RESOLVING THE ANOMALY OF *LOMATIUM ANOMALUM*: DISCOVERY OF A NEW SPECIES IN SOUTHWESTERN IDAHO (U.S.A.), *LOMATIUM ANDRUSIANUM* (APIACEAE)

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ABSTRACT

Apparent polyphyly within the unresolved clade of *Lomatium* (Apiaceae) containing *L. triternatum, L. anomalum, L. thompsonii*, and *L. packardiae* suggests conflict among current taxonomic classification schemes. To recover this clade and more clearly define species boundaries, we examined populations of *L. anomalum* from three geographic regions in Idaho and adjacent Oregon. Using phylogenetic, morphological, and ecological data, we conclude that the *L. anomalum* complex currently circumscribes multiple species. Phylogenetic analysis of the nuclear ribosomal ITS and ETS, and cpDNA *rpl32-trnLUAG*, *rps-16* intron, *trnD-trnT, ndhA* intron, and *psbA-trnH* recovered populations from the Boise foothills as a distinct, monophyletic clade. Principal Components Analysis of 30 reproductive and vegetative characters show two distinct groups: one of Boise foothills and one of the combined Mann Creek and Camas Prairie vicinities. Principal Components Analysis of 16 soil characteristics show that soils occupied by Boise foothills populations are distinct from those occupied by Mann Creek and Camas Prairie populations. Based on phylogenetic, morphometric, and ecologic criteria, populations of what had been considered *L. anomalum* from the Boise foothills and vicinity are here described as a new species—**Lomatium andrusianum.**

RESUMEN

La aparente polifilia en el clado no resuelto de *Lomatium* (Apiaceae) que contiene *L. triternatum, L. anomalum, L. thompsonii,* y *L. packardiae* supone un conflicto en los esquemas de la clasificación taxonómica actual. Para recuperar este clado y de una forma más especifica definir los límites entre sus especies, hemos examinado poblaciones de *L. anomalum* de tres regiones geográficas en Idaho y de la zona adyacente de Oregón. Utilizando datos filogenéticos, morfológicos y ecológicos, hemos concluído que el complejo de *L. anomalum* comprende a múltiples especies. El análisis filogenético del nuclear ribosómico del ITS y ETS, y del cpDNA *rpl32-trnLUAG*, el intrón *rps-16*, *trnD-trnT, el intrón ndhA*, y *psbA-trnH* recupera estas poblaciones de las estribaciones de Boise como diferentes, como un clado monofilético. El análisis en componentes principales de 30 caracteres reproductores y vegetativos muestra dos grupos distintos: uno de las estribaciones de Boise y otro del combinado de las cercanías de Mann Creek y Camas Praire. El análisis de componentes principales de 16 características edáficas muestra que los suelos ocupados por las poblaciones de las estribaciones de Boise son distintas que las de aquellos terrenos ocupados por las poblaciones de Mann Creek y Camas Prairie. Basándose en criterios filogenéticos, morfométricos y ecológicos, las poblaciones de lo que ha sido considerado como *L. anomalum* de las estribaciones de Boise y sus cercanías son aquí descritas como una nueva especie—**Lomatium andrusianum.**

INTRODUCTION

Lomatium (Apiaceae) is a western North American genus in which over 100 species will be recognized in the upcoming publication of *Flora of North America*, vol. 13 (Barbara Wilson, pers. comm.). It is part of one of the largest plant radiations in North America, the Perennial Endemic North American Apiaceae (PENA) clade, the evolution of which is poorly understood (Downie et al. 2002; Downie et al. 2010; Sun & Downie 2010; George et al. 2014).

Many species of *Lomatium* are tracked as rare by Natural Heritage Programs in several states, including *L. bentonitum, L. erythrocarpum, L. greenmanii, L. knockei, L. latilobum, L. observatorium, L. pastorale, L. stebbinsii,* and *L. tarantuloides*; two species—*Lomatium bradshawii* and *Lomatium cookii*—are federally listed under the Endangered Species Act. Close to 40% of the genus is comprised of narrowly endemic taxa (Mark Darrach,

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pers. comm.). Many species have been used as a food source by indigenous peoples due most frequently to the starch storage in the roots (Beauchamp et al. 2007). Recent biomedical efforts have assayed secondary metabolites produced by *Lomatium* taxa, as an alternative to beta blockers for treating hypertension (Bell & Koithan 2012; Goldhaber-Pasillas et al. 2012; Schneider et al. 2013). Understanding relationships among the diverse taxa within the *Lomatium* genus is of value relative to conservation efforts, ethnobotanical and medicinal research.

Lomatium presents multiple challenges to resolving its evolutionary history, exhibiting various cases of near-cryptic speciation, polyphyly, and convergent evolution across disparate clades (Carlson et al. 2011; George et al. 2014; Mansfield et al. 2016). Although species circumscriptions have traditionally been predicated on morphological distinctions, it is evident that morphology alone is frequently insufficient to accurately define species boundaries in groups such as *Lomatium*.

Lomatium triternatum (Pursh) J.M. Coult. & Rose is endemic to the Pacific Northwest. In most recent floristic treatments of the region (e.g. Hitchcock & Cronquist 1973; Cronquist 1997) this species has included *L. anomalum* M.E. Jones ex J.M. Coult. & Rose as *L. triternatum* var. *anomalum* (M.E. Jones ex J.M. Coult. & Rose) Mathias. The clade containing *L. triternatum, L. anomalum, L. thompsonii,* and *L. packardiae* (George et al. 2014; Smith et al. 2016), referred to here as the *L. triternatum* clade, represents a taxonomic challenge. Recent phylogenetic analyses suggest that *L. anomalum* is polyphyletic (George et al. 2014; Smith et al. 2018). Specimens classified within this taxon range geographically from western Montana and Wyoming discontinuously thorough northern Utah to southwestern Oregon and northern California. Originally described from "Idaho and adjacent Oregon," specimens of *L. anomalum* examined by Coulter and Rose (1900) range from Camas Prairie (*Henderson 2660*) and Nez Perce County (*Heller 3132* and *Sandberg 28*) to "Hills near Snake River" (*Cusick 1905*). Populations of *L. anomalum* appear highly variable both in morphology and ecological setting. One set of populations from the Boise foothills east to the Bennett Hills in southern Idaho seems to be particularly unique morphologically in comparison to populations from north of Weiser (e.g , Mann Creek and vicinity) to Camas Prairie south of Lewiston, Idaho (Fig. 1). In this study we analyze populations of *L. anomalum* to determine whether the Boise foothills populations satisfy species criteria using three different species concepts: phylogenetic, phenetic, and ecologic. Though recently considered as a separate species (Cronquist 1992), specimens identified as *L. packardiae* in our study are included under *L. anomalum* because other analyses (George et al. 2014) showed that *L. packardiae* resides in the same clade as *L. anomalum*.

The phylogenetic species concept defines a species as "an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent" (Cracraft 1989). According to this concept a species is based on common ancestry and genetic similarity and is delineated by a highly resolved monophyletic clade (Mallet 2007). Each individual of a species as defined by a monophyletic clade shares specific synapomorphies. These shared derived traits distinguish members of one clade/species from those of other clades/species. We thus hypothesize that populations of *L. anomalum* from the Boise foothills will resolve as a unique monophyletic clade distinct from the rest of the *L. anomalum* individuals in the *L. triternatum* clade.

