The Discovery of Two New Tufted Desertparsleys from Southeastern Oregon: *Lomatium ravenii* var. *paiutense* and *Lomatium bentonitum*

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Anyone who has ever tried to identify a biscuitroot or desertparsley (*Lomatium*) or springparsley (*Cymopterus*) can appreciate how variable these plants can be. As a consequence of my floristic study of southeastern Oregon, most recently the Owyhee region, I often encounter unusual forms of plants. Sometimes these forms are just minor variations within the range of what might be expected for a given species, and other times the variations seem different enough to warrant a closer look. Further investigation may include more field observations, locating additional populations with the unusual characters, careful measurements and comparisons of these characters between closely related species, greenhouse or experimental manipulations, or even phylogenetic analysis of DNA sequence data. At the small liberal arts college where I teach, some of these aberrant populations that "don't read the books" make for fun research projects for keen undergraduate students. That was the case in the mid-2000s when I suggested to my student, Kim Carlson, that she make some measurements on specimens of three species of *Lomatium* from southeastern Oregon and southwestern Idaho.

Figure 1. *Lomatium foeniculaceum* var. *macdougalii* is a wide-ranging, yellow-flowered, tufted biscuitroot entering southeastern Oregon from the southeast. Photo courtesy of Gerald Carr.

Flowers in these "apioids" (Apiaceae, the carrot and parsley family) are small and rather nondescript white, yellow, or sometimes purplish, reddish, or brownish-green. Easily recognized by the characteristic umbel, members of the genera *Lomatium* and *Cymopterus* harbor a wild and confusing variation in the fruits, leaves, stems and roots. Many new species are still being described, for two reasons: differences among species are subtle and many of these plants are restricted to very narrow geographic ranges (narrowly endemic). For example, within the past five years, scientists described eight new taxa within *Lomatium* in the Pacific Northwest: *L. bentonitum* from the Succor Creek area in southeastern Oregon, *L. brunsfeldianum* from northern Idaho, *L. tarantuloides* from the Greenhorn Mountains of northeastern Oregon, *L. swingerae* from west-central Idaho, *L. knokei* from central Washington, *L. ochocense,* from the Ochoco Mountains of central Oregon, *L. pastorale*[1] from northeastern Oregon [see *Kalmiopsis* 20:1-5], and *L. ravenii* var. *paiutense* from northern Nevada, southeastern Oregon and southwestern Idaho. Several more narrowly endemic species are in the process of being described.

1 Originally published as *L. pastoralis*.

This is the story of the research that led to the discovery of two of these new taxa: bentonite desertparsley (*L. bentonitum*), and Paiute desertparsley (*L. ravenii* var. *paiutense*). This research also revealed to me that our current understanding of the evolution of this group of plants is still in its infancy.

Lomatiums from Malheur County that "don't read the books"

In southeastern Oregon we commonly encounter several tufted lomatiums, three of which I'll discuss here. One of these, Macdougal's biscuitroot (*L. foeniculaceum* var. *macdougalii*), is yellow-flowered (Figure 1). It grows in shallow soils high in clay content and ranges to the east and southeast (Idaho and eastern Nevada). A very similar

Figure 2. Anomalous white-flowered desertparsley (*Lomatium ravenii* var. *paiutense*) from southeastern Oregon, northern Nevada, and southwestern Idaho. Cronquist included this as *L. nevadense* in the *Intermountain Flora*. Photo by the author.

plant growing in comparable habitats, but with white flowers and with other minor, subtle differences, enters southeastern Oregon from the southwest (western Nevada and northeastern California). This plant (Figure 2) has been called different names by different botanists, and became the focus of our research in 2005. The name Lassen parsley (*L. ravenii*) is given for this plant in the USDA Plants Database (http://plants.usda.gov). But in his treatment of *Lomatium* for the *Intermountain Flora*, Art Cronquist (1997) placed these white-flowered desertparsleys (Figure 2) under the name *L. nevadense*. This white-flowered species, commonly called Nevada biscuitroot (Figure 3), is a widespread southwestern species that reaches into Oregon from California and Nevada and grows in loamy soils often at higher elevations. In his discussion of *L. nevadense*, Cronquist noted that "a few plants with the leaves…dissected into very numerous small segments, nearly as in *L. foeniculaceum*, but with the bractlets…scarcely hirtellous, as in *L. nevadense* occur in a swath from Lassen County, California across northern Nevada…. At least some of these plants have white flowers with purple anthers, as in *L. nevadense*: these have been described as *L. ravenii*." Thus, Cronquist acknowledged that our unusual white-flowered tufted *Lomatium* specimens in southeastern Oregon (Figure 2) were similar to three species: *L. foeniculaceum*, *L. ravenii,* and *L. nevadense*. Cronquist chose to call the unusual Oregon specimens *L. nevadense*

Figure 3. White-flowered *Lomatium nevadense* var. *nevadense* is a wide-ranging and highly variable southwestern US species that extends into southeastern Oregon. Photo courtesy of Gerald Carr.

and, in the process, lumped all the other white-flowered specimens called *L. ravenii* into *L. nevadense* as well. The justification for lumping was that the morphology of the type specimen of *L. ravenii* fell within the range of the highly variable *L. nevadense*. But we were not satisfied with Cronquist's reluctance to accept *L. ravenii* as a distinct taxon, when other authors did. Thus, the taxonomy of *L. ravenii* became the focus of our research in 2005. The distributions of these three species are shown in Figure 4.

