

## Phylogenetic Analysis Reveals Multiple Cases of Morphological Parallelism and Taxonomic Polyphyly in *Lomatium* (Apiaceae)

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**Abstract**—The genera *Lomatium* and *Cymopterus*, along with many others, form a group that has been referred to previously as the perennial endemic Apiaceae subfamily Apioideae of western North America. This group of ecologically important and widespread species has been the target of numerous systematic studies, but the evolutionary relationships among these species remain elusive. Here we show that this confusion is due to high levels of morphological parallelism and homoplasy in the characters that have traditionally been used to define them, a result that is concordant with previous studies of the group. We explore patterns of evolution in traditionally important morphological characters using Bayesian stochastic character mapping on a phylogeny constructed from novel nrDNA and cpDNA sequence data for 96 specific and infraspecific taxa of the estimated 200 species in the group. We consider the implications of these results for taxonomic classification, the evolution of morphologies, and the utility of these morphologies to delimit small and large clades. *Lomatium concinnum* is newly combined as *Cymopterus glomeratus* var. *concinus* and the new combination *Cymopterus glomeratus* var. *greeleyorus* is made.

**Keywords**—Classification, convergent evolution, *Cymopterus*, homoplasy, morphology.

One of North America's largest endemic plant radiations is also one of its least understood: the perennial, endemic North American clade of Apiaceae subfamily Apioideae (hereafter, the PENA clade). The PENA clade contains approximately 200 species in 20 currently recognized genera (Table 1), and the proper circumscription of these genera has been the subject of much debate (Mathias 1928, 1930, 1938; Theobald et al. 1964; Downie et al. 2001, 2002). The largest of the PENA genera are *Lomatium* and *Cymopterus*, together containing over half of the group's species. Both are taxonomically challenging because of high levels of species sympatry and extreme morphological variability within many species.

Species of the PENA clade are ecologically important across much of western North America. Most species (especially *Lomatium* and *Cymopterus*) occur in open habitats of the Intermountain and Pacific West, and many are xeric-adapted geophytes (Hartman 2000). Several related eastern North America genera including *Zizia*, *Taenidia*, and *Polytaenia*, are associated with more mesic meadow environments. The combined range of the PENA genera covers most of North America. The greatest species density, however, is concentrated west of the Mississippi River. *Lomatium* and *Cymopterus* contain many species that are well-documented food sources for animals including insects, gophers, sage grouse, and grizzly bears (Mattson et al. 1990; Barnett and Crawford 1994; Thompson 1998), and both the tuberous roots and fruits of some species were also once an important part of many Native American diets (Hunn and French 1981). Several species of *Lomatium* are of interest to modern medicine for their antimicrobial and antiviral properties (McCutcheon et al. 1997; Chou et al. 2006; Mukhtar et al. 2008).

In addition to its ecological and cultural significance, the PENA clade is also of interest for its biodiversity. With its approximately 200 species, this group represents one of the most extensive endemic plant radiations on the continent,

comparable to others such as *Lupinus* L. (Drummond 2008; Eastwood et al. 2008) and *Castilleja* Mutis ex L. f. (Tank and Olmstead 2008, 2009; Tank et al. 2009). Like other such radiations, the PENA clade is known for its high proportion of narrowly endemic species, many of which are of conservation concern (Cronquist 1992; Grimes and Packard 1981; Carlson et al. 2011a). New species continue to be described on an almost yearly basis (Darrach et al. 2010; Helliwell 2010; Carlson et al. 2011a, b; McNeill 2012).

Morphological evolution in the PENA clade is remarkable, resulting in a great deal of variation both within and among populations. Efforts to untangle the intricacies of species relationships based on this morphology have met with limited success (Coulter and Rose 1900; Mathias 1928, 1930, 1938; Schlessman 1984). The taxonomic boundary between *Lomatium* and *Cymopterus*, for instance, has traditionally been defined by a morphological macrofeature: *Lomatium* fruits are dorsally flattened with lateral wings, whereas *Cymopterus* fruits generally are terete to dorsally compressed with dorsal wings in addition to lateral ones. This pattern, however, is not without exception. These inconsistencies have led some authors to question the value of fruit characters for classification in this group (Cronquist et al. 1997; Sun and Downie 2004, 2010a, b; Sun et al. 2004). Vegetative and floral characters show essentially similar patterns, though often with even greater degrees of variation (Hitchcock and Cronquist 1973; Schlessman 1984; Cronquist et al. 1997).

Previous phylogenetic studies have confirmed suspicions that the current morphological classification does not reflect monophyletic groups within the PENA clade. Several genera, including *Cymopterus* and *Lomatium* as they are currently circumscribed, appear to define para- or polyphyletic assemblages (Downie et al. 2002; Sun and Downie 2004, 2010a, b; Sun et al. 2004; Carlson et al. 2011a). In fact, previous studies have indicated high levels of homoplasy

TABLE 1. Genera of the perennial endemic North American (PENA) clade of Apiaceae subfamily Apioideae. Species counts follow Mabberly (2008), except as otherwise referenced in the case of recent taxonomic revisions.

Genus	Number of constituent species
<i>Aletes</i> J. M. Coult. & Rose	15–20
<i>Cymopterus</i> Raf.	32
<i>Eurytaenia</i> Torr. & A. Gray	2
<i>Harbouria</i> J. M. Coult. & Rose	1
<i>Lomatium</i> Raf.	74
<i>Musineon</i> Raf.	3
<i>Neoparrya</i> Mathias	1
<i>Oreonana</i> Jeps.	3
<i>Oreoxis</i> Raf.	4
<i>Orogenia</i> S. Watson	2
<i>Podistera</i> S. Watson	4
<i>Polytaenia</i> DC.	2
<i>Pseudocymopterus</i> J. M. Coult. & Rose	2 (Sun et al. 2006)
<i>Pteryxia</i> (Nutt. ex Torr. & A. Gray) J. M. Coult. & Rose	5
<i>Shoshonea</i> Evert & Constance	1
<i>Taenidia</i> (Torr. & A. Gray) Drude	2
<i>Tauschia</i> Schldl.	31
<i>Thaspium</i> Nutt.	3
<i>Vesper</i> Hartman & Nesom	6 (Hartman and Nesom 2012)
<i>Zizia</i> W. D. J. Koch	4

in essentially every morphological character ever used for higher classification in this group (Sun et al. 2004, 2005, 2006, 2008; Sun and Downie 2004, 2010a), suggesting that it may represent a useful model system in which to explore the patterns and processes that underlie the evolution of high levels of morphological diversity and parallelism in plants, and their relationship to ecological interactions and processes of diversification.

Here we present results characterizing morphological evolution in the PENA clade. These results bring some clarity to our understanding of morphological innovation and parallel character evolution in this group, and represent a first step toward a clearer picture of how the PENA radiation can inform our understanding of the relationship between morphological innovation and other processes such as diversification and ecology. Development of a robust phylogenetic understanding of this clade is a necessary step to facilitate this kind of research, and to this end we present novel phylogenies for 96 taxa in the PENA clade, constructed from nuclear ribosomal and chloroplast DNA sequence data using markers ITS, *matK*, *rpl32-trnL<sub>UAG</sub>*, and *rps16* intron, which corroborate and improve upon previously published trees. Using these, we employ Bayesian stochastic mapping to model the evolution of various important morphological characters within the group to assess general patterns of morphological evolution and their implication for our understanding of evolutionary history in this clade. Finally, we present new nomenclature for a single species previously recognized within *Lomatium* on the basis of a homoplastic fruit character, but which we show to be nested within a species complex of *Cymopterus*.

#### MATERIALS AND METHODS

**Sampling and Nucleotide Sequence Generation**—Leaf tissue samples representing 96 specific and infraspecific taxa of North American Apioideae were collected both directly from wild populations and from preexisting herbarium voucher specimens from populations throughout the western U. S. A. (Appendix 1). Of these 96 taxa, 58 were from

*Lomatium*, 11 from *Cymopterus*, 21 from other PENA genera, and six from a clade containing species of *Angelica* L., which is an outgroup of the PENA clade (Sun and Downie 2004, 2010a). Samples collected for this study were preserved in silica gel whenever possible; vouchers for these silica-dried specimens have been deposited at the College of Idaho herbarium (CIC; herbarium acronyms according to Thiers 2012). Those samples taken directly from pre-existing specimens were obtained from vouchers in the collections of CIC, RM, ID, and SRP.

DNA was extracted from dried leaf samples using a Qiagen DNeasy plant mini kit (Qiagen, Valencia, California). We used the polymerase chain reaction (PCR), following the methods of Smith et al. (2004), to amplify the nuclear ribosomal marker ITS and the chloroplast markers *rpl32-trnL<sub>UAG</sub>* (Shaw et al. 2007), *rps16* intron (Shaw et al. 2005), and *matK* (Wolfe et al. 1992). Amplification products were sequenced by Genewiz (South Plainfield, New Jersey).

**Alignment and Phylogeny Estimation**—Sequences were checked for mislabeled base pairs and manually aligned using PhyDE 0.9971 (Müller et al. 2005). For analyses where indels were scored, the simple indel coding of Simmons and Ochoterena (2000) as implemented in the program SeqState (Müller 2005) was used. Regions of ambiguous alignment, as well as the beginning and end of each marker sequenced (which were generally of poor quality), were excluded from final nucleotide data matrices.

Phylogenetic trees were estimated from these alignments using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) methods. The exception to this was the data matrix that rescored indels which was analyzed only with MP. Following Sun and Downie (2004, 2010a), trees were rooted manually using a clade containing species from the genus *Angelica*. The MP analyses were performed using PRAP2 (Müller 2007) in conjunction with PAUP\* v4.0 b10 (Swofford 2002). Bootstrap support (BS; Felsenstein 1985) was estimated from 1,000 heuristic replicates using PRAP2 (Müller 2007).