The phenetic, or morphological, species concept assumes that members within a species have physical characters that are both similar to other members within the species, and distinct from members of other closely related species. We thus hypothesize that individuals of *L. anomalum* from the Boise foothills populations would have at least one distinct morphological character that distinguish them from other *L. anomalum* in the *L. triternatum* clade, specifically those collected from other Idaho locations from the Camas Prairie and Mann Creek.

The ecological species concept assumes that ecological niche partitioning leads to speciation (Van Valen 1976). One species is distinct from another because it occupies a unique ecological niche that other closely related species do not. The ecological species concept is frequently used to explain endemism in plants on the premise that endemics grow in specific soils owing predominantly to unique soil chemistries (Mallet 2007). Though other ecological parameters, such as frost heave cycles in alpine environments, may drive ecological speciation, we hypothesize that *L. anomalum* from the Boise foothills will inhabit ecologically distinct

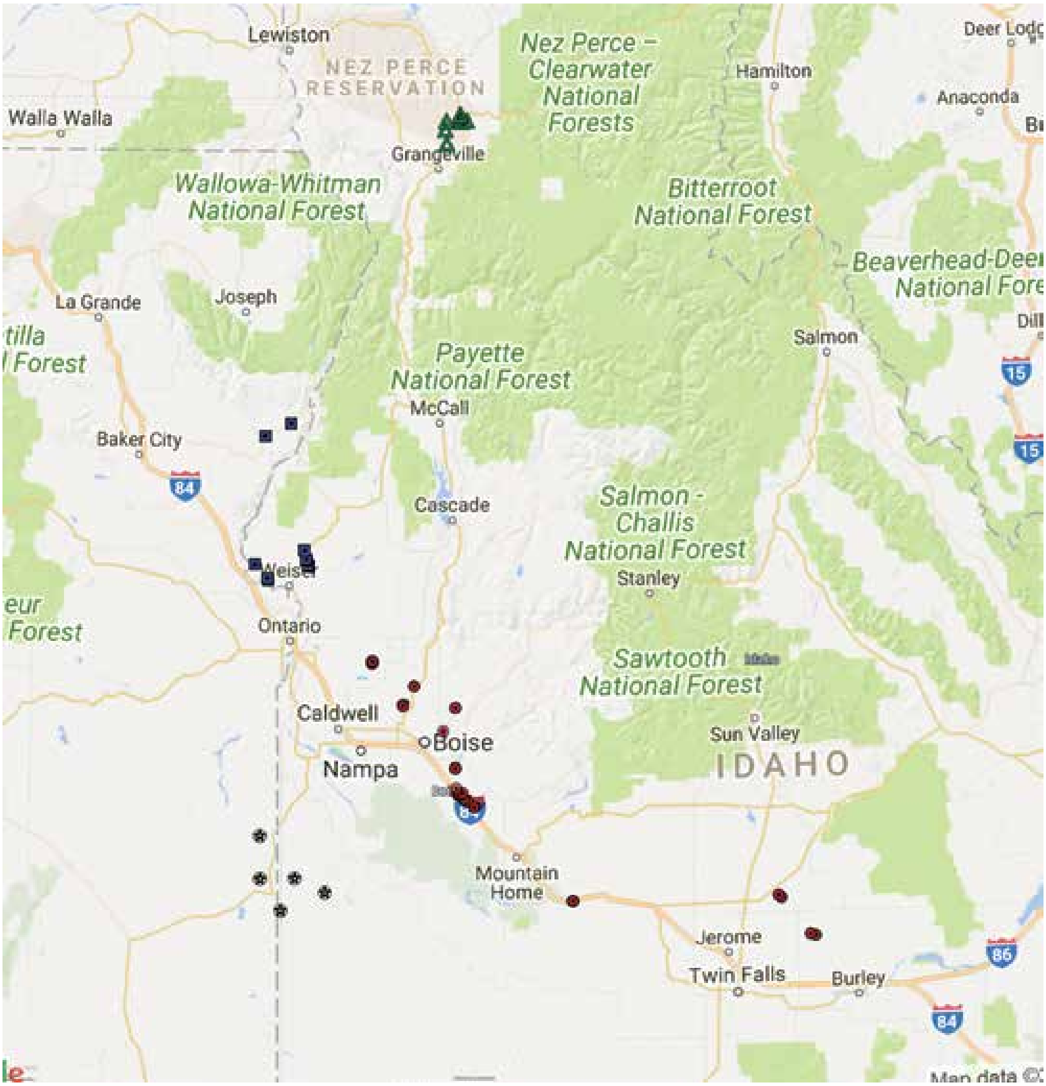

Fig. 1. Map of locations of populations studied in southwestern Idaho and eastern Oregon. *Lomatium andrusianum* (circles); *L. anomalum* [Camas Prairie (triangles), Mann Creek (diamonds), *L. packardiae* (rectangles)]

substrates from those of populations of *L. anomalum* from the Camas Prairie and Mann Creek areas. More specifically we analyzed soil texture and soil chemistry as metrics for substrate differentiation.

In this study, we sampled diverse morphologies of the *L. anomalum* complex from three localities in southwestern Idaho and adjacent Oregon: Boise foothills (BF), Mann Creek Drainage and adjacent vicinities (MCA), and Camas Prairie (CP). While *Lomatium triternatum* var. *triternatum* and *Lomatium thompsonii* reside in the *L. triternatum* clade (Smith et al. 2018), these species are morphologically distinct enough from *L. anomalum*—the former having narrower, longer leaflets and shorter fruits, the latter having more robust stature and larger fruits—that they were not included in the morphometric or ecologic study. Additionally, *L. thompsonii* is geographically removed from Idaho in northcentral Washington. We focus, instead, on *L. anomalum* populations (including *L. packardiae*) within the larger *L. triternatum* clade for our phylogenetic study. This study thus combines phylogenetic and morphometric data and soil texture and chemistry to delimit *L. andrusianum* as a new species endemic to the Boise foothills and vicinity.

METHODS AND MATERIALS

***Phylogenetic Analyses.*—**Leaf material for DNA extraction was collected from populations in the Boise foothills, Mann Creek, and Camas Prairie (Table 1). Additional samples from the *L. anomalum* complex (including 10 samples of *L. packardiae*) from eastern Oregon through southeastern Washington were included for phylogenetic studies (Fig. 1; Smith et al. 2018). DNA from all samples were extracted using Qiagen plant DNeasy mini kits (Qiagen, Valencia, California), following the manufacturer's instruction with the exception that incubation of the samples at 60°C was extended to two hours (George et al. 2014). Amplification of ITS, *rps16* intron, and *rpl32-trnLUAG* used the primers of George et al. (2014), while amplification of the nuclear ribosomal ETS region and the cpDNA regions *trnD-trnT*, *ndhA* intron, and *psbA-trnH* used primers of Feist and Plunkett (Smith et al. 2018). All DNA regions were amplified using methods of George et al. (2014). Gel electrophoresis using 1% agarose gels stained with ethidium bromide under UV light was used to determine successful amplifications which were then purified using Exo-SAPit (Affymetrix, Cleveland, Ohio) and shipped to GeneWiz (Plainfield, New Jersey) for bi-directional sequencing. Chromatograms were downloaded from the GeneWiz site and edited. Consensus sequences were generated from both strands using Phy-DE (Müller et al. 2005). The consensus sequences were compiled into a master alignment which was used to for phylogenetic reconstruction based on maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). Support for the trees was estimated using bootstrap with both MP and ML and posterior probabilities with BI.