First, Kim examined the morphological variation among specimens of these three species from our herbarium at The College of Idaho, which included a large number of specimens from Malheur County and surroundings. In the following year, she examined a few more species and varieties and from a wider geographic range. She measured 29 different morphological characters (such as length-to-width ratios of bracts below the flower clusters, flower color, and density of hairs on various structures) in plants from more than 50

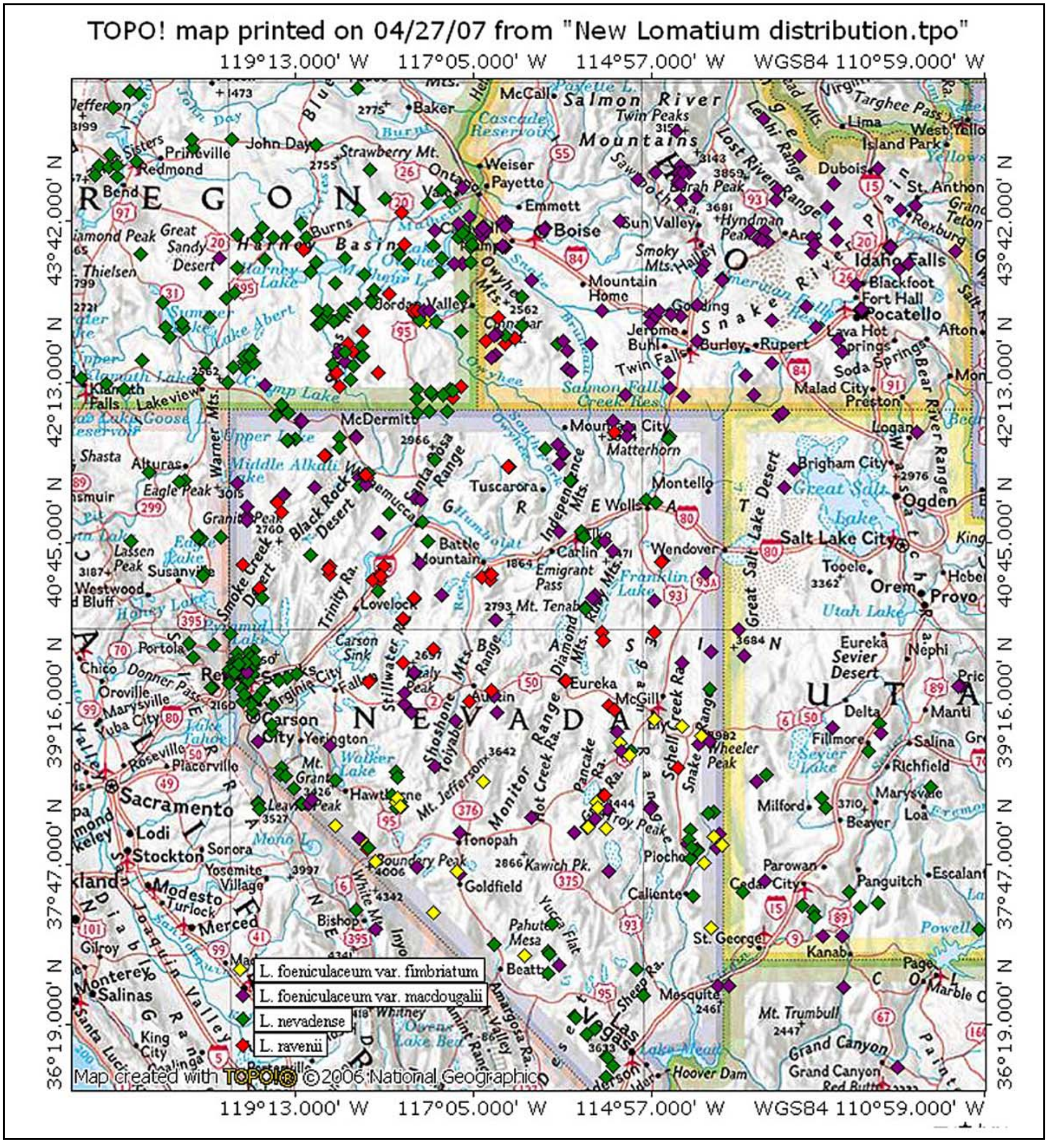


Figure 4. The distributions of *Lomatium foeniculaceum*, *L. nevadense*, and *L. ravenii* in our region (not showing the entire range of *L.foeniculaceum* and *L. nevadense*). Map by author.

populations of these three taxa and other related *Lomatium* species.

One way to visualize the results of her study is to reduce the variation among those 29 characters into a two-dimensional graph with two axes that describe much, but not all, of that variation (Carlson *et al.* 2011). Through this procedure, non-metric multidimensional scaling (NMDS), we were able to see (Figure 5) that the specimens from throughout the full geographic range of *L. ravenii* (Nevada, Idaho, California and southeastern Oregon) were distinct from both *L. foeniculaceum* and the highly variable *L. nevadense.* Data points for plants recognizable as *L. ravenii* (enclosed by a polygon in Figure 5), *L. nevadense* and *L. foeniculaceum* formed clusters distinct from one another, rather than being scattered throughout the variation typical of each species. These clusters supported distinguishing three distinct species. Among the white-flowered desertparsley specimens with tightly clustered leaves, we recognize *L. ravenii* as a species rather than including some of the specimens in *L. nevadense* and others in *L. foeniculaceum*.

