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A NEW SPECIES OF *LOMATIUM* (APIACEAE) FROM RED MOUNTAIN, A SERPENTINE ISLAND IN MENDOCINO COUNTY, CALIFORNIA

KEVIN M. MASON
28737 Colina Vista St.
Agoura Hills, California 91301
quercusboletus@gmail.com

EDWARD WILLIE
POB 254
San Anselmo, California 94979
ewillie44@aol.com

JAMES F. SMITH
Department of Biological Sciences
Boise State University
Boise, Idaho 83725
jfsmith@boisestate.edu.

JENNIFER WHEELER
Bureau of Land Management
Arcata Field Office
Arcata, California 95521
jswheele@blm.gov

BARBARA L. WILSON
Carex Working Group
2250 NW 13th Street
Corvallis Oregon 97330
bwilson@peak.org

ABSTRACT

A *Lomatium* species is endemic to Red Mountain, an ultramafic habitat island in northern Mendocino Co., California. It has been misidentified as three different species, *L. congdonii*, *L. engelmannii*, and *L. tracyi*, but differs from all of them and is described here as **Lomatium kogholiin**i Mason & Willie, **sp. nov.**, the Wailaki *Lomatium*.

When reviewing *Lomatium* for the Flora of North America project (Flora of North America Editorial Committee 1993-ongoing), we were struck by a series of specimens identified as *L. congdonii* J.M. Coulter & Rose reported from Red Mountain, Mendocino Co., California (Constance & Weatherwax 2017). This location is far from the known range of *L. congdonii*, which grows on ultramafic soils in the western foothills of the Sierra Nevada. *Lomatium* seeds are not well adapted to long-distance dispersal (Marisco & Hellman 2009), so the plants from Red Mountain were unlikely to be *L. congdonii*.

Red Mountain is a massive outcrop of ultramafic rock surrounded by sedimentary and metamorphic bedrock (USGS 2018) within the ancestral territory of the Native American Wailaki tribe. The contrast between the ultramafic mountain and surrounding geologic zones can be detected easily in aerial photos because of visible differences in vegetation density and the striking red color of the ultramafic soils on the mountain (Google LLC 2018). For plants adapted to ultramafic substrates, Red Mountain functions as a habitat island. At least 3 species are previously known to be endemic to

the site, *Arabis macdonaldiana* Eastwood, *Eriogonum kelloggii* A. Gray, and *Sedum eastwoodiae* (Britton) A. Berger (USFWS 2013).

Two *Lomatium* species occur on Red Mountain. One, confirmed by numerous herbarium specimens and our own field work, is *L. dasycarpum* (Torrey & A. Gray) J.M. Coulter & Rose. It is distinguished by its pale, tomentose petals and highly dissected leaves. It is ignored for the remainder of this article, which concentrates on smaller plants with glabrous yellow petals and less divided leaves.

This second *Lomatium* has been identified as *L. engelmannii* Mathias and *L. tracyi* Mathias & Constance, as well as *L. congdonii* (Table 2). All three of these species are similar in size and all grow on ultramafic substrates in central and northern California (Figure 3; Appendix 3). Given the limited area of Red Mountain, it seemed unlikely that more than one of these similar species could be present. More troubling, the plants from Red Mountain seemed to differ somewhat from each of the described species. Because of similarities between these species, we used DNA sequences as well as traditional taxonomic methods to compare them.

Methods – morphology

We examined specimens identified as *Lomatium congdonii*, *L. engelmannii*, and *L. tracyi* from from CAS, HSC, JEPS, ORE, OSC, and UC (herbarium acronyms from Thiers, continually updated; Appendix 1). We also examined high quality scans kept at OSC of *L. engelmannii* specimens located at SOC, and scans of the types of *L. congdonii*, *L. engelmannii*, and *L. tracyi* made available on the websites of the relevant herbaria (Table 1).

Table 1. Links to scans of type specimens of *Lomatium congdonii*, *L. engelmannii*, and *L. tracyi* available on the internet.

Species	Herbarium	URL of type or through which type can be found
L. congdonii	US	https://collections.nmnh.si.edu/search/botany/?ti=3
L. engelmannii	MO	http://www.tropicos.org/ImageSearch.aspx
L. tracyi	UC	https://webapps.cspace.berkeley.edu/ucjeps/imageserver/blobs/c81c2dd0-b160-4e46-8fab/derivatives/OriginalJpeg/content

One of us (KM) travelled through northern California to visit known sites where these three species grow, and two of us (KM and JW) visited Red Mountain to examine the plants. Samples collected from this trip were used for DNA extraction (Appendix 2). Plants were identified using the Jepson Manual (Constance & Mathias 2013, 2017) and by comparison with other labeled, and in many cases annotated, specimens (Appendix 1).

Methods – DNA

DNA was extracted from all samples using a Qiagen DNeasy plant mini kit (Qiagen, Valencia, California), following the manufacturer's instructions with the exception that incubation of the samples at 60°C was extended to 2 hours. Amplification of all regions used the primers and methods of Smith et al. (2018). Successful amplifications were determined by viewing aliquots on 1% agarose gels stained with ethidium bromide and viewed under UV illumination. All successful amplifications were purified using Exo-SAPit (Affymetrix, Cleveland, Ohio) and shipped to GeneWiz (Plainfield, New Jersey) for sequencing of complementary strands. Chromatograms were edited and assembled using Phy-DE (Müller et al. 2010). New samples for this publication are listed in Appendix 2 with GenBank numbers. All other samples were previously published in Smith et al. (2018) and voucher information as well as GenBank numbers for these samples can be found there.

Sequences were aligned for each of the seven regions separately, inserting gaps to maintain homology among characters. Ambiguous portions of the alignments and areas with large stretches of missing data were removed from the ends of all regions. A concatenated dataset for all seven regions was then generated and used as the basis for all phylogenetic analyses.

Maximum parsimony (MP) and MP bootstrap with 1,000 replicates (MPBS) were evaluated using PRAP2 (Müller 2004) in conjunction with PAUP* (Swofford 2002). Maximum likelihood (ML) was assessed using RaxML (Stamatakis, 2006) on the CIPRES Science Gateway (Miller et al. 2010) under the default GTR + G + I model and allowing bootstrapping (MLBS) using one model with joint branch length optimization to stop automatically using the default autoMRE. Consensus trees were generated and viewed in MEGA 7 (Kumar et al. 2016). The best fit model for DNA evolution was determined using jModelTest 2.1.7 (Darriba et al. 2012) and used for the Bayesian analysis (BI) with MrBayes 3.2 (Ronquist et al. 2012). Majority rule consensus trees of the output were generated in PAUP* and effective sample size (ESS) values were estimated in Tracer (Rambaut et al. 2014).

