

# Phylogenetic analyses of morphological and molecular data reveal major clades within the perennial, endemic western North American Apiaceae subfamily Apioideae<sup>1</sup>

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SUN, F.-J. AND S. R. DOWNIE (Department of Plant Biology, 265 Morrill Hall, 505 South Goodwin Avenue, University of Illinois at Urbana-Champaign, Urbana, IL 61801 USA). Phylogenetic analyses of morphological and molecular data reveal major clades within the perennial, endemic western North American Apiaceae subfamily Apioideae. *J. Torrey Bot. Soc.* 137: 133–156, 2010.—The taxonomy and phylogeny of the perennial North American Apiaceae subfamily Apioideae endemic to western North America (north of Mexico) have posed great challenges to systematists. Available classifications based on morphological characters are in general inconsistent and unsatisfactory, and cladistic analyses based on these data are limited to only a few taxa and a small number of characters. In this study, we scored 54 morphological characters from 123 taxa of North American Apioideae (representing 111 species in 21 genera) to construct an estimate of phylogenetic relationships and to compare the results obtained with those inferred for the group through previous studies using molecular data. The morphological and combined (morphological and molecular) datasets were analyzed using maximum parsimony (with equal, proportional, and successive approximations weighting strategies and Goloboff fit criterion applied to the morphological characters) and Bayesian approaches. Phylogenetic trees derived from morphological characters are largely congruent with those derived from molecular data, upon the collapse of weakly supported branches. The least number of most parsimonious trees is derived from the combined analysis when morphological characters are given proportional weights, and these trees are fully congruent with those derived from molecular data alone. The results revealed that many morphological characters used previously to delimit genera are highly homoplastic, such as the presence of a carpophore, stylopodium, pseudoscape, and dorsal wings, the number of vittae, and the orientation of fruit compression. The results also supported the monophyly of the group, in accordance with previous molecular studies. Three major clades and several well-supported subclades are tentatively circumscribed, thus facilitating future phylogenetic and revisionary studies.

Key words: *Aletes*, cpDNA, *Cymopterus*, *Glehnia*, ITS, *Lomatium*, *Podistera*, *Pseudocymopterus*, *Pteryxia*, *Zizia*.

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As one of the major centers of geographical distribution of Apiaceae, western North America (specifically, Pacific North America and the adjacent Rocky Mountains, north of Mexico) hosts some 200 species of Apiaceae subfamily Apioideae (Mathias 1965). The taxonomy of these plants has been investigated for over a century, many different classification systems have been proposed (e.g., Torrey and Gray 1840; Coulter and Rose 1900; Mathias 1930; Mathias and Constance 1944–1945; Cronquist 1997; S. Goodrich et al., unpublished data), and new species and combinations from the region are continuously being described (e.g., Hartman 1985, 1986, 2000, 2006; Hartman and Constance 1985, 1988; Kagan 1986; Hartman and Kirkpatrick 1986). Recently, however, molecular phylogenetic studies based on DNA sequence data have greatly challenged the morphology-based classifications of these taxa. While these molecular studies supported the monophyly

of this group of perennial, endemic taxa, they also revealed that most of the genera comprising the group are not monophyletic (Downie et al. 2002; Sun 2003; Sun et al. 2004; Sun and Downie 2004; Sun and Downie, 2010). As examples, *Cymopterus* Raf. and *Lomatium* Raf., the two largest genera within the group and representing over half of all of its included species (Kartesz 1994), are each highly polyphyletic, with species from each genus allying closely with many other genera. Available classifications of the group based on morphological characters are in general inconsistent and unsatisfactory, and previous cladistic studies based on morphology are limited to only a few taxa and a small number of characters (Gilmartin and Simmons 1987; Downie et al. 2002). Many taxa demonstrate overlapping patterns of morphological character variation, both at the intraspecific and interspecific levels (Mathias 1930; Hartman 1985; Hartman and Constance 1985; Sun et al. 2005, 2006, 2008), and morphological synapomorphies useful to circumscribe genera or major clades are few or heretofore unknown.

In this study, we use a phylogenetic approach to examine the morphological characters used previously to circumscribe genera within the perennial, endemic western North American (NA) Apiaceae subfamily Apioideae. The major objectives of this study are to: (1) construct an estimate of phylogenetic relationships within the group using morphological data; (2) evaluate the utility of morphological data in circumscribing genera and major clades inferred on the basis of combined morphological and molecular evidence; and (3) assess patterns in the evolution of several specific morphological characters that have been widely utilized in previous classifications of the group (i.e., the development of a pseudoscape and a stylopodium, the pattern of fruit compression, the development of a carpophore and fruit ribs, and the number of vittae in each interval of the fruit). Based on the combined morphological and molecular evidence, the monophyly of this group of perennial, endemic NA genera can be further evaluated and its major clades be circumscribed, thereby facilitating future phylogenetic and revisionary studies.

**Materials and Methods.** ACCESSIONS AND MORPHOLOGICAL CHARACTERS EXAMINED. A total of 123 taxa of primarily western NA

distribution, representing 21 genera, 111 species, 10 varieties, and two subspecies, was examined (Appendix). The ranges of several species reach into central NA; a few others extend into eastern NA, or are restricted to that region. These taxa represent the same accessions as examined previously for nrDNA ITS (Downie et al. 2002; Sun et al. 2004) and cpDNA *rps16* intron (Sun and Downie 2004) and *trnF-trnL-trnT* (hereafter *trnF-L-T*; Sun and Downie, 2010) sequence variation. For ease of comparison with the results of our earlier studies of the group, the nomenclature of the *Cymopterus acaulis* and *Pteryxia terebinthina* species complexes are maintained as in Kartesz (1994). *Cymopterus glomeratus* (Nutt.) DC. (= *C. acaulis* Raf.) traditionally has five infraspecific taxa, but on the basis of the results of numerical multivariate analyses, we proposed that plants in this species complex be recognized as a single species, with no varieties (Sun et al. 2005). Similarly, four varieties were recognized previously in *Pteryxia terebinthina*, but results of our prior multivariate analysis of this complex supported only two, vars. *foeniculacea* and *terebinthina* (Sun et al. 2008). Based on results of previous molecular studies, *Aethusa cynapium* L. was chosen in the phylogenetic analyses to root all trees.

Microscope slides of mature fruit cross-sections were prepared from two or more herbarium specimens for nearly all species examined in this study. Prior to sectioning, fruits were softened by treating them for one to two hours in warm water. Free hand sections through the middle of the mature mericarps were made using a razor blade. These sections were examined under an Olympus compound microscope for orientation of fruit and seed compression, features of the ribs, wings, and commissure, and the number and position of vittae. A total of 54 characters was scored; 26 of these were obtained from fruits, 14 from inflorescences, 11 from plant habit, and three from flowers. These characters and their character states are provided in Table 1, along with additional comments. The data matrix is presented in the Appendix. For the majority of these morphological characters, the determination of their character states was obvious due to their qualitative nature. For nine quantitative characters (Table 1; Nos. 11, 17, 18, 31, 32, 35, 45, 47, and 50), character states were determined

Table 1. Morphological characters and character states used in the phylogenetic analyses of 123 representatives of NA Apioideae.

Characters	Character states and comments
1. Plant habit	0 = acaulescent; 1 = caulescent
2. Herbage habit	0 = mat-forming; 1 = stem one-few, tufted
3. Herbage surface	0 = glabrous; 1 = pubescent; 2 = scabrous or granular
4. Root habit	0 = tap, slender or thickened; 1 = tap, tuberous or globose; 2 = fibrous, fascicled
5. Root habit	0 = branching caudex; 1 = simple, not branching root crown
6. Peduncle surface	0 = glabrous; 1 = pubescent; 2 = hirtellous or scabrous at summit
7. Pseudoscape	0 = present; 1 = absent
8. Leaf complexity	0 = ternate pinnate once; 1 = ternate-pinnately two to several times; 2 = simply pinnate or subbipinnate
9. Leaf margin	0 = irregularly toothed; 1 = evenly serrate or dentate; 2 = entire
10. Sheath	0 = not or slightly ampliate; 1 = conspicuously sheathing
11. Ratio of ultimate leaf segment length / width	0 = < 10; 1 = > 10. Two patterns of ratio values were observed: one group having most species with ratio values less than five (occasionally about six to eight), and the other group having ratio values larger than 10 (range 10–25). Therefore, the ratio value of 10 was used as a gap to distinguish these two characters states. One exception was found in <i>Pseudocymopterus montanus</i> , which has a polymorphism recorded, because no clear gap was found in the ratio values (range one to 15) in this species. This is likely due to the fact that <i>P. montanus</i> is such a variable species with regard to its leaf morphology.
12. Flower petal color	0 = white; 1 = purple or pinkish; 2 = yellow; 3 = green
13. Flower anther color	0 = purple; 1 = yellow; 2 = white
14. Pedicels of sterile flowers	0 = rigid and persistent; 1 = neither rigid nor persistent
15. Inflorescence habit	0 = spreading; 1 = compact; 2 = globose head
16. Primary ray surface	0 = glabrous; 1 = pubescent; 2 = hirtellous or scabrous at summit
17. Primary ray length	0 = equal or nearly equal (ratio of shortest ray length / longest ray length > 0.8); 1 = unequal (ratio of shortest ray length / longest ray length < 0.8). Most species having state 1 were found to have ratio values less than 0.5. Others had ratio values > 0.8. The ratio value of 0.8 was used as a gap to distinguish the two character states. Two species, <i>Polytaenia texana</i> and <i>Pseudocymopterus montanus</i> , were recorded as having polymorphisms. Both species were found to be variable in this character.
18. Maximum primary ray number	0 = less than 30; 1 = more than 30. Two patterns of maximum primary ray number were found, with one group having most species with the maximum primary ray number less than 10 (several less than 20–25), and the other group having a maximum primary ray number > 30 (range 30–50). Therefore, the number 30 was used as a gap to distinguish these two character states.
19. Bract	0 = present; 1 = absent
20. Bract texture	0 = entire herbaceous or with narrow scarious margin; 1 = mostly scarious except midvein
21. Bract top edge	0 = entire and tapering; 1 = more or less obovate; 2 = toothed
22. Involucre shape	0 = nearly complete, forming a cup underneath umbel; 1 = individual lobes, not forming a cup
23. Bractlet	0 = present; 1 = absent
24. Bractlet top edge	0 = entire and tapering; 1 = more or less obovate; 2 = toothed
25. No. of midveins on the bractlet	0 = one; 1 = more than one
26. Bractlet color	0 = white; 1 = purple or green
27. Bractlet texture	0 = entirely herbaceous; 1 = herbaceous with narrow scarious margin; 2 = mostly scarious except midvein
28. Involucel shape	0 = nearly complete, forming a cup underneath umbellet; 1 = dimidiate, not forming a cup

Table 1. Continued.

Characters	Character states and comments
29. Ovary surface	0 = glabrous; 1 = pubescent or villous; 2 = scabrous or granular
30. Stylopodium in fruit	0 = absent; 1 = present
31. Style orientation	0 = widely spreading (angle between two styles > 45 degrees); 1 = more or less erect (angle between two styles < 45 degrees). The angle between two styles was larger than 90 degrees for species having state 0, while smaller than 30 degrees for species having state 1. Therefore, the clear gap of 45 degrees was chosen to separate these two states.
32. Calyx teeth in fruit	0 = > 0.6 mm, well-developed; 1 = < 0.6 mm, not well-developed. Using calyx teeth length 0.6 mm as a gap to distinguish two character states was based on the fact that species having state 1 always had calyx teeth shorter than 0.5 mm and species having state 0 always had calyx teeth longer than 1 mm.
33. Fruit attachment	0 = sessile; 1 = pedicellate
34. Fruit surface	0 = glabrous; 1 = pubescent or villous; 2 = scabrous or granular
35. Fruit compression	0 = dorsally compressed (ratio of length of commissural face / width of two mericarps > 1.5); 1 = laterally compressed (ratio of length of commissural face / width of two mericarps < 0.6); 2 = terete (ratio of length of commissural face / width of two mericarps = 0.9–1.1). Three groups of ratio values (< 0.6, 0.9–1.1, and > 1.5) were found and used to distinguish three characters states in this continuous character.
36. Carpophore	0 = persistent; 1 = present, but falling with mericarp; 2 = absent
37. Carpophore branching	0 = entire, not bifid; 1 = bifid
38. Commissure	0 = constricted (constricted > 80% of the commissural face); 1 = not constricted (not constricted < 20% on the commissural face)
39. Corky and rib-like projection of fruit axis	0 = present; 1 = absent
40. Fruit ribs	0 = all ribs winged; 1 = only lateral ribs winged; 2 = no wings
41. Fruit ribs	0 = filiform; 1 = rounded, corky
42. Fruit wings	0 = chartaceous; 1 = thick, corky
43. Dorsal wings	0 = wavy or corrugated; 1 = not wavy or corrugated
44. Lateral wings	0 = wavy or corrugated; 1 = not wavy or corrugated
45. Lateral wings	0 = wider than fruit body (ratio of lateral wing length on cross-section / fruit body length > 1.2); 1 = equal to fruit body (ratio of lateral wing length on cross-section / fruit body length = 0.9–1.1); 2 = narrower than fruit body ratio of lateral wing length on cross-section / fruit body length < 0.8). Most species having state 0 had ratio values larger than 1.5 (a few cases 1.2–1.5) and most species having state 2 always had ratio values smaller than 0.5 (a few cases 0.6–0.8). The majority of species having state 1 had ratio values always about one. Clear gaps in this continuous character were used to distinguish these three character states.
46. Lateral wing	0 = incurved (lateral wing is almost perpendicular to commissural face); 1 = not incurved (lateral wing is parallel to the commissural face)
47. Seed compression	0 = dorsally compressed (ratio of seed length on commissural face / width of one mericarp > 1.5); 1 = laterally compressed (ratio of seed length on commissural face / width of one mericarp < 0.6); 2 = terete (ratio of seed length on commissural face / width of one mericarp = 0.9–1.1). Three groups of ratio values (< 0.6, 0.9–1.1, and > 1.5) were found in this continuous character and used to distinguish these three characters states.
48. Seed face in cross-section	0 = plane; 1 = concave (at least halfway concave into seed)
49. Wing on cross-section	0 = base enlarged; 1 = not enlarged; 2 = top enlarged

Table 1. Continued.