However, there were two unresolved questions remaining from this analysis that we pursued in the following year or so. First, it was clear that Cronquist did not accept *L. ravenii* as a good species, so we needed to find out where it fit in an analysis of the DNA of all of the *Lomatium* taxa throughout northeastern California, northern Nevada, and Malheur County in southeastern Oregon. Second, in our analysis there was one rather odd specimen from Succor Creek (marked with the blue star on Figure 5) that we had initially thought was *L. ravenii*, but differed from other *L. ravenii* specimens, both on the herbarium sheet and on the NMDS graph.

To pursue both of these questions we joined forces with Dr. James F. Smith at Boise State University, whose phylogenetic work using DNA sequences of both nuclear and chloroplast genes enabled him to distinguish among closely related species in the largely tropical family *Gesneriaceae*. So in 2007 and 2008 we returned to the field to locate both more populations of the anomalous Succor Creek specimen and to find true *L. ravenii* from the type locality. Kim and I, with help from Jim, Dr. Ron Hartman (University of Wyoming), and some of my other students collected fresh leaf samples of many populations of *L ravenii*, *L. nevadense*, *L. foeniculaceum,* the unusual Succor Creek specimen, and several other species of *Lomatium*, from which Kim began extracting DNA for analysis.

Two varieties of *Lomatium ravenii*

First, we examined plants from the population where Mildred Mathias and Lincoln Constance collected the type specimen of *L. ravenii*, which is the plant on which they based their initial description of the species and named it. We reasoned that, perhaps *L. ravenii* specimens from the type locality were different than the *L. ravenii* we had been studying. With the help of Dr. Barbara Ertter (University of California, Berkeley, and The College of Idaho) and Matt Guilliams (a UC student at the time), we were able to get leaf samples and voucher specimens of three *L. ravenii* from both the type locality and nearby locations.

After refining techniques for sequencing the same genes from all samples, we were able to decipher some presumed evolutionary relationships using techniques of phylogenetic analysis. The results of these analyses (Figure 6) demonstrate that *L. ravenii* is indeed closely related to *L. foeniculaceum.* It is within the same terminal branch, or clade, in this phylogenetic tree. *Lomatium nevadense*, the species in which Cronquist thought *L. ravenii* should be included, is in a part of this tree widely separated from *L. foeniculaceum* and *L. ravenii* by several other *Lomatium* species (Figure 6). This phylogenetic tree also revealed that *L. ravenii* specimens consist of two different, related groups, one that includes plants resembling the *L. ravenii* type specimen and another that includes other *L. ravenii* from Malheur County and northern Nevada. We named this second group of *L. ravenii* as a new variety (Carlson *et al.* 2011b): *L. ravenii* var. *paiutense* or Paiute desertparsley, in recognition of the Northern Paiute tribe, which shares a similar range throughout northern Nevada, southeastern Oregon, southwestern Idaho and whose members may have used the plant as a food source. The new variety, *L. ravenii* var. *paiutense* is more densely hairy on the leaves and bracts beneath the umbels and has broader, shorter leaf segments than the typical variety (*L. ravenii* var. *ravenii*) that is restricted to California (not overlapping the range of the Paiute