***Morphometric Analyses.*—**A total of 85 specimens identified as *L. anomalum* (or as synonym *L. triternatum* var. *anomalum*) were used in the morphometric analysis: 62 from the Boise foothills, 13 from Mann Creek and vicinity, and 10 from Camas Prairie (Table 1). Thirty characters were measured on each specimen (Table 2). Non-parametric ANOVA tests were used to determine statistically significant differences in quantitative characters between the three localities (SigmaPlot 13.0, Systat Software, Inc. San Jose, California). Non-parametric ANOVA and t-tests were preferred to corresponding parametric tests because data were not normally distributed, or, in some cases, lacked equal variance. All data were analyzed using Principal Components Analysis (PCA). Most specimens lacked both complete vegetative and reproductive characters. Accordingly, to obtain larger sample sizes, separate PCAs for reproductive data and vegetative data were performed.

Soil Analyses.—Eight populations from the Boise foothills and five from localities in Mann Creek and Camas Prairie were selected based on ease of access to analyze soil texture and chemistry. To obtain a representative soil sample from each of the populations, five plants were randomly selected within a 25-meter radius of a marked population center. A roughly cylindrical soil sample (ca. 150 g) of approximately 5 cm diameter to a depth of approximately 15 cm was collected from the root zone of each plant. Each sample was dried for at least 24 hours at 105°C. Dried samples were then weighed and passed by hand through a 2-mm mesh sieve to separate gravel from finer fractions. Larger clods were gently broken apart with a mortar and pestle and re-sieved. Two of the five soil samples from each sampled population were used for soil particle size analysis using the Bouyoucos hydrometer method (Gee & Bauder 1986). Remaining samples from each population were pooled, and approximately 400 grams of soil from each population were sent to the University of Wisconsin Soil and Forage Analysis Laboratory for pH determination and chemical composition analysis of, P, K, Ca, Mg, Na, exchangeable H, total cation exchange capacity, organic matter, sulfate, total nitrogen, nitrate, and ammonium. These thirteen chemical parameters and size fraction data were analyzed by PCA using SigmaPlot 13.0.

RESULTS

Phylogenetic Analyses.—All taxa represented in Figure 2 except *L. thompsonii* and *L. packardiae* (included within the *L. anomalum* clade) have been treated as *L. triternatum* in the recent floristic treatments of the geographic area of study (Hitchcock & Cronquist 1973; Cronquist 1997). *Lomatium andrusianum,* forms a monophyletic clade separate from *L. anomalum* (Fig. 2). The clade containing *L. andrusianum* is supported with

Table 1. Collection data for all 85 specimens studied in the morphometric analysis. Additional collections used in phylogenetic analyses (including *L. packardiae*—within *L. anomalum*) are listed in Smith et al. (2018). MCA for Mann Creek, CP for Camas Prairie, and BF for Boise foothills (*L. andrusianum*). CIC is Tucker Herbarium of College of Idaho, SRP is Snake River Plains Herbarium of Boise State University.

Group Represented	Collection Number	Herbarium	Accession Number	Latitude	Longitude
MCA	*Mansfield 16036*	CIC	50702	44.35504	-117.094
MCA	*Mansfield 07055*	CIC	34270	44.415	-116.907
MCA	*George 066*	CIC	39891	44.41554	-116.907
MCA	*Mansfield 16037*	CIC	50701	44.40155	-117.155
MCA	*Mansfield 16034*	CIC	50704	44.34809	-117.089
MCA	*Stevens 123*	CIC	50706	44.41996	-116.908
MCA	*Hinchliff 889*	CIC	43330	44.83942	-117.109
MCA	*Stevens 121*	CIC	50705	44.88277	-116.986
MCA	*Halverson 053*	CIC	41054	44.38333	-116.883
MCA	*Bowden 021*	CIC	35339	44.4	-116.9
MCA	*Tauson 311*	CIC	32539	44.4124	-116.906
MCA	*Halverson 065*	CIC	34254	44.45	-116.917
MCA	*Stucker K64*	CIC	39890	44.39697	-116.896
CP	*Lesica 10798*	CIC	44338	45.919	-116.139
CP	*Lesica 10794*	CIC	44337	46.1	-115.9
CP	*George 102*	CIC	43301	45.93866	-116.171
CP	*Mansfield 16064*	CIC	50797	45.9177	-116.1653
CP	*Mancuso 3147*	CIC	39717	45.917	-116.171
CP	*Mansfield 16063*	CIC	50796	45.91777	-116.239
CP	*Mansfield 16062*	CIC	50795	45.88782	-116.244
CP	*Mancuso 4264*	SRP	58023	45.93806	-116.171
CP	*McNeill 2016051702*	CIC	50814	45.84012	116.2367
CP	*Lingenfelter 302*	SRP	3940	NA	NA
BF	*Smith 11580*	SRP	52211	43.83515	-116.258
BF	*Ertter 19118*	SRP	46558	43.25167	-114.669
BF	*Ertter 54/2*	CIC	1032	43.62	-116.17
BF	*DeBolt 2807*	SRP	58088	43.25064	-115.65
BF	*Johnson 11*	SRP	31905	43.61535	-116.183
BF	*Ertter 75-37*	CIC	1021	43.118	-114.509
BF	*Stevens 106*	CIC	50905	43.61596	-116.181
BF	*Davidson 10991*	SRP	32014	43.91472	-116.198
BF	*Stevens 103C*	CIC	50896	44.06457	-116.595
BF	*Smith 13073*	CIC	50839	43.25963	-114.681
BF	*HRClure sn*	CIC	956	NA	NA
BF	*Stevens 101C*	CIC	50901	43.92183	-116.447
BF	*Mancuso 4046*	CIC	47685	44.07266	-116.5961
BF	*Slice 18*	SRP	31908	NA	NA
BF	*Ertter 20748*	CIC	44289	43.6035	-116.161
BF	*HMTucker sn*	CIC	937	NA	NA
BF	*Ertter 20719*	CIC	42149	43.616	-116.18
BF	*Kyle 18*	SRP	31904	43.61944	-116.183
BF	*Bratz sn.*	CIC	935	NA	NA
BF	*Smith 11580*	CIC	49955	43.83515	-116.258
BF	*Stevens 104*	CIC	50904	43.61596	-116.181
BF	*Smith 13117*	SRP	59670	43.92813	-116.447
BF	*Mansfield 16041*	CIC	50697	44.06705	-116.591
BF	*Mancuso 4046*	SRP	52913	44.07266	-116.5961
BF	*Smith 13073*	CIC	50838	43.25963	-114.681
BF	*Stevens 105*	CIC	50694	43.61596	-116.181
BF	*White 040*	SRP	58031	43.62387	-116.166
BF	*Stevens 107*	CIC	50906	43.60313	-116.161
BF	*Stevens 103A*	CIC	50898	44.06457	-116.595
BF	*Stevens 101B*	CIC	50900	43.92183	-116.447
BF	*Schlangen 15*	SRP	58021	43.64051	-116.195
BF	*Smith 13075*	SRP	59628	43.83513	-116.256
BF	*Smith 13074*	CIC	50840	43.12321	-114.534
BF	*Stevens 108*	CIC	50907	43.70712	-116.199
BF	*Schulte 031*	SRP	31907	43.59352	-116.145