The Akaike information criterion (AIC), as implemented in Modeltest 3.6 (Posada and Crandall 1998; Posada and Buckley 2004), was used to identify optimal substitution models for ML and BI analyses. The software MrBayes 3.1.1 (Huelsenbeck and Ronquist 2003) was used for two independent BI analyses: one in which a single model was used for all data (hereafter referred to as the one-model analysis or BIO); and a second in which four models were used, one for each genetic marker, which is referred to as the partitioned analysis or BIP. All analyses were run with four chains, for ten million generations. Convergence was determined by viewing the trace logs in Tracer v1.3 (Rambaut and Drummond 2005). A burn-in fraction of 50,000 generations was discarded from each posterior distribution. All BI analyses were repeated twice to ensure that parameter estimates converged to similar values; this convergence was assessed using the online version of Are We There Yet (AWTY; Nylander et al. 2008). The ML analyses were completed using GARLI v0.96 (Zwickl 2006) with 1000 bootstrap replicates, using a single model. Indel codings were excluded from both the ML and BI analyses.

**Tests of Incongruence**—The partition homogeneity test (Farris et al. 1994) was performed as implemented in PAUP\* (Swofford 2002) with 10,000 bootstrap replicates (using a heuristic search, simple addition, and no branch swapping) to test for congruence between the nrDNA and cpDNA partitions. As an additional measure of congruence among partitions, bootstrap analyses were performed on these partitions separately to assess areas of conflict and to determine if any conflict was strongly supported (Seelanen et al. 1997). Conflicts between the partitions that received BS < 70% were considered to be soft incongruence, reflecting limited resolving power of the region. Such soft incongruence was treated as insufficient to prevent combining partitions.

**Analyses of Morphology**—We mapped nine morphological characters that have been important for species and genus delimitations in the PENA group onto the BIP majority-rule consensus tree, and used the software SIMMAP v. 1.5 (Bollback 2006) to reconstruct the evolutionary history of these characters with Bayesian stochastic mapping over the last 4,000 trees from the posterior distribution of the BIP analysis. Within SIMMAP, the bias parameter was set to the empirical prior, and the rate parameter was set to the rescale tree length. All character state changes were treated as unordered. A description of these characters is presented in Table 2, and character codings for species are available in Appendix S1.

#### RESULTS

**Phylogeny Reconstructions**—Amplifications were successful for nearly all regions and for nearly all accessions

TABLE 2. Description of characters and character states used in Bayesian stochastic character mapping and the results of the ancestral state reconstruction. For coding for each species, see Appendix S1.

<b>R. Roots.</b> 0 - thickened, fibrous, often branched taproot, 1 - elongate, essentially fibrous (not fleshy), usually unbranched taproot, 2 - rounded thickened fleshy taproot or tuber. <b>F. Fruits.</b> 0 - dorsiventrally flattened with lateral wings, 1 - rounded with many wings, 2 - rounded cylindrical, with ribs but not wings. <b>S. Leaflet Structure.</b> 0 - fine, densely-clustered, and linear-cylindric, 1 - elongate linear-lanceolate, 2 - dense, lanceolate-ovate ("fern-like"), 3 - broad-connate, 4 - fine, diffuse, and narrowly-linear.
<b>N. Leaflet Arrangement.</b> 0 - essentially planar, 1 - three-dimensional. <b>H. Habit.</b> 0 - acaulescent, 1 - caulescent. <b>1. Primary Leaf Division.</b> 0 - pinnate/subpinnate, 1 - irregular. <b>2. Secondary Leaf Division.</b> 0 - none, 1 - ternate, 2 - pinnate/subpinnate, 3 - incomplete, 4 - irregular. <b>3. Tertiary Leaf Division.</b> 0 - none, 1 - ternate, 2 - pinnate/subpinnate, 3 - incomplete, 4 - irregular. <b>4. Quaternary Leaf Division.</b> 0 - none, 1 - pinnate/subpinnate, 2 - irregular.

(Appendix 1). Summary statistics for each region are presented in Table 3. The ITS data matrix included 663 base pairs (bp) of aligned data, the *rps16* intron matrix included 1,020 bp, the *rpl32-trnL<sub>UAG</sub>* matrix included 1,777 bp, and the *matK* matrix included 693 bp. Analyses using MP BS for each region separately were mostly poorly supported and with less resolution than in the combined analyses (data not shown) therefore only the combined analyses will be presented here. The MP analysis without scored indels resulted in 192 trees (L = 2,622 steps, consistency index (excluding uninformative characters, CI; Kluge and Farris 1969) = 0.48, retention index (RI, Farris 1989) = 0.73, and rescaled consistency index (RC, Farris 1989) = 0.45), whereas the MP analysis with indels scored resulted in 196 trees (L = 3,090 steps, CI = 0.45, RI = 0.72, RC = 0.43). The best tree from the ML analysis had a -lnL of 22,290.39.

For the BI analyses, results from AWTY indicated convergence for each pair of runs. The topologies from the BIO and BIP runs were largely congruent for major clades, although the latter runs resulted in slightly more resolved trees. The majority-rule consensus trees from the MP and ML bootstrap analyses showed lower resolution than the Bayesian consensus trees, but overall did not support incongruent topologies (results not shown). Therefore, we present only the topology from the BIP analysis, with support from the ML and MP bootstraps (the latter with and without indels rescored) and BIO posterior probabilities (PP) illustrated upon it (Figs. 1–3B).

**Tests of Incongruence Between ITS and cpDNA Trees—**The result of the partition homogeneity test ( $p = 0.01$ ) indicated significant differences between the ITS and cpDNA partitions. As has been reported on many occasions, however, this test often indicates incongruence when none

exists (Reeves et al. 2001; Yoder et al. 2001). A less biased method for assessing incongruence is simply to compare support values among partitions (Seelanen et al. 1997). The comparison of BS proportions between the cpDNA and ITS partitions (trees not shown) detected no incongruence.

**Phylogenetic Structure—**The monophyly of the PENA clade was strongly supported by all analyses (Fig. 1). Four subclades within the PENA clade are identified (Clades A–D) with the first three of these comprising a large clade containing most of the species of *Lomatium* and *Cymopterus* as well as species from many other PENA genera. We refer to this large clade informally as the "Lomatium clade." Within the Lomatium clade, Clade C was identified with high support by all analyses. Clades A and B, on the other hand, were each only poorly to moderately supported.

Clade A (Fig. 2) contains three subclades supported only by the BI analyses: subclade a1 contains species from five genera; subclade a2 contains *Cymopterus glomeratus* and three related taxa; and subclade a3 contains *Lomatium foeniculaceum*, *L. ravenii*, and two other taxa. Six additional species of *Cymopterus*, *Lomatium*, and *Pteryxia* were also in Clade A, but their relationship to other taxa was either unsupported, poorly supported in all analyses, or conflicted among analyses. The one exception was the sister species relationship of *C. nivalis* and *L. howellii*.

Clade B (Fig. 3) is the largest clade and consists primarily of *Lomatium* species, but also species from three other genera. Within Clade B, five supported subclades are recognized: subclade b1 contains *Lomatium cous* and related species; subclade b2 contains *Lomatium bicolor*, *Tauschia tenuissima*, and *Lomatium pastoralis*; subclade b3 contains two *Lomatium* species and *Orogenia linearifolia*; subclade b4 contains six species of *Lomatium*; and subclades b5 and b6 contain a few species of *Lomatium* each. Clade B also contains 29 taxa whose relationships were unsupported or poorly supported in all analyses except the sister relationship of the undescribed species E and F.

Clade C is placed sister to Clade B with low support (Figs. 1, 3) and includes three *Lomatium* species.

Clade D is strongly supported as sister to the Lomatium clade (Fig. 1). Unlike the other clades, however, relationships within this clade are generally strongly supported. We identify four subclades within Clade D: subclade d1 contains one species of *Aletes* and the type species for the genera *Pseudocymopterus* and *Musineon*; subclade d2 comprises *Vesper*; subclade d3 comprises *Polytaenia* and *Zizia*; and subclade d4 includes the type species of the genus *Taenidia* as well as *Musineon lineare* and *L. brandegeei*, the only *Lomatium* species in this study that falls outside the Lomatium clade of Fig. 1.

**Morphology Reconstructions—**The mappings of the nine morphological characters to the tips of the majority-rule

TABLE 3. Summary statistics of DNA regions used in this analysis

DNA region	Aligned length	Number of excluded ambiguities	Final aligned length used in the analysis	Number of parsimony informative characters	Number of parsimony un-informative characters	Number of indels
ITS	664	1	663	176	150	82
<i>rpl32-trnL<sub>UAG</sub></i>	1,829	52	1,777	257	253	259
<i>rps16</i> intron	1,050	30	1,020	104	143	83
<i>matK</i>	693	0	693	61	50	5

