748 (RM)	AF358527, AF358594	AF358650	AF444032	
<i>Zizia aurea</i> (L.) W.D.J. Koch	Downie et al. 1998	U30574, U30575	AF110535	AF444033	

**Note:** Reference citations indicate source and voucher information for previously published DNA data. ITS data have been deposited with GenBank as separate ITS-1 and ITS-2 sequences. Species nomenclature follows Kartesz (1994); standardized authors names according to Brummitt and Powell (1992); herbarium acronyms according to Holmgren et al. (1990).

and amplification, and template purification and sequencing for both ITS and *rps16* intron loci are the same as described previously (Downie and Katz-Downie 1996, 1999). Similar procedures were used for the *trnF-L-T* study, using the primers and PCR amplification protocols of Taberlet et al. (1991). Both manual and automated sequencing methods were used. Simultaneous consideration of both DNA strands across all sequenced regions permitted unambiguous base determination in nearly all cases.

### Sequence analysis

All newly procured sequences were aligned manually in the data editor of PAUP\* version 4.0 (Swofford 1998), with gaps positioned to minimize nucleotide mismatches. When alignment was ambiguous because of, for example, tracts of poly-As, -Gs, or -Ts or indirect duplications of adjacent elements in two or more taxa, these positions were eliminated from the analysis. The determination of boundary sequences for the six conserved structural domains of the *rps16* group II intron was based on similar boundary sequences inferred for tobacco and mustard (Michel et al. 1989; Neuhaus et al.

1989) and other Apiaceae (Downie et al. 2000c). A similar breakdown of the *trnL* intron was not done, given its 50% smaller size relative to *rps16*. Uncorrected pairwise distances (p) were calculated by PAUP\*, as they are commonly provided in other angiosperm ITS analyses (Baldwin et al. 1995). All sequence data have been deposited in GenBank (Table 2); aligned data in PAUP\* nexus files are available upon request.

### Phylogenetic analysis of molecular data

Initially, a maximum parsimony analysis of ITS data for all 148 taxa was carried out to confirm the placements of the *Arracacia* clade and *Cymopterus* sensu lato (including *Oreoxis*, *Pseudocymopterus*, and *Pteryxia*) and its allies within a broader phylogeny. Based on the results of this global analysis and in an effort to increase resolution by reducing the number of excluded positions because of the greater ambiguity involved in aligning sequences from more distantly related taxa, the clade comprising *Cymopterus* and allies was isolated for subsequent and more comprehensive phylogenetic analysis. For this smaller (local) set of taxa, a

maximum likelihood analysis (Felsenstein 1981) was also performed. All trees in the local analyses were rooted by *Aethusa cynapium*, as suggested by the global results. Separate analysis of each spacer region was not done. Previous studies, in Apioideae and other angiosperms, have indicated the high complementarity of spacer data and the greater phylogenetic resolution and internal support achieved in trees when both spacers are considered together than when either spacer is treated alone (Baldwin et al. 1995; Downie and Katz-Downie 1996). Data from the *rps16* intron and 3' exon portion were analyzed using maximum parsimony separately (85 species) and, for 83 taxa, in combination with ITS data. The *trnF-L-T* region was analyzed in its entirety, as well as partitioned into the two intergenic spacers and intron region for separate consideration. The 27 species common to the ITS, *rps16* intron, and *trnF-L-T* data sets were also analyzed separately and in combination using maximum parsimony, with the trees rooted by positioning the root along the branch connecting *Angelica archangelica* to the rest of the network. To examine the extent of conflict among separate data sets, the incongruence length difference test of Farris et al. (1995) was conducted using the partition homogeneity test of PAUP\*. One hundred replicates were considered for each partition, using simple addition sequence of taxa and tree bisection reconnection (TBR) branch swapping. Incongruence among data sets is identified if the additive tree lengths taken from resampled matrices are greater than the sum of the tree lengths from the original data. Prior to carrying out a maximum likelihood analysis of the 85-taxon ITS data set, the program Modeltest vers. 3.06 (Posada and Crandall 1998) was used to select an evolutionary model of nucleotide substitution (among 56 possible models) that best fits these data. The settings appropriate for the chosen model (base frequencies and among-site rate variation) were inputted into PAUP\* and a heuristic search performed using ten random addition sequence replicates and TBR branch swapping under maximum likelihood optimization.

Analyses of all but the smallest data sets were carried out initially using equally weighted maximum parsimony and the following protocol. One thousand heuristic searches were initiated using random addition starting trees, with TBR branch swapping and multrees selected, but saving no more than five of the shortest trees from each search. These trees were subsequently used as starting trees for further TBR branch swapping. The maximum number of saved trees was set at 20 000 and these trees were permitted to swap to completion. The strict consensus of these 20 000 minimal length trees was then used as a topological constraint in another round of 500–1000 random-addition replicate analyses but, in this case, only those trees that did not fit the constraint tree were saved (Catalán et al. 1997). No additional trees were found at the length of the initial shortest trees, which suggests that the strict consensus tree adequately summarizes the available evidence, even though the exact number of trees at that length is not known. Bootstrap values (Felsenstein 1985) were calculated from 100 000 replicate analyses using “fast” stepwise-addition of taxa; only those values compatible with the 50% majority-rule consensus tree were recorded. For all small (i.e., 27-taxon) data sets except that of ITS, a finite number of shortest trees was obtained

using 500 random-addition replicate searches and TBR branch swapping. Bootstrap values were calculated from 100 replicate analyses, simple-addition sequence of taxa, and TBR branch swapping. For the 27-taxon ITS matrix, the strategy used for the larger data sets was employed, with the exception that a maxtree limit of 500 trees was set for each of 100 bootstrap replicates. The number of additional steps required to force particular taxa into a monophyletic group was examined using the constraint option of PAUP\*. In all maximum parsimony analyses, gap states were treated as either missing data or a fifth base (“new state”), or were excluded.

Alignment gaps were incorporated into parsimony analyses by scoring each unambiguous insertion or deletion as a separate presence–absence (i.e., binary) character, while maintaining gap states as missing data. The resultant topology was compared to one inferred when alignment gaps were omitted as additional characters. The “Character Steps/etc.” charting option of MacClade vers. 3.08 (Maddison and Maddison 1992), under the assumption of Fitch parsimony, was used to calculate the number of steps of each gap character across all maximally parsimonious topologies. For two *Lomatium* species, two compressed regions of undetermined length were reported in ITS-1 (Soltis and Kuzoff 1993). In several other *Lomatium* species (Hardig and Soltis 1999), runs of ambiguous bases or missing data are evident within the same regions, suggestive that compressions were a problem here too. Given the discrepancies in length between these sequences and those sequenced by us for other *Lomatium* taxa, gaps were not scored as additional characters in the analyses of ITS data.

### Morphology

Characters of the fruit have been important traditionally in delimiting taxa within the group, but have yet to be analyzed cladistically across a wide spectrum of species. Thus, in the absence of a phylogenetic estimate, patterns in the evolution of these characters and their utility in circumscribing monophyletic groups could not be properly assessed. Moreover, we have observed that published fruit transections are occasionally interpreted incorrectly, because they were based on immature material or the species were misidentified. Microscope slides of mature fruit cross-sections were prepared for two or more populations of nearly all species of *Cymopterus* and several related genera (except *Lomatium*). Prior to sectioning, fruits were softened by treating them for several minutes in Pohl's Softening Agent (Radford et al. 1974). Free-hand sections through the middle of the mature mericarps were made using a razor blade and preserved using Hoyer's Mounting Medium (Radford et al. 1974). These sections were examined for orientation of fruit and seed compression, features of the ribs, wings, and commissure, and the number, position, and size of vittae. All microscope slides have been deposited at the Rocky Mountain Herbarium (RM).

Our preparations of mature fruit cross-sections and an examination of abundant representative material stored at RM uncovered 25 qualitative morphological characters that are potentially parsimony informative (see Table 5). About half of these characters were obtained from the fruits, the remainder from plant habit, inflorescence, and flowers. For

each of 27 species, 30–50 herbarium specimens were examined from throughout its range; these species represented the same ones as used in the cladistic analyses of *trnF-L-T* data. Character polymorphisms were recorded. Because the number of states differed among characters (ranging from two to five), all characters were weighted in inverse proportion to their number of steps using the scale option of PAUP\*, hence fractional weights were employed. Heuristic searches were conducted with 500 random-addition replicate searches and TBR branch swapping. All character states were assumed unordered, and the options multrees, collapse, and acctran optimization were selected. Bootstrap values were calculated from 500 replicate analyses, simple-addition sequence of taxa, and TBR branch swapping. The pattern of evolution of each morphological character across all minimal length trees was assessed using MacClade, with the goal of finding those characters most useful in the delimitation of major clades and genera.

## Results

### ITS

Alignment of all 148 ITS-1 and ITS-2 sequences resulted in a matrix of 490 positions. Thirty-one positions from ITS-1 and 50 positions from ITS-2 were eliminated from subsequent analyses because of confounding interpretations of homology; these included several small autapomorphic insertions, as well as length mutations of varying sizes in two or more taxa. These 81 positions represented 29 excluded regions, with 25 of them only 1 or 2 bp in size. The largest excluded region, encompassing 33 positions in ITS-2 near gene 5.8S, was characterized by highly variable sequences in all members of tribes Scandiceae Spreng. and Oenantheae Dumort. Characteristics of the included positions are presented in Table 3. Both spacer regions contributed comparable numbers of informative characters to the phylogenetic analysis. Measures of pairwise sequence divergence across both ITS-1 and ITS-2 ranged from identity (between the two varieties of *Cymopterus acaulis* and among the three species of *Thaspium*) to 34.6% of nucleotides (between *Daucus pusillus* and *Cynosciadium digitatum*). Excluding all *Lomatium* species, 13 unambiguous alignment gaps were parsimony informative; these ranged from 1 to 4 bp in size. Numerous autapomorphic deletions of a single bp were prevalent throughout the alignment. The two largest length mutations, each of 14 bp in size, represent deletions in *Myrrhidendron* and *Ligusticum scoticum* ITS-1 sequences relative to outgroups *Physospermum* and *Pleurospermum*. No evidence of divergent paralogous rDNA copy types was found in any of the species investigated.