TABLE 1. *cont.*

Group Represented	Collection Number	Herbarium	Accession Number	Latitude	Longitude
BF	*Mansfield 16040*	CIC	50698	44.07317	-116.591
BF	*Prentice 504*	CIC	936	43.59	-116.09
BF	*Stevens 101A*	CIC	50899	43.92183	-116.447
BF	*Smith 13074*	CIC	50841	43.12321	-114.534
BF	*Davis 511*	CIC	941	NA	NA
BF	*Ertter 20748*	CIC	42150	43.6035	-116.161
BF	*Pecunia 35*	SRP	55903	43.61606	-116.182
BF	*Johnson 026*	CIC	35454	43.93333	-116.433
BF	*Stevens 103B*	CIC	50897	44.06457	-116.595
BF	*Ertter 21352*	CIC	47868	43.575	-116.111
BF	*Carnes 013*	SRP	50216	43.61674	-116.185
BF	*Smith 13113*	SRP	59666	43.98869	-116.394
BF	*Prentice 504*	SRP	6545	43.59	-116.09
BF	*Holly.sn.*	CIC	939	NA	NA
BF	*Kunkel sn.*	CIC	10630	NA	NA
BF	*Mansfield 16042b*	CIC	50788	43.57685	-116.11
BF	*Mansfield 16031*	CIC	47656	43.71108	-116.199
BF	*Mansfield 16042*	CIC	50789	43.60312	-116.16
BF	*Ertter 20591*	NA	NA	43.59583	-116.143
BF	*DeBolt 2807a*	SRP	58137	43.25064	-115.65
BF	*Mansfield 16033*	CIC	47654	43.61596	-116.181
BF	*Ertter 19851*	NA	NA	43.596	-116.143
BF	*Ertter 75-37*	SRP	6537	43.118	-114.509
BF	*Debolt 931-471*	SRP	59435	43.25139	-115.649
BF	*Kreamer 003*	SRP	49059	43.61647	-116.181
BF	*Kreamer 4*	SRP	58020	43.61584	-116.182

100% posterior probability from the BI majority-rule consensus tree (MP bootstrap = 63, ML bootstrap = 77; Fig. 2). *Lomatium anomalum* from Mann Creek and Camas Prairie, however, do not resolve into distinct subclades (Fig. 2). Non-Boise foothills *L. anomalum* (including *L. packardiae*) thus remain ambiguous with unclear species boundaries. *Lomatium* sp. nov. 2 and *L.* sp. nov. 3 represent clades of other novel species within the *L. triternatum* clade. Sequences for all genes used in these analyses are reported in Smith et al. (2018).

Morphometric Analyses.—*Lomatium andrusianum* (Boise foothills clade) is also distinguishable morphologically from the Camas Prairie and Mann Creek populations in the *L. anomalum* clade. Amongst 30 characters evaluated Table 3 shows 19 quantitative variables that differ significantly ($p<0.05$) between *L. andrusianum* and the combined Mann Creek/Camas Prairie populations of *L. anomalum* (see also Fig. 4). *Lomatium andrusianum* has shorter, narrower ultimate leaflets and shorter tertiary leaf divisions than Mann Creek and Camas Prairie populations (Table 3; Fig. 4). The peduncles, petioles, and inflorescence rays are also notably shorter in *L. andrusianum* (Table 3; Fig. 4). Finally, *L. andrusianum* has shorter mature fruits with wider wings, accounting for 63% of the total fruit width on average (Table 3). Results of PCA of morphological data (Fig. 3) show two geographically distinct groups: one group includes populations from the Boise foothills (*L. andrusianum*) and the second includes the combined Mann Creek/Camas Prairie populations (part of *L. anomalum*). With 88% of the variation explained in the first two principal component axes of the PCA performed on vegetative characters, *L. andrusianum* is distinct from the other populations (Fig. 3A). Reproductive characters do not adequately separate the two species (Fig. 3B) despite 77% of variation explained in the first two axes. However, in the limited number of specimens possessing both measurable reproductive and vegetative characteristics, *L. andrusianum* was distinct from all other *L. anomalum* with 59% of the variation explained by the first two axes (Fig. 3C). While some reproductive characters (pedicel length, inflorescence length, and ray length) were significantly longer ($p<0.01$, $p<0.05$, $p<0.05$, respectively; data not shown) in Camas Prairie populations than either *L. andrusianum* or Mann Creek populations, fruits were significantly longer in Mann Creek populations than either *L. andrusianum* or Camas Prairie populations.

Table 2. Character list for morphological analysis (Veg = vegetative characters; Repro = reproductive characters).

1. Veg: Mean length of 4 longest ultimate segments on largest basal 1° leaflet (mm)
2. Veg: Mean width of 4 longest ultimate segments on largest basal 1° leaflet (mm)
3. Veg: Mean Aspect Ratio length: width of ultimate segments on largest basal 1° leaflet (mm)
4. Veg: Hairs on basal leaf segments (0=glabrous; 1=present)
5. Veg: Hairs on stem leaf segments (0=glabrous; 1=present)
6. Veg: Hairs on base of stem (0=glabrous; 1=present)
7. Veg: Hairs on rays (0=glabrous; 1=present)
8. Veg: Length of longest leaf from proximal-most 1° to tip (cm)
9. Veg: Length of longest 2° leaflet (cm)
10. Veg: Length of longest 3° leaflet (cm)
11. Veg: Length of petiole on stem
12. Veg: Width of sheath at widest (mm)
13. Veg: Number of stem leaves per stem
14. Veg: Scape length (cm) from base of peduncle of inflorescence
15. Repro: Mature fruit length (mean of 5) (mm)
16. Repro: Mature fruit width (mean of 5) (mm)
17. Repro: Mature pedicel length (mm) (mean of longest in 5 umbels)
18. Repro: Ratio of fruit length:fruit width
19. Repro: Infructescence length (cm) (length of primary umbel)
20. Repro: Infructescence width at widest point (cm) (width of primary umbel)
21. Repro: Ratio of infructescence length:width (primary umbel)
22. Repro: Wing width (mm)
23. Repro: Wing width as % of fruit width (two wings/fruit width)
24. Repro: Ultimate umbel length (mm)
25. Repro: Ultimate umbel width (mm)
26. Repro: Ratio of ultimate umbel length: width
27. Repro: Inflorescence length in flower (mm)
28. Repro: Inflorescence width at widest point in flower (mm)
29. Repro: Ratio of inflorescence length:width in flower
30. Repro: Average ray length (average of 5 longest of all umbels; mature fruiting only--cm)

Soil Analyses.—Soils occupied by *L. andrusianum* had significantly higher sand fraction content and levels of Na and significantly fewer exchangeable H^+ than soils occupied by *L. anomalum* in Mann Creek and Camas Prairie populations (Table 4). Two groups of soils are distinguishable in PCAs of the 16 soil chemistry and texture variables: Boise foothills soils are distinct from a combined Mann Creek/Camas Prairie group with 60% of the variation explained by PCA axes 1 and 2 (Fig. 6A). When the PCA includes only the three significant variables shown in Table 4, 80% of the variation is explained by PCA axis 1 and PCA axis 2 of the PCA, and the same two groups are distinguishable (Fig. 6B). Sample sizes for Mann Creek and Camas Prairie were too small to conclusively distinguish these soils as individual groups. Combined, however, they serve to distinguish soils of *L. andrusianum* from *L. anomalum* (Fig. 6).