Results – morphology

The Wailaki *Lomatium* and the species most similar to it differed in several traits, including ray number and the size and oil tubes of the fruit (Table 3). Details of how the leaves were divided among species were the most useful traits for distinguishing the taxa but the hardest to communicate (Figs. 2, 4). Sample sizes for traits of mature fruits were limited, because, as is true for most *Lomatium* (KM, BLW pers. obs.), specimens are usually collected in flower or with young fruit.

The trait that most easily distinguishes the Wailaki *Lomatium* from the two similar species that grow in northwest California (*L. engelmannii* and *L. tracyi*) is its lack of bractlets. This is a trait the Wailaki *Lomatium* shares with *L. congdonii*.

Petal color is a useful trait for identifying the Wailaki *Lomatium*, but confusion surrounds the color because in *Lomatium* both yellow and white flowers often dry white or cream-colored. The Wailaki *Lomatium* and *L. congdonii* both have yellow flowers (Fig. 4; KM pers. obs.; CalPhotos continually updated). *Lomatium engelmannii* petals are white (pers. observ.; CalPhotos 2017) or purplish (Constance & Wetherwax 2012, 2017), although they were originally described as "yellow (?)" (Mathias 1938). Petals were originally reported as yellow in *L. tracyi* (Mathias & Constance 1942), based on a series of Tracy specimens collected 1923-1936 in Humboldt and Trinity counties, and they still are reported as yellow (Constance & Wetherwax 2012, 2017). However, the plants we have seen from Trinity County have white petals [KM pers. observ.; Photo 0000 0000 1009 2993 (2009-10-30) posted by J.K. Nelson on Cal Photos]. We are uncertain about the petal color of *L. tracyi* growing in Humboldt County because it usually cannot be judged from dried specimens.

Two CAS specimens labeled *Lomatium tracyi* and collected south of Red Mountain (*Smith 6203* and *Smith & Wheeler 6229A*) turned out to be *L. caruifolium* (Hook. & Arnold) J.M. Coulter & Rose. *Lomatium caruifolium* has yellow flowers and much wider bractlets than *L. tracyi*.

Clarifying the morphology of the similar *Lomatium* of ultramafic habitats also clarified their ranges (Fig. 3). Distances from Red Mountain to the range of *L. congdonii* is 284 km east-southeast, to *L. engelmannii* is 167 km northeast, and to *L. tracyi* is 61 km north. Comparison with a geologic map of California revealed that each taxon (including the Wailaki *Lomatium*) is associated with a different ultramafic bedrock that formed at a different time and has somewhat different components (USGS 2018; Appendix 3).

Table 2. Earlier names given to *Lomatium* herbarium specimens from Red Mountain that have no bractlets, yellow flowers, and little-divided leaves, here described as *L. kogholiini*.

Earlier name	Herb.	Collector	Coll. #	Day	Month	Year
L. congdonii	UC	L. Constance & R. C. Rollins	3003	21	5	1942
L. congdonii	UC	A. Eastwood & J. T. Howell	6131	7	7	1938
L. congdonii	UC	M. E. Mathias & L. Constance	6527			1867
L. congdonii	UC	T. Nelson & J. Nelson	4566	7	4	1979
L. tracyi	CAS	R. Gankin , R. Hildreth, and W. & I. Knight	2719	15	7	1969
L. tracyi	UC	G. F. Hrusa, H. Townsend, & T. Nosall	11884	8	6	1994
L. engelmannii	HSC	T. Nelson & A. Goes	2394	3	5	1976
L. engelmannii	HSC	T. Nelson & A. Goes	2400	3	5	1976
L. engelmannii	HSC	T. Nelson, A. Goes, & J. Nelson	2427	4	5	1976
L. engelmannii	HSC	T. Nelson, A. Goes, & J. Nelson	2434	4	5	1976
L. engelmannii	HSC	T. Nelson & A. Goes	2570	23	5	1976
L. engelmannii	HSC	T. Nelson & A. Goes	2571	23	5	1975
L. engelmannii	HSC	J. Sawyer & T. Nelson	2878	30	4	1977

Table 3. Morphological differences among the *Lomatium* taxa studied. ULS = ultimate leaf segments, the smallest units into which the leaf is divided. Sources: Constance & Weatherwax 2012, 2017, and measurement of herbarium specimens (Appendix 1). ULS = ultimate leaf segment.

	L. kogholiini	***L. congdonii***	***L. engelmannii***	***L. tracyi***
Petal color	yellow	yellow	white or purplish-white	white or yellow?
Bractlets	usually absent	usually absent	present or absent	present
Bractlets, if present	linear to lanceolate	linear to lanceolate	linear, lanceolate, or obovate	obovate or oblanceolate
Leaf color	green	gray-green	blue-green or gray-green, seldom green	green or blue-green
Rays	4–7	6–18	2–12	6–12
Oil ducts on commissure	4–6	2–4	2–6	7
Fruiting Pedicel	3–16 mm	5–12 mm	(2–) 3–9 mm	1–5 (–6) mm
Fruit Length	7.8–10 mm	7–10 mm	7–14 mm	4.8–10 (–11.5) mm
Leaf Surface	glabrous	glabrous or scabrous	glabrous, scabrous, or sparsely puberulent	glabrous
ULS callus tip length	0–0.1 mm	0.1–0.2 mm	0.1–0.2 mm, generally more pointed	0–0.1 mm, generally less pointed
ULS length	0.5–4 (–6.5) mm	3–10 mm	1–3 (–6) mm	0.5–3 (–7) mm