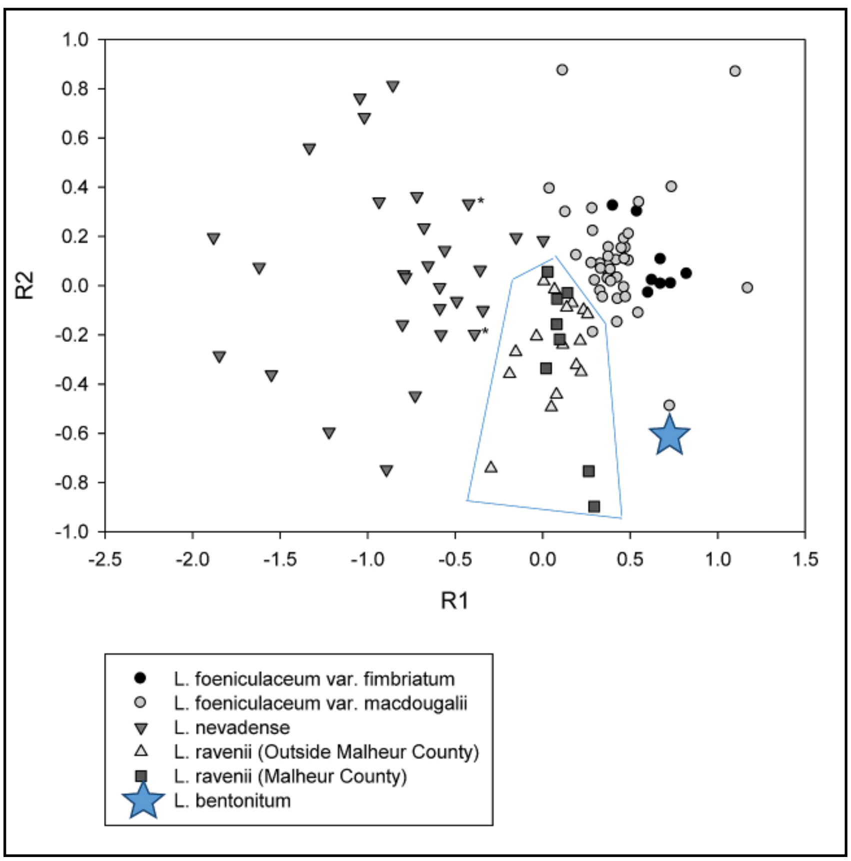


Figure 5. An NMDS graph illustrating variation among plants in the three species of *Lomatium* that the author and his student Kim Carlson investigated in 2007, showing also the unusual specimen that led to the discovery of *Lomatium bentonitum*. The two axes represent a composite of the greatest amount of variation possible in two dimensions from among the 29 variables measured among the 50 plants observed. Each point on the graph represents one plant from a unique population. (adapted from Carlson *et al.* 2011a)

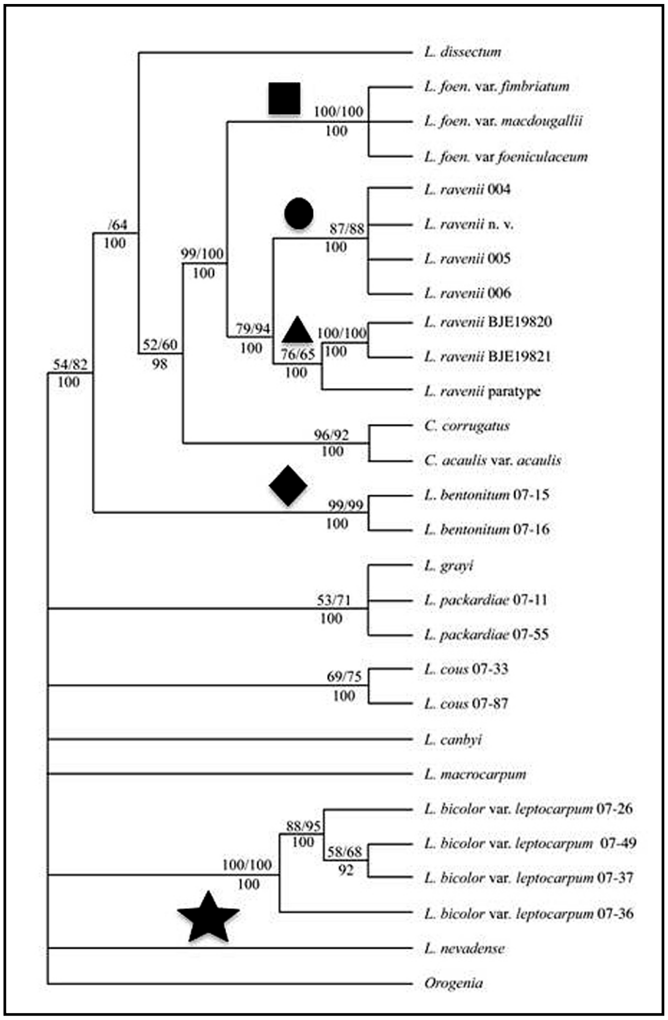


Figure 6. A phylogenetic tree (cladogram) of *Lomatium ravenii*, its closest relative, *L. foeniculaceum*, and other less closely related species of biscuitroots and desertparsleys. The groups (clades) discussed in this article are marked on the figure: *L. foeniculaceum* (square), L. *ravenii* var. *paiutense* (circle), *L. ravenii* var. *ravenii* (triangle), *L. bentonitum* (diamond), and *L. nevadense* (star). The numbers are degrees of support (likelihood of true phylogenetic relationship) for each branch based on different methods of analysis. (adapted from Carlson *et al.* 2011b)

desertparsley—see Figure 7). Also, *L. ravenii* var. *ravenii* has other characteristics more closely resembling *L. nevadense* than does *L. ravenii* var. *paiutense.* Cronquist may well have recognized the difference between what we are calling two varieties of *L. ravenii*, but preferred to lump all plants resembling *L. ravenii* in the widespread and variable *L. nevadense*. His note suggesting that what we now call *L. ravenii* var. *paiutense* might have merely been another form (possibly a variety?) of *L. foeniculaceum* was indeed insightful, as the results of the DNA cladogram illustrate (Figure 6).

Bentonite desertparsley (*Lomatium bentonitum*) is a new species

Having settled the *L. ravenii* enigma to our satisfaction, the phylogenetic tree revealed that the unusual Succor Creek specimens (shown by the blue star in Figure 5) not only represented a different branch on the tree (labeled as *L. bentonitum* on Figure 6), but the specimens were so different that they were separated from specimens of the two *Lomatium* species, *L. ravenii* and *L. foeniculaceum* by specimens from a different genus (*Cymopterus*)! Indeed the DNA analysis strongly indicated that we had turned up another species.