TAXONOMY

Lomatium andrusianum McK. Stevens & Mansfield, sp. nov. (**Fig. 4 left, Fig. 5**). Type: U.S.A. Idaho. Ada Co.: on top of Chukar Butte, ½ mi W of Sweet Connie trail in Boise foothills, on shallow, rocky, clay soils developed on basalt substrate, plants only found on flat on top, not in similar soils on slopes nearby, 43.71108°N, 116.19908°W, 4000 ft, 29 May 2016, D.H. Mansfield 16031 (holotype: CIC 47656; isotypes: OSC, WIS, ID, WTU).

Lomatium andrusianum is similar to *Lomatium anomalum* but is distinguishable morphologically in having: more, narrower and shorter ultimate leaflets, narrower fruits with proportionately wider fruit wings and smaller length/width ratios, and generally less pubescence on the foliage.

Herbs: Perennial, erect, remotely aromatic, glabrous to, more often, sparsely puberulent or sparsely hirsute, acaulescent, or more typically caulescent with one stem leaf, 15–42(–55) cm in height, typically 30–35 cm in height when in mature fruit. Root: elongate taproot 5–17 mm thick from 10–>30 cm long, rarely, if ever, with tuberous thickening. Root surmounted by a short, simple or branching caudex bearing 1–3 (—10) stems. Older

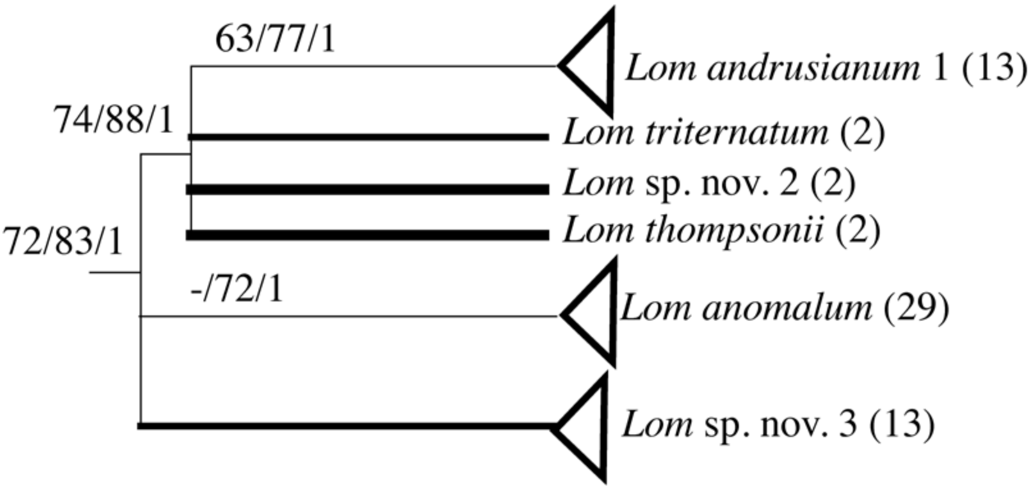

Fig. 2. Bayesian majority rule tree with maximum parsimony bootstrap (MPBS), maximum likelihood bootstrap (MLBS) and Bayesian inference posterior probabilities (BIPP) shown. Values shown are MPBS/MLBS/BIPP. A dash indicates support was below 50% for that analysis at that node. Branches with bootstraps > 75 and posterior probabilities > 0.95 are thickened to 2 point width and branches that were maximally supported in all analyses are thickened to 3 point width. Monophyletic groups where multiple individuals per species were sampled have been collapsed and replaced by a triangle where more than three individuals were sampled, otherwise the number of individuals is shown in parentheses following the species name. Boise foothills populations (*L. andrusianum)* have been recovered in a monophyletic clade separate from all other *L. anomalum* (including all samples from Mann Creek and Camas Prairie and including 10 *L. packardiae* samples). All specimens and Gen Bank sequence references included in this condensed phylogeny can be found in Smith et al. 2018 .

Table 3. Means and standard deviations of vegetative and reproductive characters for Boise foothills (*L. andrusianum*) and Mann Creek/Camas Prairie populations of *L. anomalum.* Significance determined by two-tailed t-test. Differences at p<0.05 denoted by "*" and p<0.001 denoted by "**".

Character\Location	**Boise Foothills** *L. andrusianum*	**Mann Creek/Camas Prairie** *L. anomalum*	**Significance**
Ultimate Leaflet Length (mm)	24.71±8.93	39.37±6.65	**
Ultimate Leaflet Width (mm)	3.11±1.06	7.72±4.57	**
Leaf Hairs on Basal Leaf Segments	0.38±0.48	0.61±0.49	**
Leaf Hairs on Stem Leaf Segments	0.46±0.50	0.95±0.20	**
Length Longest Leaf: Proximal to Primary Tip (cm)	12.01±2.65	13.25±2.35	*
Length of Longest Secondary Leaflet (cm)	5.85±1.46	7.79±1.46	**
Length Longest Tertiary Leaflet (cm)	2.79±1.04	4.89±1.05	**
Length Petiole on Stem Leaf (cm)	5.91±4.09	11.23±3.82	**
Scape Length From Base of Peduncle of Inflorescence (cm)	24.24±6.48	33.26±8.10	**
Mature Fruit Length (mm)	11.96±1.40	14.14±2.62	**
Mature Fruit Width (mm)	4.58±0.64	5.63±0.84	*
Length:Width Ratio of Mature Fruit	2.69±0.63	2.57±0.62	*
Infructescence Length (cm)	9.73±2.96	11.71±3.54	**
Length:Width Ratio of Infructescence	0.86±0.16	1.01±0.16	**
Wing as Percentage of Total Fruit Width (%)	63.05±17.12	43.84±6.85	**
Length of Inflorescence (mm)	17.64±2.82	21.63±2.82	**
Width of Inflorescence (mm)	30.84±6.32	30.28±7.73	*
Length:Width Ratio of Inflorescence	0.58±0.09	0.76±0.19	**
Length Ray (cm)	7.78±2.62	9.40±2.99	**