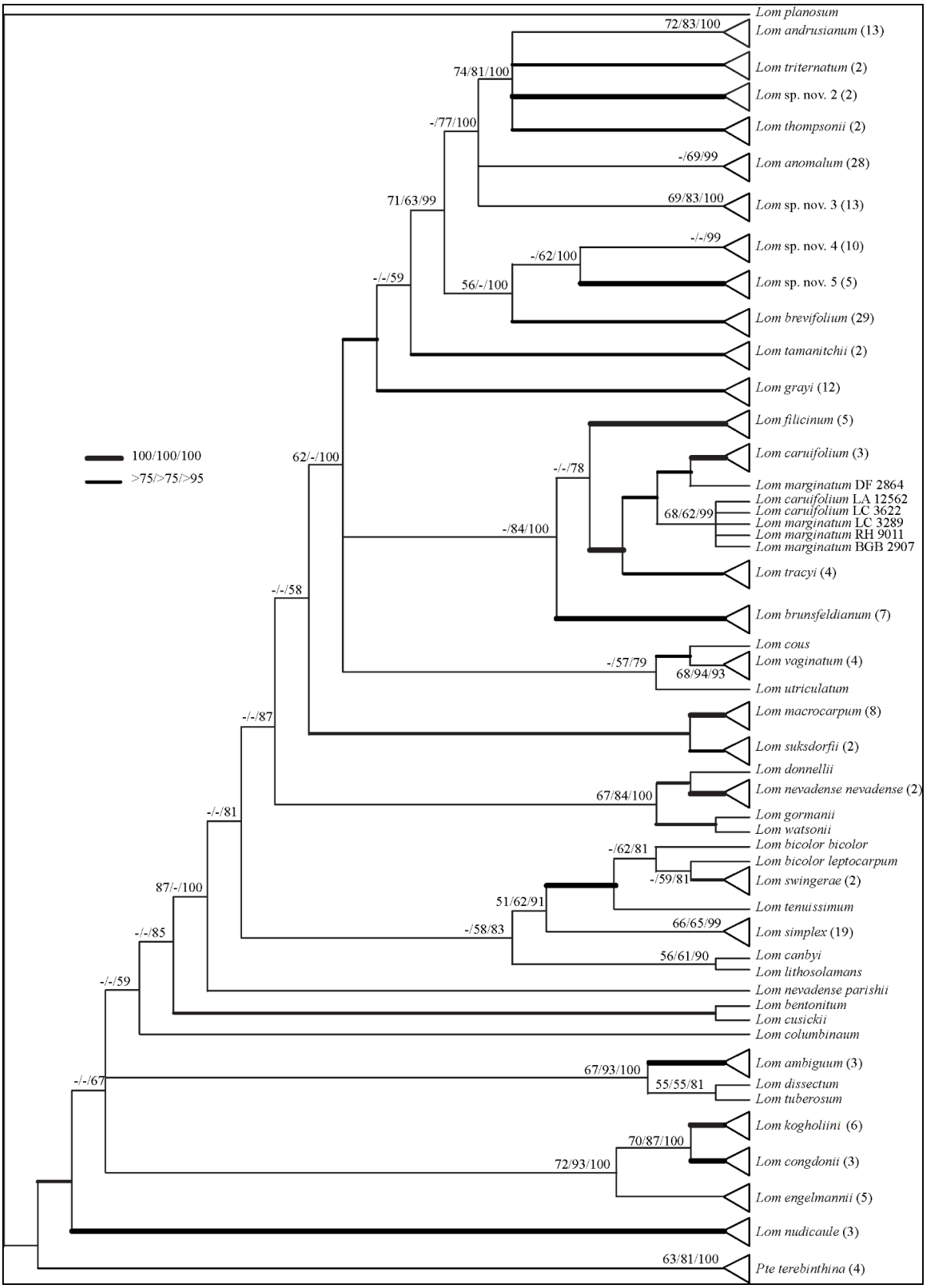
100/100/100
>75/>75/>95
Lom planosum
72/83/100
Lom andrusianum (13)
Lom triternatum (2)
74/81/100
Lom sp. nov. 2 (2)
-/77/100
Lom thompsonii (2)
-/69/99
Lom anomalum (28)
71/63/99
69/83/100
Lom sp. nov. 3 (13)
-/-/99
Lom sp. nov. 4 (10)
-/62/100
-/-/59
56/-/100
Lom sp. nov. 5 (5)
Lom brevifolium (29)
Lom tamanitchii (2)
Lom grayi (12)
Lom filicinum (5)
62/-/100
Lom caruifolium (3)
-/-/78
Lom marginatum DF 2864
Lom caruifolium LA 12562
Lom caruifolium LC 3622
68/62/99
Lom marginatum LC 3289
-/84/100
Lom marginatum RH 9011
Lom marginatum BGB 2907
Lom tracyi (4)
-/-/58
Lom brunsfeldianum (7)
Lom cous
-/57/79
Lom vaginatum (4)
68/94/93
Lom utriculatum
-/-/87
Lom macrocarpum (8)
Lom suksdorfii (2)
Lom donnellii
67/84/100
Lom nevadense nevadense (2)
-/-/81
Lom gormanii
Lom watsonii
-/62/81
Lom bicolor bicolor
Lom bicolor leptocarpum
-/59/81
Lom swingerae (2)
87/-/100
51/62/91
Lom tenuissimum
66/65/99
-/-/85
-/58/83
Lom simplex (19)
56/61/90
Lom canbyi
Lom lithosolamans
-/-/59
Lom nevadense parishii
Lom bentonitum
Lom cusickii
Lom columbinaum
67/93/100
Lom ambiguum (3)
-/-/67
55/55/81
Lom dissectum
Lom tuberosum
Lom kogholiini (6)
70/87/100
72/93/100
Lom congdonii (3)
Lom engelmannii (5)
Lom nudicaule (3)
63/81/100
Pte terebinthina (4)

Figure 1. Majority-rule consensus tree from Bayesian inference analysis with maximum parsimony and maximum likelihood support on corresponding branches. Numbers above branches are maximum parsimony bootstrap/maximum likelihood bootstrap/Bayesian inference posterior probabilities. A dash indicates bootstrap support less than 50. Maximal support from all three analyses are indicated with branches of triple thickness, and support that was greater or equal to 75 for both bootstrap values and greater or equal to 95 posterior probabilities are shown with branches of double thickness. Lom = *Lomatium,* Pte = *Pteryxia.* Letters and numbers following taxon names indicate individuals that are cited in Appendix 2. Where species are recovered as monophyletic, the clades are collapsed and the number of species sampled in each clade is indicated in parentheses following the name

Results – DNA

Amplifications were successful for nearly all regions and all samples, but some of the herbarium material did not amplify for all regions (Appendix 2). The three methods of phylogenetic analyses were congruent with each other, with the greatest resolution from the BI analyses. The two separate runs of the BI analyses were fully congruent and posterior probability support differed between the two by only a single point. The majority rule consensus of the BI trees is presented in Fig. 1 with MPBS and MLBS mapped onto the tree where clades were the same. Maximum parsimony resulted in 199 most-parsimonious trees (length = 2704 steps, consistency index (CI) excluding uninformative positions = 0.4473, retention index (RI) = 0.8467, rescaled consistency index (RC) = 0.4625). The TVM + I + G model was selected by jModelTest and implemented in the BI analyses. The ESS values were 1717.6 and 1,833.8 for the two runs.