We decided to examine the morphology of specimens in more detail, such as the root form and additional features related to form, density and location of surface hairs. Fortunately, we had some additional specimens in our herbarium that had been collected a few years earlier. A subsequent NMDS analysis of these specimens distinguished this new species from the other species similar to it, including *L. nevadense*, *L. ravenii*, *L. foeniculaceum*, and *L. canbyi* (Figure 8). We named it *Lomatium bentonitum* because the only place where we found it (or have found it since we described it) is a bentonite clay mine in Succor Creek basin (Figure 9).

Lomatium bentonitum, or bentonite desertparsley (Figure 10), is found only in azonal soils on outcrops of Miocene ash of the Sucker Creek Formation in Succor Creek drainage where light colored ash has weathered to bentonite clay, a shrink-swell clay with tremendous capacity to absorb water. The similar species, *L. ravenii* var. *paiutensis*, Paiute desertparsley, lives nearby but not on the bentonite-rich outcrops. Though similar in appearance to Paiute desertparsley, bentonite desertparsley has more planar leaves, which are less hairy, making the plant appear more green than gray. The root is perhaps its most distinctive feature. Figure 11 shows how the top of the root is abruptly narrowed in *L. bentonitum* but tapered in *L. ravenii* var. *paiutense*. However, now that we have been able to recognize *L. bentonitum* as a distinct species, and know how rare it is, I recommend against digging

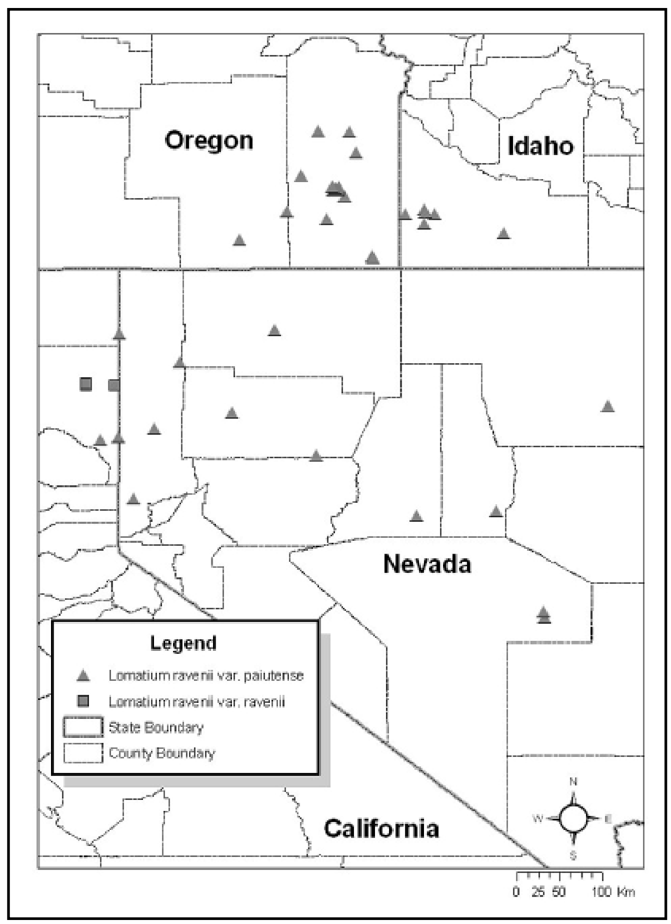


Figure 7. The distributions of the two varieites of *L. ravenii*. Map by author.

it up to examine its root. We know of just one population of this species, though we have not searched exhaustively in this region. Other clay rich substrates in the area should be investigated for this extremely rare endemic. Originally we had thought that an additional population existed deep in the desert plateaus in southern Owyhee County, Idaho because we had one specimen that resembled *L. bentonitum* in our herbarium (still cited in PLANTS USDA (http://plants.usa.gov). But in 2012 we revisited populations from that area and realized that, although some plants in the *L. ravenii* var. *paiutense* populations have a distinctive abrupt narrowing to the bulbous root, most root tops are tapered. Furthermore, those plants were not in bentonite clay outcrops, but rather are growing in rocky soil having a clay substructure, which is the typical habitat of *L. ravenii* var. *paiutense*. Furthermore, the surfaces of leaves were much more typical of *L. ravenii* var. *paiutense*.

The Succor Creek location of the new bentonite desertparsley is in the vicinity of several other unusual soil outcrops from weathered ash deposits high in clay content where other rare plants are found, including *Lomatium packardiae*, *Cymopterus glomeratus* var. *greeleyorus* (*C. acaulis* var. *greeleyorum*), *Mentzelia mollis*, and others. This area is unusually rich in rare plants restricted to specific substrates. *Lomatium bentonitum* is one more to add to the growing list of narrow endemic *Lomatium* species found in southeastern Oregon's deserts.