Maximum parsimony analysis of 148 ITS-1 and ITS-2 sequences, with gap states treated as missing data, resulted in over 20 000 minimal length trees. The strict consensus of these trees, rooted with *Physospermum* and *Pleurospermum*, is presented in Fig. 1A. Those tribes and major clades outlined previously in subfamily Apioideae (Downie et al. 2001) are maintained, whereas resolution of relationships among *Cymopterus* sensu lato (including *Oreoxis*, *Pseudocymopterus*, and *Pteryxia*) and allies is quite poor, with only a few clades supported strongly in a large polytomy. In accordance with previous studies, the *Arracacia* group is

monophyletic but supported weakly (with < 50% bootstrap value); its sister group is not realized. The genera *Arracacia*, *Coulterophytum*, and *Prionosciadium* are each not monophyletic. The same can be said for western NA genera *Aletes*, *Cymopterus*, *Lomatium*, *Musineon*, *Oreoxis*, and *Pteryxia*, and several other genera represented by more than one species. In contrast, *Thaspium* and *Zizia* are each monophyletic. Given the large polytomy with many weakly supported clades, such an analysis is unsatisfactory in resolving relationships among *Cymopterus* and its allies. However, this global analysis does suggest that *Aethusa cynapium* or members of tribe Coriandreae W.D.J. Koch may be appropriate outgroups for further local analyses of *Cymopterus* and relatives.

Upon reduction of the global ITS matrix to include only those members comprising the large polytomy (except those of the *Arracacia* clade, which were also removed to facilitate analysis), a heuristic search was repeated using *Aethusa cynapium* as a functional outgroup. Alignment of 85 ITS sequences resulted in a matrix of 454 positions, with none excluded (Table 3). Maximum pairwise sequence divergence estimates approached 10.5% over both spacers, and 117 positions were parsimony informative (representing an increase of six positions relative to the same subset of taxa in the global analysis). Parsimony analysis of these sequence data, with gap states treated as missing, resulted in 20 000 minimal length trees whose strict consensus is presented in Fig. 1B. Once more, little resolution of relationships is achieved, with the results highly comparable to those obtained by the global analysis. However, in the local analysis, six of seven species of *Angelica* (plus *Sphenosciadium*) arise as a clade sister to all other ingroup taxa; *Angelica sylvestris*, however, is basal to this group. Rooting the trees with either *Bifora radians* or *Coriandrum sativum* (both of tribe Coriandreae) resulted in trees (not shown) consistent to those when *Aethusa cynapium* is used to root the network, the only exception being that all seven species of *Angelica* (plus *Sphenosciadium*) formed a monophyletic group arising from a large, basal polytomy. Constraining the 17 species (18 taxa) of *Cymopterus* to monophyly resulted in trees 21 steps longer than those most parsimonious. A monophyletic *Lomatium* resulted in trees 30 steps longer, whereas constraining the six narrowly endemic species comprising the *Euryptera* group of *Lomatium* (*Lomatium howellii*, *Lomatium lucidum*, *Lomatium parvifolium*, *Lomatium repostum*, *Lomatium rigidum*, and *Lomatium shevockii*) to monophyly, one of the few natural assemblages within the genus (Hardig and Soltis 1999), resulted in trees five steps longer than those most parsimonious. Repeating the local analysis with gap states treated as a fifth base ("new state" in PAUP\*) resulted in 20 000 minimal length trees, each of 621 steps. Their strict consensus is presented in Fig. 2A. Differences from the previous analyses include an increased resolution of relationship (albeit with many clades still supported weakly), the placements of *Pseudocymopterus montanus* and the clade of *Spermolepis* and *Ciclospermum* as successive sister groups to a large polytomous clade of NA Apiaceae, the union of *Thaspium*, *Zizia*, and *Polytaenia*, and a monophyletic *Euryptera* species group (with 83% bootstrap support). Excluding gapped positions from the analysis resulted in a strict consensus tree of identical topol-

**Table 3.** Sequence characteristics of the nuclear rDNA ITS and cpDNA *rps16* intron and 3' exon regions, separately and combined, used in the phylogenetic analyses of Apiaceae subfamily Apioideae.

Region	Length variation (bp)	No. of aligned positions	No. of positions eliminated	No. of positions constant	No. of positions informative	No. of positions autapomorphic	No. of unambiguous gaps informative	Maximum pairwise sequence divergence (%)
<b>Nuclear rDNA ITS</b>								
Global analysis ( <i>n</i> = 148)								
ITS-1	202–221	244	31	35	151	27		40.7
ITS-2	207–231	246	50	29	143	24		36.4
ITS-1 and ITS-2	417–443	490	81	64	294	51		34.6
Local analysis ( <i>n</i> = 85)								
ITS-1	207–218	224	0	108	65	51		12.1
ITS-2	221–226	230	0	122	52	56		10.9
ITS-1 and ITS-2	427–441	454	0	230	117	107		10.5
<b>Chloroplast DNA <i>rps16</i> intron and 3' exon (<i>n</i> = 85)</b>								
Intron								
Domain I	476–506	575	118	313	68	76	12	7.9
Domain II	67–108	123	64	32	15	12	3	11.9
Domain III	64–76	78	23	39	8	8	1	12.7
Domain IV	85–153	192	82	57	25	28	3	15.5
Domain V	34–34	34	0	32	2	0	0	5.9
Domain VI	35–35	35	1	27	3	4	0	5.9
Entire intron	801–884	1059	288	518	123	130	19	6.6
3' exon (partial)	110–110	110	1	99	5	5	0	5.5
Intron and 3' exon	911–994	1169	289	617	128	135	19	6.2
<b>Combined ITS and <i>rps16</i> intron and 3' exon (<i>n</i> = 83)</b>								
Entire matrix	1349–1432	1645	356	703	377	209	19	13.9

**Note:** Alignment gaps were not scored as additional characters in the analyses of ITS data.

ogy to that produced when gap states were treated as missing. The lack of resolution in the ITS trees derived from maximum parsimony precludes unambiguous hypotheses of relationship, but does show clearly that many NA genera, where resolved, are not monophyletic. The two largest genera within the complex, *Cymopterus* and *Lomatium*, are each highly polyphyletic.

Based on the hierarchical likelihood ratio test statistic, Modeltest selected the TrN + G model (Tamura and Nei 1993) as fitting the ITS data best (base frequencies: 0.2501, A; 0.2416, C; 0.2474, G; 0.2609, T; estimates of substitution rates: A→C, 1; A→G, 2.2111; A→T, 1; C→G, 1; C→T, 4.7219; G→T, 1; proportion of invariable sites = 0; gamma distribution shape parameter = 0.5188). Using these parameters, a single most-likely tree was recovered in PAUP\*, with a  $-\ln$  likelihood score of 3968.51683; this tree is presented in Fig. 2B. The relationships suggested by this phylogram include the monophyly of all *Angelica* species (plus *Sphenosciadium*), and the position of this clade, along with that comprising *Spermolepis* and *Ciclospermum*, as sister to

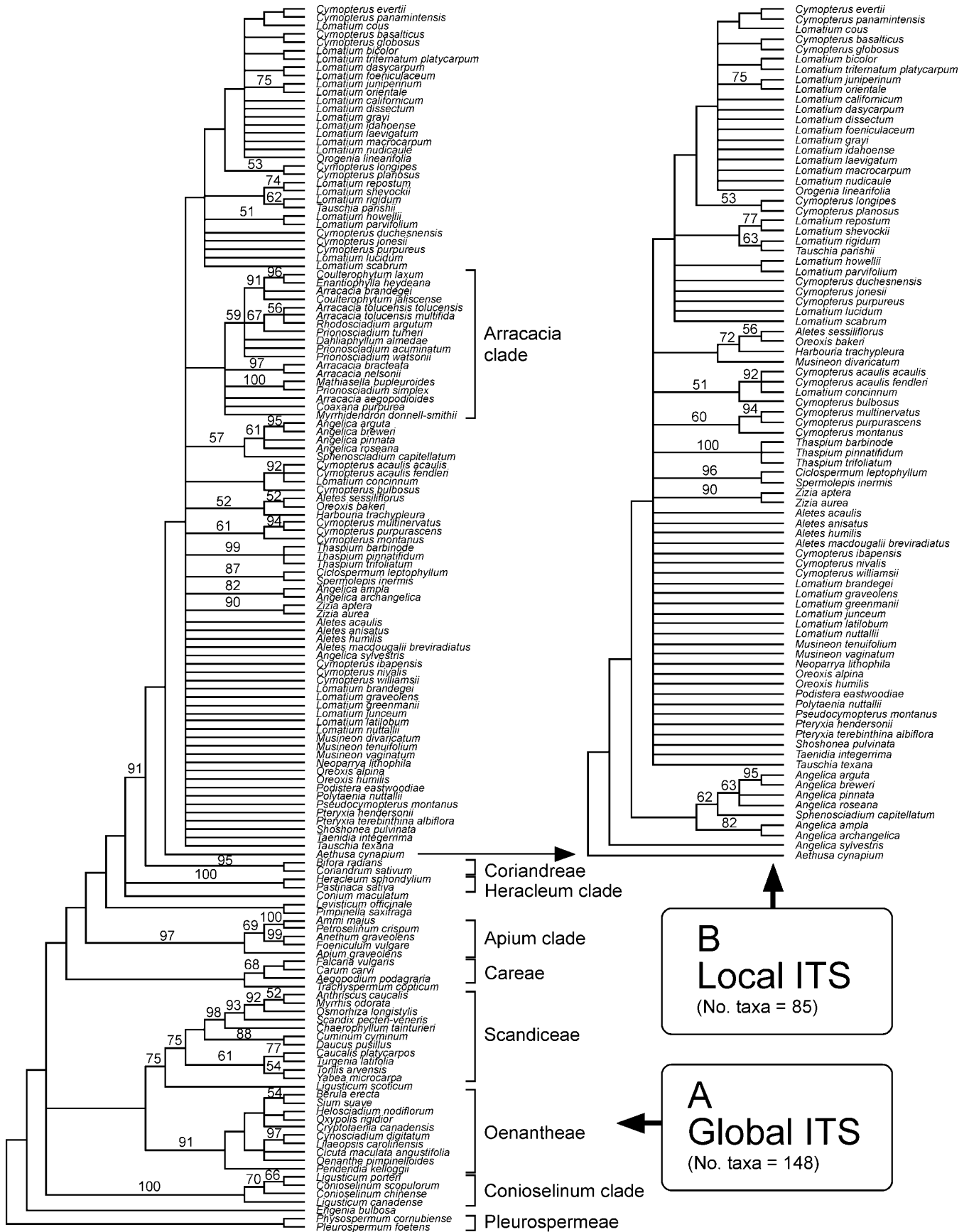
all NA endemic species. The major clades inferred are similar to those presented by the maximum parsimony tree when gaps are treated as new character states (Fig. 2A), with no resolution among them. Many genera are not monophyletic (*Aletes*, *Musineon*, *Oreoxis*, *Pteryxia*, and *Tauschia*), and *Cymopterus* and *Lomatium* are grossly polyphyletic. Members of the *Euryptera* species group are closely allied, but do not form a clade.