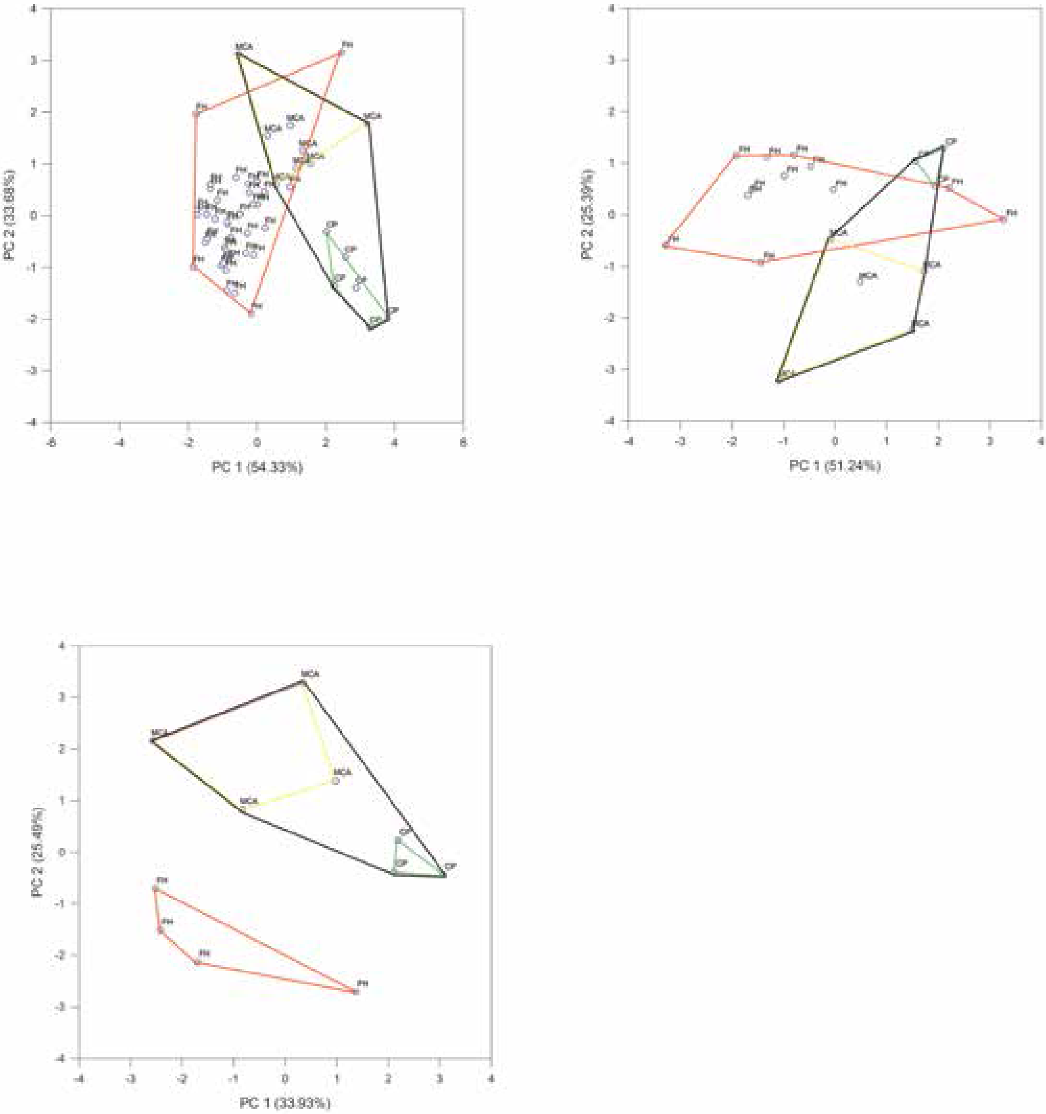

Fig. 3. A) Principal Components Analysis (PCA) capturing variation in vegetative characters listed in Table 2. The first (PCA 1) and second (PCA 2) axes account for 88% of the variation among the 14 variables used in this analysis (see Table 2). **B)** PCA capturing variation among 16 reproductive characters listed in Table 2. The first and second axes presented account for 77% of variation. **C)** PCA capturing variation in 30 reproductive and vegetative characters listed in Table 2. The first and second axes presented account for 59% of variation. Independent clustering in all three figures illustrates morphologic distinction between *L. andrusianum* (BF-red) and *L. anomalum* [black: the combination of MCA (yellow) and CP (green)].

plants up to at least 15 years of age. Pseudoscape absent. Leaves: Leaves 2–3(–5). Petioles (3–)5–12 (–14) cm long, with anthocyanic to stramineous sheaths at the base; brown leaf sheaths from prior 1–2 years occasionally present, often obscuring up to 10 cm of stem; sheaths glabrous, prominently 10–20 nerved up to 10 × 0.9 cm. Leaves obovate in outline, (6.5–)10–17(–22) cm in length from the distal end of the petiole, (3–)5–15 cm wide; branched venation evident in leaflets; petioles and rachises glabrous to puberulent or hirsute. Primary divisions of leaves typically ternate, but often with one or two additional leaflets at base; secondary divisions pinnate, occasionally with one or two additional leaflets at base; tertiary divisions (linear) elliptic to

Table 4. Quantitative composition of soils from nine populations from Boise foothills (*L. andrusianum*) localities and five populations from combined Mann Creek and Camas Prairie localities (grouped as *L. anomalum*). The three soil characters which are significantly different between Boise foothills and Mann Creek/Camas Prairie at $p<0.001$ are demarcated with ** in significance column.

	Boise Foothills *L. andrusianum*		Mann Creek/Camas Prairie *L. anomalum*		
Ecological Parameter	Mean	±Standard Deviation	Mean	±Standard Deviation	Significance
pH	7.1	0.2	6.5	0.2	
P(ppm)	32.1	12.9	81.7	29.6	
K (ppm)	310.4	87.9	416.0	140.7	
Ca (ppm)	3070.9	906.8	3097.3	238.8	
Mg (ppm)	581.8	267.6	834.3	90.3	
Na (ppm)	64.6	54.2	32.2	9.6	**
H+ (meq/100g)	0.0	0.0	2.8	0.6	**
CEC summation	17.5	5.5	21.1	2.5	
OM (%)	2.5	0.5	5.1	0.4	
Sulfate S (ppm)	5.2	3.4	5.2	4.2	
Total nitrogen (ppm)	1253.9	429.9	2625.1	79.7	
Nitrate (ppm)	2.4	0.3	5.0	1.4	
Ammonium (ppm)	23.1	16.0	45.2	45.1	
% sand	49.5	10.1	37.5	10.8	**
% clay	27.7	8.8	20.4	5.3	
% gravel	15.0	9.0	30.0	19.0	

Fig. 4. Representative vouchers of *L. andrusianum* (**left**) and *L. anomalum* from Mann Creek (middle) and Camas Prairie (**right**).

oblanceolate or further divided unevenly into linear-elliptic to oblanceolate segments. Ultimate leaflets approximately 100–200 per leaf, (5–)10–30(–78.9) mm long, (0.8–)1–3(–6.3) mm wide, (3–)7–12(–16) times as long as wide, glabrous to puberulent, rarely hirsute. Leaflets with minute (up to 0.15 mm) non-photosynthetic translucent obtuse to acute or acuminate tip. Inflorescences: comprised of compound umbels, typically 1(–2) per stem, involucre none. Peduncles discontinuously pithy, glabrous to sparsely puberulent or sparsely hirsute, erect, terete, green to sometimes anthocyanic at the base becoming stramineous with age. Peduncle length in flower (6–)8–26(–32) cm with typical specimens around 15–20 cm, peduncle length in fruit 13–37 cm typically 19.5–25 cm. Peduncles 1.8–2.9(–5.3) mm wide, typically 2.1–2.3 mm wide, 1 cm below the apex.