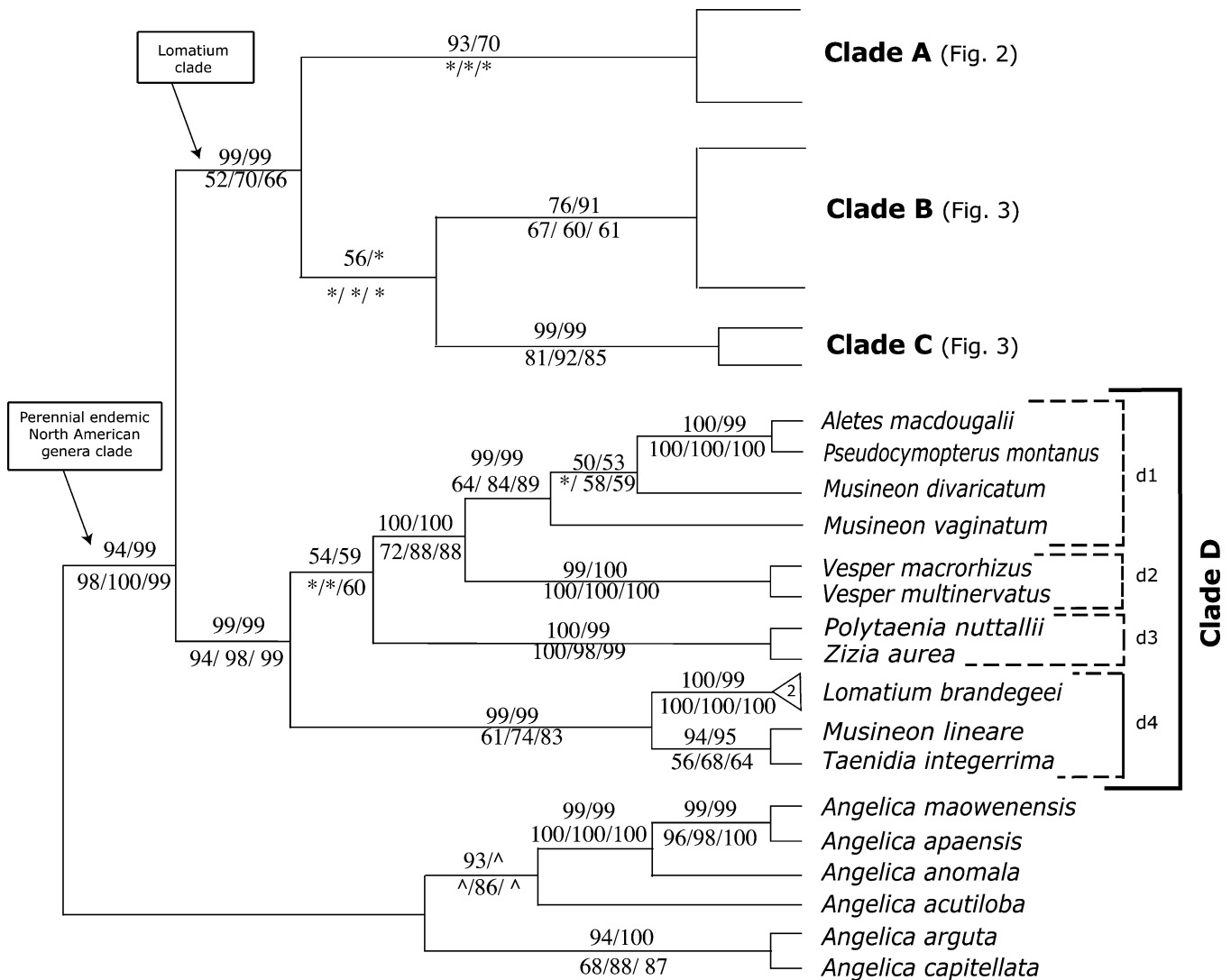


FIG. 1. Majority rule consensus topology from the Bayesian inference partitioned model (BIP) analyses. Values above branches are posterior probabilities, and follow the pattern: BIP / 1-model Bayesian analysis. Values below the branches are bootstrap values, and follow the pattern: MP with indels scored as missing / MP with indels rescored / ML. Asterisks (\*) mark analyses in which the indicated clade collapses into a polytomy, and caret symbols (^) mark analyses in which the clade is resolved with a topology differing from the BIP topology shown. Lettered clades and subclades are discussed in the text. Where multiple individuals of the same taxon were recovered as monophyletic they have been condensed into a triangle with the number of individuals that comprise that clade presented in the triangle.

BIP consensus topology are presented in Fig. 4. Stochastic mapping reconstructions of all internal nodes for each of these characters are presented in Appendix S2. The BIP majority-rule consensus topology, with the internal nodes numbered according to SIMMAP output node codings, is presented in Fig. S1. Individual ancestral character reconstructions showing internal probabilities for each character are presented in Appendix S3.

Some characters clearly evolve more rapidly than others, but these patterns differ among the major clades. Characters that evolve quickly across all clades include root structure (Fig. 4, character R), leaflet structure (character S), and leaflet division above the primary level (characters 2–4). Fruit structure (character F) remains relatively constant (with some exceptions) in Clades B and C, whereas in Clades A and D this trait is more homoplastic. In contrast, plant habit (character H) is more stable in Clade A than in Clade B. Leaflet arrangement (character N) and primary

leaflet divisions (character 1) change at a moderate frequency throughout the tree. Overall, Clade D exhibits the highest level of morphological variation with respect to the number of taxa it contains.

To identify the extent of overlap among overall morphologies for species in the group, we grouped taxonomic exemplars (tips in the phylogeny) on the basis of unique combinations of states for all nine characters. Of the 96 specific and infraspecific taxa of the PENA clade that were sampled for this study, 18 shared the same distribution of character states with at least one other taxon, while 78 had a unique combination of states. These data are presented in the supplemental Appendix S4.

#### DISCUSSION

**Morphology and Classification**—The morphology of the PENA clade has presented a conundrum for their classification

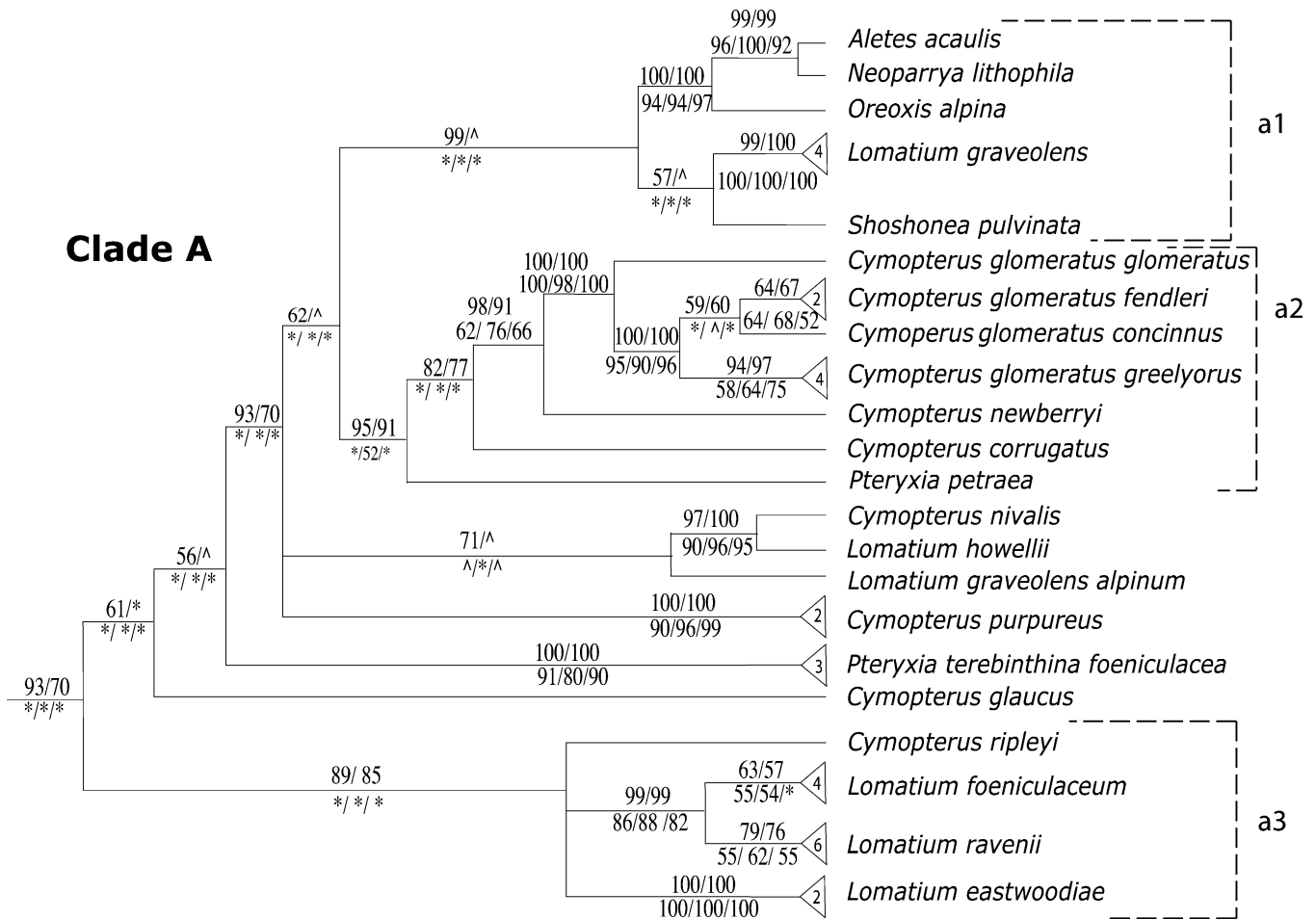


FIG. 2. Majority rule consensus from the Bayesian inference partitioned model (BIP) analyses showing complete sampling of Clade A from Fig. 1. All label formatting and abbreviations are as described for Fig. 1.

(Coulter and Rose 1900; Mathias 1930, 1938; Schlessman 1984; Plunkett et al. 1996; Sun and Downie 2004, 2010a, b; Sun et al. 2004); even Cronquist in the *Intermountain Flora*, went as far as describing “the taxonomic definition of *Cymopterus*

[as] a vexed question” (Cronquist et al. 1997). Although species often have clearly differentiated morphologies (Appendix S4), major clades do not, and homoplasy is rampant in many characters (Sun and Downie 2010a). We

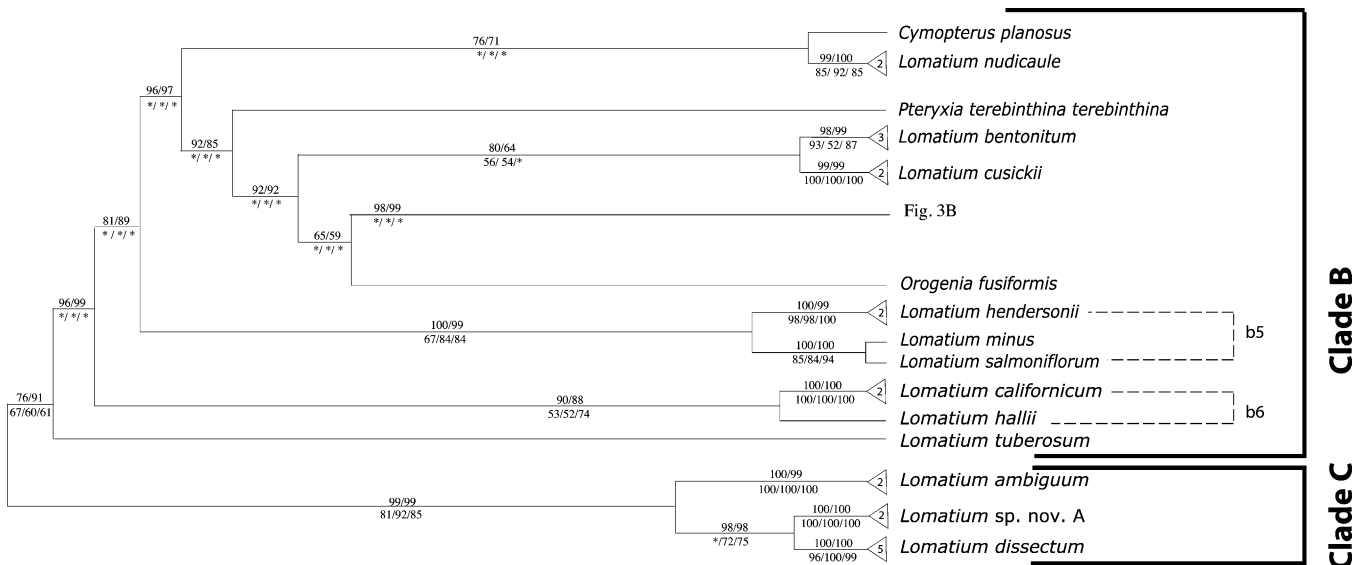


FIG. 3A. Majority rule consensus from the Bayesian inference partition (BIP) model analyses showing part of Clade B and complete sampling of Clade C from Fig. 1. All label formatting and abbreviations are as described for Fig. 1.