Evolutionary relationships in *Lomatium*

The observation (in Figure 6) that two species of the genus *Cymopterus* are situated between very similar and closely related species of *Lomatium* is curious and rather unsettling. After all, shouldn't all species within a genus be more closely related to each other than to species in a different genus? On the surface, this does not seem to be true in

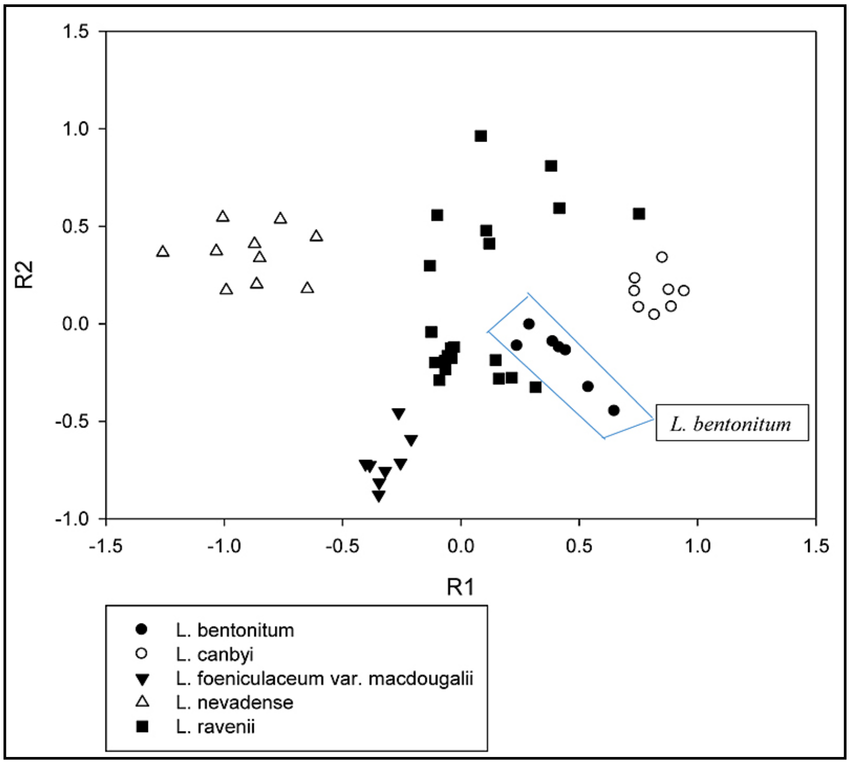


Figure 8. An NMDS graph illustrating variation among samples of *Lomatium bentonitum* and nearby species resembling it. (adapted from Carlson *et al.* 2011a)

Figure 9. The bentonite clay mine in Succor Creek drainage in Malheur Co., Oregon—the only known locality of *Lomatium bentonitum*. Photo by the author.

Figure 10. The habit of *Lomatium bentonitum* in its native habitat. Photo by the author.

this group of desertparsleys. In the past few years we, and others, are continuing to examine the genetic and morphologic relationships among other members of this group. Within the group of plants that includes *Cymopterus* and *Lomatium,* at least 10 cases have been identified where species of one of the genera appear to be more closely related to species of the other genus than to members of their own genus (George *et al.* 2014, Sun and Downie 2010). This situation termed "polyphyly[2]" indicates that our understanding of the evolutionary relationships among species in the two genera is not yet clear. Some characters that we thought defined a genus are more than likely ones that appear repeatedly in multiple evolutionary lineages, and do not indicate that the groups share a common ancestor. For example, one character used to separate *Cymopterus* from *Lomatium* is the multiple elaborated wings on the fruits of *Cymopterus*, which are normally absent on fruits of *Lomatium* — but there are exceptions (*L. packardiae* var. *tamanitchii, L. thompsonii, L. suksdorfii, C. glomeratus* var. *concinnus*). As we continue to study this group of interesting plants, we expect that the coming years will reveal dramatic reinterpretations of their evolutionary relationships and plenty of new names for botanists to learn.

Acknowledgements

I wish to acknowledge many people who have contributed to this project. I could not have become so engaged with *Lomatium* without my collaboration with Dr. James F. Smith at Boise State University. Kim Carlson's interest, keen eye, and careful attention to detail got this all off the ground. Emma George moved the project forward by tireless work that demonstrated the incredible polyphyly in the group. Many of my students have worked to the project, including Lauren Polito, McKayla Stevens, Kelsey Nelson; many more in field botany classes have contributed to important field collections. Several others including Richard Heliwell, Mark Darrach, Rick McNeil, Cody Hinchliff, and Jim Duncan have contributed invaluable samples and vouchers. I continue to appreciate collaborations with Barbara Ertter, Ron Hartman, Cody Hinchliff, and Stephen Downie. Mark Darrach read and contributed to the final manuscript. Finally, I wish to thank Cindy Roché and Kareen Sturgeon for their many helpful editing suggestions.

2 Polyphyly refers to branches of a phylogenetic tree that do not include their common ancestor.

References

Carlson KM, Mansfield DH, Smith JF. 2011a. A new species in the *Lomatium foeniculaceum* (Apiaceae) clade revealed through combined morphometric and phylogenetic analyses. Systematic Botany 36(2):495-507.

Carlson KM, Mansfield DH, Smith JF. 2011b. A new variety of *Lomatium ravenii* (Apiaceae) from the northern Great Basin and adjacent Owyhee region. Aliso 29(2):105-114.

Cronquist A. 1997. *Lomatium* Pp. 394-419 *in* Volume Three, Part A: Subclass Rosidae (except Fabales). Intermountain Flora by Cronquist A, Holmgren NH, Holmgren PK. New York Botanical Garden Press, Bronx, NY.