Fig. 5. Representative leaves of *L. andrusianum*. All photos are of leaves taken from the distal end of the petiole to the distal end of the leaf (or nearly so). Bar = 10 mm.

Peduncles typically overtopping leaves by 5–13 cm in flower and 6.3—16 cm in fruit. Inflorescence (2.5–)6–15 cm wide. Rays 3–12, unequal in length, from (0.6–)1.5–7(–10) cm in flower to (2.5–)3–9(–13) cm in fruit. Rays mostly ascending, up to 20% erect, up to 50% spreading, and up to 10% reflexed. Shortest, central rays usually bearing umbellets with entirely male flowers that do not lengthen with plant maturity; male umbellets 3–8 per inflorescence; typically 4 or 5; fruiting umbellets 4–13 per inflorescence, typically 7–10, also bearing male flowers. Pedicels spreading to erect, glabrous to sparsely puberulent/hirsute, 1.7–4.8 mm long in flower, 2.1–6.2 (–8.0) mm in fruit. Involucel: bractlets 0–8 typically 2–4, green, herbaceous, lanceolate to linear, with radial distribution. Bractlets 2.0–6.2 × 0.1–0.3 mm, glabrous to very rarely sparsely puberulent/hirsute, free to base, lacking or with a very narrow scarious margin, never ciliate. Flowers: glabrous 10–55 per umbellet, petals yellow, 0.55–0.90 × 0.55–0.80 mm, ovate with incurved apiculus; stamens incurved; anthers yellow, 0.30–0.40 × 0.20–0.30 mm; pollen yellow; filaments ca. 1.0 mm. Stylopodia yellowish green to greenish, 0.15 mm high. Styles 0.6–1.3 mm, strongly incurved. Ovaries green, glabrous to puberulent. Fruit: hemispherically arranged with 5–13 fruits per fruiting umbellet, typically 9–10. Fruits glabrous to sparsely, or rarely densely puberulent, (8.5–)9.8–13.3(–15.5) mm, typically 10–13 mm long, 3.5–6.3 mm, typically 4.5–5.5 mm wide. Fruit wing width 1.0–2.2 mm, not obviously thickened, strongly dorsiventrally compressed with rounded base and distal obtuse margin. Wing width to body width 0.50–0.81, typically about ⅔. Fruits elliptical with length/width ratio 1.81–3.33, typically between 2.0 and 3.0. Dorsal fruit surfaces with 3(4) stramineous, slightly elevated ribs; oil tubes obscure, 3–4 in the intervals, 2 along the commissure, 0 on the wings. Photographs are in Figs. 4 (left) and 5.

Specimens examined (in addition to those cited in Table 1). **Idaho. Ada Co.:** Military Reserve along NW side of hill, surrounded by sagebrush and grasses. 43°37'N, 116°10'W, 870 m, 19 Apr 2012, *Jarolimek s.n.* (SRP). **Payette Co.:** along ridge SE of Bannister Basin major ash outcrops. Up Bannister Basin Rd, ca. ½ mi W of the Dry Ck. turnoff of Big Willow Ck. Rd., 8–10 mi E of Hwy 52 in the Payette River valley, on heavy clay of decomposed ash, but not on ash barrens, 100% vegetation cover, population in the thousands, 44.0727°N, 116.59139°W, 3050 ft, 13 Apr 2016, *D. Mansfield 16004* (CIC).

Phenology.—Flowers from early April through early June. Fruits are produced from mid-May through mid-June.

Etymology.—The epithet "*andrusianum*" commemorates the much-respected, former 4-term governor of Idaho and Secretary of the Interior, Cecil Andrus. The name was suggested by Chris Jensen of Boise Idaho as a crowd funding to support continued research in *Lomatium* and was supported by over 40 donors.

Habitat.—*Lomatium andrusianum* is known from heavy clay soils along the Boise Front. It is found on flats and gradual slopes in mainly *Artemisia tridentata*-dominated communities, including *A. tridentata/Poa secunda* (*sandbergii*), *A. tridentata/Ericameria nauseosa*, and less commonly *A. tridentata/Purshia tridentata*. It is also found in association with *Astragalus purshii* var. *glareosus*, *Balsamorhiza sagittata* or *B. hookeri*, *Elymus elymoides*, *Microseris nutans*, *Phlox longifolia*, *Eriophyllum lanatum* or *Penstemon cusickii*. It can tolerate much disturbance and is often found only with exotic annual grasses, primarily *Taeniatherum caput-medusae*, yet also *Poa bulbosa*, or *Bromus tectorum*. See also Discussion.

Range.—*Lomatium andrusianum* is known from a narrow band of lower foothills along the northeast side of the Snake River plain of southwestern Idaho from Bannister Basin in the Big Willow Creek drainage of eastern Payette Co. (44.07°N, 116.59°W) southeast roughly parallel to the Snake River through Gem, Ada (e.g., 43.61°N, 116.16°W), Elmore, Camas, and Gooding cos. to Lincoln Co. at the southeastern extent of the range (43.12°N, 114.53°W). Elevation ranges from 820 to 1500 m.

DISCUSSION

Analyses of phylogeny, morphometrics, and soil properties suggest that populations formerly treated as *L. anomalum* (*L. triternatum* var. *anomalum*) from the Boise foothills are distinct from other members of the *L. anomalum* complex in the *L. triternatum* clade. Phylogenetically, populations from the Boise foothills were resolved as monophyletic and separate from all other populations of *L. anomalum* including those previously referred to as *L. packardiae* (Fig. 2). Thus, we believe that the phylogenetic species concept is satisfied in treating Boise foothills populations of *L. anomalum* as a novel species. However, we have been unable to place Jones' type specimen of *L. anomalum* in our study, because we have been unable to obtain a tissue sample for DNA analysis. So, whether the *anomalum* epithet should be assigned to the Boise foothills clade or the clade containing the remainder of *L. anomalum* populations (including those from Mann Creek and Camas Prairie) is problematic. We have searched unsuccessfully for two years in "the hills above Indian Valley" (Coulter & Rose 1900) for any population that might approximate Jones' type population of *L. anomalum*. Based on our study of images of the type, it appears to be comparable to our Mann Creek populations, though the type is fragmentary, lacking leaves. Thus, we believe that Jones' epithet should remain with the populations of *L. anomalum* (including Mann Creek and Camas Prairie populations) exclusive of the novel species, and we assign the new name, *L. andrusianum*, to populations from the Boise foothills.

Insufficient genetic resolution between the Mann Creek and Camas Prairie populations of *L. anomalum* and *L. packardiae* populations suggests that additional methods will need to be utilized to more accurately define the remaining elements of the *L. anomalum* complex. More specifically, Mann Creek populations, Camas Prairie populations, and populations of *L. packardiae* do not resolve as distinct sub-clades within the 29 individuals studied here and indicated as *L. anomalum* in Figure 2. Henceforth, we refer to all populations of that unresolved *L. anomalum* clade as the *L. anomalum* complex.