Characters	Character states and comments
50. Ratio of wing length / wing width on cross-section	0 = < 5; 1 = > 5. Most species having state 0 had the ratio values about one to three, whereas species having state 1 had the ratio values larger than six. Therefore, the ratio value of five was selected as a gap to distinguish these two character states.
51. Strengthening cells	0 = present; 1 = absent
52. No. of oil tubes in the interval	0 = one; 1 = more than one; 2 = inconspicuous; 3 = none. State 2 indicates that the boundaries of the oil tubes are inconspicuous, such that their numbers cannot be counted.
53. No. of oil tubes in the commissure	0 = two; 1 = more than two; 2 = inconspicuous. State 2 indicates that the boundaries of the oil tubes are inconspicuous, such that their numbers cannot be counted.
54. Accessory oil tube in rib	0 = present; 1 = absent

by detecting gaps in the character variation (Stevens 1991). Character polymorphism and uncertainties were observed and specified in the data matrix (Appendix). Approximately 10% of the cells in the data matrix were scored as unknown or inapplicable.

**PHYLOGENETIC ANALYSIS.** The matrix of morphological characters was first analyzed using maximum parsimony (MP), with the character state changes either equally or proportionally weighted. The latter was done because the number of states differed among characters (ranging from two to four), so all characters were weighted in inverse proportion to their minimum number of steps using the scale option of PAUP\* (Swofford 2003). Another character weighting approach, successive approximations (Farris 1969), was also used. Here, two successive weighting searches were done, one starting with equal weights and the other with proportional weights, and the results from both searches were compared. In this approach, characters were weighted by the maximum values of their rescaled consistency (RC) indices, and searches were ended when the RC values became stable for at least three iterations. The matrix was also analyzed using equally weighted MP with Goloboff fit criterion selected (Goloboff 1993;  $K = 2$ , default in PAUP\*). All character states were assumed unordered, and the options multrees, collapse, and acctran optimization were chosen. Due to the large number of taxa, MP trees were sought using the heuristic search strategies of PAUP\* and the inverse constraint approach described in Catalán et al. (1997) and later implemented by Downie et al. (1998). Boot-

strap (BS) values (Felsenstein 1985) were calculated from 100,000 replicate analyses using “fast” stepwise addition of taxa; only those values compatible with the majority rule consensus tree were recorded. The number of additional steps required to force particular taxa into a monophyletic group was examined using the constraint option of PAUP\*. The pattern of evolution of each morphological character across one arbitrarily selected minimal length tree was assessed using MacClade vers. 4.0 (Maddison and Maddison 2003), with the goal of finding those characters most useful for delimiting clades and, ideally, genera. MacClade’s trace character or chart option was used to determine the number of steps of each character over a randomly chosen tree or all MP trees.

Bayesian analysis running four million generations was carried out using MrBayes vers. 3.0 (Ronquist and Huelsenbeck 2003), with tree sampling occurring every 100 generations. This was done using the standard model for unordered characters with a standard gamma distribution to accommodate the rate variation across sites. Starting trees were chosen at random and four simultaneous Markov chain Monte Carlo chains were used to model the character rate heterogeneity. The posterior probability (PP) values (expressed as percentages) for each bipartition of the phylogeny were determined from the remaining trees after the removal of “burn-in” trees.

By using a “total evidence” analysis (Kluge 1989; Kluge and Wolf 1993), also called a “simultaneous analysis” (Nixon and Carpenter 1996), both molecular (ITS, *rps16* intron, and *trnF-L-T*) and morphological data were

combined into a single matrix for simultaneous consideration. For each taxon with multiple accessions in the molecular datasets (i.e., two accessions each of *Aletes acaulis*, *Pseudocymopterus montanus*, *Pteryxia terebinthina* var. *albiflora*, and *Pteryxia terebinthina* var. *calcareo*, and three accessions of *Aletes macdougalii* subsp. *breviradiatus*), the same morphological character states were assigned to each taxon based on an examination of their voucher specimens. Therefore, the final combined dataset contained 129 taxa. The protocols for searching for the most parsimonious trees using MP are the same as those performed for morphological data. The successive approximations (Farris 1969) and the MP with Goloboff fit criterion selected (Goloboff 1993) were not performed. In the Bayesian analysis, different models of maximum likelihood were given to different molecular partitions (ITS, *rps16* intron, *trnF-L-T*) of the combined data, as described previously (Sun 2003; Sun et al. 2004, Sun and Downie 2004; Sun and Downie, 2010).

**Results. DATA MATRICES.** The combination of molecular and morphological data for 129 taxa resulted in a matrix of 3586 (3532 molecular, 54 morphological) characters, with no positions excluded from the molecular partition because of alignment ambiguity. The combined dataset had a total of 408 parsimony informative characters (354 molecular, 54 morphological). The values of the *g1* statistics for 10,000 and 100,000 random trees of both morphological (-0.148 to -0.172) and combined (-0.235 to -0.276) datasets were significantly more skewed than random data (-0.09 to -0.11,  $P < 0.01$ ), indicating that these data contain significant amounts of phylogenetic signal (Hillis and Huelsenbeck 1992).

**MORPHOLOGY.** The results of all phylogenetic analyses of morphological data showed similar results, differing primarily in their degree of resolution and branch support. To show these relationships, we present only the results of the MP analysis using proportional weights because the strict consensus tree resulting from this analysis (Fig. 1) showed greatest resolution and branch support overall. In general, upon the collapse of weakly supported branches (i.e., BS or PP values  $< 50\%$ ), phylogenetic trees derived from mor-

phological characters are congruent with those derived from molecular data from our previous studies. All morphological analyses support the monophyly of the group of perennial, endemic NA taxa.

**MORPHOLOGY: MAXIMUM PARSIMONY USING PROPORTIONAL WEIGHTS.** MP analysis of 54 morphological characters using proportional weights (i.e., 31 characters with a weight of 1.00, 21 characters with a weight of 0.50, and two characters with a weight of 0.33) resulted in the preset limit of 20,000 most parsimonious trees, each of 331.83 steps [consistency index (CI) = 0.16; retention index (RI) = 0.68; RC = 0.11]. By using the inverse constraint approach, the strict consensus of the 20,000 most parsimonious trees served as a topological constraint in a further heuristic search. In this search, five more trees of the same length as these 20,000 trees were obtained. The strict consensus tree of these 20,005 trees is given in Fig. 1. On this tree, *Angelica capitellata* is sister to the perennial endemic NA genera group, the latter comprising a large polytomy, and a clade of all remaining *Angelica* species is successively basal to the aforementioned taxa. Coming off this polytomy, eight branches contain four or more taxa, but the BS values for all of these branches are low ( $< 50\%$ ). Among the 54 characters examined, six occur without homoplasy (CI = 1.00) on one arbitrarily selected MP tree (Nos. 14, 20–22, 39, and 46; Table 1). Of those genera traditionally recognized within the group, only two are monophyletic (*Oreonana* and *Orogenia*), and these genera are supported by non-homoplastic characters. Rigid and persistent pedicels of sterile flowers (No. 14, state 0) support the clade of *Oreonana*, and the presence of corky and rib-like projections on fruit axes (No. 39, state 0) and incurved lateral wings (No. 46, state 0) support the clade of *Orogenia*. Characters having high CI values ( $> 0.70$ ) but show some homoplasy include plant habit (No. 1; CI = 0.87), flower petal color (No. 12; CI = 0.72), and shape of the top of the bractlet (No. 24; CI = 0.82). Many characters emphasized in previous classification systems show high levels of homoplasy, such as the presence/absence of a pseudoscape (No. 7; CI = 0.53), fruit compression patterns (No. 35; CI = 0.14), development of a carpophore (No. 36; CI = 0.43), development of fruit wings (No. 40; CI = 0.35), develop-

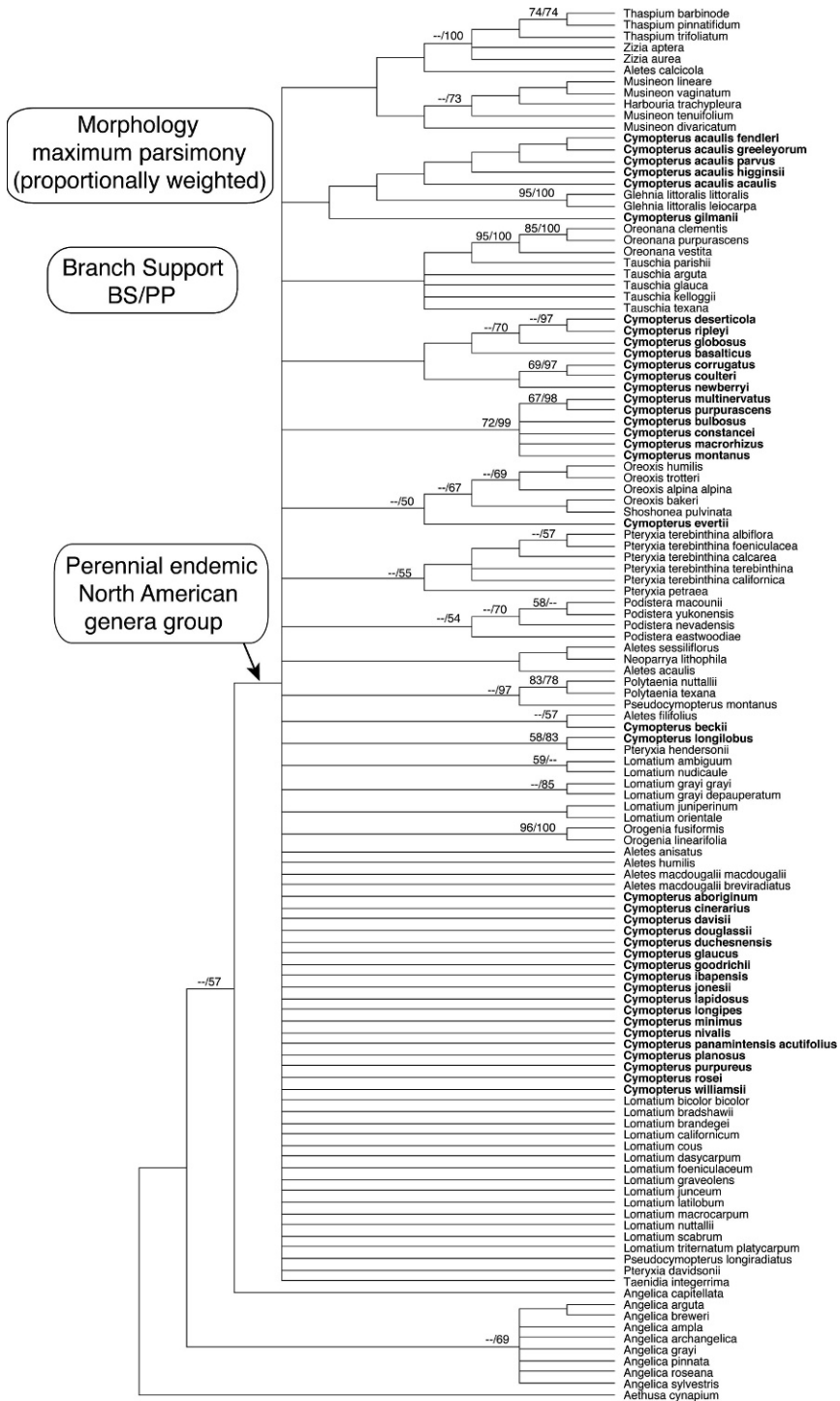


FIG. 1. Strict consensus tree of 20,005 minimal length trees derived from proportionally weighted MP analysis of 54 morphological characters from 123 members of NA Apioideae. Numbers on branches are bootstrap estimates (BS) for 100,000 replicate analyses using “fast” stepwise addition and Bayesian posterior probability (PP) values expressed as percentages, respectively; values <50% for both support values are not indicated or indicated by “--”.

ment of a stylopodium in fruit (No. 30, CI = 0.50), and number of oil tubes in the interval and on the commissure of the fruit (Nos. 52 and 53; CIs = 0.26 and 0.23, respectively). Characters exhibiting the highest levels of homoplasy (CI  $\leq$  0.13) include primary ray length (No. 17; CI = 0.10), length of calyx teeth in fruit (No. 32; CI = 0.13), width of lateral wings (No. 45; CI = 0.13), ratio of wing length/width in cross-section (No. 50; CI = 0.11), presence/absence of strengthening cells in fruits (No. 51; CI = 0.08), and the presence/absence of an accessory oil tube in the ribs (No. 54; CI = 0.07). Overall, the homoplastic characters have CI values ranging from 0.07 to 0.87.