### *Rps16* intron

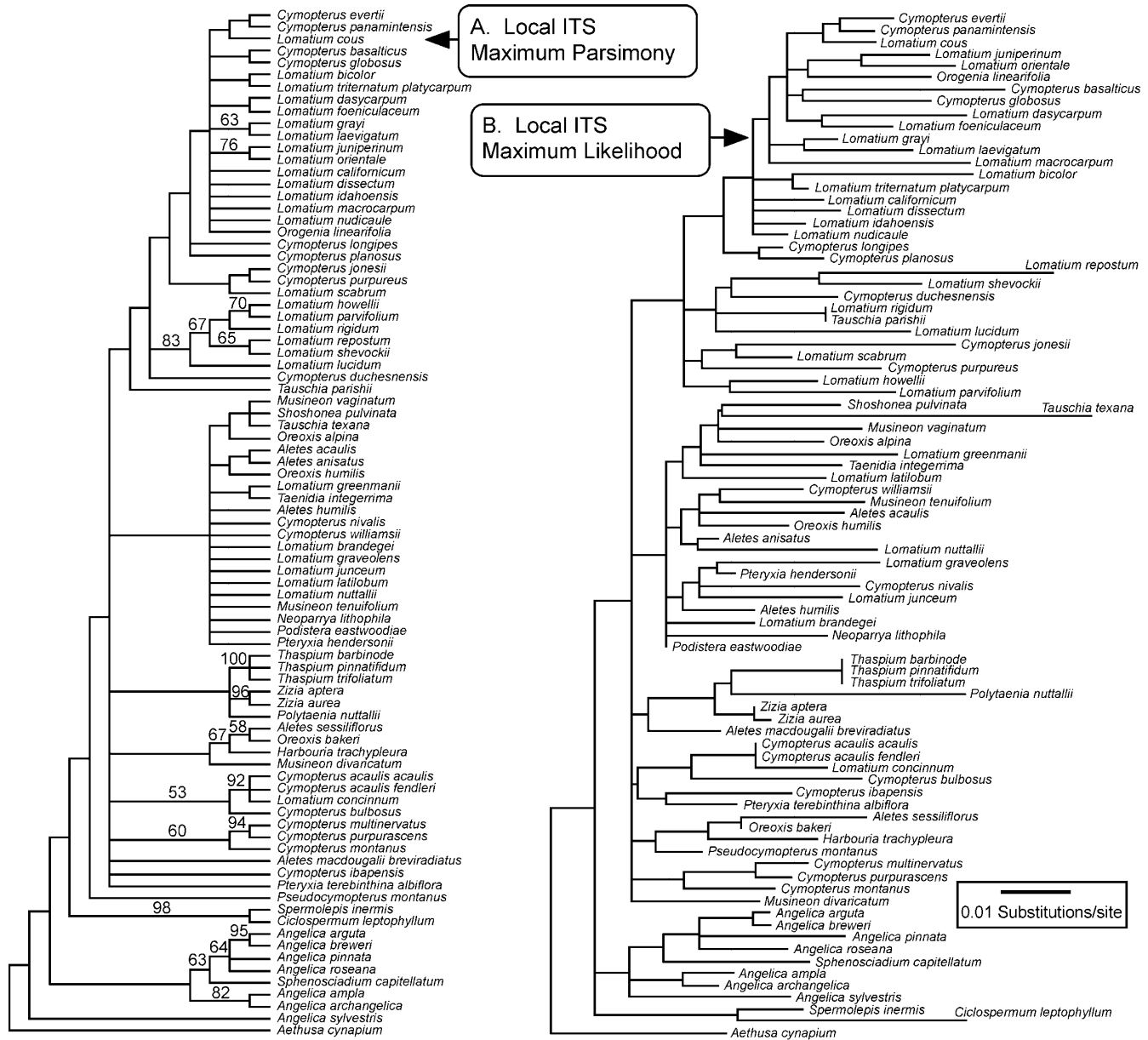
Among the 85 species examined for *rps16* intron sequence variation, the length of the intron varied from 801 to 884 bp. Juxtaposed was 110 bp of sequence from the 3' exon. Alignment of these intron and flanking exon data resulted in a matrix of 1169 positions, of which 289 were excluded from subsequent analyses because of alignment ambiguities. These ambiguous regions ranged from 1 to 43 bp in size, averaging 11 positions each. Characteristics of all unambiguous positions, including the number of constant, autapomorphic, and parsimony informative sites, are

**Fig. 1A.** Strict consensus of 20 000 minimal length 2242-step trees derived from equally weighted maximum parsimony analysis of 148 taxa and 409 unambiguously aligned ITS-1 and ITS-2 nucleotide positions, with gap states treated as missing data (CIs = 0.3189 and 0.2979, with and without uninformative characters, respectively; RI = 0.6335; RC = 0.2020). Numbers at nodes are bootstrap estimates for 100 000 replicate analyses using "fast" stepwise-addition; values  $\leq$  50% are not indicated. Brackets indicate major clades of Apioideae (Downie et al. 2001). **Fig. 1B.** Strict consensus of 20 000 minimal length 567-step trees derived from equally weighted maximum parsimony analysis of 85 nuclear rDNA ITS-1 and ITS-2 sequences, with gap states treated as missing data (CIs = 0.5485 and 0.4298, with and without uninformative characters, respectively; RI = 0.6139; RC = 0.3367). Numbers at nodes are bootstrap estimates for 100 000 replicate analyses using "fast" stepwise-addition; values  $\leq$  50% are not indicated. Complete taxon names, including ranks of infraspecific taxa which have been omitted for brevity, are provided in Table 2.





**Fig. 2A.** Strict consensus tree of 20 000 minimal length 621-step trees derived from equally weighted maximum parsimony analysis of 85 nuclear rDNA ITS-1 and ITS-2 sequences, with gap states treated as a fifth base (“new character state”; CIs = 0.5588 and 0.4408, with and without uninformative characters, respectively; RI = 0.6432; RC = 0.3594). Numbers at nodes are bootstrap estimates for 100 000 replicate analyses using “fast” stepwise-addition; values ≤ 50% are not indicated. **Fig. 2B.** Most-likely tree derived from maximum likelihood analysis of ITS sequence data, based on the TrN + G model of nucleotide substitution (–Ln likelihood = 3968.51683). Complete taxon names are provided in Table 2.



presented in Table 3. Nineteen unambiguous alignment gaps were potentially parsimony informative, ranging from 1 to 11 bp in size. Pairwise sequence divergence ranged from identity (between three pairs of sequences) to 6.2% of nucleotides (between the *Lomatium bicolor* – *Lomatium californicum* pair and *Scandix*).

The secondary structure of the *rps16* intron, like other plastid group II introns, is characterized by six major domains. For each domain and across all 85 species compared, features of the aligned sequences are presented in Table 3. Domain I is the largest, ranging between 476 and 506 bp in size, whereas domains V and VI are the smallest, each rang-

ing between 34 and 35 bp in size. Domains V and VI are also the most conserved, with five informative positions collectively, low nucleotide sequence divergence, and no inferred gaps. These two small domains provide as much information to the phylogenetic analysis as does the 3' exon portion. Relative to their size, domains II and IV provide the most phylogenetic information, with some 23 to 25% of all included positions parsimony informative.

Maximum parsimony analysis of 880 unambiguously aligned *rps16* intron and 3' exon nucleotide positions plus 19 binary-scored informative gaps, with gap states treated as missing data, resulted in over 20 000 minimal length trees,

of which their strict consensus (with accompanying bootstrap values) is shown in Fig. 3A. Here, the positions of all alignment gap changes are indicated, with the 14 non-homoplastic changes shown by solid circles and homoplasies (reversals and parallel gains of gaps 1 to 9 bp in size) by open circles. Repeating the analysis without the 19 scored gaps resulted in trees 27 steps shorter and collapse of the four branches indicated by asterisks in Fig. 3A. Treating gap states as a fifth base ("new state") or excluding them altogether made no appreciable difference to the resultant consensus tree topologies. However, regardless of analysis, resolution of relationships among *Cymopterus* and its allies is poor. Moreover, the genera *Heracleum* and *Pastinaca* (the *Heracleum* clade) and *Aethusa cynapium* fall within a large, polytomous group. The four included species of *Angelica* and *Sphenosciadium* do not form a clade, but arise within the same lineage as two species of *Lomatium*, *Aletes anisatus*, *Cymopterus globosus*, and *Shoshonea pulvinata*. While this lineage is weakly supported (with or without scored gaps) it does suggest that *Lomatium*, *Aletes*, and *Cymopterus* may each not be monophyletic. Upon consideration of binary-scored gaps as additional characters, *Tauschia* and *Pteryxia* may also not be monophyletic. Pairwise sequence divergence estimates among the 58 species comprising the large polytomy barely exceed 3.0% of nucleotides. Within this same group, the number of characters potentially informative for parsimony analysis is 47 (excluding scored gaps), and their distribution is inadequate to resolve more than only a few clades. Clearly, these intron and exon data are insufficient by themselves to resolve relationships among the perennial, endemic, apioid umbellifers of western NA. However, basal resolutions in the tree are generally strongly supported, with the major clades identified similar to those resolved in the global analysis of ITS data (Fig. 1A).