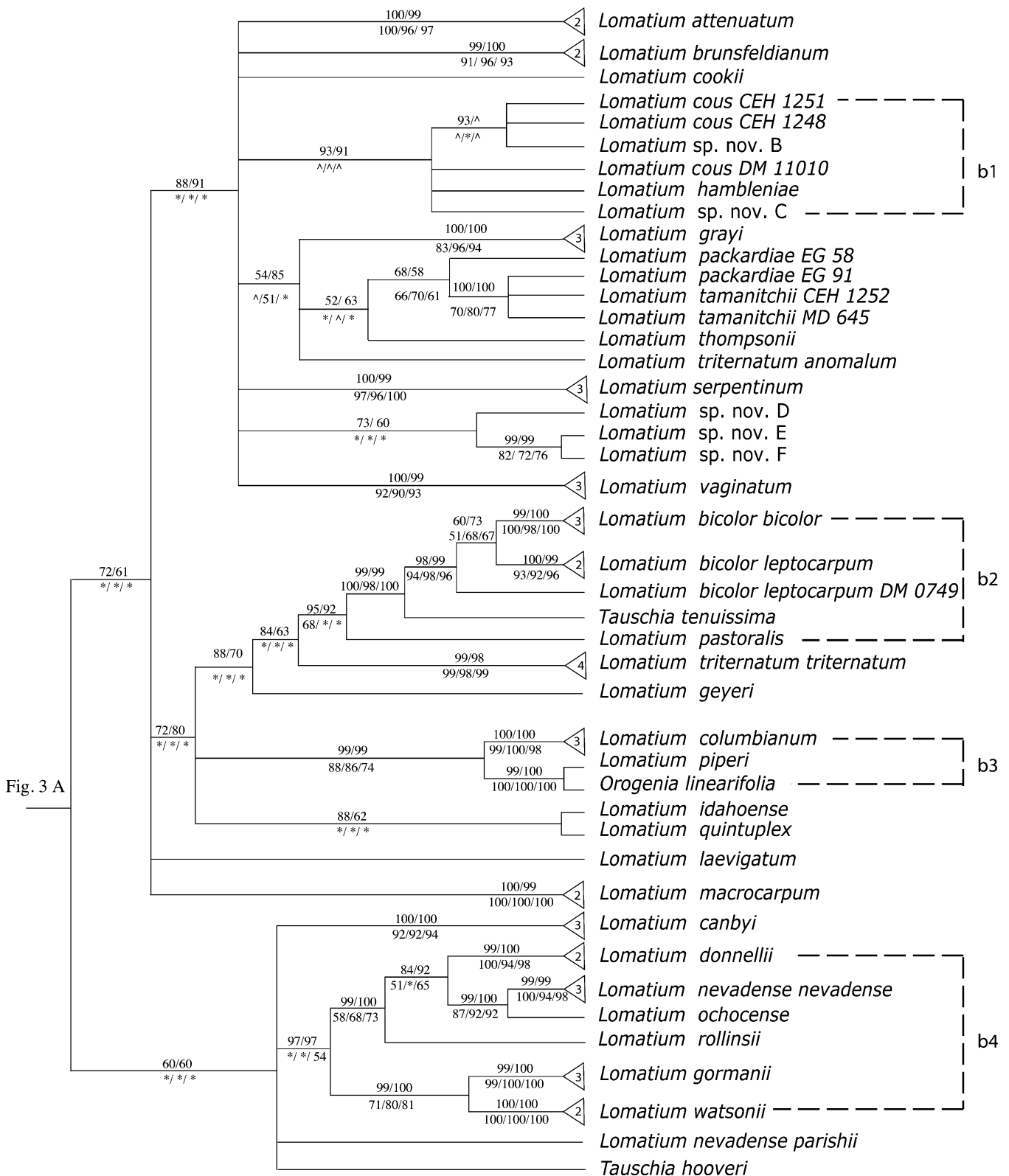


FIG. 3B. Majority rule consensus from the Bayesian inference partition (BIP) model analyses showing complete sampling of the remainder of Clade B from Fig. 3A. All label formatting and abbreviations are as described for Fig. 1.

used stochastic character mapping and simple visualization of character states on the tips of the phylogeny to examine the congruence between evolutionary history and the taxonomic use of nine morphological traits that have been important for

defining taxa in the PENA clade. Our results are largely congruent with those of Sun and Downie (2010a), which followed a similar line of inquiry using a different suite of characters and methods.

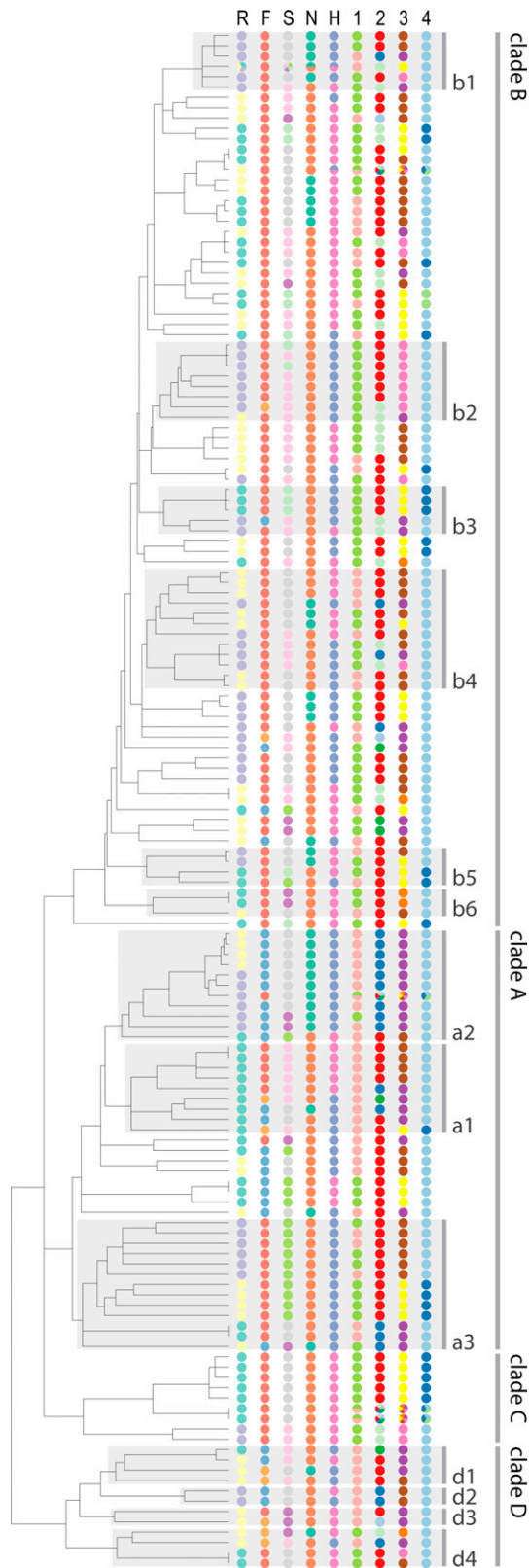


FIG. 4. Majority-rule consensus topology of the Bayesian partitioned analysis (BIP), with states for all morphological characters plotted for all tips. Clade labels correspond to those used in Figs. 1–3. Legends for colors are presented in Appendix S4. Pies with multiple equal-sized pieces represent unknown states for those taxa. Column labels represent characters as follows: R = roots; F = fruits; S = leaflet structure; N = leaflet arrangement; H = habit; 1 = primary leaf divisions; 2 = secondary leaf divisions; 3 = tertiary leaf divisions; 4 = quaternary leaf divisions.

Of the nine morphological characters we analyzed, none stand out as particularly well-suited for the identification of major clades in the group, as many or all character states are represented for most major clades (Fig. 4). Although this study sampled less than half of the known species in the PENA clade, one general observation that is likely to hold with the addition of more taxa is that morphological change in this group is both rapid and complex. This complexity is likely only to increase as the inclusion of more species reveals new instances of parallel character change. Compared to Sun and Downie (2010a), who examined 123 taxa of North American Apioideae, we have included more species of *Lomatium* and fewer species of *Cymopterus* and other genera. Despite differences in characters analyzed, species sampled, and methodology, the general patterns observed here are essentially similar to the findings of Sun and Downie (2010a): we identify (1) high levels of homoplasy in nearly all characters, (2) dynamic morphological change over short phylogenetic depths, and (3) no morphological synapomorphies for any named clades.

The ancestral state reconstructions illustrate high rates of change in PENA clade morphology. Differences among these rates may have implications for systematics, as characters evolving at fast rates are generally not useful for distinguishing broadly related groups, but may be useful in the development of species-specific tools such as synoptical keys. As yet, general fruit structure (Fig. 4, character F) seems to be one of the most phylogenetically conserved traits that we have examined but it certainly does not provide synapomorphies for any currently recognized taxa. Root characteristics (character R), such as those used by Schlessman (1984) to define the tuberous lomatiums, are even less well-suited to diagnosing clades, as are fine leaf structural characteristics (characters 2–4) and plant habit (character H). Primary leaf divisions and leaflet arrangement (characters 1, N) may be valuable in diagnosing some smaller clades, and when combined with other leaf division characteristics, may be valuable at deeper levels.