Two clusters of taxa are relevant to this study (Fig. 1). One consists of *Lomatium caruifolium, L. marginatum,* and *L. tracyi*. The other consists of *L. engelmannii, L. congdonii,* and the Wailaki *Lomatium.*

Discussion

We initially hypothesized that the Wailaki *Lomatium* from Red Mountain was closely related to *L. tracyi* because Red Mountain is within what was reported to be the range of *L. tracyi,* and the Wailaki *Lomatium* has yellow petals, as *L. tracyi* was reported to have (Mathias & Constance 1942, 1944-1945; Constance & Weatherwax 2012, 2017). However, our hypothesis was false for several reasons. First, Red Mountain is not within the range of *L. tracyi*; *L. tracyi* specimens reported from south of Red Mountain are *L. caruifolium.* Second, *L. tracyi* in Trinity County has white to purplish petals and cream to purple anthers (K Mason 137, 138, and 146; Appendix 1, specimens examined). We have not yet found strong evidence about the fresh petal color of Humboldt County populations of *L. tracyi*. Most important, an analysis of DNA sequences indicates that *L. tracyi* is related to *L. caruifolium* and *L. marginatum,* not the plants from Red Mountain and its relatives (Fig. 1). A Humboldt County specimen of *L. tracyi* (*Chambers 5517*) was included in the study. Whatever its petal color, it clustered with the other *L. tracyi,* not with the Wailaki *Lomatium* (Fig. 1). The Wailaki *Lomatium* also differs from *Lomatium tracyi* in ultimate leaf segments shape, bractlet presence and (when present) shape, leaf color, and other morphologic characters (Table 3).

The Wailaki *Lomatium* is morphologically and genetically similar to *L. congdonii*. Both lack bractlets and have yellow petals and relatively long fruiting pedicels. They differ in several traits including number of rays, ultimate leaf segment length, and the size and oil ducts of the fruit (Table 3), but molecular data indicate that they are sister taxa (Figure 1). The Wailaki *Lomatium* is relatively geographically separated from *L. engelmannii* and differs from it in petal color and bractlet presence (Table 3). However, its leaves are more similar to those of *L. engelmannii* than those of *L. tracyi.* We conclude that the *Lomatium* plants from Red Mountain are distinct from *L. congdonii, L. engelmannii,* and *L. tracyi* and describe it as a species, *L. kogholiini.*

LOMATIUM KOGHOLIINI K.M. Mason & E. Willie, **sp. nov**. **TYPE: California**. Mendocino Co.: Red Mountain summit, 1222 m, 8 May 2018, *K.M. Mason* & *Wheeler 121* (holotype: OSC; isotypes: CAS, HSC).

Similar to *Lomatium congdonii* but with fewer rays and more oil ducts on commissure; similar to *L. engelmannii* but petals yellow and bractlets absent.

Herbs 0.5–3.8 dm, acaulous, glabrous, green; taproot slender; caudex simple, with basal sheaths of previous years present or absent, with or without persistent peduncles; pseudoscape absent. **Leaves** green, glabrous; basal leaves with petioles 50–150% as long as blades, partially or wholly sheathing; blades broadly ovate to triangular, 3–15 × 2.2–16 cm; ultimate leaf segments 80–400, elliptic to lanceolate, 0.5–4(–6.5) × 0.5–1 mm, entire, acute, apiculate, with calluses 0–0.1 mm. **Peduncles** 1–2 per plant, 4.5–28 cm, exceeding leaves, 0.5–1.8 mm wide 1 cm below apex, decumbent, ascending, or erect, not inflated, glabrous. **Umbels**: 2.2–3.4 cm wide in flower, 2.5–6(–10.5) cm wide in fruit; rays 4–7, 2–5 of them fertile, 0.5–3(–13.2) cm long in fruit, glabrous, unequal, ascending to spreading; involucel usually absent, if present not dimidiate; bractlets 0(-2), if present usually vestigial, linear to lanceolate, 1.5–5 mm, shorter than flowers, glabrous, distinct, margins narrowly scarious, not ciliate, entire. **Pedicels** 3–16 mm in fruit, shorter or longer than the fruit. **Flowers:** petals yellow, glabrous; anthers yellow; ovary and fruit glabrous. **Mericarps** dorsiventrally compressed, broadly oblong, 7.8–10 × 3.5–5 mm, length/width ratio 1.8–2.2, obtuse to rounded; wings 0.5–1.3 mm wide, 28–52% of body width, paler than body; dorsal ribs slightly or not raised; oil ducts 1 in intervals, 4–6 on commissure, conspicuous. **Chromosome number**, *n*=11, (note on *Nelson & Nelson 4566* from UC). Figures 2 and 4.

Flowering early April–June, fruiting June–July. Open jeffrey pine (*Pinus jeffreyi*) plant communities with sugar pine (*Pinus lambertiana*), on serpentine soil, elevation 400–1250 m, characteristically with *Pinus attenuata, Calocedrus decurrens, Arctostaphylos manzanita, Ceanothus pumilus, Quercus vaccinifolia, Allium falcifolium Pedicularis densiflora,* and *Sedum eastwoodiae*. Endemic to Wailaki Territory, specifically Red Mountain and Little Red Mountain of Mendocino Co., California, north of Cummings.

"Kogholiini" (accent on the first i; *kog-oh-LI-in-ee*) is Wailaki for "daylight coming." The plant was found on Wailaki ancestral land. The Wailaki name was chosen to honor the connection between the plant and the Wailaki people, a name worthy of the special standing of *Lomatium* in the herbal and native worlds. The phrase was found in the lyrics of an old traditional female puberty song.

Other collections examined. USA. California. Mendocino Co.: Summmit, "Big" Red Mountain, 5 mi SE of Bell Springs, 4000 ft, 21 May 1942, *Constance & Rollins 3003* (UC); near Cummings P. O., 7 Jul 1938, *Eastwood & Howell 6131* (UC); Red Mountain, 3400 ft, 15 Jul 1969, *Gankin et al. 2719* (CAS); on summit, 1250 m, 8 Jun 1994, *Hrusa et al. 11884* (UC); Red Mtns., 1867, *Mathias & Constance 6527* (UC); along road on E side of Red Mountain, 3800 ft, 3 May 1976, *Nelson & Goes 2394* (HSC); E of road along E side of Red Mountain, 4000 ft, 3 May 1976, *Nelson & Goes 2400* (HSC); at S end of BLM road to School Section Creek, just above creek, 2800 ft, 4 May 1976, *Nelson et al. 2427* (HSC); along ridge beween the forks of School Section Creek, 3200 ft, 4 May 1976, *Nelson et al. 2434* (HSC); along road to Little Red Mountain, 2700 ft, 23 May 1976, *Nelson et al. 2570* (HSC); along road to Little Red Mountain, 2700 ft, 23 May 1975, *Nelson & Goes 2571* (HSC); at S end of BLM road to Red Mountain, across School Section Creek from end of road, 2800 ft, 7 Apr 1979, *Nelson & Nelson 4566* (UC); Cedar Spring Road to Red Mountain, 3400 ft, 30 Apr 1977, *Sawyer & Nelson 2878* (HSC).