**MORPHOLOGY: MAXIMUM PARSIMONY USING EQUAL WEIGHTS.** MP analyses of 54 morphological characters, using equal weights, resulted in the preset limit of 20,000 most parsimonious trees, each of 491 steps (CI = 0.16; RI = 0.67; RC = 0.11; strict consensus tree not shown). Again, resolution of relationships and BS support values are generally low, and over half of the branches (28 out of 54) occurring in Fig. 1 are maintained. In this analysis, five characters (vs. six in the proportionally weighted analysis) occur without homoplasy (Nos. 14, 20, 25, 39, and 46). Two previous non-homoplastic characters are now homoplastic (No. 21, CI = 0.75; No. 22, CI = 0.67). One previous homoplastic character is now non-homoplastic (No. 25, CI = 1.00). Again, many characters emphasized in previous classification systems show high levels of homoplasy. Characters exhibiting the highest levels of homoplasy are the same as those identified in the proportionally weighted MP analysis and have similar CI values. Overall, the homoplastic characters have CI values ranging from 0.05 to 0.83.

**MORPHOLOGY: MAXIMUM PARSIMONY USING SUCCESSIVE APPROXIMATIONS.** MP analyses of 54 morphological characters using successive approximations starting with proportional or equal weights each resulted in the preset limit of 20,000 most parsimonious trees, each of 52.04 and 51.67 steps, respectively (CIs = 0.38 and 0.38, RIs = 0.81 and 0.82, and RCs = 0.31 and 0.31, respectively; strict consensus trees not shown). For both of these analyses, five iterations were needed to stabilize the RC values, both from initially 0.11 to 0.31. *Glehnia*

is the sister taxon of the NA genera group and *Angelica* (excluding *A. capitellata*) is placed one node away. *Angelica capitellata* is sister to a clade comprising all aforementioned taxa. The relationships within the NA genera group are poorly resolved and similar to those inferred in the proportional weighting approach.

**MORPHOLOGY: MAXIMUM PARSIMONY USING GOLOBOFF CRITERION.** MP analyses of morphological data with Goloboff criterion selected resulted in the preset limit of 20,000 most parsimonious trees, each of 549 steps (CI = 0.14; RI = 0.62; RC = 0.09; G-fit = -24.37). The topology of the strict consensus tree (not shown) is very similar to that of the successive approximations approach, but slightly less resolved.

**MORPHOLOGY: BAYESIAN.** Among a total of 40,000 trees generated in the Bayesian analysis of 54 morphological characters, 10,000 trees were discarded as "burn-in" before the *Ln* likelihood values stabilized. The remaining 30,000 trees were used to generate a majority rule consensus tree (not shown). The *-Ln* values of these 30,000 trees ranged from 2176.31 to 2296.60, averaged 2227.62, with a standard deviation of 14.50. Relationships inferred by the Bayesian tree are very similar to, or consistent with, those estimated by proportionally or equally weighted MP methods (Fig. 1).

**MORPHOLOGY: PHYLOGENETIC RESOLUTIONS.** The results of each morphological analysis showed that the resolution of relationships among these NA taxa is low, with many clades not very well-supported. *Cymopterus* (bold-faced in Figs. 1 and 2) and *Lomatium*, two of the largest genera, are highly polyphyletic, as are many other genera within the group. Constraining the 40 examined taxa of *Cymopterus* to monophyly and rerunning the equally or proportionally weighted MP analysis of morphological characters resulted in trees of 11 or 9.5 steps longer than those most parsimonious trees obtained without the constraint invoked (491 or 331.83 steps, respectively). *Lomatium* arose as monophyletic in trees of 7 or 6.17 steps longer than those without the constraint. Similar analyses revealed that *Aletes*, *Musineon*, *Oreoxis*, *Podistera*, *Pseudocymopterus*, *Pteryxia*, and



*Tauschia* are each monophyletic in trees 2 to 7 steps greater than those most parsimonious. Given the large number of steps required to force monophyly of most of these genera, it is highly unlikely that they represent natural groups. With few exceptions, none of the major clades or subclades revealed coincide with traditionally recognized genera or informally recognized species groups based on morphology. Only *Oreonana*, *Orogenia*, *Glehnia*, *Polytaenia*, and *Podistera* are each revealed as monophyletic, while *Thaspium*, *Zizia*, *Oreoxis*, and *Pseudocymopterus* are monophyletic only in some of the analyses. The monophyly of the outgroup *Angelica* is supported, but with the exclusion of *A. capitellata*. This species is different from its congeners by having its umbellets covered by a woolly indumentum. Other characters distinguishing this taxon from its congeners include an irregularly toothed leaf margin, herbaceous bractlets with narrow scarious margin, longer calyx teeth in fruit, thick and corky fruit wings, and the absence of strengthening cells in the fruit. Previously, this striking species was recognized as *Sphenosciadium capitellatum* A. Gray, but was subsequently transferred into *Angelica* on the basis of molecular data (Spalik et al. 2004). Molecular and combined morphological/molecular data (presented immediately below) support the monophyly of all *Angelica* species.

COMBINED MORPHOLOGICAL AND MOLECULAR CHARACTERS: MAXIMUM PARSIMONY. MP analyses of combined (morphological and molecular) data, giving either proportional or equal weights to the morphological characters, resulted in either 240 minimal length trees (each of 2239.33 steps, CIs = 0.44 and 0.30, with and without uninformative characters; RI = 0.64; RC = 0.28) or the preset limit of 20,000 minimal length trees (each of 2454 steps; CIs = 0.41 and 0.28, with and without uninformative characters; RI = 0.62; RC = 0.26), respectively. Less resolution was achieved in the strict consensus tree derived from equally weighted MP analysis of combined data. In this tree (not shown), the monophyly of the perennial, endemic NA genera group is weakly supported (BS value 52%). A basal trichotomy is identified, with the first branch containing the two subspecies of *Glehnia littoralis* (BS value 75%), the second branch containing all nine accessions of

*Angelica* (BS value <50%), and the third branch comprising all other accessions of the perennial, endemic NA genera group. The latter comprises a highly branched polytomy. Greater resolution of ingroup relationships is obtained when the morphological characters are given proportional weights in the combined analysis. In the strict consensus tree derived from this analysis (Fig. 2), the monophyly of the perennial, endemic NA genera group continues to be supported, with *Glehnia* being its basalmost lineage. The nine accessions of *Angelica* constitute a clade that is sister group to all aforementioned taxa. Constraining *Cymopterus* to monophyly and rerunning the MP analysis, with morphological characters given either equal or proportional weights, resulted in trees 44 and 54.33 steps longer than those most parsimonious obtained without the constraint invoked (2454 and 2239.33 steps, respectively); *Lomatium* arose as monophyletic in trees 25 and 35.33 steps longer. Similar analyses revealed that *Aletes*, *Musineon*, *Oreoxis*, *Podistera*, *Pseudocymopterus*, *Pteryxia*, and *Tauschia* are each monophyletic in trees six to 38.83 steps greater than those most parsimonious.

COMBINED MORPHOLOGICAL AND MOLECULAR CHARACTERS: BAYESIAN. Among a total of 20,000 trees generated in the Bayesian analysis, 5,000 trees were discarded as “burn-in” before the *Ln* likelihood values stabilized; 15,000 of these trees were used to generate a majority rule consensus tree (not shown). The *-Ln* values of these 15,000 trees ranged from 19578.08 to 19676.28, averaging 19618.10, with a standard deviation of 13.55. Relationships inferred by the Bayesian tree are identical to, or highly consistent with, those estimated by MP analysis with morphological characters given proportional weights. Bayesian PP values are presented on the MP strict consensus tree (Fig. 2).

COMBINED MORPHOLOGICAL AND MOLECULAR CHARACTERS: PHYLOGENETIC RESOLUTIONS. The least number of most parsimonious trees is derived from the combined analysis when morphological characters are given proportional weights, and these trees are largely congruent with those trees derived from molecular data alone (Sun 2003; Sun and Downie, 2010). In fact, these trees are better resolved and, in general, their branches more

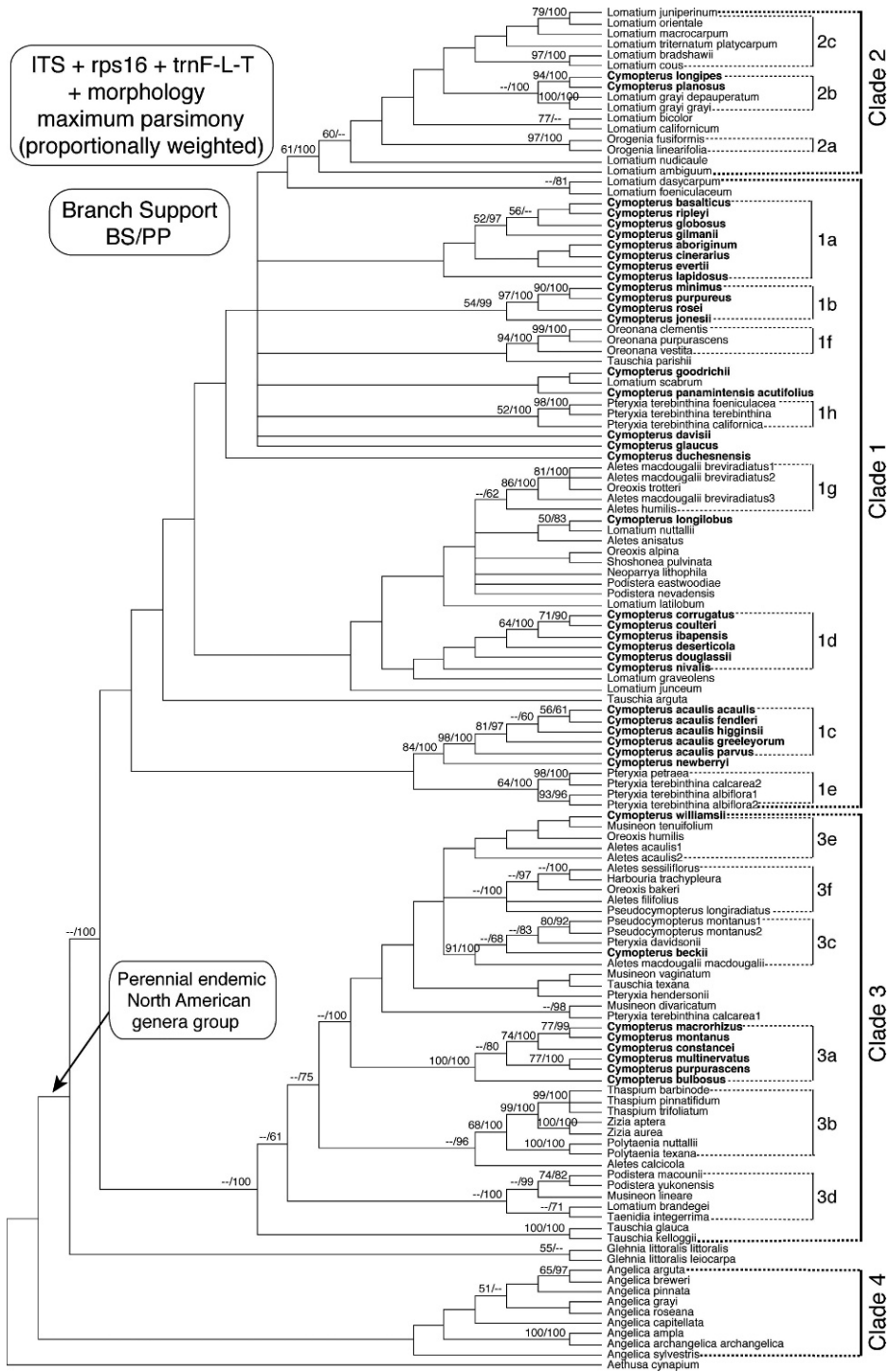


FIG. 2. Strict consensus tree of 240 minimal length trees derived from MP analysis of combined molecular (ITS, *rps16* intron, and *trnF-L-T*) and morphological (proportionally weighted) characters for 129 accessions of NA Apioidae. The four major clades of Apioidae circumscribed previously (Sun 2003; Sun and Downie, 2010) are indicated. Numbers on branches are bootstrap estimates (BS) for 100,000 replicate analyses using “fast” stepwise addition and Bayesian posterior probability (PP) values expressed as percentages, respectively; values <50% for both support values are either not indicated or indicated by “--”.