Although synapomorphies are lacking, many of the morphological characters examined herein do at least represent apomorphies for shallow clades. All the species of clade b1 (Figs. 3, 4), for instance, which is a species complex involving *Lomatium cous*, have flattened fruits, leaves with fern-like leaflets that lack quaternary leaf divisions, and tuberous roots (assuming that these leaflet and root morphologies also apply to the otherwise similar *Lomatium* sp. nov. C, which could not be scored for this study). These features, however, are not unique to this clade, but also extend (at least) to *Lomatium hendersonii* of subclade b5. A similar example is offered by subclade b2 (Figs. 3, 4), which contains *Lomatium bicolor* var. *leptocarpum*, *L. pastoralis*, and one species of *Tauschia*. These species have pinnate leaves that lack quaternary leaf divisions and have a 3-dimensional structure, and all are acaulescent. However, *Orogenia linearifolia* from clade b3 also shares these characters. It is worth noting that *O. linearifolia* may easily be distinguished from all species of clade b2 on the basis of a variety of other characters, especially overall plant size. Regardless, the failure of the examined characters to serve as synapomorphies stands. Other labeled subclades show similar patterns.

Our failure to identify morphological synapomorphies is not to suggest that these clades are not morphologically cohesive. In the case of the *L. cous* complex (subclade b1), these species are all morphologically similar, as are the species of the *L. bicolor* clade (subclade b2). Indeed, this pattern follows for other identified subclades of clade B. Species of subclade b4 are generally acaulescent herbs of mid-elevations in the sagebrush steppe, with similar leaf and fruit morphologies. Subclade b5 contains specialists of talus slopes and rocky outcrops from the Blue Mountains region of eastern Oregon, which have distinctive foliar and inflorescence morphologies. Subclade b6 species have similar leaf architectural and inflorescence features.

Subclade a1 contains high-elevation, xeric-adapted species of the central Intermountain region, which generally have a thick epidermis, and rugged, reduced leaves and inflorescences, while subclade a2 contains the infraspecific taxa of *Cymopterus glomeratus* and *Lomatium concinnum* (as *C. glomeratus* var. *concinus* in Fig. 2), whose congruent morphology is discussed below. Subclade a3 contains *L. foeniculaceum* and *L. ravenii*, which are so similar in size and morphology they are frequently confused, and *L. eastwoodiae*, whose similarity to the others is less obvious. The placement of *Cymopterus ripleyi* in this clade is somewhat surprising, as this species is entirely morphologically divergent from the others, but this clade is only poorly to moderately supported and *C. ripleyi* has been placed with morphologically similar taxa in other analyses (Sun and Downie 2004, 2010a, b), which are not included here. Clade C consists of species related to *L. dissectum*, all of which are large, caulescent plants with finely divided leaves that thrive in disturbed hill slopes. Similarly, the subclades of Clade D each have a set of traits that unite their species.

The challenge in defining taxonomic units in the PENA clade based on morphology has less to do with entirely chaotic patterns of character change than it does with “character recycling.” For any single character state examined here (and many combinations of these as well), distantly related taxa can be found that exemplify it. The use of such traits to define taxa has resulted in many cases of non-monophyletic classifications in plants (Knapp 2002; Eriksson et al. 2003; Sun and Downie 2010a; Clark et al. 2012; Degtjareva et al. 2013; Smith and Clark 2013). Resolving these issues often involves exploring other potential characteristics to identify synapomorphies for large clades, as well as assessing taxonomic circumscriptions to define monophyletic, morphologically diagnosable taxa (Al-Shehbaz et al. 2006; Hall et al. 2011; Liu et al. 2012). In the PENA clade, many characters remain underexplored within a phylogenetic context, including fruit characters such as oil tubes and dehiscence mechanisms (although see Sun and Downie 2010a), floral traits, and epidermal structures such as trichomes or glands (Hartman and Larson 2011).

In addition, the utility of biochemical diversity, internal anatomy, and developmental sequences of complex organs such as leaves and inflorescences is virtually undocumented with respect to their utility for evolutionary classifications in this group. These features should be examined in future studies.

**Phylogenetic Patterns and Congruence with Previous Studies**—We recognize four major clades within the PENA clade (Clades A–D, Figs. 1–3). Relationships within these

clades are moderately well-supported, at least by the BIP analysis, but relationships among them are only weakly resolved, indicating the potential for their composition and arrangement to change with the addition of data. Despite issues of low resolution for the MP and ML analyses, the Bayesian phylogenies show increased resolution when compared to previous studies (Sun and Downie 2004, 2010a; Sun et al. 2004), and similar resolution to the Bayesian trees of Sun and Downie (2010b), although the topology presented by that study differs from the one presented here.

Clade A received moderate support from the BIP analysis. This clade was also observed in one previous study (Sun and Downie 2010b), although its subclades a1 and a2 have been observed, in part, in several others (Sun and Downie 2004, 2010a; Sun et al. 2004). Subclade a3 corresponds to the *L. foeniculaceum* clade of Carlson et al. (2011a, b). Clade A contains most of the *Cymopterus* species included in this study.

Clade B consists primarily of *Lomatium* species, as well as species from several other genera, and is moderately supported by the BIO and MP with indels analyses. Here we present a more thorough sampling of *Lomatium* species than any previous study (Sun and Downie 2004, 2010a, b; Sun et al. 2004). Thus, although our Clade B corresponds to clade 2 of Sun and Downie (2010a, b), many of the subclades that we recognize in Clade B cannot be observed in those studies because the taxa they contain are absent. Within our trees, deep relationships in Clade B are moderately or weakly supported (by the BIP analyses only), but many relationships defining shallower clades are strongly supported across methods. As discussed above, the morphology and ecology of these subclades is cohesive, suggesting the possibility that they may represent real evolutionary groups. Additional sampling will be required to better assess this.

The two constituent species of the genus *Orogenia* were also placed in Clade B. This genus has previously been resolved as a monophyletic group (Sun and Downie 2010a, b), and this was supported by the unique morphology of its species. Here, however, *Orogenia* is resolved as polyphyletic (Fig. 3). This difference may be due to the use of different genetic loci in this study and the inclusion of additional *Lomatium* taxa.

The phylogenetic backbone of Clade B (Fig. 4) displays a pattern that is suggestive of a rapid radiation: many short branches concentrated in a narrow slice of time. This implies that this clade may have originated in a burst of diversification (Downie et al. 2002; Sun et al. 2004; Sun and Downie 2010b). It is certainly concordant to observe that *Lomatium*, the most species-rich genus in the PENA clade, is (with a few exceptions) nearly entirely contained within Clade B in our trees.

Clade C contains only three species (including a previously undescribed species from central Washington state), and it is strongly supported by the Bayesian analyses and moderately so by the MP and ML bootstraps. The position of *L. ambiguum* in Sun and Downie (2004, 2010a) and Sun et al. (2004), is consistent with the position of Clade C in our trees. *Lomatium dissectum* was not included in Sun and Downie (2010b) and *L. ambiguum* was at the base of clade 2 of Fig. 3 in the Bayesian topology of Sun and Downie (2010b).

Clade D contains species from several polyphyletic genera and is strongly supported by all analyses. This clade



corresponds to clade 3 from Sun and Downie (2010a, b) and also to an unlabeled clade in Sun and Downie (2004). Several subclades of Clade D appear as elements of a polytomy in Sun et al. (2004). Relationships within this clade are largely congruent with these previous studies. *Lomatium brandegeei*, is placed here, as it was in Sun and Downie (2004, 2010a, b). Clade D also includes *Pseudocymopterus*, *Polytaenia*, *Zizia*, and *Vesper*. *Vesper* is a recently described genus that consists of six species previously classified as *Cymopterus*, and it is one of the few identified subclades within the PENA clade that is united by several morphological synapomorphies (Coulter and Rose 1900; Mathias 1930; Hartman 2000; Sun and Downie 2010a; Hartman and Nesom 2012). *Thaspium*, *Zizia*, and *Polytaenia* each was monophyletic in Sun and Downie (2004, 2010a, b) and Sun et al. (2004), but their sampling in the current study (one exemplar each) precludes further assessment of monophyly.

Relationships in Clade D are more strongly supported than they are within other parts of the PENA clade, and this pattern holds across studies and analysis methods (Sun and Downie 2004, 2010a, b; Sun et al. 2004). This may be due to (1) differences in rates of molecular evolution among these clades for the sampled markers, (2) slower rates of lineage diversification in Clade D than elsewhere, which have allowed more time for the fixation of informative mutations, or (3) a lower prevalence of processes that may be contributing to confounding phylogenetic signal in Clade D than elsewhere, such as lateral gene transfer. The observation that divergences in Clade D are relatively deep compared to the rest of the tree (Fig. 4) supports a role for hypothesis 2, longer intervals between lineage splitting events. This is further corroborated by the corresponding long branches in this clade in other studies (Sun and Downie 2004, 2010a, b; Sun et al. 2004), and the higher degree of morphological variation over narrower phylogenetic spans in Clade D than elsewhere within the PENA clade. This does not preclude a role for lateral gene transfer however, as suggested by Schlessman (1984).

In general, we corroborate the findings of previous studies (Downie et al. 2002; Sun and Downie 2004, 2010a, b; Sun et al. 2004), and the premonitions of others (Theobald 1971; Mathias 1930, 1938; Cronquist et al. 1997), that morphologically-defined taxa in the PENA clade are largely not monophyletic. Of the ten genera from which we sampled two or more species, all except *Vesper* were resolved as either para- or polyphyletic. Eight species and infraspecific taxa for which we included more than a single individual were also not recovered as monophyletic.

In many of the species cases (e.g. *Lomatium cous* and *L. packardiae* in Fig. 3), the support for non-monophyly was weak, suggesting that phylogenetic error or population-level genetic processes such as incomplete lineage sorting may be responsible. Within *Lomatium nevadense*, *L. triternatum*, and *Pteryxia terebinthina*, however, lineages corresponding to morphologically diagnosable, recognized subspecific taxa were placed with strong support in distant locations within the phylogeny. The simplest explanation for this is that the similar morphologies used to combine these species' nominate varieties and subspecies are probably the product of parallel evolution rather than evolutionary relatedness. A straightforward solution would involve simply elevating these infrageneric taxa to the level of species, which has

also been suggested by Lesica and Kittelson (2013) based on morphological and ecological evidence for *L. triternatum* var. *anomalum*.