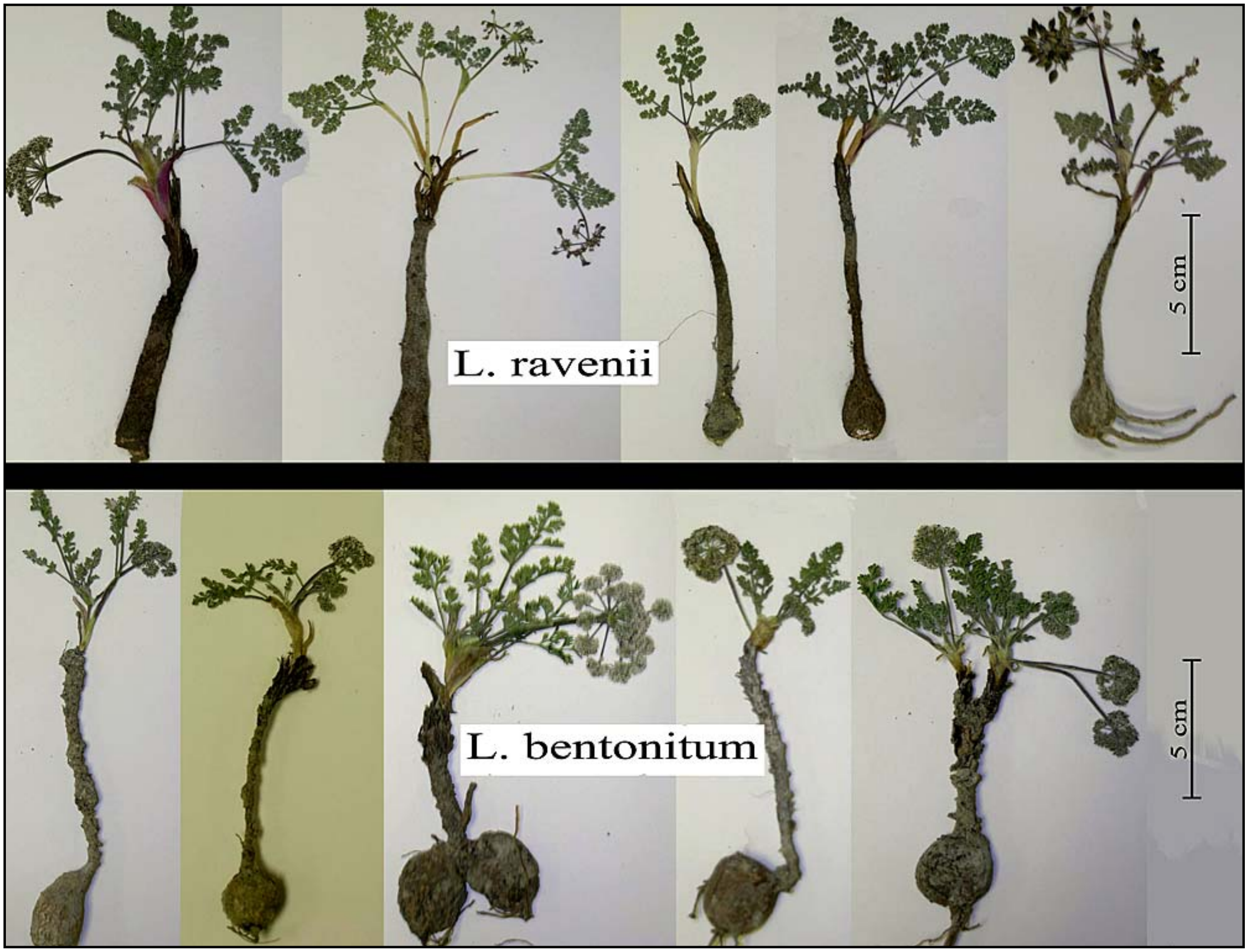
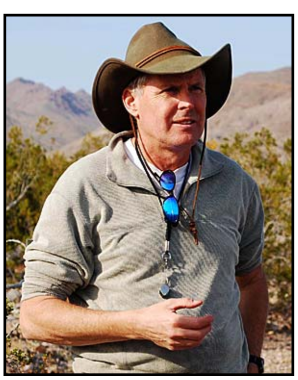


Figure 11. The two new desertparsleys of southeastern Oregon: *Lomatium ravenii* var. *paiutense* and *Lomatium bentonitum*. They are distinguished by their tapering and bulbous roots, respectively, and by their grayer, more hairy and greener, less hairy foliage, respectively. (from Carlson *et al.* 2011a)

George E, Mansfield DH, Smith JF, Hartman R, Downie S, Hinchliff C. 2014. Phylogenetic analysis reveals multiple cases of morphological parallelism and taxonomic polyphyly in *Lomatium* (Apiaceae). Systematic Botany 39 (2):662-675.

Sun FJ, Downie SR. 2010. Phylogenetic relationships among the perennial, endemic Apiaceae subfamily Apioideae of western North America: additional data from the cpDNA trnF-trnL-trnT region continue to support a highly polyphyletic *Cymopterus*. Plant Diversity and Evolution 128:151–172.