strongly supported than any phylogenetic tree for the group heretofore available, thus we use these results to tentatively circumscribe major clades and subclades to facilitate future phylogenetic and revisionary studies of this problematic group. For consistency with our earlier studies, we identify the four major clades circumscribed previously on the basis of MP analysis of all available molecular data (Clades 1–4, Fig. 2), even though Clade 2 arises from within a paraphyletic Clade 1 in all MP analyses of combined morphological and molecular data presented herein. The results of the Bayesian analysis of these same combined data, however, revealed Clades 1 and 2 as monophyletic sister groups. Here, we continue to treat Clade 2 as separate from Clade 1, as previous molecular studies and the Bayesian analysis of combined data have revealed. The monophyletic genus *Glehnia* cannot be assigned to any of the three major ingroup clades, thus further studies are warranted to clarify its phylogenetic relationships. Of the four major clades identified, one represents the outgroup genus *Angelica* and will not be discussed further. Each of the other three major clades contains three to eight subclades, several of which are moderately or well-supported in either the MP or Bayesian analyses. Overall, while the combined analyses confirmed the monophyly of the perennial, endemic NA Apioideae, many clades and subclades are weakly supported, with most of these having no resemblance to pre-established groups. Only five traditionally recognized genera (*Oreonana*, *Orogenia*, *Thaspium*, *Zizia*, and *Polytaenia*) are revealed as monophyletic in the combined analyses. For those species with infraspecific taxa or those represented by more than one accession, only three (*Cymopterus acaulis*, *Glehnia littoralis*, *Pseudocymopterus montanus*) are revealed as monophyletic; three other species (*Aletes acaulis*, *Aletes macdougali*, *Pteryxia terebinthina*) are paraphyletic or polyphyletic.

Clade 1 contains 60 accessions, representing 10 genera. The genera *Neoparrya*, *Oreonana*, and *Shoshonea* occur exclusively in this clade. Thirty accessions of *Cymopterus* (representing 75% of all accessions of *Cymopterus* included in this study) also occur here. Eight subclades (1a–h), each containing three to eight accessions, are recognized. Most of these subclades have BS values of 51–86% and PP values of 90–100%. Subclade 1a is composed of eight

species of *Cymopterus* (*C. aboriginum*, *C. basalticus*, *C. cinerarius*, *C. evertii*, *C. gilmanii*, *C. globosus*, *C. lapidosus*, *C. repleyi*). *Cymopterus aboriginum* is not allied with this group on the Bayesian tree (not shown). These eight species share dorsally compressed fruits and the absence of a carpophore (except *C. aboriginum* and *C. lapidosus*). Although most of these species were at one time recognized in the genus *Aulospermum* (Mathias 1930), there is no unique and obvious morphological synapomorphy supporting this subclade. A putative close relationship among *C. aboriginum*, *C. cinerarius*, and *C. evertii* was suggested by Hartman and Kirkpatrick (1986). Three character state changes occurred along the branches leading to Subclade 1a: No. 12, changing from states 2 to 0; No. 15, changing from states 0 to 1; and No. 41, changing from state 0 to equivocal; however, all of these character state changes have reversals within the subclade. Subclade 1b contains four species of *Cymopterus* (*C. jonesii*, *C. minimus*, *C. purpureus*, *C. rosei*). These species were also circumscribed in *Aulospermum* (Mathias 1930) and all are morphologically very similar. Indeed, *C. jonesii*, *C. minimus*, and *C. rosei* were treated as varieties of *C. purpureus* (Goodrich 1986). All species share the presence of a pseudoscape. Subclade 1c comprises the five varieties of *Cymopterus acaulis* (i.e., vars. *acaulis*, *fendleri*, *greeleyorum*, *higginsii*, and *parvus*), with *C. newberryi* closely allied. *Cymopterus newberryi* has a similar leaf morphology to that of *C. acaulis*, but it varies greatly in wing development (the latter has well-developed wings, whereas the former has dorsal wings similar to the lateral or often narrower and irregularly developed, or they may even be obsolete, thus resembling the situation in *Lomatium*). Based on their similar habit, *C. newberryi* was treated as a variety of *C. fendleri* (Jones 1908). This group is supported by the presence of a pseudoscape, dorsally compressed fruits, and dorsal wings, and the absence of a carpophore. Subclade 1d represents another six species of *Cymopterus* (*C. corrugatus*, *C. coulteri*, *C. deserticola*, *C. douglassii*, *C. ibapensis*, *C. nivalis*). This group is paraphyletic on the Bayesian tree (not shown), with Subclade 1e arising from within it. *Cymopterus corrugatus* and *C. coulteri* are very similar morphologically, both having wavy wings and ternate or pinnate leaves; on the basis of this similarity, Jones (1908) treated

*C. coulteri* as a variety of *C. corrugatus*. All species are acaulescent and possess irregularly toothed leaf margins. Subclade 1e contains four accessions of *Pteryxia*, i.e., *P. petraea*, *P. terebinthina* var. *albiflora* (two accessions), and *P. terebinthina* var. *calcareae*. These taxa all bear dorsally compressed fruits with dorsal wings. *Pteryxia petraea* has sometimes been treated as a variety of the *P. terebinthina* complex (Goodrich 1986; Constance 1993). Subclade 1f is composed of three species of *Oreonana* (*O. clementis*, *O. purpurascens*, *O. vestita*). The monophyly of this group is supported by the rigid and persistent pedicels of its sterile flowers. Subclade 1g contains three accessions of *Aletes macdougallii* subsp. *breviradiatus* and one accession of *Oreoxis trotteri*. These two taxa are considered as being conspecific (S. Goodrich et al., unpublished data). They share an extremely similar leaf morphology, laterally compressed fruits, and the presence of one oil tube in each interval of their fruits. *Aletes humilis* is closely allied to this group in both MP and Bayesian trees. Subclade 1h constitutes three varieties of *Pteryxia terebinthina* (i.e., vars. *californica*, *foeniculacea*, and *terebinthina*). These taxa also share an extremely similar leaf morphology.

Clade 2 comprises 16 accessions from three genera, representing two accessions of *Orogenia*, 12 accessions of *Lomatium* (60% of all *Lomatium* accessions examined), and two accessions of *Cymopterus*. Three subclades are designated within this clade. Subclade 2a contains both species of *Orogenia* (*O. fusiformis* and *O. linearifolia*). The monophyly of *Orogenia* is supported by two unique morphological synapomorphies: corky, rib-like projections on its fruit axes, and incurved lateral wings. Subclade 2b is composed of two species of *Cymopterus* (*C. longipes*, *C. planosus*) and two varieties of *Lomatium grayi* (vars. *depauperatum* and *grayi*). Both *C. longipes* and *C. planosus* were also recognized in *Aulospermum* by Mathias (1930), but differ from each other in flower color. The two varieties of *L. grayi* are very similar morphologically, although var. *grayi* has more ultimate leaf segments and relatively larger fruits than those of var. *depauperatum*. MacClade revealed only one character state change along the branches leading to Subclade 2b: No. 10, changing from states equivocal to 0. Subclade 2c is composed of six species of *Lomatium* (i.e., *L. bradshawii*, *L. cous*, *L. juniperinum*, *L. macro-*

*carpum*, *L. orientale*, *L. triternatum* subsp. *platycarpum*). This subclade is not revealed by the Bayesian analysis. The group is characterized by dorsally compressed fruits without dorsal wings, features typical of *Lomatium* species.

Clade 3 comprises 41 accessions. These represent 14 genera, with seven (i.e., *Harbouria*, *Musineon*, *Polytaenia*, *Pseudocymopterus*, *Taenidia*, *Thaspium*, and *Zizia*) found exclusively in this clade. Six subclades are circumscribed, supported by BS values ranging from less than 50% to 100% and mostly high PP values (96–100%). Subclade 3a contains six species of the *Phellopterus* group (Coulter and Rose 1900; Mathias 1930; Hartman 2000) of *Cymopterus* (*C. bulbosus*, *C. constancei*, *C. macrorhizus*, *C. montanus*, *C. multinervatus*, *C. purpurascens*). These plants share large and showy bractlets that are often basally connate. However, similar bractlets also occur in *C. basalticus* (Subclade 1a). The species of the *Phellopterus* group and *C. basalticus* differ in their leaf morphology; the latter has palmately dissected leaves with three overlapping leaflets, whereas those of the former have pinnately and more openly dissected leaves. Subclade 3a is also supported by homoplastic characters, such as the presence of a pseudoscape, dorsally compressed fruits, and dorsal wings. Subclade 3b comprises all species of *Polytaenia*, *Thaspium*, and *Zizia*, and each of these genera is monophyletic. The species of *Thaspium* and *Zizia* are remarkably similar in appearance and this group is supported by the unique synapomorphy of a fibrous and fascicled root system. The generic limits of *Thaspium* and *Zizia* have been questioned (Ball 1979; Lindsey 1982; Cooperider 1985), but in this study they comprise well-supported monophyletic sister groups. Three character state changes occur along the branches leading to Subclade 3b: No. 17, changing from states 1 to equivocal; No. 52, changing from states equivocal to 0; and No. 53, changing from states 1 to 0. Two of these character state changes (Nos. 52 and 53) have no reversals within the subclade. Subclade 3c comprises five accessions representing four genera, representing *Aletes macdougallii* subsp. *macdougallii*, *Cymopterus beckii*, *Pseudocymopterus montanus* (two accessions), and *Pteryxia davidsonii*. These plants share a linear leaf morphology. *Aletes macdougallii* subsp. *macdougallii*, *C. beckii*, and *P. davidsonii*

resemble each other morphologically, and the first two taxa have been suggested as conspecific (Hartman 2006). MacClade revealed no morphological character state changes along the branches leading to Subclade 3c. Subclade 3d contains five species representing four genera (*Podistera macounii*, *P. yukonensis*, *Lomatium brandegei*, *Musineon lineare*, and *Taenidia integerrima*). The two species of *Podistera* share a stylopodium. This subclade is not supported by the morphological analyses. Three character state changes occur along the branches leading to Subclade 3d: No. 9, changing from states 0 to 2; No. 20, changing from states 2 to equivocal; and No. 50, changing from states 1 to equivocal. Among these character state changes, only one (No. 9) has no reversals within the subclade. Subclade 3e is composed of five accessions representing four genera [*Cymopterus williamsii*, *Musineon tenuifolium*, *Oreoxis humilis*, and *Aletes acaulis* (two accessions)]. *Cymopterus williamsii* was once indicated as possibly belonging to *Oreoxis* (Hartman and Constance 1985). MacClade revealed four character state changes along the branches leading to Subclade 3e: No. 6, changing from states 0 to 1; No. 16, changing from states 0 to 1; No. 32, changing from states equivocal to 0; and No. 54, changing from states 1 to 0. Subclade 3f contains *Aletes sessiliflorus*, *A. filifolius*, *Harbouria trachypleura*, *Oreoxis bakeri*, and *Pseudocymopterus longiradiatus*. Neither subclade 3e nor subclade 3f is supported by the morphological analyses. Two character state changes occurred along the branches leading to Subclade 3f: No. 6, changing from states 0 to 2; and No. 41, changing from states 0 to equivocal.