In the case of *P. terebinthina*, we find phylogenetic support for Sun et al.'s (2008) hypothesis recognizing the varieties *P. terebinthina* var. *terebinthina* (Fig. 3) and *P. terebinthina* var. *foeniculacea* (Fig. 2) as distinct and cohesive lineages. These varieties are also ecologically differentiated, with *P. terebinthina* var. *terebinthina* typically found on sand dunes at lower elevations in the Columbia basin of central Oregon and Washington while *P. terebinthina* var. *foeniculacea* grows on rocky substrates and has a distribution that stretches from the southern half of Montana west to central Idaho with disjunct populations in California, Oregon, and Washington (Hitchcock and Cronquist 1973; Sun et al. 2008).

**Recognition of *Cymopterus glomeratus* var. *concinnum***—*Lomatium concinnum* is a morphologically distinctive, narrowly endemic species, restricted to three counties in west central Colorado. It has vegetative and floral characteristics that resemble the varieties of *C. glomeratus* (Mathias 1938), although these species do differ, most notably through its production of flattened fruits that lack dorsal wings in *L. concinnum* (Fig. 5). Phylogenetically, *L. concinnum* has been placed in a position nested among the varieties of *C. glomeratus* by this study (Fig. 2, clade a2) and that of Sun and Downie (2004). The flattened fruit, devoid of dorsal wings of *L. concinnum* is, in fact, the only reason for its placement within the genus *Lomatium* (Mathias 1938). The treatment of this species in *Lomatium* alongside the varieties of *C. glomeratus* (which it otherwise closely resembles), illustrates the inadequacy of this fruit character for defining evolutionary units in this group.

Sun et al. (2005) recognized *C. glomeratus* as a single species with no varieties, a decision that was based in part on issues of non-identifiability among them. Here, however, we choose to recognize these varieties on the basis that (1) the recognition at the species level of *L. concinnum* renders a unified *C. glomeratus* paraphyletic and (2) there appears to be some phylogenetic support for the differentiation of (at least some of) the varieties of *C. glomeratus* (Fig. 2, clade a2). We propose that these nominate varieties may provide a useful starting point for taxonomic concepts defining morphologically diagnosable, independently evolving lineages in this group. We begin this process by proposing nomenclatural changes assigning *L. concinnum* to the genus *Cymopterus* and make the combination of *C. acaulis* var. *greeleyorum* into *C. glomeratus*.

#### TAXONOMIC TREATMENT

***Cymopterus glomeratus* var. *concinnum*** (Osterh.) R. L. Hartman, comb. et stat. nov. *Cogswellia concinna* Osterh., *Muhlenbergii* 8: 44. 1912. *Lomatium concinnum* (Osterh.) Mathias, *Ann. Missouri Bot. Gard.* 25: 276. 1937.—TYPE: U. S. A. Colorado, Delta Co.: Paonia, G. E. Osterhout 4515 (holotype: RM!; isotype: RM!).

This species is restricted to southeastern Delta, eastern Montrose, and northern Ouray counties in adobe hills and plains on rocky soils derived from Mancos Formation shale associated with *Artemisia tridentata* Nutt., *Atriplex confertifolia* (Torr. & Frém.) S. Watson, *Sarcobatus vermiculatus*



FIG. 5. Specimen on the left is *Cymopterus glomeratus* var. *fendleri*; on the right is *Cymopterus glomeratus* var. *concinnus*.

(Hook.) Torr., or *Quercus gambelii* Liebm., from 1,680–2,130 m (Spackman et al. 1997). *Cymopterus glomeratus* var. *fendleri* is found on sandy soils in the foothills with *Pinus edulis* Engelm. and *Juniperus osteosperma* (Torr.) Little along the western portion of Colorado and adjacent Utah.

***Cymopterus glomeratus* var. *greeleyorus*** (J. W. Grimes & P. L. Packard) R. L. Hartman, comb. nov. *Cymopterus acaulis* (Pursh) Raf. var. *greeleyorum* J. W. Grimes & P. L. Packard, Brittonia 33: 430. 1981. —TYPE: U. S. A. Oregon. Malheur Co.: Rockville area, just s. of Leslie Gulch road junction with Succor Creek road, T26S R46E S16, 2 May 1976, P. L. Packard 76–3, (holotype: NY digital image!)

This variety is restricted to barren, tan, volcanic ash outcrops of the Sucker Creek formation in the Succor Creek region of Malheur County, Oregon.

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- APPENDIX 1. Species names, herbarium accession numbers, vouchers, collection localities and GenBank accession numbers for individuals used in this study. NA refers to sequences obtained directly from GenBank. GenBank numbers are on the order ITS, *rpl32-trnL*UAG, *rps16* intron, and *matK*. A dash (-) indicates the sequence was not obtained for that accession. Accession numbers in bold are ones not newly generated for this study.
- Aletes acaulis* (Torr.) J. M. Coult. & Rose. U. S. A. Colorado: Boulder Co., T. Hogan 1739 (RM 577080), KF619603, KF619879, KF619742, KF620016. *Aletes macdougalii* J. M. Coult. & Rose. Arizona: Coconino Co., C. E. Hinchliff 1293 (CIC 040906), KF619604, KF619880, KF619743, KF620017. *Angelica acutiloba* (Siebold & Zucc.) Kitag. NA, NA, NA, **AB569093**, **GU395095**, **JF279395**, **AB697585**. *Angelica anomala* Avé-Lall. NA, NA, NA, **JX022893**, **GU395097**, **JF279397**, **JN033545**. *Angelica apaensis* Shan & C. Q. Yuan. NA, NA, NA, **JX022898**, **GU395098**, **JF279398**, **FJ986060**. *Angelica arguta* Nutt. Oregon: Harney Co., D. Mansfield 12-718 (CIC 043702), KF619605, KF619881, KF619744, -. *Angelica capitellata* Spalik, Reduron & S. R. Downie. Oregon: Harney Co., D. Mansfield 12-719 (CIC 043701), KF619735, KF620009, KF619873, KF620104. *Angelica maowenensis* C. C. Yuan & Shan. NA, NA, NA, **JX022924**, **GU395106**, **JF279412**, -. *Cymopterus corrugatus* M. E. Jones. Oregon: Malheur Co., K. Carlson 004 (CIC 035388), **HQ426079**, **HQ426130**, **HQ426105**, -. *Cymopterus glaucus* Nutt. Idaho: Elmore Co., D. Mansfield 11-019, KF619613, KF619888, KF619751, KF620019. *Cymopterus glomeratus* var. *concinus* (Osterh.) Mathias. Colorado: Delta Co., C. E. Hinchliff 1323 (CIC 041348), KF619643, KF619916, KF619779, KF620038. *Cymopterus glomeratus* var. *fendleri* (A. Gray) R. L. Hartm. Arizona: Navajo Co., C. E. Hinchliff 1286B (CIC 040915), KF619608, KF619883, KF619746, -; Colorado: Mesa Co., C. E. Hinchliff 1314 (CIC 040930), KF619607, KF619882, KF619745, KF620018. *Cymopterus glomeratus* Raf. var. *glomeratus*. Idaho: Canyon Co., D. Mansfield 07002 (CIC 034363), **HQ426080**, **HQ426131**, **HQ426106**, -. *Cymopterus glomeratus* var. *greeleyorus* (J. W. Grimes & P. L. Packard) R. L. Hartman. Oregon: Malheur Co., D. Mansfield 10-005 (CIC 039181), KF619885, KF619748, -; Oregon: Malheur Co., J. Raino 46 (CIC 039906), KF619609, KF619884, KF619747, -; Oregon: Malheur Co., E. George 092 (CIC 039940), KF619612, KF619887, KF619750, -; Oregon: Malheur Co., E. George 087 (CIC 039945), KF619611, KF619886, KF619749, -. *Cymopterus newberryi* (S. Watson) M. E. Jones. Arizona: Coconino Co., C. E. Hinchliff 1299 (CIC 040927), KF619614, KF619889, KF619752, KF620020. *Cymopterus nivalis* S. Watson. Oregon: Harney Co., D. Mansfield 12-718 (CIC 043702), KF619615, KF619890, KF619753, KF620021. *Cymopterus planosus* (Osterh.) Mathias. Colorado: Delta Co., C. E. Hinchliff 1322 (CIC 040916), KF619617, KF619891, KF619754, KF620022. *Cymopterus purpureus* S. Watson. New Mexico: Rio Arriba Co., C. E. Hinchliff 1279 (CIC 040925), KF619618, KF619892, KF619755, KF620023; Utah: Emery Co., C. E. Hinchliff 1312 (CIC 040928), KF619619, KF619893, KF619756, KF620024. *Cymopterus ripleyi* Barneby var. *ripleyi*. Nevada: Lincoln Co., C. E. Hinchliff 1310 (CIC 041345), KF619620, KF619894, KF619757, KF620025. *Lomatium ambiguum* (Nutt.) J. M. Coult. & Rose. Idaho: Gem Co., J. F. Smith 9561 (SRP 44525), KF619622, KF619896, KF619759, -; Idaho: Idaho Co., C. E. Hinchliff 1273 (CIC 041353), KF619621, KF619895, KF619758, KF620026. *Lomatium attenuatum* Evert. Montana: Beaverhead Co., C. E. Hinchliff 1349 (CIC 043319), KF619623, KF619898, KF619760, -; Wyoming: Park Co., E. Evert 16359 (RM 577251), KF619624, KF619897, KF619761, -. *Lomatium bentonitum* K. M. Carlson & D. H. Mansfield. Oregon: Malheur Co., E. George 089 (CIC 039943), KF619625, KF619899, KF619762, KF620027; Oregon: Malheur Co., D. Mansfield 07015 (CIC034356), **HQ426090**, **HQ426140**, **HQ426116**, -; Oregon: Malheur Co., D. Mansfield 07016 (CIC 034355), **HQ426091**, **HQ426141**, **HQ426117**, -. *Lomatium bicolor* (S. Watson) J. M. Coult. & Rose var. *bicolor*. Idaho: Franklin Co., B. Moseley 1768 (ID 107870), KF619626, KF619898, KF619763, -; Idaho: Franklin Co., R. McNeill 83 (ID 132553), KF619627, KF619901, KF619764, -; Idaho: Oneida Co., B. Baker 075-038 (ID 156442), KF619628, KF619902, KF619765, -. *Lomatium bicolor* var. *leptocarpum* (Torr. & A. Gray) Jeps. Idaho: Elmore Co., D. Mansfield 07049 (CIC 034335), **HQ426087**, **HQ426138**, **HQ426113**, -; Idaho: Adams Co., D. Mansfield 07026 (CIC 034346), **HQ426086**, **HQ426137**, **HQ426112**, -; Idaho: Washington Co., E. George 064 (CIC 039892), KF619629, KF619903, KF619766, KF620028. *Lomatium brandegeei* (J. M. Coult. & Rose) J. F. Macbr. Washington: Chelan Co., C. E. Hinchliff 1327 (CIC 041351), KF619631, KF619904, KF619767, KF620029; Washington: Kittitas Co., D. Mansfield 11-477, (CIC 041532), KF619632, KF619905, KF619768, KF620030. *Lomatium brunsfeldianum* Kempter & R. P. McNeill. Idaho: Idaho Co., S. Walker 218 (ID 133382), KF619634, KF619907, KF619770, -; Idaho: Kootenai Co., C. R. Bjork 6481 (ID 122120), KF619633, KF619906, KF619769, -. *Lomatium californicum* (Nutt.) Mathias & Constance. Oregon: Josephine Co., R. Helliwell 3949 (CIC 039924), KF619636, KF619909, KF619772, KF620031; Oregon: Jackson Co., J. T. Duncan 06 (CIC 041667), KF619635, KF619908, KF619771, KF620032. *Lomatium canbyi* (J. M. Coult. & Rose) J. M. Coult. & Rose. Idaho: Owyhee Co., E. George 028 (CIC 039904), KF619638, KF619912, KF619774, KF620035; Washington: Yakima Co., C. E. Hinchliff 1243 (CIC 041460), KF619637, KF619910, KF619773, KF620034; Oregon: Malheur Co., E. George 086 (CIC 039946), KF619639, KF619911, KF619775, KF620033. *Lomatium columbianum* Mathias & Constance. Oregon: Wasco Co., C. E. Hinchliff 1262 (CIC 041356), KF619640, KF619913, KF619776, KF620036; Washington: Klickitat Co., M. Darrach 623 (CIC 042008), KF619641, KF619914, KF619777, KF620037; Washington: Klickitat Co., C. E. Hinchliff 1265 (CIC 041352), KF619642, KF619915, KF619778, -. *Lomatium cookii* Kagan. Oregon: Josephine Co., R. Helliwell 3951 (CIC 039919), KF619644, KF619917, KF619780, KF620039. *Lomatium cous* (S. Watson) J. M. Coult. & Rose. Oregon: Umatilla Co., D. Mansfield 11-010, (CIC 040130), KF619647,