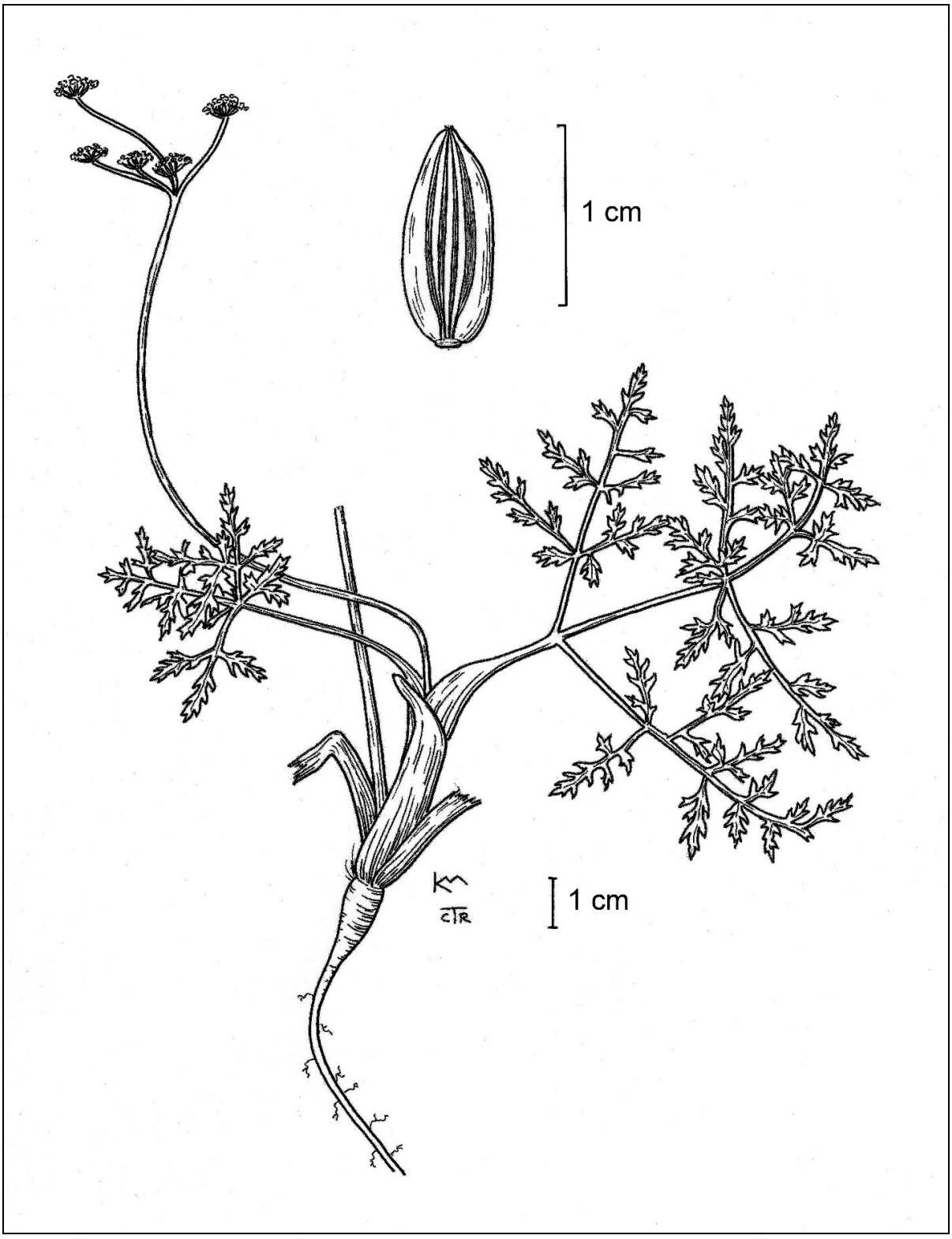

Figure 2. *Lomatium kogholiini* habit and fruit. Drawing by Kevin M. Mason and Cindy T. Roché.

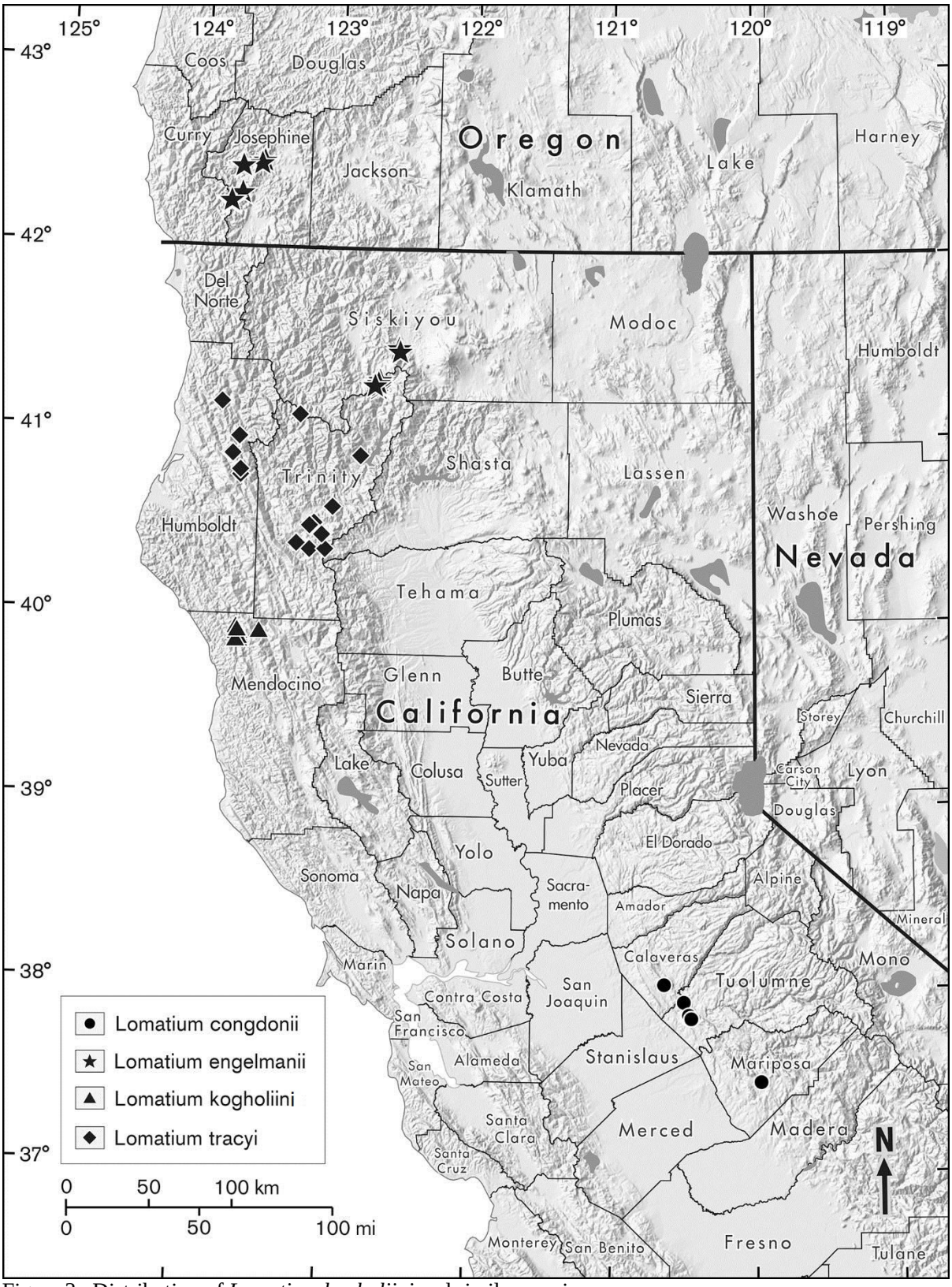

Figure 3. Distribution of *Lomatium kogholiini* and similar species.