Though no evident morphological synapomorphies distinguish *L. andrusianum* from other closely related taxa, many quantitative characters differ between *L. andrusianum* and the collective Mann Creek and Camas Prairie populations of the *L. anomalum* complex. The absence of evident morphological synapomorphies, however, is frequently observed in the PENA clade (George et al. 2014). *Lomatium andrusianum* has shorter ultimate leaflet segments and shorter tertiary leaf divisions than those of *L. anomalum* from further northwest (Mann Creek) and north (Camas Prairie; Table 3, Fig. 4). Though the PCAs of vegetative characters alone (Fig. 3A) and of vegetative and reproductive characters combined (Fig. 3C) show clear separation of *L. andrusianum* from *L. anomalum,* the reproductive characters alone do not sufficiently distinguish *L. andrusianum* from *L. anomalum* (Fig. 3B). While fruits from Mann Creek populations are longer than those of either Camas Prairie populations or *L. andrusianum*, infructescences, rays, and pedicels of Camas Prairie populations are longer than those of Mann Creek populations and *L. andrusianum*. Though leaflets of *L. andrusianum* are significantly narrower than those of combined populations of the *L. anomalum* complex (Table 3), they are not significantly narrower than those of Mann Creek populations (data not shown; Fig. 4). However, leaflets of Camas Prairie populations are significantly wider ($p<0.01$) than those of *L. andrusianum* and specimens of the *L. anomalum* complex from Mann Creek (Fig. 4; data not shown), which accounts for the difference between *L. andrusianum* and the collective populations of the *L. anomalum* complex. Thus, leaflet width may not be a helpful character in distinguishing *L. andrusianum* from the *L. anomalum* complex in general. Clearly morphological variability in both vegetative and reproductive characters among geographically separate populations of the *L. triternatum* clade have long obscured species boundaries (Table 3, Fig. 3C, Fig. 4).

Soil texture and chemistry differ between *L. andrusianum* and the combined Mann Creek and Camas Prairie populations of the *L. anomalum* complex (Table 4, Fig. 6). *Lomatium andrusianum* grows on soils with higher sand content and Na levels and lower $H+$ than soils on which the *L. anomalum* complex plants grow. Though soils associated with *L. andrusianum* are relatively high in clay content, like all those in the *L. anomalum* complex, the higher sand content reflects the location of populations in the lacustrine deposits of the shores of ancient Lake Idaho. The soils occupied by *L. andrusianum* are recognizably different than those occupied by the *L. anomalum* complex (Fig. 6). Yet many other attributes of the habitat are apparently overlapping. Populations of both *L. andrusianum* and the *L. anomalum* complex (including *L. packardiae*) typically occupy sites of relatively high clay content (see Table 4). Both *L. andrusianum* and the *L. anomalum* complex can be found on flat or slightly sloping terrain, though the Camas Prairie form (Fig. 4C) of *L. anomalum* seems restricted to flat sites. Populations of both can be found in several *Artemisia tridentata*-dominated communities, including. *A. tridentata/Poa secunda* (*sandbergii*), *A. tridentata/Purshia tridentata*, and *A. tridentata/Ericameria nauseosa*, but Mann Creek and Camas Prairie forms of the *L. anomalum* complex can also be found

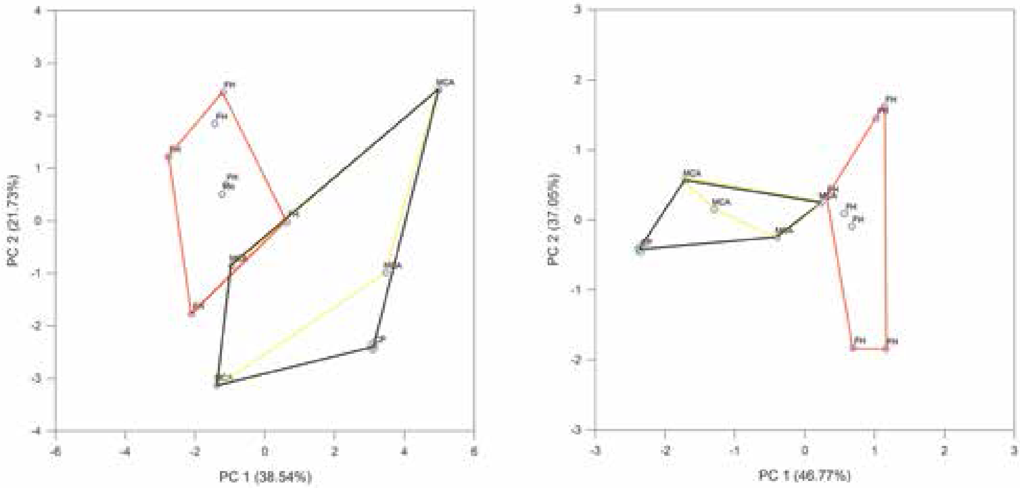

Fig. 6. PCA capturing variation in soil characters (Table 4). A) PCA of all 16 soil chemistry and texture variables shown in Table 4. B) PCA of the three significant soil variables shown in Table 4. Distinct clustering suggests distinct niche requirements for two groups [*L. andrusianum* (BF-red); *L. anomalum* (black: the combination of MCA (yellow) and CP (green))].

in *Pinus ponderosa/Festuca idahoensis* and/or *Pinus ponderosa/Pseudotsuga menzesii* communities. While both *L. andrusianum* and the *L. anomalum* complex may be associated with species such as *Lomatium nudicaule*, *Balsamorhiza* spp., *Lupinus* spp., and weedy annual grasses such as *Poa bulbosa*, only the latter, and not *L. andrusianum*, seem to ever be associated with meadow species such as *Camassia quamash*, *Delphinium nuttallianum*, *Ranunculus alismifolius* var. *davisii, Lomatium dissectum* or introduced taxa of similar habitats such as *Bromus inermis*, *Phleum pratensis* or *Cirsium canadensis*.

It seems probable that a combination of geographic isolation and edaphically driven speciation have been foremost factors in differentiating *L. andrusianum* from members of the *L. anomalum* complex. We are uncertain of the extent to which edaphic factors have driven phenotypic separation. The study of edaphic factors should likely be included in future investigations of the *L. triternatum* clade (Fig. 6).

Regardless of the ambiguities within the remainder of the *L. triternatum* clade, it is evident that *L. andrusianum* represents a distinct species as indicated by phylogenetic, morphologic, and edaphic criteria presented here. While the Mann Creek and Camas Prairie populations of the *L. anomalum* complex remain poorly understood genetically relative to plants presently assigned to *L. packardiae*, it is clear that *L. andrusianum* occupies a single monophyletic clade (Fig. 2). While *L andrusianum* possesses no apparent morphological synapomorphies relative to other members of the genus *Lomatium*, it is quantitatively distinct from other *L. anomalum* complex populations northeast of the Snake River, most notably in its shorter, more numerous leaflets, narrower fruits with proportionately wider wings, and sparser pubescence throughout the plant. But variation among other morphological characters is less clear; *L. andrusianum* has shorter fruits than Mann Creek populations but not Camas Prairie populations, and it has shorter inflorescences, pedicels, and rays and narrower leaves than Camas Prairie populations but not Mann Creek populations. Additional morphometric analyses within the *L. anomalum* complex (including *L. packardiae*) are warranted once cladistic subgroups can be better resolved.

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