KF619920, KF619783, -; Oregon: Morrow Co., C. E. Hinchliff 1251 (CIC 040910), KF619645, KF619918, KF619781, KF620041; Washington: Whitman Co., C. E. Hinchliff 1248 (CIC 041470), KF619646, KF619919, KF619782, KF620040. *Lomatium cusickii* (S. Watson) J. M. Coult. & Rose. Idaho: Valley Co., J. Handley 2430 (CIC 042724), KF619649, KF619922, KF619785, -; Idaho: Idaho Co., B. E. Nelson 50572 (CIC 042753), KF619648, KF619921, KF619784, -. *Lomatium dissectum* (Nutt.) Mathias & Constance. Oregon: Jackson Co., J. T. Duncan 11 (CIC 041663), KF619652, KF619925, KF619788, -; Oregon: Douglas Co., R. Helliwell 3957 (CIC 044305), KF619654, KF619927, KF619790, -; Idaho: Washington Co., E. George 059 (CIC 039898), KF619653, KF619926, KF619789, KF620042; Washington: Asotin Co., C. E. Hinchliff 1249 (CIC 040923), KF619650, KF619923, KF619786, -; Arizona: Coconino Co., C. E. Hinchliff 1296 (CIC 040902), KF619651, KF619924, KF619787, KF620043. *Lomatium donnellii* (J. M. Coult. & Rose) J. M. Coult. & Rose. Oregon: Jefferson Co., C. E. Hinchliff 1258 (CIC 040912), KF619656, KF619929, KF619792, KF620044; Oregon: Wheeler Co., C. E. Hinchliff 1254 (CIC 040920), KF619655, KF619928, KF619791, KF620045. *Lomatium eastwoodiae* (J. M. Coult. & Rose) J. F. Macbr. Colorado: Mesa Co., C. E. Hinchliff 1319 (CIC 041347), KF619657, KF619930, KF619793, KF620046; Colorado: Mesa Co., C. E. Hinchliff 1317 (CIC 04929), KF619658, KF619931, KF619794, -. *Lomatium foeniculaceum* (Nutt.) J. M. Coult. & Rose var. *macdougalii* (J. M. Coult. & Rose) Cronquist. Nevada: Lincoln Co., C. E. Hinchliff 1306 (CIC 040903), KF619659, KF619932, KF619795, KF620047; Idaho: Canyon Co., D. Mansfield 07-001 (CIC 034364), KF619660, KF619933, KF619796, -. *Lomatium foeniculaceum* (Nutt.) J. M. Coult. & Rose var. *fimbriatum* (W. L. Theobald) B. Boivin. Oregon: Malheur Co., K. Carlson 002 (CIC 035387), HQ426076, HQ426127, HQ426102, -. *Lomatium foeniculaceum* (Nutt.) J. M. Coult. & Rose var. *foeniculaceum*. Montana: Stillwater Co., R. Hartman 85466 (RM 865326), HQ426077, HQ426128, HQ426103, -. *Lomatium geyeri* (S. Watson) J. M. Coult. & Rose. Washington: Yakima Co., C. E. Hinchliff 1244 (CIC 041478), KF619661, KF619934, KF619797, KF620048. *Lomatium gormanii* (Howell) J. M. Coult. & Rose. Washington: Yakima Co., C. E. Hinchliff 1238 (CIC 041453), KF619663, KF619936, KF619799, KF620050; Washington: Walla Walla Co., C. E. Hinchliff 1212 (CIC 041451), KF619664, KF619937, KF619800, -; Washington: Yakima Co., C. E. Hinchliff 1236 (CIC 041475), KF619662, KF619935, KF619798, KF620049. *Lomatium graveolens* var. *alpinum* (S. Watson) Dorn & R. L. Hartm. Nevada: Lincoln Co., C. E. Hinchliff 1307 (CIC 040904), KF619687, KF619959, KF619822, KF620068. *Lomatium graveolens* (S. Watson) Dorn & R. L. Hartm. var. *graveolens*. Idaho: Franklin Co., J. F. Smith 5233 (SRP 028339), KF619665, KF619940, KF619801, KF620051; Idaho: Franklin Co., M. Mancuso 2334 (CIC 032806), KF619666, KF619941, KF619802, KF620052; Idaho: Bear Lake Co., D. Mansfield 12-598, KF619667, KF619938, KF619803, KF620053; Idaho: Bear Lake Co., D. Mansfield 12-663, KF619668, KF619939, KF619804, KF620054. *Lomatium grayi* (J. M. Coult. & Rose) J. M. Coult. & Rose. Washington: Yakima Co., C. E. Hinchliff 1240 (CIC 041459), KF619670, KF619943, KF619806, KF620056; Oregon: Malheur Co., E. George 050 (CIC 039901), KF619669, KF619942, KF619805, KF620055. *Lomatium hallii* (S. Watson) J. M. Coult. & Rose. Oregon: Douglas Co., R. Helliwell 3955 (CIC 039930), KF619671, KF619944, KF619807, KF620057. *Lomatium hambleniae* Mathias & Constance. J. Bent 11-43, KF619672, KF619945, KF619808, KF620058. *Lomatium hendersonii* (J. M. Coult. & Rose) J. M. Coult. & Rose. Oregon: Wheeler Co., C. E. Hinchliff 1257 (CIC 040919), KF619674, KF619947, KF619810, KF620059; Oregon: Crook Co., R. Helliwell 3944 (CIC 039909), KF619673, KF619946, KF619809, -. *Lomatium howellii* (S. Watson) Jeps. Oregon: Josephine Co., R. Helliwell 3959 (CIC 044307), KF619675, KF619948, KF619811, KF620060. *Lomatium idahoense* Mathias & Constance. Idaho: Owyhee Co., D. Mansfield 11-231 (CIC 041525), KF619676, KF619949, KF619812, KF620061. *Lomatium laevigatum* (Nutt.) J. M. Coult. & Rose. Oregon: Wasco Co., C. E. Hinchliff 1261 (CIC 041342), KF619678, KF619950, KF619813, KF620062. *Lomatium macrocarpum* (Hook. & Arn.) J. M. Coult. & Rose. Idaho: Adams Co., D. Mansfield 07032 (CIC 034342), HQ426093, HQ426142, HQ426119, -; Idaho: Ada Co., M. Fisk s. n. (CIC 041521), KF619679, KF619951, KF619814, KF620063. *Lomatium minus* (Rose ex Howell) Mathias & Constance. Oregon: Wasco Co., R. Helliwell 3939 (CIC 039914), KF619680, KF619952, KF619815, KF620064. *Lomatium nevadense* (S. Watson) J. M. Coult. & Rose var. *nevadense*. Nevada: Elko Co., D. Mansfield 11-081 (CIC 041519), KF619682, KF619954, KF619817, -; Idaho: Owyhee Co., E. George 082 (CIC 039897), KF619683, KF619955, KF619818, KF620065; Oregon: Harney Co., D. Mansfield 07295 (CIC 034424), KF619684, KF619956, KF619819, -. *Lomatium nevadense* (S. Watson) J. M. Coult. & Rose var. *parishii* (J. M. Coult. & Rose) Jeps. Arizona: Apache Co., C. E. Hinchliff 1283 (CIC 040914), KF619681, KF619953, KF619816, KF620066. *Lomatium nudicaule* (Pursh) J. M. Coult. & Rose. Idaho: Washington Co., E. George 065 (CIC 039895), KF619685, KF619957,