Figure 4. Morphological variation in flowering *Lomatium kogholiini*. Photos taken on Red Mountain, Mendocino Co., California, on 8 May 2018 by Jennifer Wheeler

Identification key to *Lomatium kogholiini* and similar species

These *Lomatium* species have similar leaf dissection. Bractlets are often wide and obovate, sometimes lobed or dissected, less often absent. Fruit walls are thick, and therefore oil ducts are obscure. Fruit wings are often curved down, making schizocarps elliptic in cross section, and usually about the same color as the fruit bodies. These species occur west of the Cascade Range and Sierra Nevada, mostly in California, though four occur in Oregon and southwest Washington.

1. Bractlets much dissected, sometimes 2-pinnate; Oregon (Willamette Valley) and southwest Washington ..... **Lomatium bradshawii**
1. Bractlets entire or sometimes few toothed or lobed, not pinnate, sometimes absent; southern Oregon and California.

2. Petals dark purple or dark red; nw. and central California.

3. Ultimate leaf segments ovate; mericarps length/width ratio 1.7–2.3 ..... **Lomatium ciliolatum** (in part)
3. Ultimate leaf segments linear; mericarps length/width ratio 1.1–2.

4. Peduncle densely scabrous; bractlets broadly scarious margined, rarely narrowly scarious margined; mericarps length/width ratio 1.4–2 ..... **Lomatium hooveri**
4. Peduncle glabrous to sparsely scaberulous; bractlets narrowly scarious margined; mericarps length/width ratio 1–1.6(–1.8) ..... **Lomatium marginatum** (in part)

2. Petals white, purplish-white, cream, or yellow; California and Oregon.

5. Petals white, purplish-white, or cream when fresh; anthers yellow, yellow-green, purple, or purple turning to cream; fruiting rays 1–4(–8) per umbel; mericarps 7–15 mm; s. Oregon and n. California.

6. Ultimate leaf segments (5–)10–84 mm; leaves green ..... **Lomatium marginatum** (in part)
6. Ultimate leaf segments 0.5–7(–18) mm, if segments up to rarely (–18) mm then leaves gray green (as in *L. peckianum*).

7. Ultimate leaf segments (1–)3–7(–18) mm; mericarps length/width ratio 2–3.8 (–4.4); fruit wings 1.2–2.8 mm wide; substrate volcanic ..... **Lomatium peckianum**
7. Ultimate leaf segments 0.5–3(–7); mericarps length/width ratio 1.7–3.6; fruit wings 0.5–1.5 mm wide; substrate strictly serpentine.

8. Ultimate leaf segment callus tips 0–0.1 mm; petals white; leaves green or blue-green; mericarps 4.8–10(–11.5) mm; fruiting pedicel 1–5(–6) mm; leaf surfaces glabrous; n. California ..... **Lomatium tracyi** (in part)
8. Ultimate leaf segment callus tips 0.1–0.2 mm, generally more pointed; petals purplish-white or white; leaves blue-green or gray-green, seldom green; mericarps 7–14 mm; fruiting pedicel (2–)3–9 mm; leaf surfaces glabrous, scabrous, or sparsely puberulent; s. OR and n. California ..... **Lomatium engelmannii**

5. Petals yellow when fresh; anthers yellow; fruiting rays 1–15 per umbel; mericarps 4.8–12(–13) mm; central California to s. Oregon.

9. Bractlets absent on most umbellets, if present on some then linear to lanceolate; ultimate leaf segments 0.5–10 mm; fruit wings 0.5–1.3 mm wide; California.

10. Rays 6–18 per umbel; leaf surfaces green or gray-green; oil tubes on the commissure 2–4; Red Hills of Tuolumne Co., California ..... **Lomatium congdonii**
10. Rays 4–7 per umbel; leaf surfaces green; oil tubes on the commissure 4–6; Red Mountain of Mendocino Co., California ..... **Lomatium kogholiini**

9. Bractlets present on most umbellets, or if absent on some umbellets then bractlets obovate to oblanceolate; ultimate leaf segments 0.5–60 mm; fruit wings 0.5–2.8 mm wide; California and Oregon.

11. Ultimate leaf segments elliptic to broadly ovate, 0.5–8 mm; peduncle 0.5–2 mm wide in fruit 1 cm below the umbel; California.

12. Leaves, peduncles, and/or rays glabrous or scabrous; bractlets obovate or oblanceolate, 1–2.5(–4) mm long; leaves pinnate to 1–2-pinnatifid; peduncle 0.5–1 (–1.2) mm wide in fruit; n. California ..... **Lomatium tracyi** (in part)
12. Leaves peduncles, and/or rays typically pubescent, sometimes glabrous or scabrous; bractlets usually obovate, 3–4 mm long; leaves usually more divided 1–2-pinnate to 2–3-pinnatifid; peduncle 0.5–2 mm wide in fruit; central and n. California.

13. Ultimate leaf segments 0.3–1 mm wide; substrate volcanic soil; range San Francisco Bay area (in Santa Clara and Stanislaus cos.) ..... **Lomatium observatorium**
13. Ultimate leaf segments 0.3–2.5 mm wide; substrate serpentine; range nw. California ..... **Lomatium ciliolatum**

11. Ultimate leaf segments linear, 2–60 mm; peduncle 0.5–4 mm wide in fruit 1 cm below the umbel; bractlets 1–10 mm; California and Oregon.

14. Leaves pinnate to 1–2-pinnatifid; peduncle 0.5–1(–1.2) mm wide in fruit; leaves, peduncles, and/or rays glabrous or scabrous; n. California ..... **Lomatium tracyi** (in part)
14. Leaves usually more divided 2–3-pinnate to 2–3-pinnatifid; peduncle 1–4 mm wide 1 cm below the umbel; leaves peduncles, and/or rays glabrous, scabrous, or pubescent; central and n. California.