### ITS and *rps16* intron combined

ITS and *rps16* intron data for the same set of 83 taxa were combined for simultaneous consideration, as separate analyses of these data failed to provide adequate resolution among *Cymopterus* and its allies. Given the lack of resolution and poorly supported nodes in the *rps16* intron-derived trees, a test of incongruence was considered unnecessary. Details of the alignment are provided in Table 3, with 377 characters potentially informative. Maximum parsimony analysis of both data partitions including the 19 informative intron gaps, with gap states treated as missing data, resulted in 20 000 minimal length trees; their strict consensus is presented in Fig. 3B. Identical results were obtained when gap states were treated as a fifth base; slightly less resolution among the western NA endemics was achieved when gap positions were excluded from the analysis. The consensus tree (Fig. 3B) shows more resolution than either of the separate analyses and, in general, greater bootstrap support for many clades. Nevertheless, a large polytomy of western NA taxa is maintained. Greater resolution is achieved, but many genera are still not monophyletic. *Cymopterus* (with 13 included species in the combined analysis) is highly polyphyletic, comprising 10 separate lineages occurring in all major branches of the polytomy. *Lomatium* (12 species) is also polyphyletic, but in this case more than half of its species

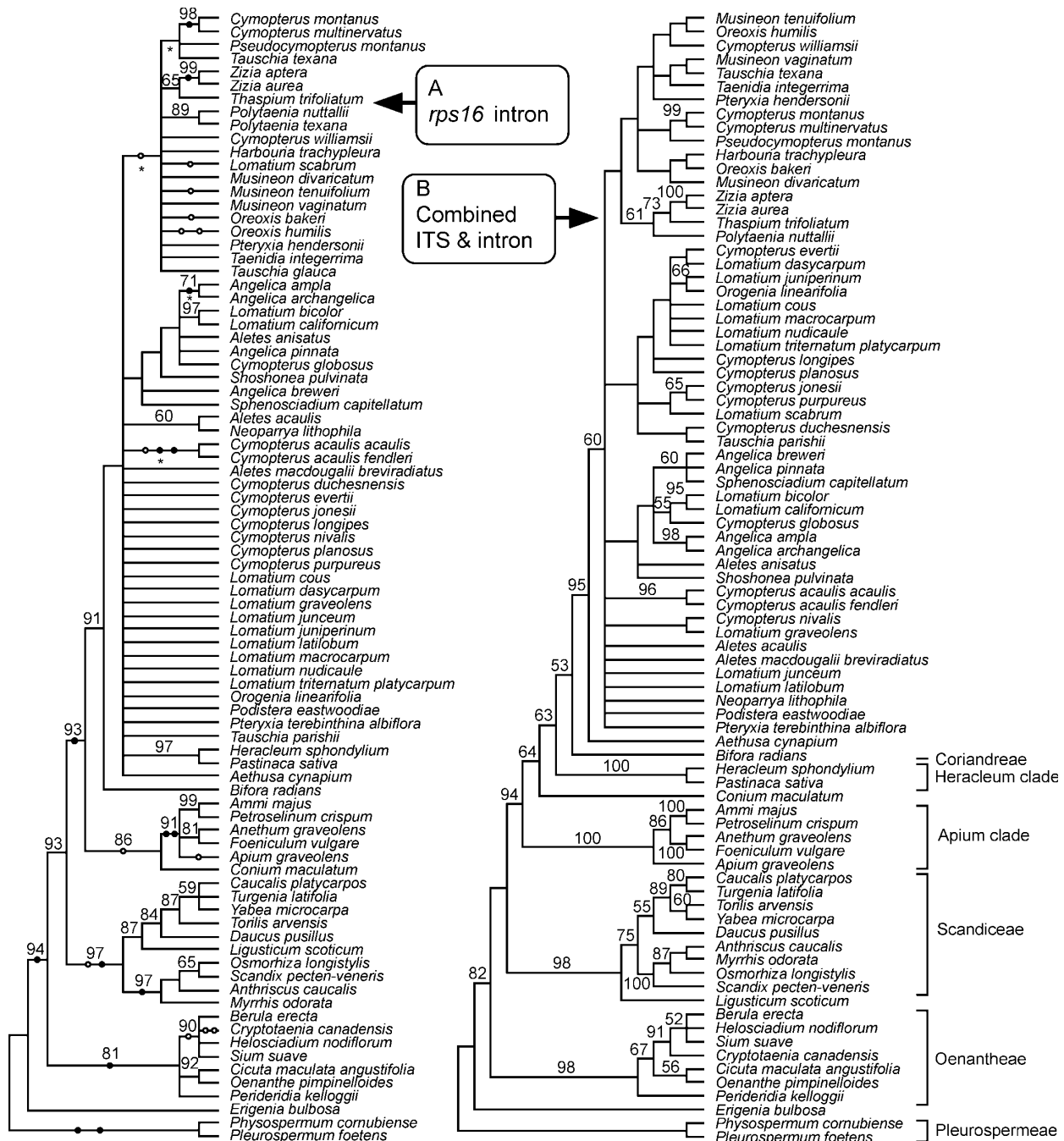
are found in just one major branch. Constraining *Cymopterus* to monophyly resulted in trees 24 steps longer than those produced without the constraint; trees of similar length resulted when *Lomatium* was constrained as monophyletic. *Aletes*, *Musineon*, *Oreoxis*, *Pteryxia*, and *Tauschia* are also each not monophyletic. *Angelica* and *Sphenosciadium* form a clade alongside the same five species as in the separate analysis of intron data. Other noteworthy results include the close association of *Zizia*, *Thaspium*, and *Polytaenia*; the sister relationship between *Aethusa cynapium* and the large polytomous clade of western NA taxa; and the highly resolved and strongly supported relationships among the basal elements of the phylogeny.

### *trnF-trnL-trnT*

Length variation of the entire *trnF-L-T* region for the 27 species studied ranged from 1693 to 1816 bp, and alignment of these data resulted in a matrix of 1884 positions. Forty-six positions, representing tracts of poly-A's or insertions of dubious homology in two or more taxa, were eliminated. Characteristics of these unambiguously aligned data, including partitions representing the two intergenic spacers and the *trnL* intron, are presented in Table 4. No length variation was exhibited by the *trnL* exons (50 and 35 bp for the 3' and 5' exons, respectively) and from gene portions *trnF* and *trnT* (39 and 17 bp, respectively). The *trnL* intron ranged in size from 456 to 508 bp. The proportion of nucleotide differences ranged from identity to 2.5% for the *trnF-L* spacer and from identity to 2.9% for the *trnL-T* spacer; however, the *trnL* intron, intermediate in size between the two intergenic spacers, was more conserved, with a maximum pairwise sequence divergence of 1.6%. Overall, 42 positions were potentially informative, with over half of these coming from the *trnL-T* spacer. Twenty-seven gaps, ranging in length from 1 to 46 bp, were required to facilitate alignment; these represented 15 insertions (1–17 bp) and 12 deletions (2–46 bp) relative to the *Angelica archangelica* sequence. Seven of these gaps were potentially informative for parsimony analysis (size range 2–40 bp; representing two insertions and five deletions).

Maximum parsimony analysis of the entire *trnF-L-T* region, with gap states treated as missing, resulted in 220 minimal length trees, each of 145 steps (see Table 4 for measures of character fit); the strict consensus of these trees is shown in Fig. 4A. *Angelica archangelica* was used to root these trees, as suggested by the local analyses of ITS data (Figs. 1B, 2A, and 2B). The strict consensus reveals three major clades, two of which are largely unresolved. One major clade (with 91% bootstrap support) consists exclusively of *Lomatium* species. *Cymopterus* and *Pteryxia* are each divided between the two remaining major clades. Additionally, *Harbouria*, *Musineon*, *Thaspium*, and *Zizia* are placed in one clade (with 73% bootstrap support), and *Aletes*, *Lomatium*, *Neoparrya*, *Podistera*, and *Shoshonea* occur in the other (with 82% bootstrap support). The latter is sister to the *Lomatium* clade. *Cymopterus*, *Lomatium*, and *Pteryxia* are each not monophyletic, and the results are equivocal in establishing the monophyly of *Musineon* and *Zizia*. Phylogenetic analyses of the three *trnF-L-T* data partitions yielded trees (not shown) highly consistent with respect to their major groups, and results of a partition

**Fig. 3A.** Strict consensus of 20 000 minimal length 474-step trees derived from equally weighted maximum parsimony analysis of 85 cpDNA *rps16* intron and 3' exon sequences plus 19 binary-scored alignment gaps, with gap states treated as missing data (CIs = 0.6983 and 0.5600, with and without uninformative characters, respectively; RI = 0.8281; RC = 0.5783). Numbers at nodes are bootstrap estimates for 100 000 replicate analyses using "fast" stepwise-addition; values  $\leq 50\%$  are not indicated. The positions of all state changes for the 19 informative gaps are indicated: solid circles indicate nonhomoplastic changes; open circles indicate homoplastic changes. Asterisks indicate branches that collapse when the 19 informative gaps are excluded and the analysis rerun (tree length = 447 steps; CIs = 0.6980 and 0.5470, with and without uninformative characters, respectively; RI = 0.8183; RC = 0.5712). **Fig. 3B.** Strict consensus of 20 000 minimal length 1907-step trees derived from equally weighted maximum parsimony analysis of combined ITS and *rps16* intron and 3' exon data (1289 unambiguously aligned positions and 19 informative gaps) for 83 taxa (CIs = 0.4803 and 0.4059, with and without uninformative characters, respectively; RI = 0.6875; RC = 3302). Treating gap states as either missing data or a fifth base resulted in identical topologies. Numbers at nodes are bootstrap estimates for 100 000 replicate analyses using "fast" stepwise-addition; values  $\leq 50\%$  are not indicated. Brackets indicate major clades of Apioideae (Downie et al. 2001). Complete taxon names are provided in Table 2.



**Table 4.** Characteristics of the *trnF-L-T*, ITS, and *rps16* intron regions, separately and combined, used in the maximum parsimony analyses of 27 species of western North American Apiaceae subfamily Apioidae.