#### MORPHOLOGICAL CHARACTER OPTIMIZATIONS.

To assess evolutionary patterns of individual morphological characters and their usefulness in genus and major clade determinations, each of the 54 morphological characters were optimized onto all of the 240 trees inferred by MP analysis of combined morphological and molecular data. The results revealed that only two traditionally recognized genera, *Oreonana* and *Orogenia*, are supported by unique synapomorphies. As stated above, *Oreonana* is supported by having rigid and persistent pedicels on its sterile flowers, and *Orogenia* is supported by having corky and rib-like projections on its fruit axes and

incurved lateral wings. The group of *Thaspium* + *Zizia* is supported by having fibrous and fascicled roots (No. 4, state 2). The *Phellopterus* group of *Cymopterus* (*C. bulbosus*, *C. constancei*, *C. macrorhizus*, *C. montanus*, *C. multinervatus*, and *C. purpurascens*) is supported by having a bract (No. 19, state 0) and a complete involucl (No. 28, state 0), but these two characters also occur elsewhere on the tree, such as in *Podistera yukonensis*, *P. macounii*, *C. glaucus*, and *C. basalticus*. The genera *Thaspium*, *Zizia*, and *Polytaenia*, while each revealed as monophyletic in the combined analyses, are also supported by a suite of homoplastic characters. None of the three major ingroup clades, circumscribed previously on the basis of molecular evidence and recovered herein in the Bayesian analysis of combined data, are supported by unique morphological synapomorphies. Similarly, many of the subclades circumscribed herein on the basis of combined morphological and molecular data are not supported by unique morphological synapomorphies either. Clade 1 is supported by only molecular data, with no morphological character state changes identified. Three morphological character state changes occur on the branch leading to Clade 2, and three along the branch leading to Clade 3 (Fig. 3). Reversals, however, are apparent for each of these characters within these clades. These three major clades are not easily delimited, or cannot be delimited whatsoever, on the basis of morphology.

The distribution of six morphological characters (seven character states) widely used in traditional treatments of the group is provided in Fig. 3. Like most other morphological characters, these six characters are highly homoplastic, each arising or being lost multiple times during the evolution of the group. Optimization of the character "presence/absence of a pseudoscape" (No. 7) revealed that it required 20 steps on each of the 240 MP trees. There are at least 13 gains for state 0, the presence of this character. Three lineages characterized by a pseudoscape each contain four to six accessions of *Cymopterus*. One of these lineages is composed of the six species of the *Phellopterus* group (Subclade 3a); a second comprises the five varieties of *Cymopterus acaulis* (Subclade 1c); and the third consists of four species of *Cymopterus* (Subclade 1b). The remaining lineages contain one to three accessions each, representing *Cymopterus* (15

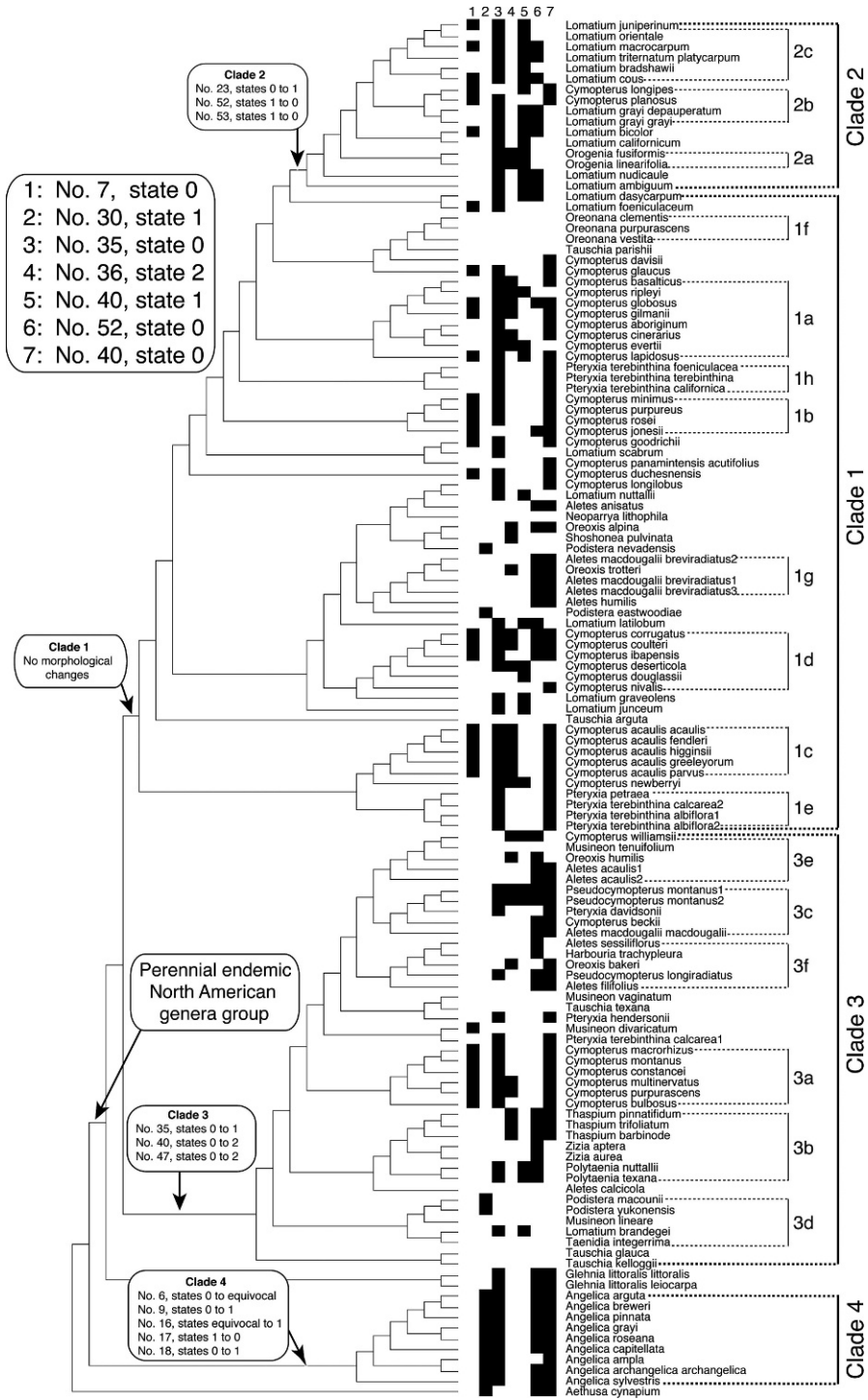


FIG. 3. Distribution of seven morphological character states on a randomly selected minimal length tree derived from MP analysis of combined molecular (ITS, *rps16* intron and *trnF-L-T*) and morphological (proportionally weighted) characters for 129 accessions of NA Apiodeae. Mapped character states are indicated on the figure and are as follows: 1, a pseudoscape is present (No. 7, state 0); 2, a stylopodium is present (No. 30, state 1); 3, fruits are dorsally compressed (No. 35, state 0); 4, a carpophore is absent (No. 36, state 2); 5, dorsal wings are absent (No. 40, state 1); 6, one oil tube is present in each interval (No. 52, state 0); 7, dorsal wings are present (No. 40, state 0).

accessions), *Lomatium* (five accessions), and *Musineon* (one accession). The ancestral condition is identified as the absence of a pseudoscape (state 1). Optimization of the character “presence/absence of a stylopodium in fruit” (No. 30) revealed that this character required four steps on one randomly chosen tree. Across all 240 MP trees, it required either three or four steps. The ancestral condition is revealed as the presence of a stylopodium in fruits (state 1), for this character occurs in *Angelica* (nine accessions) and *Aethusa*. Within the perennial, endemic NA Apioideae group, only *Podistera* (four species in three lineages) is characterized by having a prominent stylopodium, although the genus is polyphyletic. Optimization of the character “dorsally/laterally compressed or terete fruits” (No. 35) indicated that this character required 21 steps on one arbitrarily selected tree, and 21–22 steps when all of the 240 MP trees were considered. While the ancestral condition of this character is equivocal, there are at least 10 losses and seven gains for character state 0 (dorsally compressed fruits), eight gains for state 1 (laterally compressed fruits), and four gains for character state 2 (terete fruits). The last state occurs in *Cymopterus williamsii*, *C. douglassii*, *Shoshonea*, and *Thaspium*. Five of the lineages with dorsally compressed fruits contain six to 10 accessions (Subclades 1a, 1c + 1e, 2c, 3a, and *Angelica*). Two of the lineages with laterally compressed fruit contain five to six accessions. One is composed of *C. davisii*, *Oreonana* (three accessions), and *Tauschia parishii*, the other contains Subclade 1g and *Podistera eastwoodiae*. Optimization of the character “development of a carpophore” (No. 36, CI = 0.43) showed that this character required 19 steps on each of the 240 MP trees. This character contains three character states: a carpophore is persistent (state 0), a carpophore is present but falling with the mericarp (state 1), and a carpophore is absent (state 2). State 0 is revealed as the ancestral condition. There are at least 9 gains for character state 2. Two of the lineages without a carpophore each contain six accessions of *Cymopterus* (Subclade 1c with *C. newberryi* included, and Subclade 1a excluding *C. lapidosus* and *C. aboriginum*). Optimization of the character “development of wings on fruit ribs” (No. 40) revealed that this character required 30 steps on each of the 240 MP trees. This character is divided into three character states: both lateral

and dorsal ribs are winged (state 0), only lateral ribs are winged (state 1), and no ribs are winged (state 2). State 0 is revealed as the ancestral condition. There are eight and four gains for character states 1 and 2, respectively. Three of the lineages with dorsal wings (Subclades 1c + 1e, 3a, and *Angelica*) contain six to 10 accessions of *Cymopterus* or *Pteryxia*. One of the lineages without dorsal wings (state 1) contains six accessions of *Lomatium* (Subclade 2c). All other lineages contain one to two accessions. The monophyly of *Thaspium* (three accessions) is supported by the presence of both dorsal and lateral wings. Optimization of the character “number of oil tubes in the interval of the fruit” (No. 52) indicated that this character required 25 steps on each of the 240 MP trees. The ancestral condition is the presence of one oil tube in each interval in the fruits (state 0). There are at least 10 losses and 9 gains for character state 0. Two of the lineages with a single oil tube in each interval contain six accessions each: one lineage contains all but one species of *Angelica*; the other is composed of three monophyletic genera: *Polytaenia*, *Thaspium*, and *Zizia*. All remaining lineages characterized by one oil tube in an interval are composed of one to five accessions each.

**Discussion.** The results of diverse analyses of both morphological and combined morphological and molecular data are in agreement with our earlier studies based exclusively on molecular evidence in revealing that many NA Apioideae genera are not monophyletic. The two largest genera, *Lomatium* and *Cymopterus*, are each highly polyphyletic, with their species inextricably linked with each other and those of *Aletes*, *Oreoxis*, *Pseudocymopterus*, *Pteryxia*, and several other smaller genera of the region. The results of the combined analysis when morphological characters are given proportional weights offer the most resolved and best supported trees heretofore available for the group. These trees are also fully congruent with those derived from molecular data alone. Four major clades are recognized, one of which represents the out-group taxon *Angelica*. Numerous subclades are also revealed, although very few are supported by uniquely occurring morphological synapomorphies and many are supported poorly in the combined analyses. The *Phellopterus* group of *Cymopterus* (*C. bulbosus*, *C.*

*constancei*, *C. macrorhizus*, *C. montanus*, *C. multinervatus*, and *C. purpurascens*) may very well be the only previously identified species groups within the complex that is supported by molecular and morphological evidence. Therefore, until these subclades receive confirmation through additional study, we do not formally recognize new assemblages of taxa at the present time. These clades and subclades are only provisionally recognized and, pending support from further studies, will be used as a framework in future phylogenetic and revisionary studies of NA Apioideae.

The monophyly of the entire group of perennial, endemic Apiaceae subfamily Apioideae of NA is supported by both morphological and molecular analyses. The restricted distribution of many of these plants to elevated regions of similar habitat, their similar life history and overall general habit, and their overlapping patterns of morphological character variation suggested previously that this group of umbellifers was closely related. The absence of a prominent conical stylopodium in all taxa except *Podistera*, where the stylopodium is otherwise well developed, as it is in most other umbellifers, is a synapomorphy uniting the group. Further support for their monophyly comes from the shared presence of a protogynous breeding system (and associated reproductive characteristics), an atypical feature in a family where floral protandry prevails (Schlessman et al. 1990). Protogyny is presumed derived in the apioid umbellifers, a response to an early flowering season and unreliable pollinators (Schlessman and Graceffa 2002).

Fruit and other morphological characters traditionally have been used to delimit taxa within Apioideae. However, heretofore, these characters have not been analyzed cladistically across a wide spectrum of NA taxa. 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. In this study, we have determined that only two traditionally recognized genera, *Oreonana* and *Orogenia*, are supported by uniquely-occurring morphological character states. The genera *Thaspium*, *Zizia*, and *Polytaenia* are also each revealed as monophyletic in the combined analyses, but none of them are supported by morphological synapomorphies. In general, morphological characters have

very limited use in delimiting genera and major clades. The six characters used widely in previous classifications of the group are highly homoplastic, resulting in many different treatments for the group and difficulties in circumscribing taxa unambiguously.