15. Mature mericarps length/width ratio 1.7–3(–3.2); peduncle glabrous or distally scaberulous; southwest Oregon ..... **Lomatium cookii**
15. Mature mericarps length/width ratio 1–2.2; peduncle glabrous, scabrous, or pubescent; west-central California.

16. Bractlets usually >5 per fruiting umbellet, broadly obovate to narrowly oblanceolate, rarely lanceolate; mature fruiting pedicels 0.5–5(–6) mm, shorter than or equal to fruit length; peduncle glabrous, scabrous, or pubescent; elevation 50–600 m ..... **Lomatium caruifolium**
16. Bractlets usually <5 per fruiting umbellet, filiform to lanceolate, rarely narrowly oblanceolate; mature fruiting pedicels 3.5–13 mm shorter than or longer than fruit length; peduncle glabrous; elevation 250–1000 m ..... **Lomatium marginatum** (in part)

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Appendix 1. Additional specimens examined.

***Lomatium caruifolium*. USA. California.** Butte Co.: 8 mi N of Oroville, 17 Apr1914, *A. A. Heller 11303* (OSC); 8 mi N of Oroville, 6 Mar 1915, *Heller 11769* (OSC). Mendocino Co.: Hog Hole Ridge, 552 m, 18 May 2018, *K. M. Mason 135A-135C* (OSC, SRP, UC); along Mountain House Road 9.6 km S of Hopland, 213 m, 20 May 1981, *Smith 6203* (CAS); wet serpentine outcrop at E edge of town of Boonville, Rte. 128, 400 ft, 21 May 1981, *Smith & Wheeler 6229A* (CAS). Sacramento Co.: Sacramento Valley; along Ca-104/Twin Cities Rd., 0.7 mi W of the Amador County Line (Carbondale 7.5' Q), 63 m, 7 Apr 2014, *Hemkamp & Barnes 22698* (OSC). San Francisco Co.: San Francisco, 25 Jun 1903, *E.R.S. S.10520* (ORE); San Francisco, Sierra and Missouri streets, 6 May 1956, *Howell 31353* (OSC); San Francisco, Hunters Point, 6 May 1957, *Howell 32217* (OSC); San Francisco, Bayview Hills, 18 Mar 1950, *Raven 1440* (OSC); San Francisco, McLaren Park, 30 Mar 1956, *Raven 8901* (OSC); San Francisco, NE of Mountain Lake, Presidio, 7 Apr 1957, *Raven 10595* (OSC); San Francisco, about the E summit of the San Miguel Hills, 13 Apr 1957, *Raven 10658* (OSC); San Francisco, Presidio Golf Links, 7 Apr 1956, *Rubtzoff 2181* (OSC). San Mateo Co.: E of SE end of San Andreas Lake; just W of Burlingame, near Millbrae, near junction of Trousdale Drive and Skyline Boulevard, between NW and SE versions of a new highway, 19 Apr 1968, *French 2858* (OSC [2 sheets]). Santa Barbara Co.: Santa Cruz Island, Central Valley, near valley Road 100 yards W of Reparo Viejo overlook., 1000 ft, 8 May 1990, *Junack sc-1670a* (OSC). Sonoma Co.: 4 mi N of Geyserville, 200 ft, 10 May 1942, *Constance & Rollins 2862* (ORE). Tuolumne Co.: S outskirts of Chinese Camp, 6 Apr 1968, *Constance et al. 3624* (OSC); along Hwy. #49, 2.1 mi. S of the jct of Hwy. #120 at Chinese Camp, 17 Apr 1973, *McNeal 1268* (OSC).

***Lomatium congdonii*. USA. California.** Calavaras Co.: Highway 4 2.5 road mi N of Copperopolis; watershed Black Creek on gentle slope 0.3 mi E of the highway; Salt Spring Valley 7.5' USGS Quadrangle, 30 Apr 1998, *Taylor 16362* (UC); Highway 4 2.5 road mi N of Copperopolis, watershed Black creek on gentle slope 0.3 mi E of the highway, Salt Spring Valley 7.5' USGS Quadrangle, 6 Jun 1998, *Taylor 16487* (UC). Mariposa Co.: W Water Ditch [illegible] Mariposa, Jun 1896, *Congdon s.n.* (UC); Mariposa, 16 Apr 1893, *Congdon s.n.* (UC); West Water Ditch, 17 May 1903, *Congdon* (UC); West Water Ditch, Mariposa, 24 Jun 1894, *Congdon s.n.* (UC); Mariposa, 21 Apr 1897, *Congdon s.n.* (UC); Mariposa, 19 Apr 1996, *Congdon s.n.* (UC). Tuolumne Co.: 3 mi S of Chinese Camp on dirt road to La Grange, 1000 ft, 30 Mar 1956, *Constance et al. 3621* (UC); 3 mi S of Chinese Camp, 15 May 1937, *Hoover 2448* (UC); 3 mi S of Chinese Camp, 2 May 1939, *Hoover 4071* (UC); 3 mi S of Chinese Camp, rocky hills, 16 Jun 1967, *Hoove 10638* (UC); Jamestown, Red Hills, on Serpentine Loop Road, 338.5 m, 16 May 2018, *Mason 124* (UC); Red Hills, on the side of Red Hills Road, 351.4 m, 16 May 2018, *Mason 126* (SRP); Red Hills, rest stop off of Red Hills Rd closest to La Grange Road on a trail S side of rest stop, 368.6 m, 16 May 2018, *Mason 127* (OSC); Red Hills, NE-facing slope along dirt road into Sixbit Gulch., 1000 ft, 25 May 1984, *Taylor 8515* (UC); Peoria Basin, slopes at SE edge of basin ca. 1 mi E of Peoria Pass Rd, New Melones Dam 7.5' USGS Quadrangle, 900 ft, 15 Apr 1996, *Taylor 16332* (UC); Red Hills (ca. 3 air mi SW of Chinese Camp), 22 Apr 1998, *Taylor 16359* (UC).