	<i>trnF-L-T</i>			ITS	<i>rps16</i> intron	Combined ( <i>trnF-L-T</i> , ITS, and <i>rps16</i> intron)	
	Entire region	<i>trnF-L</i> intergenic spacer	<i>trnL-T</i> intergenic spacer				
No. of total characters	1884	382	511	850	444	997	3325
Length variation (bp)	1693–1816	330–368	456–508	733–809	437–439	911–976	3096–3229
No. of eliminated characters	46	15	0	31	7	20	73
No. of constant characters	1721	343	487	753	321	902	2944
No. of autapomorphic characters	75	18	15	39	74	41	190
No. of informative characters	42	6	9	27	42	34	118
% informative characters <sup>a</sup>	2.3	1.6	1.8	3.3	9.6	3.5	3.6
% divergence (range)	0.1–1.7	0–2.5	0–1.6	0–2.9	0.2–6.7	0.2–3.2	0.3–2.6
No. of unambiguous gaps	27	8	6	13	6	13	46
No. of unambiguous gaps parsimony informative	7	4	0	3	3	4	14
No. of minimal length trees	220	4	27	30	> 20 000	6	16
Length of shortest trees	145	28	27	81	196	94	478
Consistency index <sup>b</sup>	0.6769	0.8571	0.7500	0.7250	0.4955	0.6604	0.4926
Retention index	0.8727	0.9565	0.9000	0.9018	0.5912	0.8583	0.6783
Rescaled consistency index	0.7463	0.9224	0.8000	0.7793	0.4223	0.6939	0.4825

<sup>a</sup>No. of informative characters / (no. of total characters – no. of eliminated characters).

<sup>b</sup>Excluding uninformative characters.

homogeneity test showed that these data sets do not yield significantly different phylogenetic estimates. Greatest resolution of relationships was obtained with *trnL-T* data, given its higher number of informative characters. Poorest resolution was achieved using *trnL* intron data, with only four clades resolved within a large, basal polytomy.

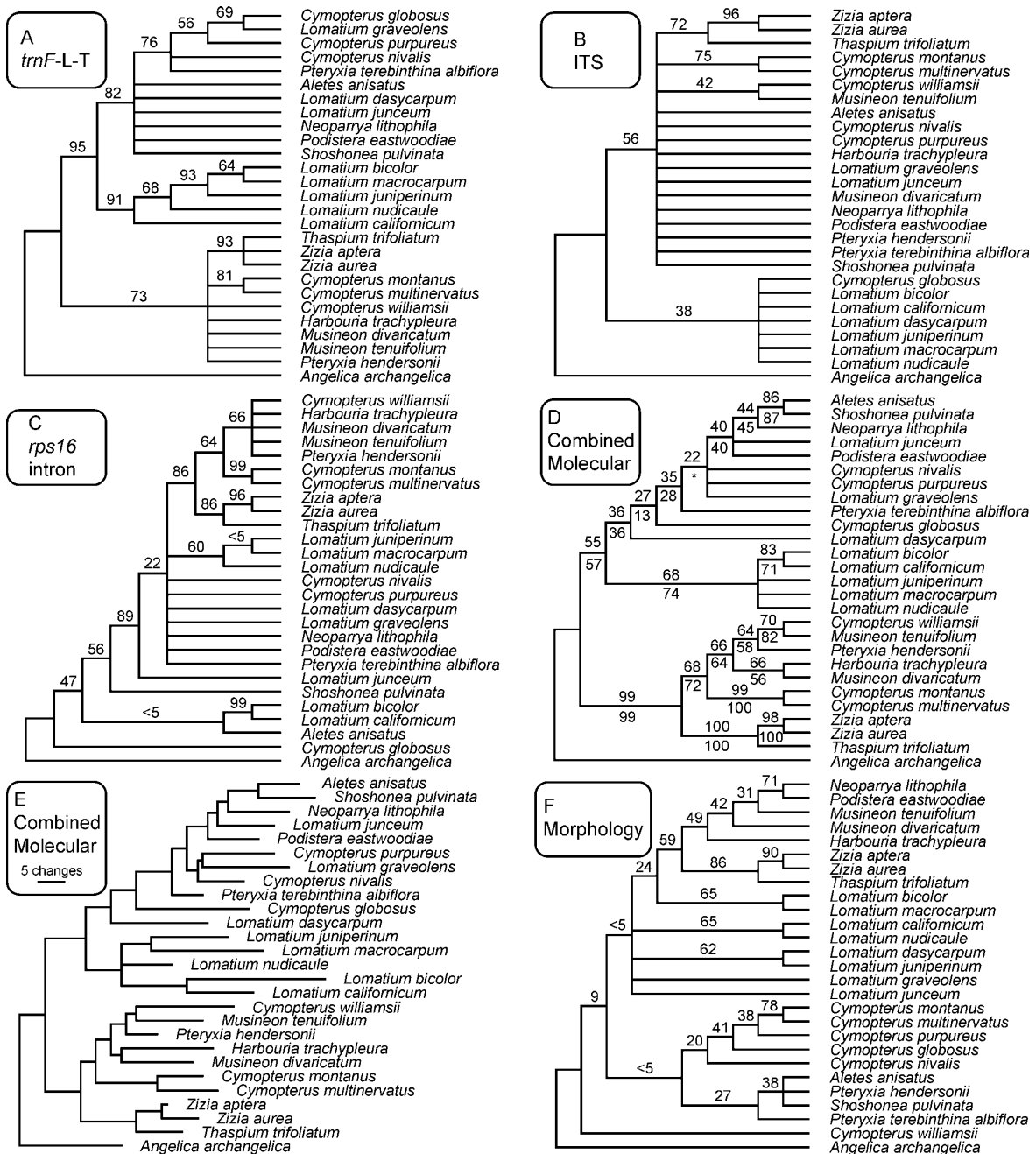
#### Comparative analysis of molecular data

The *trnF-L-T* results were compared to those obtained using ITS and *rps16* intron data for the same set of 27 taxa (Table 4). The proportion of nucleotide differences in the ITS partition was two to three times higher than either the *trnF-L-T* or intron partition, and relative to its size the ITS region contributed the greatest percentage of informative characters to the analysis (9.6%). The strict consensus trees resulting from separate analyses of these molecular data are shown in Figs. 4A–4C. Phylogenetic resolution within the ITS tree (Fig. 4B) is poor, with all clades but one (*Zizia aptera* + *Zizia aurea*, with 96% bootstrap value) supported weakly. Somewhat better resolution is achieved in the *rps16* intron tree (Fig. 4C), but several of its basal branches are also very weakly supported. The *trnF-L-T* tree (Fig. 4A) offers a comparable level of resolution to that of intron tree, but with generally higher bootstrap values. Despite a four-fold greater size, the entire *trnF-L-T* region yielded almost exactly the same numbers of autapomorphic and potentially informative characters as did the ITS region, yet the ITS tree was less resolved, possessed lower consistency index (CI), retention index (RI), and rescaled consistency (RC) values, and showed lower bootstrap support overall than did those trees derived from *trnF-L-T* (or intron) data.

Visual inspection of the trees derived from these three data partitions indicates discordance among them, largely attributable to poorly supported nodes, and results of a parti-

tion homogeneity test indicate significant incongruence. However, by collapsing those branches with bootstrap values < 80%, the trees become highly consistent with respect to their major groupings. Some disagreement persists between the *trnF-L-T* and *rps16* intron trees, but since these loci are both found on the chloroplast genome and are inherited as a single linkage group, the differences seen are not likely the result of, for example, hybridization and (or) introgression, but rather weaknesses of the data themselves. Maximum parsimony analysis of the combined data (using 118 potentially informative characters and treating gap states as missing) resulted in 16 minimal length trees, each of 478 steps; their strict consensus, with accompanying bootstrap support, is shown in Fig. 4D. Bootstrap estimates ranged between 22 and 100%, with 6 of 19 nodes supported by values > 80%. A similar tree was obtained (not shown) when 14 informative gaps were included, with only one node collapsing upon addition of these gap data. Seven gaps are synapomorphic, and support relationships based on nucleotide substitutions alone. The remaining gaps each required two to three steps to explain their distribution across all minimal length trees, as determined by MacClade. The inclusion of gaps did little to increase resolution or bolster bootstrap support. A single, arbitrarily selected, maximally parsimonious tree (Fig. 4E) illustrates that most character state changes occur at the tips of the branches, with many internal branches of short length. Repeating the analysis with gap states treated as a fifth base resulted in a consensus tree of similar topology to that when gaps were treated as missing, with only minor shuffling of the most distal branches in the tree. Compared to the results of the partitioned analyses, consideration of combined molecular data yielded a strict consensus tree of greatest resolution. Three major clades are recognized, in which the composition of each is identical to

**Fig. 4.** Trees resulting from equally-weighted maximum parsimony analyses of (A) *trnF-L-T*, (B) ITS, (C) *rps16* intron, (D and E) combined molecular, and (F) morphological data sets for 27 members of Apiaceae subfamily Apioideae. Trees A–D and F represent strict consensus trees; tree E represents one of 16 minimal length trees. Measures of character fit for the molecular data sets are presented in Table 4; those for the morphological data set are presented in the text. Complete taxon names are provided in Table 2. Bootstrap values are indicated at the nodes. The asterisk in tree D indicates the one branch that collapses when the 14 scored gaps are included in the analysis (tree length = 502 steps; CIs = 0.7052 and 0.5000, with and without uninformative characters, respectively; RI = 0.6831; RC = 0.4817). Bootstrap values, for analyses without and with scored informative gaps, are presented above and below the branches, respectively.



that inferred by the separate analysis of *trnF-L-T* data. Once more, *Cymopterus*, *Lomatium*, *Musineon*, and *Pteryxia* are each not monophyletic. *Cymopterus* is highly polyphyletic, and constraining its six species to monophyly resulted in trees 25 steps longer (excluding scored gaps) than those without the constraint. Forcing each of *Lomatium* (eight species), *Musineon* (two species), and *Pteryxia* (two species) to monophyly resulted in trees seven, four, and 20 steps longer, respectively.