In *Cymopterus*, Cronquist (1997) reported that some species (*C. acaulis*, *C. bulbosus*, *C. purpurascens*) have a pseudoscape (a scape-like stalk of a leaf cluster that originates from the root-crown) with a subterranean root crown, whereas other species (*C. aboriginum*, *C. cinerarius*, *C. nivalis*) have a taproot surmounted by a branching, surficial caudex. However, some species do not fit completely into either of these categories. As examples, *C. megacephalus* and *C. ripleyi* have a simple subterranean root crown, but lack a pseudoscape. *Cymopterus duchesnensis* has a taproot capped by a surficial crown or more often by a branched caudex. Several other species have a surficial or subterranean root crown, but do or do not have a pseudoscape. Our results show that the ancestral condition is the absence of a pseudoscape and that the derivation of a pseudoscape has been achieved multiple times during the evolution of the group. A pseudoscape is also present in some species of *Lomatium* (*L. juniperinum*, *L. cous*, *L. macrocarpum*, *L. bicolor*) and *Musineon* (*M. divaricatum*), thus its presence has limited utility for reliably delimiting taxa. Similarly, plants having a taproot surmounted by a branching, surficial caudex are also found in multiple separate lineages (not shown).

The presence of a prominent conical stylopodium (a disc-like to long-tapering enlargement borne atop the ovary at the base of the styles) is commonly present in many species of Apiaceae, therefore, the absence of a stylopodium is considered as prime evidence supporting the monophyly of perennial, endemic NA Apiaceae subfamily Apioideae (Mathias and Constance 1944–1945; Downie et al. 2002; Sun et al. 2004). Only the genus *Podistera* within the ingroup possesses a stylopodium. However, because this genus is not monophyletic in the combined analyses, the presence of a stylopodium arises three times independently. This character is readily observable, but its presence does not unambiguously circumscribe any one particular genus within the ingroup, as previously considered.

In Apiaceae, fruit compression patterns have been used to distinguish taxonomic



groups at various levels. In western NA Apiaceae, dorsally compressed fruits are present in many genera, such as *Cymopterus*, *Lomatium*, *Orogenia*, *Pteryxia*, *Pseudocymopterus*, *Polytaenia*, *Glehnia*, and *Angelica*. 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 individual’s point of view” (Mathias 1930). Fruit cross-sections reveal a complex series, from fruits that are subterete to somewhat compressed laterally (*C. douglassii*, *C. jonesii*, *C. longipes*, *C. nivalis*, *C. panamintensis*) to those that are markedly compressed dorsally (*C. deserticola*, *C. newberryi*). Our results show that dorsally compressed fruits support many separate subclades, as do laterally compressed fruits. These results agree with those obtained in other studies of Apiaceae, where the orientation of fruit compression, a feature used widely in traditional systems of classification of the family, is an unreliable character for circumscribing taxa (Cronquist 1982; Downie et al. 2001).

Nearly half of the species of *Cymopterus* lack a carpophore, a remnant of the floral axis to which the mericarps are attached (Hartman and Constance 1985; Cronquist 1997; Hartman 2000). Our results show that the loss of the carpophore (through adnation of its halves to the mericarps) has been independently achieved several times within *Cymopterus*. The absence of a carpophore also occurs in all or some accessions of *Aletes*, *Thaspium*, *Oreoxis*, *Pseudocymopterus*, *Shoshonea*, and *Orogenia*, supporting the monophyly of *Orogenia* and *Thaspium*. The presence of a carpophore supports the monophyly of *Oreonana*, *Zizia*, *Angelica*, and *Polytaenia*. In total, this character is lost at least nine times within the group, and only serves to distinguish two of the subclades designated herein.

The outer surface of the mericarp normally has five primary ridges or ribs (three dorsal and two lateral), in which the dorsal and/or lateral ribs may develop into wings. In general, species of *Cymopterus* bear (one to three) wings on their dorsal fruit ribs, whereas in *Lomatium*, the dorsal ribs are generally filiform and wingless or occasionally very narrowly winged. However, the absence of (or obsolete) dorsal wings found in some species of *Cymopterus* (*C. corrugatus*, *C.*

*deserticola*, *C. douglassii*, *C. longipes*, *C. megacephalus*, *C. newberryi*, *C. ripleyi*, *C. williamsii*) makes this character unreliable to separate *Cymopterus* from *Lomatium*. Similar fruits to those of typical *Lomatium* are also seen in some species of *Pteryxia* (*P. terebinthina*, *P. hendersonii*) and *Pseudocymopterus* (*P. montanus*). The presence of fruits with both lateral and dorsal wings supports seven of the subclades designated herein, as well as several other taxa (such as, *Thaspium*, *Glehnia*, and *Angelica*). Two subclades and *Polytaenia* are supported by the absence of dorsal wings.

The number of vittae (oil tubes) in the intervals between the primary ribs of the fruits was used to distinguish primarily between *Aletes* (mostly solitary) and *Neoparrya* (numerous; Theobald et al. 1963). Cronquist (1997) submerged *Aletes* into *Musineon* because the distinction between some species of *Aletes* and *Musineon* is no more than the number of oil tubes (two or more in the latter). In *Cymopterus*, this number varies from 3 to 5. All but one species of *Angelica* are supported by the presence of one oil tube in each fruit interval, as are *Glehnia*, *Polytaenia*, *Thaspium*, and *Zizia*. Subclade 1g is the only subclade designated herein having a single interval vitta in all included taxa. The genus *Aletes* is polyphyletic in all trees, thus the presence of a solitary vitta in the intervals of the fruit is a highly homoplastic character (arising at least four times independently in nine accessions) and cannot be used by itself to delimit genera.

In conclusion, our study confirms that morphological characters are of limited value for delimiting most traditionally-defined genera within the group of perennial, endemic NA apioid umbellifers. Many of these genera are ill-formed, being based on highly homoplastic and overlapping characters. Thus, the emphasis placed on these characters in previous systems of classification of the group has led to highly artificial assemblages of taxa. Such a conclusion is not surprising, given the common disagreement 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). Generic delimitation in Apiaceae is often vague and arbitrary (Constance 1987; Cronquist 1997), and many species-rich genera are polyphyletic (Downie et al. 2000a, 2000b; Spalik et al. 2001). Unfortunately, the results of this study do little to refute these statements. Of all the perennial, endemic apioid genera of NA, only *Oreonana*, *Orogenia*, *Polytaenia*, *Thaspium*, and *Zizia* are each resolved as monophyletic on the basis of phylogenetic analyses of combined molecular and morphological data. Furthermore, all but a few of the major clades and subclades circumscribed herein are supported by homoplastic morphological characters. The systematics of the group is nowhere near satisfactory, and a complete reassessment of the generic limits of these taxa is required. The systematic investigation of the perennial, endemic genera of NA Apioideae needs to be continued with the goal of uncovering morphological synapomorphies useful for clade 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 morphological 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 the perennial, endemic NA Apioideae will be required. Indeed, such changes appear to be underway already. In accordance with previous floristic studies (Goodrich 1986; Cronquist 1997), the genera *Aletes* (in part), *Oreoxis*, *Pseudocymopterus*, and *Pteryxia* have been recently included within a broadly defined *Cymopterus* in a flora of the San Juan Basin region (S. Goodrich et al., unpublished data). The distinction between *Lomatium* and *Cymopterus* also remains very unclear, with no obvious character consistently separating these taxa. Given this trend and overlapping character variation among genera, it may very well be possible that future studies will indicate that all or most members of the group should be combined into one large, polymorphic genus, an extreme but possibly inevitable action.

#### Literature Cited

- BALL, P. W. 1979. *Thaspium trifoliatum* (meadow-parsnip) in Canada. *Can. Field Naturalist* 93: 306–307.
- CATALÁN, M. P., E. A. KELLOGG, AND R. G. OLMSTEAD. 1997. Phylogeny of Poaceae subfamily Pooideae based on chloroplast *ndhF* gene sequences. *Mol. Phylogenet. Evol.* 8: 150–166.
- CONSTANCE, L. 1987. *Neogeozia* (Apiaceae), a very distinct and elegant genus of Mexican Umbelliferae. *Opera Bot.* 92: 59–71.
- CONSTANCE, L. 1993. Apiaceae [Umbelliferae]: carrot family, p. 136–166. In J. C. Hickman [ed.], *The Jepson Manual: higher plants of California*. University of California Press, Berkeley and Los Angeles, CA.
- COOPERRIDER, T. S. 1985. *Thaspium* and *Zizia* (Umbelliferae) in Ohio. *Castanea* 50: 116–119.
- COULTER, J. M. AND J. N. ROSE. 1900. Monograph of the North American Umbelliferae. *Contr. U.S. Natl. Herb.* 7: 1–256.
- CRONQUIST, A. 1982. Reduction of *Pseudotaenidia* to *Taenidia* (Apiaceae). *Brittonia* 34: 365–367.
- CRONQUIST, A. 1997. Apiaceae, p. 340–427. In A. Cronquist, N. H. Holmgren, and P. K. Holmgren [eds.], *Intermountain Flora: Vascular Plants of the Intermountain West, USA., Vol. 3, Part A*. The New York Botanical Garden, Bronx, NY.
- DAVIS, P. H. 1972. Umbelliferae, p. 265–538. In *Flora of Turkey and the East Aegean Islands*, Vol. 4. University Press, Edinburgh.
- DOWNIE, S. R., R. L. HARTMAN, F.-J. SUN, AND D. S. KATZ-DOWNIE. 2002. Polyphyly of the spring-parsleys (*Cymopterus*): Molecular and morphological evidence suggest complex relationships among the perennial, endemic genera of western North American Apiaceae. *Can. J. Bot.* 80: 1295–1324.
- DOWNIE, S. R., D. S. KATZ-DOWNIE, AND M. F. WATSON. 2000a. A phylogeny of the flowering plant family Apiaceae based on chloroplast DNA *rpl16* and *rpoC1* intron sequences: Towards a suprageneric classification of subfamily Apioideae. *Am. J. Bot.* 87: 273–292.
- DOWNIE, S. R., G. M. PLUNKETT, M. F. WATSON, K. SPALIK, D. S. KATZ-DOWNIE, C. M. VALIEJO-ROMAN, E. I. TERENTIEVA, A. V. TROITSKY, B.-Y. LEE, J. LAHAM, AND A. EL-OQLAH. 2001. Tribes and clades within Apiaceae subfamily Apioideae: The contribution of molecular data. *Edinb. J. Bot.* 58: 301–330.
- DOWNIE, S. R., S. RAMANATH, D. S. KATZ-DOWNIE, AND E. LLANAS. 1998. Molecular systematics of Apiaceae subfamily Apioideae: phylogenetic analyses of nuclear ribosomal DNA internal transcribed spacer and plastid *rpoC1* intron sequences. *Am. J. Bot.* 85: 563–591.
- DOWNIE, S. R., M. F. WATSON, K. SPALIK, AND D. S. KATZ-DOWNIE. 2000b. Molecular systematics of Old World Apioideae (Apiaceae): relationships among some members of tribe Peucedaneae sensu lato, the placement of several island-endemic species, and resolution within the apioid superclade. *Can. J. Bot.* 78: 506–528.
- FARRIS, J. S. 1969. A successive approximations approach to character weighting. *Syst. Zool.* 18: 374–385.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