Don was born in Salem, Oregon, and grew up all over the US. He took his first biology class from Dr. Martha Springer at Willamette University and transferred to Colorado College where he completed a BA in biology in 1973, discovering field botany in his senior year studying under Dr. Jack L. Carter. After completing his MSc in botany at University of British Columbia, working with Dr. Iain E.P. Taylor on a biochemical problem, but also studying with Dr. Wilf Schofield and others, Don decided that he loved both teaching and botanical research. He earned his Doctor of Arts degree in biology at Idaho State University (1979) working with Dr. Jay Anderson. There he began studying the botany of Steens Mountain in eastern Oregon, often studying with Dr. Karl Holte. After brief post-doctoral employment at University of California, Davis, where he worked on post-harvest physiology while spending weekends studying vernal ponds of northern California, he taught botany and physiology at Colorado College (1981-1984). While Assistant Professor of Biology at Rollins College in Florida (1984-1989), Don returned each summer to Steens Mountain and Colorado to pursue his growing love of floristics. In 1989 he took a faculty position at The College of Idaho in Caldwell, where he teaches field botany and a variety of biology courses and serves as Curator of the Harold M. Tucker Herbarium. His floristic research resulted in the Flora of Steens Mountain (2000), and he continues to study the floristics of SE Oregon, SW Idaho, and N Nevada. His work has turned up many interesting problems, such as the ones described in this article, which he continues to pursue with his wonderful and talented undergraduate students.

Key to the low-growing (generally < 1.5 dm), tufted desertparsleys, springparsleys, and related biscuitroots (*Lomatium* and *Cymopterus*) of SE Oregon and SW Idaho

(These are species with highly dissected leaves with very short ultimate leaf segments.)

1a. Foliage lacking hairs or with sparse, short stubbly hairs

2a. Mature fruits lacking papery ribs between the two lateral wings; roots swollen and spherical (smelling of turpentine), sometimes only at the base of an elongate upper portion; widespread in clay soils in SE Oregon and SW Idaho .... Chucklusa (*Lomatium canbyi*)

2b. Mature fruits with papery ribs between the two lateral wings; roots elongate, cylindrical and never spherical .... *Cymopterus*

3a. Leaves dissected 1-2 times with one to a few pairs of distinct leaflets; bracts beneath the terminal umbels of flowers narrow and finger-like, not fused to one another at their bases; flowers white; plants of sandy soils in southern Malheur and Harney Counties .... Corrugated springparsley (*C. corrugatus*)

3b. Leaves dissected 2-3 times into small segments; bracts beneath the terminal umbels of flowers broad and generally fused to one another at the base; flowers white or yellow; plants generally of clay soils, in Malheur County .... Plains Cymnopoterus *(C. glomeratus* (=*C. acaulis*))

4a. Flowers yellow; plants restricted to brown to tan Sucker Creek Formation ash outcrops that have weathered to clay........................ Greeley springparsley (var. *greeleyorus*)

4b. Flowers white; plants in clay soils other than those of the brown to tan ash outcrops in Succor Creek .... Plains springparsley (var. *glomeratus*)

1b. Foliage distinctly hairy, though sometimes sparsely so

5a. Flowers yellow; anthers yellow........................ *L. foeniculaceum*

6a. Petals with a fringe of hairs on their margins; plants known only from barrens a few miles west of Rome, OR (not known in ID) .... Fringe-petal biscuitroot (var. *fimbriatum*)

6b. Petals entire, lacking a fringe of hairs on their margins; plants scattered throughout SE Oregon and SW ID .... Macdougal's biscuitroot (var. *macdougalii*)

5b. Flowers white; anthers generally purple

7a. Plants with spherical thickening in the roots (see Figure 11) abruptly narrowing at the top; foliage similar to *L. nevadense* (see lead 8a); plants restricted to azonal soils of white ash outcrops in the Sucker Creek Formation that have weathered to bentonite clay .... Bentonite desertparsley (*L. bentonitum*)

7b. Plants with either elongate roots or, if roots are thickened then tapering gradually at the top of the thickened base (see Figure 11); plants widely distributed in SE Oregon and SW Idaho generally on zonal, loamy or rocky (with clay subsurface) soils

8a. Leaves divided about 2.5 times; leaflets somewhat open, with ultimate leaf segments neither narrowly linear (pencil-shaped) nor narrowed at the base; foliage sparsely hairy; bracts beneath the umbels with few hairs; plants generally of well-developed loamy soils........................ Nevada biscuitroot (*L. nevadense*)

8b. Leaves divided 3 or more times; leaflets tightly clustered, with tiny ultimate segments that are either much longer than wide or narrowed at the base; foliage densely to sparsely hairy; bracts beneath the umbels densely to sparsely hairy; plants of rocky soils with clay substructure .... (*L. ravenii*)

9a. Ultimate leaf segments wider in the middle or near the tip than at the base, generally < 3.0 times longer than wide; bracts at base of umbels densely hairy; stems generally 1-2 per plant; leaf bases rarely persistent; plants widespread in N NV, SE OR, and SW ID................ Paiute parsley (var. *paiutense*)

9b. Ultimate leaf segments generally uniformly narrow, generally > 3.5 times longer than wide; bracts at base of umbels hairless or nearly so; stems generally 2-4 per plant; leaf bases generally persistent; plants from vicinity of Ravendale, CA (see Figure 7) .... Lassen parsley (var. *ravenii*)