### Morphology

The characters and states considered in the cladistic analysis of morphological data are presented in Table 5; the data matrix is presented in Table 6. Cladistic analysis of 25 morphological characters, using fractional weights, revealed 19 most parsimonious trees each of 49.91667 steps (CI = 0.5008; RI = 0.6843; RC = 0.3427). The strict consensus of these trees (Fig. 4F) shows much resolution, but only two clades, *Zizia aptera* + *Zizia aurea* and *Zizia* + *Thaspium*, are well supported, with bootstrap values  $\geq 86\%$ . Of the five genera represented by at least two species, only *Zizia* is monophyletic. *Cymopterus* is monophyletic upon the exclusion of *Cymopterus williamsii*; this species is unique among the six members of the genus examined in that its dorsal mericarp ribs are prominent, rounded, and corky rather than winged and its fruits are terete (to subterete) in outline rather than compressed dorsally. *Lomatium* is paraphyletic, albeit with very weak bootstrap support. Constraining *Lomatium* to monophyly requires trees of 50.16667 steps, whereas *Cymopterus*, *Musineon*, and *Pteryxia* are each monophyletic at 50.41667 steps. In trees of 51.6667 steps, all genera occur as monophyletic. The results of the analysis of morphological data yield trees that are not at all congruent to those achieved through separate or combined analysis of molecular data, nor are the relationships proposed in agreement with any historical or contemporary treatment of the group.

Across all 19 minimal length trees, seven characters occur without homoplasy (Nos. 6, 7, 10, 13, 15, 22, and 24; CI = 1.00; Table 5); however, only two of these (Nos. 22, terete seed compression, and 24, constricted commissure) support clades consisting of three or more species: the clade of *Neoparrya*, *Podistera*, *Musineon*, *Harbouria*, *Zizia*, and *Thaspium*; and the clade consisting of only the first four of these genera. Filiform fruit ribs (No. 18; CI = 0.500) occur in all taxa from *Neoparrya* through *Lomatium junceum*, but are absent in *Harbouria* (where the ribs are instead obtuse and corky). The presence of sepals  $> 0.6$  mm (No. 14; CI = 0.500) occurs in the *Aletes anisatus* – *Pteryxia terebinthina* clade, as well as in *Neoparrya* and *Podistera*. Dorsally compressed fruits (No. 21; CI = 0.500) bearing conspicuous dorsal and marginal wings (No. 16; CI = 0.400) and the absence of a carpophore (No. 23; CI = 0.400) are each homoplastic. Characters exhibiting the highest levels of homoplasy include the presence of a conspicuously sheathing leaf (No. 8; CI = 0.250), the occurrence and type of peduncle pubescence (No. 5; CI = 0.286), the presence of a pseudoscape and rosette of leaves (No. 4; CI = 0.333), and habit (No. 1; CI = 0.333). A prominent conical stylopodium is absent in all taxa but *Podistera* and the outgroup *Angelica*. No unique character supports the monophyly of *Cymopterus*, either with or without *Cymopterus williamsii*.

## Discussion

### Historical accounts of taxonomic confusion

Torrey and Gray (1840) provided the first treatment of *Cymopterus*, recognizing a heterogeneous assemblage of eight species in four sections, with the names of three of these sections based on unpublished genera of Nuttall: *Leptocnemia* Nutt. ex Torr. & A. Gray, *Phellopterus* Nutt. ex Torr. & A. Gray, and *Pteryxia* Nutt. ex Torr. & A. Gray. These sections differed by subtleties in calyx teeth development, pericarp composition, the number of vittae in the commissure, and persistence of a carpophore. Coulter and Rose (1888), summarizing the accounts of the previous four decades in their *Revision of North American Umbelliferae*, recognized 13 species in *Cymopterus* and erected the genera *Coloptera* J.M. Coult. & Rose and *Pseudocymopterus* for plants either similar to or previously referable to *Cymopterus*. These genera were distinguished from *Cymopterus* by their strongly dorsally compressed fruits with broad, thick (and occasionally corky), lateral wings. *Cymopterus* was restricted to those plants with five generally broad, thin, and equal wings and fruits not at all dorsally flattened. *Oreoxis*, *Podistera*, and *Phellopterus* Benth. (= *Glehnia*), each containing species that had previously been described under *Cymopterus*, and the monotypic *Aletes* and *Harbouria*, were also listed in their revision. *Lomatium*, comprising species then referred to the Eurasiatic genus *Peucedanum* L., was separated from *Cymopterus* and allies by having fruits with narrowly winged or wingless dorsal ribs and broad, thin lateral wings.

Twelve years later and during a time of much botanical exploration in NA, Coulter and Rose (1900) reduced *Coloptera* to synonymy under *Cymopterus* and transferred the NA species of *Peucedanum* to *Lomatium*. Eight species were recognized in *Cymopterus*, but its composition was vastly different from that they had circumscribed earlier. Many previously described *Cymopterus* species were instead placed in *Aulospermum*, *Glehnia*, *Oreoxis*, *Phellopterus*, *Rhysopterus*, *Pteryxia*, *Podistera*, and *Pseudocymopterus*. Characters such as the degree and direction of fruit compression, the shape of the endosperm, and features of the carpophore, vittae and mericarp ribs were again stressed, in addition to leaf habit. Great variation was evident in *Cymopterus* with regard to the development of its dorsal wings, with stark differences apparent even on the same plant. Subsequently, Jones (1908) reduced the genera *Aulospermum*, *Oreoxis*, *Phellopterus*, *Rhysopterus*, *Pteryxia*, and *Pseudocymopterus* to sectional ranks under *Cymopterus*, recognizing seven sections, 34 species, and 12 varieties within the genus. The composition of each section, however, was not always equivalent to its generic counterpart (for instance, species of *Aulospermum* were placed into three sections). Species bridging the sections were numerous, leading Jones to comment that it was futile to divide these species into separate genera.

Mathias (1930) followed the treatment of Coulter and Rose (1900) in her monograph of *Cymopterus* and allies by treating *Aulospermum*, *Glehnia*, *Oreoxis*, *Phellopterus*, *Rhysopterus*, *Pteryxia*, and *Pseudocymopterus* as generically distinct. Characters distinguishing the genera included the orientation of fruit compression, the occurrence and relative

**Table 5.** Morphological characters and states used in the phylogenetic analysis of western North American Apiaceae subfamily Apioideae.

Character no.	Character	States
1	Habit	0 = caulescent; 1 = subcaulescent to subacaulescent; 2 = acaulescent
2	Habit	0 = stems one-few, tufted; 1 = stems cushion-forming
3	Roots	0 = tap, slender; 1 = tap, thickened; 2 = tap, globose; 3 = tap, branched woody caudex; 4 = fibrous, fascicled
4	Scape	0 = no pseudoscape or rosette of leaves; 1 = pseudoscape and rosette present
5	Peduncle	0 = glabrous; 1 = generally pubescent; 2 = hirtellous/scabrous at summit
6	Peduncle	0 = not swollen at summit; 1 = swollen at summit
7	Leaf margin	0 = variously toothed or entire; 1 = evenly serrate or dentate
8	Sheath	0 = not or slightly ampliate; 1 = conspicuously sheathing
9	Bracts	0 = present; 1 = absent
10	Bractlets	0 = present; 1 = absent
11	Bractlets	0 = herbaceous; 1 = herbaceous with thin scarios margins; 2 = mostly scarios
12	Flower color	0 = white; 1 = purplish; 2 = yellow; 3 = greenish
13	Central flowers	0 = pedicellate; 1 = sessile
14	Calyx in fruit	0 = >0.6 mm; 1 = <0.6 mm
15	Style in fruit	0 = more or less erect; 1 = widely spreading
16	Fruit ribs	0 = all ribs winged; 1 = lateral ribs winged only; 2 = none winged
17	Fruit wings	0 = chartaceous; 1 = thick, corky
18	Fruit ribs	0 = filiform; 1 = rounded, corky
19	Fruit apex	0 = normal; 1 = constricted
20	Fruit surface	0 = glabrous; 1 = pubescent; 2 = granulose; 3 = scabrose
21	Fruit compression	0 = dorsally compressed; 1 = terete; 2 = laterally compressed
22	Seed compression	0 = dorsally compressed; 1 = terete
23	Carpophore	0 = present; 1 = present, falling with mericarp; 2 = absent
24	Commissure	0 = not constricted; 1 = constricted
25	Stylopodium	0 = absent; 1 = present

development of lateral and (or) dorsal wings, the shape of the wing in cross-section, and features of the involucre and involucl. She included nine species in *Cymopterus* (Table 1). Mathias and Constance (1944–1945) subsequently placed *Phellopterus* and *Aulospermum* into synonymy under *Cymopterus*, recognizing 32 species within the genus (Table 1). *Pseudocymopterus* was considered monotypic, with other species previously referable to this genus transferred to *Cymopterus* or *Pteryxia*. The lack of substantial distinguishing characters separating genera — for example, *Pteryxia* differs from *Cymopterus* mainly in its development of conspicuous calyx teeth — prompted Cronquist (1961) to expand the limits of *Cymopterus* to include *Pteryxia* and *Pseudocymopterus*, as well as other segregates included by Mathias and Constance (1944–1945). With the additional transfer of *Oreoxis* to *Cymopterus*, this system was maintained by Cronquist (1997) in his treatment of the group for *Intermountain Flora* (Table 1).

The genus *Aletes*, as initially described (Coulter and Rose 1888), was characterized as having a single large vitta in the broad intervals between its filiform ribs, two vittae on the commissural side of the fruit, and a small one in each rib. Based on the presence of a single vitta in most of its fruit intervals, Theobald et al. (1963) transferred *Pteryxia anisata* (A. Gray) Mathias & Constance into *Aletes*. Weber expanded the concept of *Aletes* by permitting considerable variation in flower color, the number, size, and disposition of vittae, and the compression and development of the lateral and dorsal wings of the mericarps, such that species of

*Cymopterus*, *Lomatium*, *Pteryxia*, and *Neoparrya* were all brought into the genus (Weber 1984; Weber and Wittmann 1992; Table 1). Emphasizing a similarity in acaulescent habit, Weber (1991) also placed *Musineon tenuifolium* in *Aletes*. Cronquist (1997) has reported that the distinction between some species of *Aletes* and *Musineon* is nothing more than the number of oil tubes in the intervals between the ribs (one in *Aletes*, and two or more in *Musineon*) and, as such, submerged *Aletes* into *Musineon*.