- GILMARTIN, A. J. AND K. S. SIMMONS. 1987. Relationships of *Lomatium* among other genera of Apiaceae. *Plant Syst. Evol.* 157: 95–103.
- GOLOBOFF, P. A. 1993. Estimating character weights during tree search. *Cladistics* 9: 83–91.
- GOODRICH, S. 1986. Utah flora: Apiaceae (Umbelliferae). *Great Basin Naturalist* 46: 66–106.
- HARTMAN, R. L. 1985. A new species of *Cymopterus* (Umbelliferae) from southern Idaho. *Brittonia* 37: 102–105.
- HARTMAN, R. L. 1986. Studies in Rocky Mountain species of *Cymopterus* (Apiaceae). *Am. J. Bot.* 73: 765–766 (Abstract).
- HARTMAN, R. L. 2000. A new species of *Cymopterus* (Apiaceae) from the Rocky Mountain region, U. S. A. *Brittonia* 52: 136–141.
- HARTMAN, R. L. 2006. New combinations in the genus *Cymopterus* (Apiaceae) of the southwestern United States. *SIDA* 22: 955–957.
- HARTMAN, R. L. AND L. CONSTANCE. 1985. Two new species of *Cymopterus* (Umbelliferae) from western North America. *Brittonia* 37: 88–95.
- HARTMAN, R. L. AND L. CONSTANCE. 1988. A new *Lomatium* (Apiaceae) from the Sierran crest of California. *Madroño* 35: 121–125.
- HARTMAN, R. L. AND R. S. KIRKPATRICK. 1986. A new species of *Cymopterus* (Umbelliferae) from northwestern Wyoming. *Brittonia* 38: 420–426.
- HEYWOOD, V. H. 1971. Systematic survey of Old World Umbelliferae, p. 31–42. *In* V. H. Heywood [ed.], *The Biology and Chemistry of the Umbelliferae*. Academic Press, New York.
- HILLIS, D. M. AND J. P. HUELSENBECK. 1992. Signal, noise, and reliability in molecular phylogenetic analyses. *J. Hered.* 83: 189–195.
- JONES, M. E. 1908. New species and notes. *Contr. West. Bot.* 12: 1–81.
- KAGAN, J. S. 1986. A new species of *Lomatium* (Apiaceae) from southwestern Oregon. *Madroño* 33: 71–75.
- KARTESZ, J. T. 1994. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland, Second edition. *Biota of the North American Program of the North Carolina Botanical Garden*. Timber Press, Portland, OR.
- KLUGE, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among Epicrates (Boidae, Serpentes). *Syst. Zool.* 38: 7–25.
- KLUGE, A. G. AND A. J. WOLF. 1993. Cladistics: What's in a word? *Cladistics* 9: 183–199.
- LINDSEY, A. H. 1982. Floral phenology patterns and breeding systems in *Thaspium* and *Zizia* (Apiaceae). *Syst. Bot.* 7: 1–12.
- MADDISON, D. R. AND W. P. MADDISON. 2003. *MacClade 4: Analysis of phylogeny and character evolution*, version 4.06. Sinauer Associates, Sunderland, MA.
- MATHIAS, M. E. 1930. Studies in the Umbelliferae. III. A monograph of *Cymopterus* including a critical study of related genera. *Ann. Missouri Bot. Gard.* 17: 213–476.
- MATHIAS, M. E. 1965. Distribution patterns of certain Umbelliferae. *Ann. Missouri Bot. Gard.* 52: 387–398.
- MATHIAS, M. E. AND L. CONSTANCE. 1944–1945. Umbelliferae, p. 43–295. *In* *North American flora*, Vol. 28B. The New York Botanical Garden, Bronx, NY.
- NIXON, K. C. AND J. M. CARPENTER. 1996. On simultaneous analysis. *Cladistics* 12: 221–241.
- RONQUIST, F. AND J. P. HUELSENBECK. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- SCHLESSMAN, M. A. AND L. M. GRACEFFA. 2002. Protogyny, pollination, and sex expression of andromonoecious *Pseudocymopterus montanus* (Apiaceae, Apioideae). *Int. J. Plant Sci.* 163: 409–417.
- SCHLESSMAN, M. A., D. G. LLOYD, AND P. P. LOWRY II. 1990. Evolution of sexual systems in New Caledonian Apiaceae. *Mem. N. Y. Bot. Gard.* 55: 105–117.
- SPALIK, K., J.-P. REDURON, AND S. R. DOWNIE. 2004. The phylogenetic position of *Peucedanum* sensu lato and allied genera and their placement in tribe Selineae (Apiaceae, subfamily Apioideae). *Plant Syst. Evol.* 243: 189–210.
- SPALIK, K., A. WOJEWÓDZKA, AND S. R. DOWNIE. 2001. Delimitation of genera in Apiaceae with examples from Scandiceae subtribe Scandicinae. *Edinb. J. Bot.* 58: 331–346.
- STEVENS, P. F. 1991. Character states, morphological variation, and phylogenetic analysis: A review. *Syst. Bot.* 16: 553–583.
- SUN, F.-J. 2003. A phylogenetic study of *Cymopterus* and related genera (Apiaceae). Ph.D. dissertation—University of Illinois at Urbana-Champaign, Urbana, IL.
- SUN, F.-J. AND S. R. DOWNIE. 2004. A molecular systematic investigation of *Cymopterus* and its allies (Apiaceae) based on phylogenetic analyses of nuclear (ITS) and plastid (*rps16* intron) DNA sequences. *S. African J. Bot.* 70: 407–416.
- SUN, F.-J. AND S. R. DOWNIE. 2010. Phylogenetic relationships among the perennial, endemic Apiaceae subfamily Apioideae of western North America: additional data from the cpDNA *trnF-trnL-trnT* region continue to support a highly polyphyletic *Cymopterus*. *Botanische Jahrbücher*, in press.
- SUN, F.-J., S. R. DOWNIE, AND R. L. HARTMAN. 2004. An ITS-based phylogenetic analysis of the perennial, endemic Apiaceae subfamily Apioideae of western North America. *Syst. Bot.* 29: 419–431.
- SUN, F.-J., G. A. LEVIN, AND S. R. DOWNIE. 2005. A multivariate analysis of *Cymopterus glomeratus*, formerly known as *C. acaulis* (Apiaceae). *Rhodora* 107: 359–385.
- SUN, F.-J., G. A. LEVIN, AND S. R. DOWNIE. 2006. A multivariate analysis of *Pseudocymopterus* (Apiaceae). *J. Torrey Bot. Soc.* 133: 499–512.
- SUN, F.-J., G. A. LEVIN, AND S. R. DOWNIE. 2008. A multivariate analysis of *Pteryxia terebinthina* (Apiaceae). *J. Torrey Bot. Soc.* 135: 81–93.
- SWOFFORD, D. L. 2003. PAUP\*. *Phylogenetic Analysis Using Parsimony (\*and other methods)*, version 4 edition. Sinauer Associates, Sunderland, MA.
- THEOBALD, W. L. 1971. Comparative anatomical and developmental studies in the Umbelliferae, p. 177–197. *In* V. H. Heywood [ed.], *The Biology and Chemistry of the Umbelliferae*. Academic Press, New York.

- THEOBALD, W. L., C. C. TSENG, AND M. E. MATHIAS. 1963. A revision of *Aletes* and *Neoparrya* (Umbelliferae). *Brittonia* 16: 296–315.
- TORREY, J. AND A. GRAY. 1840. Umbelliferae, p. 598–645. *In* A Flora of North America. Wiley & Putnam, New York.

Appendix. Data matrix of 54 morphological characters used in the cladistic analyses of 123 taxa of NA Apiioideae. The symbol “?” indicates an inapplicable character state. Character states of polymorphic characters are indicated as letters: A = 0, 1, or 2; B = 0, 1, or 3; C = 0, 2, or 3; D = 0 or 1; E = 0 or 2; F = 0 or 3; G = 1 or 2; H = 1 or 3; and I = 2 or 3.

Taxon	Morphological characters									
	10	20	30	40	50					
<i>Aethusa cynapium</i> L.	1100101101	00G100101?	??00010101	0110201110	?111210010					
<i>Aletes acaulis</i> (Torr.) J.M. Coult. & Rose	01E0011200	021101101?	??00010100	0010101110	?111211010					
<i>Aletes anisatus</i> (A. Gray) W.L. Theob. & C.C. Tseng	0100001100	021100101?	??00010100	0010101110	?111211010					
<i>Aletes calcicola</i> Mathias & Constance	D1E0121100	031102101?	??00010100	1110101112	1?2?2?120??					
<i>Aletes filifolius</i> Mathias, Constance & W.L. Theob.	D100021120	121100101?	??00010100	0010101110	?111211010					
<i>Aletes humilis</i> J.M. Coult. & Rose	01E0011200	02G100001?	??00010100	0010101112	0?2?2?110??					
<i>Aletes macdougallii</i> J.M. Coult. & Rose subsp. <i>macdougallii</i>	01E0001200	0211100001?	??00010100	0010101110	?111211010					
<i>Aletes macdougallii</i> subsp. <i>breviradiatus</i> W.L. Theob. & C.C. Tseng	01E0001200	0211100001?	??00010100	0010101110	?1?1211010					
<i>Aletes sessiliflorus</i> W.L. Tseng & C.C. Tseng	0100001220	021100101?	??00010100	0000101112	1?2?2?110??					
<i>Angelica ampla</i> A. Nelson	1100121111	00G102011?	??00010101	0110001110	?111210010					
<i>Angelica archangelica</i> L. subsp. <i>archangelica</i>	1100121111	0CG101011?	??00010101	0110001110	?111210010					
<i>Angelica arguta</i> Nutt. ex Torr. & A. Gray	11E0101111	0D2102011?	??1?2?2?01	0110001110	?111210011					
<i>Angelica breweri</i> A. Gray	11D0111111	002101111?	??1?2?2?11	0111001110	?111210011					
<i>Angelica capitellata</i> (A. Gray) Spalik, Reduron & S.R. Downie	1100101101	0D1101001?	??00011111	0101001110	?011210010					
<i>Angelica grayi</i> (J.M. Coult. & Rose) J.M. Coult. & Rose	1120121111	011102111?	??000DG101	0110001110	?111210010					
<i>Angelica pinnata</i> S. Watson	11E0101111	0D2102101?	??1?2?2?21	0110001110	?111210010					
<i>Angelica roseana</i> L.F. Hend.	11E0101111	0D2102111?	??00010121	0112001110	?111210000					
<i>Angelica sylvestris</i> L.	1100121111	0DG101011?	??00010101	0110001110	?111110011					
<i>Cymopterus aboriginum</i> M.E. Jones	0120001100	00011010D?	??00012100	01100D1110	?011112111					
<i>Cymopterus acaulis</i> (Pursh) Raf. var. <i>acaulis</i>	D100100100	002110101?	??0A01D100	010002?110	?100110021					
<i>Cymopterus acaulis</i> var. <i>fendleri</i> (A. Gray) S. Goodrich	D100100100	0211110101?	??0A01D100	010002?110	?100010021					
<i>Cymopterus acaulis</i> var. <i>greeleyorum</i> J.W. Grimes & P.L. Packard	D100100100	0211110101?	??0A01D100	010002?110	?100010011					
<i>Cymopterus acaulis</i> var. <i>higginsii</i> (S.L. Welsh) S. Goodrich	D100100100	010110101?	??0A010100	010002?110	?100210011					
<i>Cymopterus acaulis</i> var. <i>parvus</i> S. Goodrich	D100100100	021110101?	??0A01D100	010002?110	?100210011					
<i>Cymopterus basalticus</i> M.E. Jones	D100101000	0G1100101?	??00002000	010002?110	?11D210010					
<i>Cymopterus beckii</i> S.L. Welsh & S. Goodrich	1100001E20	121110101?	??0001D100	0110110110	?111211010					
<i>Cymopterus bulbosus</i> A. Nelson	D100100100	0DE1100001	1001002000	0110001110	?0DD110001					
<i>Cymopterus chierarius</i> A. Gray	01G0001100	01112?2?1?	??00?1?100	010002?110	?000010101					
<i>Cymopterus constancei</i> R.L. Hartm.	D100100100	0D01101001	210G102000	0000001110	?011010001					
<i>Cymopterus corrugatus</i> M.E. Jones	D100100200	000100001?	??00012100	011002?110	?100210020					
<i>Cymopterus coulteri</i> (M.E. Jones) Mathias	D100100200	000120101?	??000012100	01D002?110	?100110100					

Appendix. Continued.