KF619820, -; Oregon: Josephine Co., R. Helliwell 3950 (CIC 039921), KF619686, KF619958, KF619821, KF620067. *Lomatium ochocense* Helliwell & Constance. Oregon: Crook Co., R. Helliwell 3961 (CIC 044308), KF619688, KF619960, KF619823, KF620069. *Lomatium packardiae* Cronquist. Oregon: Malheur Co., E. George 058 (CIC 039889), KF619689, KF619961, KF619824, KF620071; Oregon: Malheur Co., E. George 091 (CIC 039941), KF619690, KF619962, KF619825, KF620070. *Lomatium pastoralis* D. H. Wagner ex M. E. Darrach & D. H. Wagner. Oregon: Umatilla Co., M. Darrach 675 (CIC 042000), KF619691, KF619963, KF619826, KF620072. *Lomatium piperi* J. M. Coult. & Rose. Oregon: Crook Co., R. Helliwell 3941 (CIC 039912), KF619692, KF619964, KF619827, KF620073. *Lomatium quintuplex* Schlessman & Constance. Washington: Yakima Co., C. E. Hinchliff 1232 (CIC 041468), KF619693, KF619965, KF619828, KF620074. *Lomatium ravenii* Mathias & Constance var. *paiutense* K. Carlson & Mansfield. Oregon: Malheur Co., K. Carlson 76 (CIC 035486), KF619694, KF619966, KF619829, KF620075; Oregon: Malheur Co., K. Carlson 006 (CIC 035391), HQ426084, HQ426135, HQ426110, -; Oregon: Malheur Co., K. Carlson 005 (CIC 035390), HQ426083, HQ426134, HQ426109, -; Oregon: Malheur Co., K. Carlson 003, KF619695, KF619967, KF619830, -; Oregon: Malheur Co., K. Carlson 007, KF619696, KF619968, KF619831, -. *Lomatium ravenii* Mathias & Constance var. *ravenii*. California: Lassen Co., B. Ertter 19820 (CIC 039493), HQ426085, HQ426136, HQ426111, -. *Lomatium rollinsii* Mathias & Constance. Idaho: Idaho Co., C. E. Hinchliff 1274 (CIC 040924), KF619697, KF619969, KF619832, KF620076. *Lomatium salmoniflorum* (J. M. Coult. & Rose) Mathias & Constance. Washington: Whitman Co., C. E. Hinchliff 1209 (CIC 041450), KF619698, KF619970, KF619833, KF620077. *Lomatium serpentinum* (M. E. Jones) Mathias. Idaho: Adams Co., R. Hartman 64247 (CIC 042725), KF619701, KF619971, KF619834, -; Idaho: Adams Co., J. Handley 4700 (CIC 042754), KF619700, KF619973, KF619836, -; Idaho: Nez Perce Co., C. E. Hinchliff 1210 (CIC 041449), KF619699, KF619972, KF619835, KF620078. *Lomatium* sp. nov. A. Washington: Chelan Co., M. Darrach 649 (CIC 042007), KF619704, KF619975, KF619837, KF620079; Washington: Kittitas Co., D. Mansfield 11-493 (CIC 041533), KF619703, KF619976, KF619838, KF620080. *Lomatium* sp. nov. B. Oregon: Grant Co., C. E. Hinchliff 955 (CIC 043314), KF619706, KF619977, KF619841, KF620083. *Lomatium* sp. nov. C. Idaho: Valley Co., B. Ertter 19498 (CIC 043783), KF619707, KF619981, KF619842, -. *Lomatium* sp. nov. D. Washington: Clark Co., C. E. Hinchliff 978 (WS 385696), KF619708, KF619980, KF619843, KF620084. *Lomatium* sp. nov. E. Washington: Kittitas Co., C. E. Hinchliff 1358 (CIC 043307), KF619677, KF619978, KF619839, KF620081. *Lomatium* sp. nov. F. Oregon: Grant Co., C. E. Hinchliff 1364 (CIC 043316), KF619705, KF619979, KF619840, KF620082. *Lomatium tamanitchii* M. E. Darrach & K. K. Thie. Oregon: Grant Co., M. Darrach 645 (CIC 042005), KF619709, KF619982, KF619844, KF620085; Oregon: Morrow Co., C. E. Hinchliff 1252 (CIC 040931), KF619710, KF619983, KF619845, KF620086. *Lomatium thompsonii* (Mathias) C. L. Hitchc. Washington: Kittitas Co., C. E. Hinchliff 1355 (CIC 043318), KF619711, KF619984, KF619846, KF620087. *Lomatium triternatum* var. *anomalum* (M. E. Jones ex J. M. Coult. & Rose) Mathias. Oregon: Jackson Co., J. T. Duncan 01 (CIC 041672), KF619712, KF619985, KF619847, -. *Lomatium triternatum* (Pursh) J. M. Coult. & Rose var. *triternatum*. Idaho: Ada Co., E. George 095 (CIC 039937), KF619713, KF619986, KF619849, -; Oregon: Harney Co., D. Mansfield 11-007 (CIC 040127), KF619715, KF619988, KF619851, -; New Mexico: Rio Arriba Co., C. E. Hinchliff 1280 (CIC 040913), KF619714, KF619987, KF619850, -; Washington: Benton Co., M. Darrach 630 (CIC 042001), KF619702, KF619974, KF619848, -. *Lomatium tuberosum* Hoover. Washington: Yakima Co., C. E. Hinchliff 1270 (WS 384418), KF619716, KF619989, KF619852, KF620088. *Lomatium vaginatum* J. M. Coult. & Rose. Oregon: Jefferson Co., C. E. Hinchliff 1259 (CIC 040922), KF619718, KF619991, KF619854, KF620089; Oregon: Harney Co., D. Mansfield 11-005 (CIC 039932), KF619717, KF619990, KF619853, -; Oregon: Harney Co., D. Mansfield 11-006 (CIC 039931), KF619719, KF619992, KF619855, -. *Lomatium watsonii* (J. M. Coult. & Rose) J. M. Coult. & Rose. Washington: Klickitat Co., C. E. Hinchliff 1269 (CIC 041350), KF619720, KF619993, KF619856, KF620091; Washington: Klickitat Co., C. E. Hinchliff 1247 (CIC 041455), KF619721, KF619994, KF619857, KF620090. *Musineon divaricatum* (Pursh) Nutt. Nevada: White Pine Co., C. E. Hinchliff 1311 (CIC 041346), KF619722, KF619996, KF619858, KF620093. *Musineon lineare* (Rydb.) Mathias. Idaho: Bear Lake Co., D. Mansfield 12-692, KF619723, KF619995, KF619859, KF620092. *Musineon vaginatum* Rydb. Montana: Missoula Co., P. Lesica 10620 (CIC 041462), KF619724, KF619997, KF619860, KF620094. *Neoparrya lithophila* Mathias. New Mexico: Taos Co., C. E. Hinchliff 1275 (CIC 040908), KF619725, KF619998, KF619861, KF620095. *Oreoxis alpina* (A. Gray) J. M. Coult. & Rose. Colorado: Larimer Co., S. Nunn 2078 (RM 765899), KF619726, KF619999, KF619862, KF620096.

- Orogenia fusiformis* S. Watson. Oregon: Jackson Co., J. T. Duncan 7A (CIC 041668), KF619727, KF620000, KF619863, KF620097. *Orogenia linearifolia* S. Watson. Idaho: Adams Co., D. Mansfield 07023 (CIC 034349), **HQ426099**, **HQ426147**, **HQ426125**, -. *Polytaenia nuttallii* DC. Texas: McLellan Co., F. R. Barrie 1406 (RM 529215), KF619728, KF620001, KF619864, KF620098. *Pseudocymopterus montanus* (A. Gray) J. M. Coult. & Rose. Arizona: Gila Co., C. E. Hincliff 1288 (CIC 040926), KF619729, KF620002, KF619865, KF620099. *Pteryxia petraea* (M. E. Jones) J. M. Coult. & Rose. Oregon: Malheur Co., D. Mansfield 12-496 (CIC 043140), KF619730, KF620003, KF619866, KF620100. *Pteryxia terebinthina* var. *foeniculacea* (Torr. & A. Gray) Mathias. Idaho: Adams Co., E. George 160 (CIC 041535), KF619731, KF620005, KF619867, -; Idaho: Adams Co., E. George 161 (CIC 041534), KF619732, KF620006, KF619868, KF620101; Idaho: Custer Co., C. E. Hincliff 1344 (CIC 043327), KF619616, KF620004, KF619869, -. *Pteryxia terebinthina* var. *terebinthina* (Hook.) J. M. Coult. & Rose. Washington: Grant Co., C. E. Hincliff 1271 (CIC 040911), KF619733, KF620007, KF619870, KF620102. *Shoshonea pulvinata* Evert & Constance. Wyoming: Park Co., W. Fertig 15327 (RM 613328), KF619734, KF620008, KF619871, KF620103. *Taemidia integerrima* (L.) Drude. West Virginia: Pocahontas Co., R. B. Clarkson 2138 (RM 406422), KF619736, KF620010, KF619873, KF620105. *Tauschia hooveri* Mathias & Constance. Washington: Yakima Co., C. E. Hincliff 1237 (CIC 041479), KF619737, KF620011, KF619874, KF620106. *Tauschia tenuissima* (Geyer ex Hook.) Mathias & Constance. Idaho: Shoshone Co., C. E. Hincliff 1272 (CIC 041355), KF619738, KF620012, KF619875, KF620107. *Vesper macrorhizus* (Buckley) R. L. Hartman & G. L. Nesom. Texas: Burnet Co., C. E. Hincliff 1231 (CIC041471), KF619739, KF620013, KF619876, KF620108. *Vesper multinervatus* (Coulter & Rose) R. L. Hartman & G. L. Nesom. Nevada: Clark Co., M. Darrach 622 (CIC 042013), KF619740, KF620014, KF619877, KF620109. *Zizia aurea* Koch. Kansas: Cherokee Co., R. L. McGregor 32898 (RM 527763), KF619741, KF620015, KF619878, KF620110.