#### **Polyphyly of *Cymopterus* and their relationships among the endemic perennial genera of Apiaceae (north of Mexico)**

Contemporary treatments of *Cymopterus* include some 35–45 species (Kartesz 1994; Cronquist 1997), with no formally recognized infrageneric taxa. The results of phylogenetic analyses of molecular and morphological data indicate that *Cymopterus*, sensu Kartesz or Cronquist, is clearly polyphyletic, and in the molecular analyses, trees of much greater length than those most parsimonious are required to invoke monophyly of the genus. Moreover, no unique morphological synapomorphy supports the monophyly of *Cymopterus*, and the characters used traditionally to delimit the genus show overlapping patterns of variation with those of many other endemic, perennial apioid umbellifers of western NA. *Cymopterus* is inextricably linked with *Aletes*, *Harbouria*, *Lomatium*, *Musineon*, *Neoparrya*, *Oreoxis*, *Orogenia*, *Podistera*, *Pseudocymopterus*, *Pteryxia*, *Shoshonea*, and *Tauschia*. As such, the genera *Lomatium*, *Musineon*, and *Pteryxia* (and perhaps *Aletes*, *Oreoxis*, and



**Table 6.** Matrix of morphological data.

Taxon	Morphological characters					
	1–5	6–10	11–15	16–20	21–25	
<i>Aletes anisatus</i>	2 0000	00010	0 2001	10100	00000	
<i>Angelica archangelica</i>	0 0102	00110	0 0011	11100	00001	
<i>Cymopterus globosus</i>	{12}0110	00010	1 0011	01?00	00200	
<i>Cymopterus montanus</i>	{12}0112	00000	2{01}011	00?00	00000	
<i>Cymopterus multinervatus</i>	{12}0110	00000	2 1011	00?00	00200	
<i>Cymopterus nivalis</i>	2 0300	00010	1 0011	00?00	00000	
<i>Cymopterus purpureus</i>	{12}0110	00010	1{12}011	00?00	00000	
<i>Cymopterus williamsii</i>	2 0300	00010	1 2011	11100	10200	
<i>Harbouria trachypleura</i>	0 0302	00010	1 2011	2?102	21010	
<i>Lomatium bicolor</i>	1 0202	00010	1 2011	10010	00000	
<i>Lomatium californicum</i>	0 0100	10111	? 2011	10000	00000	
<i>Lomatium dasycarpum</i>	{12}0001	00110	1 3011	10001	00000	
<i>Lomatium graveolens</i>	2 0300	00010	1 2011	10000	00000	
<i>Lomatium junceum</i>	2 1310	00110	1 2011	10000	00000	
<i>Lomatium juniperinum</i>	{12}0001	00110	1 2011	10000	00000	
<i>Lomatium macrocarpum</i>	1 0101	00010	1{01}011	10010	00000	
<i>Lomatium nudicaule</i>	2 0100	10011	? 2011	10000	00000	
<i>Musineon divaricatum</i>	0 0111	00010	1 2011	2?012	21010	
<i>Musineon tenuifolium</i>	2 0302	00010	1 2011	2?012	21010	
<i>Neoparrya lithophila</i>	2 0300	00010	1 2001	2?010	21010	
<i>Podistera eastwoodiae</i>	2 0100	00010	0 3001	2?010	21011	
<i>Pteryxia hendersonii</i>	2 0300	00010	0 2001	00?00	00000	
<i>Pteryxia terebinthina</i>	{01}0000	00110	1 2001	00?00	00000	
<i>Shoshonea pulvinata</i>	2 1300	00010	0 2001	2?103	10100	
<i>Thaspium trifoliatum</i>	0 0402	01010	1 1010	00?00	11200	
<i>Zizia aptera</i>	0 0402	01000	1 2110	2?000	21000	
<i>Zizia aurea</i>	0 0402	01000	1 2110	2?000	21000	

**Note:** Characters and states are described in Table 5. Question marks denote inapplicable data; polymorphisms are scored in parentheses.

*Tauschia* as well) are each not monophyletic either. Affinity also extends to four other indigenous perennial genera of primarily central to eastern North American distribution (i.e., *Polytaenia*, *Taenidia* (including *Pseudotaenidia*; Cronquist 1982), *Thaspium*, and *Zizia*), and while it is evident that all of these NA genera are undoubtedly closely related, our results suggest an evolutionary history of the group much more complicated than previously considered. The species of *Cymopterus* examined herein permeate many of the clades resolved in the trees derived from molecular data, and thus further study of all of these taxa (which should include a re-evaluation of the generic limits of many) is necessary to properly circumscribe *Cymopterus* and to ascertain its phylogenetic position within the group.

#### Monophyly of the endemic perennial apioid genera of NA

The restricted distribution of many of our indigenous apioid genera to dry habitats in western NA, their shared life history and general habit, and overlapping patterns of fruit variation suggest that this group of umbellifers (with the addition of *Polytaenia*, *Taenidia*, *Thaspium*, and *Zizia*) is monophyletic. An obsolete stylopodium in all genera save *Podistera* (where the stylopodium is well-developed (conical), as it is in most other umbellifers (Mathias and Constance 1944–1945)) is a synapomorphy adding credence to this hypothesis. Further support for the monophyly of the

group comes from the shared presence of a protogynous breeding system, atypical in a family where floral protandry prevails (Lindsey and Bell 1980; Lindsey 1982; Barrie and Schlessman 1987; Schlessman et al. 1990; Schlessman and Graceffa 2002). In contrast, the NA representatives of the perennial circumboreal genera *Angelica*, *Seseli* L., *Selinum* L., and *Peucedanum* all have a breeding system that is protandrous (Barrie and Schlessman 1987). Other differences between the protogynous and protandrous groups of NA Apiaceae include flowering time, habitat preference, nectary morphology, and patterns of variation in sex expression (Schlessman and Barrie 2003). Many species of *Cymopterus*, *Lomatium*, and *Pteryxia* have also been reported as hosts for a morphologically distinct species group of larvae of the holarctic moth genus *Depressaria*, often with a single species of *Depressaria* seemingly restricted to a single (or rarely few) species of *Cymopterus* or *Lomatium* (Clarke 1952; Hodges 1974; Thompson 1983; McKenna 2000). In western NA, there has been a striking radiation of Apiaceae-feeding *Depressaria*, and the host specificity of these insects, coupled with the rich diversity of substituted coumarins occurring in the host plants serving a defensive role (Murray et al. 1982), might imply an association consistent with reciprocal coevolutionary interactions (McKenna 2000; Berenbaum 2001) and, thus, monophyly of each of their interacting groups.

However, in the present study, the assumption of monophyly of these indigenous NA genera is confounded by the phylogenetic placements of the perennial circumboreal genus *Angelica* (with included *Sphenosciadium*) and members of the meso-American *Arracacia* group. (Protogyny has also been reported for *Myrrhidendron*; Webb 1984.) All of these taxa, including the examined NA endemics, occur within the *Angelica* and *Arracacia* clades of the apioid superclade, the latter a heterogeneous assemblage of both New and Old World genera (Downie et al. 2001). Included within this assemblage are the circumboreal genera *Seseli*, *Selinum*, and *Peucedanum*, whose distribution in NA is restricted to the eastern U.S.A. (Kartesz 1994), and prior analyses of this superclade using ITS and cpDNA sequences, albeit with very limited sampling of the NA endemic species, show little resolution of relationships among these taxa (Downie and Katz-Downie 1996; Downie et al. 1996, 1998, 2000b; Plunkett et al. 1996). Cladistic analysis of cpDNA restriction sites, however, does provide weak support for a monophyletic group of NA apioid taxa, but with the inclusion of the *Arracacia* clade (Plunkett and Downie 1999). Confirmation of monophyly of the endemic perennial apioid genera of NA must therefore await further study that includes additional representation of these and other Old World genera of circumboreal distribution.

The phylogenetic position of *Spermolepis* and *Ciclospermum* is not fully resolved. Both genera unite as a strongly supported clade, but only in the trees derived from analyses using maximum parsimony (with gap states treated as a fifth base; Fig. 2A) or maximum likelihood (Fig. 2B) do they fall outside of the large, polytomous clade of NA umbellifers. *Spermolepis* and *Ciclospermum* are taprooted annuals possessing threadlike to linear leaf segments and are widely distributed throughout the southern U.S.A., and other warm, temperate areas. Their placement away from the clade of perennial, endemic, apioid umbellifers is consistent with their unique life history and overall general habit. Their putative sister-group relationship to the latter, as seen in Fig. 2A, needs confirmation through further study with greater outgroup representation.

### Fruit characters as indicators of phylogeny

Our examination of relevant herbarium material, our observations of mature fruit cross-sections of nearly all species of *Cymopterus* and many related genera (see also Hartman 1983, 1985), and the results of the cladistic analysis of morphological data presented herein confirm that characters of the fruit can be quite variable and, thus, poor indicators of phylogeny. As examples, both *Cymopterus* and *Lomatium* have well-developed lateral wings. In most *Cymopterus* species, one or more (and often all three) of the dorsal ribs bear wings, with the dorsal wings often narrower than the lateral ones, whereas in *Lomatium*, the dorsal ribs are generally filiform and wingless or occasionally very narrowly winged. However, some *Cymopterus* lack dorsal wings. In *Cymopterus newberryi* (S. Watson) M.E. Jones and *Cymopterus megacephalus* M.E. Jones, the one or two wings on the dorsal surface of each mericarp vary from nearly as large as the lateral ones to often narrower and irregularly developed, or are more frequently obsolete. Fruits with scarcely developed or obsolete dorsal wings are also seen in *Cymopterus*

*deserticola* Brandegee, *Cymopterus douglassii* R.L. Hartm. & Constance, *Cymopterus ripleyi* Barneby, and *Cymopterus williamsii*, as well as in some species of *Pteryxia* (e.g., *Pteryxia terebinthina* and *Pteryxia hendersonii*) and *Pseudocymopterus* (e.g., *Pseudocymopterus montanus*), and all show similarities to fruits of typical *Lomatium*. Throughout most of its range, *Cymopterus longipes* has saliently winged fruits, but in populations from southwestern Wyoming and adjacent Utah the dorsal wings are reduced to narrow ridges (Hartman and Constance 1985). These latter populations have been referred to as *Cymopterus lapidosus* (M.E. Jones) M.E. Jones (Hartman 1986), and their fruits superficially resemble those of some species of *Lomatium*. In *Cymopterus corrugatus* M.E. Jones, the fruits have strongly corrugated narrow wings when young, but at maturity the ribs are merely raised and thickened, with or without an irregular vestige of a wing (Hitchcock and Cronquist 1961). Thus, the distinction among some species of *Cymopterus*, *Lomatium*, *Pteryxia*, and *Pseudocymopterus* based on characters of the fruit wing is subject to failure, and their differentiation is not improved upon consideration of other morphological data.