Taxon	Morphological characters				
	10	20	30	40	50
<i>Cymopterus davisi</i> R.L. Hartm.	D100001200	0211100001?	??000011120	0112101110	?111212110
<i>Cymopterus deserticola</i> Brandegee	0100101100	01E12??1?	??1????10	010102?111	00?1210020
<i>Cymopterus douglassii</i> R.L. Hartm. & Constance	0100001200	0211100001?	??0E011100	0010201111	11?1210010
<i>Cymopterus duchesnensis</i> M.E. Jones	D100D00200	0211000101?	??000010100	0110001110	?0DD010011
<i>Cymopterus evertii</i> R.L. Hartm. & R.S. Kirkp.	0120002100	0EA112101?	??000D1110	001202?111	11?1210010
<i>Cymopterus gilmanii</i> C. Morton	D1001000000	0D0110001?	??00001D100	011002?110	?111110011
<i>Cymopterus glaucus</i> Nutt.	D100100100	02G1001001	01000011100	0110000110	?011212110
<i>Cymopterus globosus</i> (S. Watson) S. Watson	D10010D100	0D212??1?	??00002100	0110002?110	?111210020
<i>Cymopterus goodrichii</i> S.L. Welsh & Neese	1100000100	0DG1000001?	??0D011100	0110000110	?000212110
<i>Cymopterus ibapensis</i> M.E. Jones	D1E0100100	000110001?	??00001D100	0110000110	?011012111
<i>Cymopterus jonesii</i> J.M. Coult. & Rose	D100D00100	0111100101?	??000010100	0110101110	?0DD012101
<i>Cymopterus lapidosus</i> (M.E. Jones) M.E. Jones	D100100100	0011100001?	??000010100	011000011D	?011210011
<i>Cymopterus longilobus</i> (Rydb.) W.A. Weber	0100001100	0211100101?	??000010100	10D0001110	?011210011
<i>Cymopterus longipes</i> S. Watson	D100100100	0EG110101?	??000010100	011010111D	0011012111
<i>Cymopterus macrorhizus</i> Buckley	D100120100	0D010E1001	0101002000	01100001110	?000110001
<i>Cymopterus minimus</i> (Mathias) Mathias	D1G01D100	0D2110101?	??000010100	01D00001110	?011110001
<i>Cymopterus montanus</i> Nutt. ex Torr. & A. Gray	D1D0120100	0D011E0001	1101002000	01100001110	?000110001
<i>Cymopterus multinervatus</i> (J.M. Coult. & Rose) Tidestr.	D100100100	0DE12000001	100111D000	01D002?110	?0DD010001
<i>Cymopterus newberryi</i> (S. Watson) M.E. Jones	D120121200	0211100101?	??000010100	01D002?11D	?101210020
<i>Cymopterus nivalis</i> S. Watson	01000001100	0D01100001?	??000011100	0110101110	?011210000
<i>Cymopterus panamintensis</i> J.M. Coult. & Rose var. <i>acutifolius</i> (J.M. Coult. & Rose) Munz	0100001100	0I111000001?	??000010100	0110101110	?011112011
<i>Cymopterus planosus</i> (Osterh.) Mathias	D100100100	0H2102101?	??000010100	01100001110	?111212110
<i>Cymopterus purpurascens</i> (A. Gray) M.E. Jones	D100100100	0D012000001	1001102000	01D002?110	?0DD010001
<i>Cymopterus purpureus</i> S. Watson	D1E0D0D100	0G11000101?	??000011100	01100D1110	?0DD012101
<i>Cymopterus ripleyi</i> Barneby	0100101000	0BG12??1?	??00002110	010102?111	1111210020
<i>Cymopterus rosei</i> (M.E. Jones ex J.M. Coult. & Rose) M.E. Jones	D1E0D2D200	0G1102101?	??000010100	01100001110	?0DD110001
<i>Cymopterus williamstii</i> R.L. Hartm. & Constance	0100001220	0211100001?	??000011100	011022?111	11?1210010
<i>Glehnia littoralis</i> F. Schmidt ex Miq. subsp. <i>littoralis</i>	D1D0111201	000111101?	??000010110	0101000110	?111110011
<i>Glehnia littoralis</i> subsp. <i>leiocarpa</i> (Mathias) Hultén	D110111201	000111101?	??000010100	0100001110	?111110011
<i>Harbouria trachypleura</i> (A. Gray) J.M. Coult. & Rose	1100021120	1211D2001?	??000011120	0112101012	1???120??
<i>Lomatium ambiguum</i> (Nutt.) J.M. Coult. & Rose	11001101121	1211000101?	??1????00	01100001111	00?1210010
<i>Lomatium bicolor</i> (S. Watson) J.M. Coult. & Rose var. <i>bradshawii</i> (Rose ex Mathias) Mathias & Constance	D101100100	021102101?	??000011100	01100001111	00?1210010
<i>Lomatium brandegei</i> (J.M. Coult. & Rose) J.F. Macbr.	D100101121	0211000101?	??02011100	01100001111	01?1210020
<i>Lomatium californicum</i> (Nutt.) Mathias & Constance	1100101120	12G1000101?	??000011100	01100001111	00?1210010
	1100101101	0211000001?	??1????00	01100001111	01?1210010

## Appendix. Continued.

Taxon	Morphological characters				
	10	20	30	40	50
<i>Lomatium cous</i> (S. Watson) J.M. Coult. & Rose	D10112D101	021102101?	??010111110	0112001111	00?1210011
<i>Lomatium dasycarpum</i> (Torr. & A. Gray) J.M. Rose subsp. <i>dasycarpum</i>	D1D01D1101	0H110D101?	??000111110	011D001111	00?1210010
<i>Lomatium foeniculaceum</i> (Nutt.) J.M. Coult. & Rose subsp. <i>foeniculaceum</i>	01D001D101	021101001?	??00D111110	0111001111	00?1210010
<i>Lomatium graveolens</i> (S. Watson) Dorn & R.L. Hartm. var. <i>graveolens</i>	0100001120	121100001?	??000111100	0110001111	00?1210010
<i>Lomatium grayi</i> (J.M. Coult. & Rose) J.M. Coult. & Rose var. <i>grayi</i>	D100001100	021100101?	??000111100	0110001111	00?1210011
<i>Lomatium grayi</i> var. <i>depauperatum</i> (M.E. Jones) Mathias	D100001100	021100101?	??000111100	0110001111	00?1210011
<i>Lomatium junceum</i> Barneby & N.H. Holmgren	0100001221	121100101?	??00010100	0110001111	00?1210011
<i>Lomatium juniperinum</i> (M.E. Jones) J.M. Coult. & Rose	D110110101	0EA101101?	??000121E0	0110001111	00?1210010
<i>Lomatium latilobum</i> (Rydb.) Mathias	0100001220	021100001?	??000111100	0010001111	01?1210010
<i>Lomatium macrocarpum</i> (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose	11DD11D101	0A2101101?	??000101D0	011D001111	00?1210011
<i>Lomatium nudicaule</i> (Pursh) J.M. Coult. & Rose	0100101101	021100101?	??1?P?P00	0110001111	00?1210010
<i>Lomatium nuttallii</i> (A. Gray) J.F. Machr.	0100001100	121100101?	??00011100	0010001111	00?1210010
<i>Lomatium orientale</i> J.M. Coult. & Rose	1110011101	002101101?	??0D011100	0110001111	00?1210010
<i>Lomatium scabrum</i> (J.M. Coult. & Rose) Mathias var. <i>scabrum</i>	01200D1100	021100101?	??00010100	0110001111	00?1210010
<i>Lomatium triternatum</i> (Pursh) J.M. Coult. & Rose subsp. <i>platycarpum</i> (Torr.) Cronquist	D110111121	121101101?	??000111110	0110001111	00?1210011
<i>Musineon divaricatum</i> (Pursh) Nutt. ex Torr. & A. Gray var. <i>divaricatum</i>	110000E0G00	02111E001?	??00011100	0112101012	0?P?P121?P
<i>Musineon lineare</i> (Rydb.) Mathias	D100001220	1E2112001?	??00010120	0112101012	0?P?P120?P
<i>Musineon tenuifolium</i> Nutt. ex Torr. & A. Gray	0100021G20	1E1112001?	??00011120	011210D012	0?P?P120?P
<i>Musineon vaginatum</i> Rydb.	1100021121	1E1112101?	??000101E0	0112100012	0?P?P120?P
<i>Neoparrya lithophila</i> Mathias	0100001220	021100101?	??00010100	0010101112	0?P?P120?P
<i>Oreonana clementis</i> (M.E. Jones) Jeps.	0010111100	000021001?	??02011120	0001101112	0?P?P121?P
<i>Oreonana purpurascens</i> Shevock & Constance	0010101200	000021011?	??02012120	0001101112	0?P?P121?P
<i>Oreonana vestita</i> (S. Watson) Jeps.	0010111100	0G1021001?	??00010120	0101101112	0?P?P121?P
<i>Oreoxis alpina</i> (A. Gray) J.M. Coult. & Rose subsp. <i>alpina</i>	0020011200	0211111101?	??00010110	000112?110	?111210010
<i>Oreoxis bakeri</i> J.M. Coult. & Rose	0010021100	0E1112101?	??02010100	010012?110	?111210010
<i>Oreoxis humilis</i> Raf.	0000021200	021112001?	??00010100	000012?110	?111110010
<i>Oreoxis trotteri</i> S.L. Welsh & S. Goodrich	0020021200	021112001?	??00010100	000012?110	?111210010
<i>Oreogenia fusiformis</i> S. Watson	0100101D20	100110101?	??1?P?P00	010002?101	0111200010
<i>Oreogenia linearifolia</i> S. Watson	0101101D20	100110101?	??1?P?P00	011002?101	0111200010

Appendix. Continued.

Taxon	Morphological characters					
	10	20	30	40	50	
<i>Podistera eastwoodiae</i> (J.M. Coult. & Rose) Mathias & Constance	0100001200	0I11100001?	??02010101	0010101012	0?? ??120??	0111
<i>Podistera macounii</i> (J.M. Coult. & Rose) Mathias & Constance	0100021220	01G1100000	E100010101	0010101012	0?? ??120??	0111
<i>Podistera nevadensis</i> (A. Gray) S. Watson	0020021220	02G11???1?	??01010101	0000101012	0?? ??120??	0111
<i>Podistera yukonensis</i> Mathias & Constance	0120021220	0EG1100000	0200010101	0010101012	0?? ??120??	0300
<i>Polytaenia nuttallii</i> DC.	1120?21101	021102001?	??00010100	0110001111	0111210011	0000
<i>Polytaenia texana</i> (J.M. Coult. & Rose) Mathias & Constance	1120?21101	021102001?	??00010100	0110001111	0111210011	0000
<i>Pseudocymopterus longiradiatus</i> Mathias, Constance & W.L. Theob.	D100021101	021102101?	??00010100	0110001110	?D11210010	0001
<i>Pseudocymopterus montanus</i> (A. Gray) J.M. Coult. & Rose	D1A0021GED	DG1102D01?	??0D010100	01D00E111D	0011210011	0DD0
<i>Pteryxia davidsonii</i> (J.M. Coult. & Rose) Mathias & Constance	1100021120	0GG112101?	??00010110	0010001110	?011211010	0111
<i>Pteryxia hendersonii</i> (J.M. Coult. & Rose) Mathias & Constance	0100001100	021100101?	??0E010100	10D0001110	?011210011	0111
<i>Pteryxia petraea</i> (M.E. Jones) J.M. Coult. & Rose	1100001100	021100101?	??00010100	0010001110	?011110011	0110
<i>Pteryxia terebinthina</i> (Hook.) J.M. Coult. & Rose var. <i>terebinthina</i>	D100001101	021100101?	??0E010100	0010001110	?000010011	0110
<i>Pteryxia terebinthina</i> var. <i>albiflora</i> (Nutt. ex Torr. & A. Gray) Mathias	D100001101	002110101?	??0E010100	0010001110	?011210011	0110
<i>Pteryxia terebinthina</i> var. <i>calcareo</i> (M.E. Jones) Mathias	D100001101	02G110101?	??0E010100	0010001110	?011110011	0110
<i>Pteryxia terebinthina</i> var. <i>californica</i> (J.M. Coult. & Rose) Mathias	1100001101	021100101?	??0E010100	0010001110	?011110011	1110
<i>Pteryxia terebinthina</i> var. <i>foeniculacea</i> (Nutt. ex Torr. & A. Gray) Mathias	D100001101	021110101?	??0E010100	0010001110	?011210011	0110
<i>Shoshonea pulvinata</i> Evert & Constance	0020021220	021112101?	??00010120	00022G1112	1?? ??100??	0110
<i>Taenidia integririma</i> (L.) Drude	1100101121	021100101?	??1?? ??00	1110101112	0?? ??120??	1111
<i>Tauschia arguta</i> (Torr. & A. Gray) J.F. Macbr.	1100101210	021100101?	??00010100	0110101112	0?? ??121??	1111
<i>Tauschia glauca</i> (J.M. Coult. & Rose) Mathias & Constance	1100101100	0G1100101?	??00010100	0100101112	0?? ??121??	1111
<i>Tauschia kelloggii</i> (A. Gray) J.F. Macbr.	0120101100	021100101?	??00010100	0110101112	0?? ??121??	1111
<i>Tauschia parishii</i> (J.M. Coult. & Rose) J.F. Macbr.	0100101100	021100001?	??00010100	0100101112	0?? ??121??	1111
<i>Tauschia texana</i> A. Gray	0100121200	021100101?	??00010100	0100101112	0?? ??121??	1111
<i>Thaspium barbinode</i> (Michx.) Nutt.	11D2121100	021102001?	??000111D0	111022?110	?011212010	0001
<i>Thaspium pinnatifidum</i> (Buckley) A. Gray	1112121100	021102001?	??00011100	101222?110	?011212010	0001
<i>Thaspium trifoliatum</i> (L.) A. Gray	1102121E10	01G102101?	??00011100	111022?110	?011212010	0000
<i>Zizia aptera</i> (A. Gray) Fernald	1102121E10	021102101?	??00011100	1110101112	0?? ??120??	0000
<i>Zizia aurea</i> (L.) W.D.J. Koch	1102121G10	021102101?	??00011100	1110101112	0?? ??120??	0000