The genus *Pseudocymopterus* has been described as “one of the most complex situations in the family” (Mathias 1930), reflecting its great morphological variability and uncertain generic position, with the only character separating it from most species of *Cymopterus* being the characteristic short stiff pubescence at the top of the peduncle (Cronquist 1997). Populations of *Pseudocymopterus montanus* (= *Cymopterus lemmonii* (J.M. Coult. & Rose) Dorn, *Pseudocymopterus tidestromii* J.M. Coult. & Rose) from higher elevations throughout much of Utah have fruits with wings that are equally well-developed. Conversely, populations elsewhere exhibit fruits with dorsal wings reduced to low ridges (New Mexico, Colorado, Wyoming) or are completely absent (Arizona; Hartman and Constance 1985). In other words, populations of *Pseudocymopterus montanus* from Utah are indistinguishable from *Cymopterus* and those from Arizona look like *Lomatium* (and, thus, have been described as *Lomatium lemmonii* (J.M. Coult. & Rose) J.M. Coult. & Rose). Additional study of this polymorphic genus is currently being carried out (Sun et al. 2000; F.-J. Sun, data not included).

We observed that other characters of the fruit are also highly variable. While definite laterally or dorsally compressed fruits are readily distinguishable in *Cymopterus*, there are numerous intermediate stages such that “the interpretation [of orientation of fruit compression] depends on the individuals point of view” (Mathias 1930). Fruit cross-sections reveal a complex series, from fruits that are subterete to somewhat compressed laterally (e.g., *Cymopterus davisii* R.L. Hartm., *Cymopterus douglassii*, *Cymopterus jonesii*, *Cymopterus longipes*, *Cymopterus nivalis*, and *Cymopterus panamintensis*) to fruits that are markedly compressed dorsally (e.g., *Cymopterus deserticola* and *Cymopterus newberryi*). In *Cymopterus*, loss of the carpophore (through adnation of its halves to the mericarps) has been independently achieved several times. Its absence has been reported from nearly half the species in the genus (Hartman and Constance 1985; Cronquist 1997; Hartman 2000), and in our cladistic analysis of morphological data at

least two losses and one reversal must be postulated to explain the distribution of this character over the six species of *Cymopterus* examined. The number, size, and position of vittae may also be quite variable, sometimes even within a genus (Mathias 1930). *Aletes* is characterized by usually a single vitta in the interval between the ribs, whereas most other genera have between two and six vittae per interval lying in a uniform row around the seed. In *Cymopterus*, the number of vittae in the intervals varies from 3 to 5, but in some species there may be only one. However, in *Neoparrya*, the oil tubes are numerous and are scattered throughout the pericarp. Some or all species of *Aletes*, *Musineon*, *Neoparrya*, *Oreoxis*, *Podistera*, and *Shoshonea* have fruits that are either subterete or slightly compressed laterally. With the exception of *Oreoxis*, with its very thick, corky-winged ribs, the aforementioned genera all have fruits that are not obviously winged and instead have ribs that may or may not be well developed. As examples, *Musineon* and *Shoshonea* have conspicuously ribbed fruits, *Aletes* and *Podistera* have ribs that may be inconspicuous or prominent and variously corky-winged, whereas *Neoparrya* shows practically no development of ribs at all.

The variation exhibited by fruit morphology and anatomy among these western NA umbellifers severely limits their utility in delimiting genera unambiguously. The repeated occurrences of dorsal flattening and wing formation in *Cymopterus* and its allies are undoubtedly adaptations for various modes of seed dispersal (Theobald 1971; Heywood 1986) and, therefore, are susceptible to convergence. Patterns of development leading to similar dorsal flattening and gross morphology of umbellifer fruits can also be quite different (Theobald 1971). In contrast, putative sister species which are otherwise indistinguishable (*Taenidia integerrima* and *Taenidia montana* (Mack.) Cronquist) can differ substantially in their orientation of fruit compression (Cronquist 1982). The number and arrangement of resin-filled vittae (containing active compounds that are toxic to insects; Berenbaum 1981) and the presence of thick, corky ribs may confer protection to the endosperm (Spalik et al. 2001a), and it is not unrealistic to presume that these characters too may be susceptible to homoplasy. Interspecific hybridization may also obscure generic limits, but such hybridization among NA umbellifers is rare (Mathias and Constance 1959; Brehm and French 1966; Schlessman 1984; Cronquist 1997), as it is in the family in general (Bell and Constance 1957; Heywood 1982). Postmating isolating mechanisms in *Lomatium*, *Thaspium*, and *Zizia* are strong (Lindsey 1982; Schlessman 1984), and polyploids are rarely found, with the few reported cases known for *Oreoxis alpina*, *Pteryxia terebinthina*, and some species of *Lomatium* (Bell and Constance 1957, 1960, 1966; Moore 1971; Crawford and Hartman 1972; Schlessman 1984).

In summary, our study confirms that fruit characters are of limited value for delimiting taxa and estimating phylogenetic relationships in this group of western NA umbellifers. Such a conclusion is not surprising, given the common dissatisfaction among systematists in using these characters to circumscribe higher-level taxa within the family (e.g., Heywood 1971; Theobald 1971; Davis 1972; Cronquist 1982). Indeed, the results of numerous molecular systematic investigations provide very little support for all but a few suprageneric taxa

erected on the basis of anatomical and morphological features of the mature fruit (summarized in Downie et al. 2001). In contrast, and unlike the results presented herein, fruit morphology may be quite useful at lower taxonomic levels. For example, in Apiaceae tribes Scandiceae and Oenantheae, whose members are also well represented in NA, the distribution of fruit characteristics is highly consistent with ITS-derived trees and cladistic analyses of both morphological and molecular data corroborate the monophyly of nearly every genus within these tribes (Spalik and Downie 2001; Spalik et al. 2001a; S. Downie, data not included). However, in other groups, such as the *Angelica* clade and the apioid superclade, many species-rich genera are polyphyletic (Downie et al. 2000b, 2000c; Spalik et al. 2001b). Additional study is required to define and delimit the various generic elements which have been confused with *Cymopterus*, and to circumscribe *Cymopterus* itself. Whether or not we will eventually find morphological synapomorphies delimiting each of these genera remains to be seen.

#### Phylogenetic utility of molecular data

Separate analyses of ITS, *rps16* intron, and *trnF-L-T* sequences failed to resolve relationships among the perennial, endemic genera of NA Apiaceae. Several clades were delimited in each of these analyses, but were not always reproduced by the different data sets, nor were many supported strongly. Data from the ITS region were most variable and yielded trees with the least resolution and highest homoplasy. Differential resolution between the plastid-derived *rps16* intron and *trnF-L-T* trees was apparent, largely attributable to poorly supported nodes. Greatest resolution of relationship was achieved by including all molecular data in a simultaneous analysis, yet divergence estimates were still low, approaching 2.6% of nucleotides, and very few nodes were supported by high bootstrap values. As additional molecular data become available, perhaps from a more rapidly-evolving locus, greater resolution of relationships may be achieved and regions of discordance, if any, more rigorously addressed.

The limited ability of these nuclear and organellar sequences to resolve relationships among the western NA apioid umbellifers might also reflect a real biological phenomenon — the rapid evolutionary radiation of this lineage. Such a hypothesis is consistent with trees exhibiting short internal branches and (or) a large basal polytomy comprising several distinct lineages (Futuyma 1997). Many species of western NA umbellifers are narrowly distributed and have strict edaphic requirements (Mathias 1930), and all exhibit low levels of sequence divergence. This, coupled with the prevalent and pronounced intergradation of morphological characters making species and generic delimitation difficult, suggests a recent origin and rapid diversification of these genera. This pattern of rapid radiation has been proposed for *Lomatium* (Soltis et al. 1995; Hardig and Soltis 1999), and has been suggested for other genera of western NA distribution (e.g., Hershkovitz and Zimmer 2000). Given the intercalation of members of *Lomatium* among other western NA Apiaceae, this pattern may very well be prevalent for the entire group. However, to evaluate the hypothesis of recent, rapid diversification, it is necessary to compare the degree of

evolutionary divergence within a clade with the degree of divergence within its sister clade (Jensen 1990). Pending further study, information on a definitive sister group is lacking (although the data presented herein suggest that *Angelica* may be a likely candidate). Clearly, a more resolved phylogeny confirming sister group relationships is in order before hypotheses of evolutionary success can be tested.

We are continuing our systematic investigation of the perennial endemic genera of western NA with the goal of uncovering morphological synapomorphies useful for generic determination. If such synapomorphies cannot be identified, we would have to accept that the task of reclassifying this group is to be accomplished on the basis of molecular evidence rather than on traditional taxonomic data. If future studies support the conclusions presented herein, and if further resolution of relationships can be achieved, radical changes to the prevailing classification of western NA Apioideae will be required.

## Acknowledgements

The authors thank Christine Desfeux, Jonathan Luttrell, and Erica Rogers for assistance in the laboratory; Lincoln Constance and Tim Chumley for providing leaf material; and Mark Schlessman and two anonymous reviewers for comments on the manuscript. This work was supported by National Science Foundation grants DEB 9407712 and DEB 0089452.

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