***Lomatium engelmannii*. USA. California.** Siskiyou Co.: Scott Mts 5 mi above Callahan, 17 May 1954, *Barneby 11534* (CAS); 5.8 air mi SE of Callahan and 19 air mi SW of Weed, 15 May 2016, *McNeill s.n.* (CIC); margins of Carmen L., ca. 1.5 mi E of Scott Mt. road, 5700 ft, 28 May 1950, *Wiggins 12361* (OSC). **Trinity Co.**: Scott's Mountain Summit Campground off of Highway 3, 1650 m, 30 Jun 3028, *Mason 147* (SRP); about 1 mi S of Scott's Mountain Summit Campground off of Hwy 3 on the right hand side of the road heading north, 1584 m, 30 Jun 2018, *Mason 148* (OSC). **Oregon.** Curry/Josephine Co. line: E side of Kalmiopsis Wilderness Area, ridge N of Onion Camp, 7 Jun 1980, *Stansell s.n.* (OSC); Curry Co.: Ridge on divide between Chetco and Illinois Rivers, 4250 ft, 26 May 2004, *Duncan s.n.* (SOC); ridge, head of Slide Creek, 18 Jun 1930, *Leach 3034* (ORE). Josephine Co.: Along trail to Whetsone Butte from end of FR 4201, 4166 ft, 19 Jun 2013, *Duncan s.n.* (SOC); Chrome Ridge, 3990 ft, 17 May 1988, *Kagan 5178801* (OSC); E of Onion Mt., ca. 13 mi W of Grants Pass, 18 Apr 1989, *Paetzel s.n.* (OSC); Upper Pickett Cr. Region, ca. 12 mi W of Grants Pass, 25 May 1990, *Paetzel s.n.* (OSC); near a saddle about 2/5 mile ESE of Pearsoll Peak Summit, 4400 ft, 7 Jun 1992, *Rolle 551* (OSC); Chrome Ridge, 4000 ft, 29 May 1995, *Rolle 896* (OSC); Chrome Ridge, on Road 2402 0.5 mi north of jct with Road 2512, 21 Jun 1985, *Stansell & Planeto s.n.* (OSC).

***Lomatium tracyi*. USA. California.** Humboldt Co.: Horse Mtn., off Titlow Hill Rd. S of its junction with Hwy 2999 E of Arcata, 4900 ft, 23 Jun 1990, *Chambers 5517* (OSC); 1/4 mi from Horse Mtn Road, 1/2 mi below turnoff to summit, near end of unused gravel road, 1 May 1978, *Kelly 587* (UC); 1/4 mile from Horse Mtn Road, 1/2 mi below turnoff to summit, near end of unused gravel road, 1 May 1978, *Kelly 588*, *589*, *590*, and *591* (UC); intersection with road sign saying Grouse Mtn. L.O. 2 mi. Horse Mtn. 15 mi, 1 May 1978, *Kelly 592* (UC); Horse Mountain, 5000 ft, 20 Jun 1926, *Tracy 7610* (UC); Brannan Mountain, 10 Jul 1930, *Tracy 8869* (CAS, UC); Brannan Mountain, 3500 ft, 9 Jul 1933, *Tracy 12650* (UC); French Camp Ridge, 3500 ft, 23 Jun 1935, *Tracy 13971* (UC); Grouse Mountain, 5000 ft, 19 Jul 1949, *Tracy 18390* (UC). Lassen Co.: 4.5 mi E of Westwood on State Hwy 36, 16 Jun 1968, *Raven & Solbrig 13248* (UC). Shasta Co.: along road from Shingletown to Manton, 0.2 mi S of jct. with Rt. 44., roadside, 3200 ft, 16 Apr 1968, *Brehm 2907* (OSC); 2.6 mi NE of Ragan Meadow Public Camp where the Round Bottom Mine Road branches off, 2 Jul 1950, *Hoffman 3275* (UC). Trinity Co.: 1.5 mi above Peanut on State Hwy 36, 11 Jun 1948, *Ferris & Lorraine 11698* (CAS, UC); 3 mi NE of Douglas City, 26 Apr 1954, *Howell 29167* (CAS); top of low flat ridge that is partially encircled by a U-shaped bend in USFS road 35N23Y, ca. 100 m SE of its jct w/ USFS road 35N32Y, just W of Mule Creek, 2850 ft, 27 Jun 1984, *Jokerst 2078* (CAS); S of Peanut off Interstate 3 in the Trinity National Forest; Trinity stop #1, 870 m, 18 May 2018, *Mason 137* (SRP); on left hand side of heading E on Interstate 36 before Interstate 3 in Trinity National Forest, Trinity stop #2, 950 m, 19 May 2018, *Mason 138A* (SRP); on left hand side of heading E on Interstate 36 before Interstate 3 in Trinity National Forest, Trinity stop #2, 950 m, 19 May 2018, *Mason 138B* (UC); Hayfork Mountain, N of the town of Hayfork off Interstate 3 in the Shasta-Trinity National Forest, 1060 m, 19 May 2018, *Mason 146* (OSC); SW of South Dubakella Mtn W of road to Mud Springs, 5000 ft, 6 May 1978, *Nelson 4004* (UC); Dubakella Quad, Shasta-Trinity National Forest, Hill above road 29N55 at jct. with spur road, 5.6 mi S of jct with State Route 36., 5500 ft, 20 Jun 1980, *Nelson & Nelson 5683* (UC); Burns Ranch, 1500 ft, 28 Jun 1923, *Tracy 6393* (UC); Hay Fork Mountain, near summit on Weaverville Road., 3600 ft, 30 Jun 1923, *Tracy 6457* (UC); Mary Blaine Mt, 6400 ft, 3 Aug 1935, *Tracy 14462* (UC). Trinity-Shasta co. line: Jct. of Wildwood and Regan Meadow roads, 5000 ft, 2 Jul 1950, *Hoffman 3273* (UC). Trinity-Tehama co. line: Jct. of Wildwood and Regan Meadow roads, 5000 ft, 2 Jul 1950, *Hoffman 3273* (UC).

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Appendix 2. Samples used in the analyses, vouchers, GenBank numbers, and herbarium code following Thiers (continuously updated). All new samples are included here; data on other samples is available in Smith et al. 2018. DNA regions where amplification was not successful are indicated with NA. Voucher includes both the abbreviation used in Figure 1 and the collector and collection number as presented in Appendix 1. *Lomatium kogholiine* specimens listed as RMA to RME were leaves from additional Red Mountain plants, vouchered by *Mason 120*.

Taxon	Voucher	Herb.	State	County	Genbank Numbers						
					ITS	ETS	*rpl32-trnL*	*rps16* intron	*trnD-trnT*	*ndhF-rpl32*	*psba-trnH*
L. caruifolium	HH1 = Mason 135A	UC	CA		MK178380	MK178330	MK178405	MK178455	MK178479	MK178430	MK178355
	HH2 = Mason 135B	OSC	CA		MK178381	MK178331	MK178406	MK178456	MK178480	MK178431	MK178356
	HH3 = Mason 135C	SRP	CA		MK178382	MK178332	MK178407	MK178457	MK178481	MK178432	MK178357
	LC = Constance 3622	OSC	CA	Amador	NA	MK178334	NA	NA	NA	NA	MK178359
	LA = Ahart 12562	OSC	CA	Butte	MK178383	MK178333	MK178408	MK178458	MK178482	MK178433	MK178358
L. congdonii	RH1 = Mason 124	UC	CA		MK178384	MK178335	MK178409	MK178459	MK178483	MK178434	MK178360
	RH2 = Mason 126	SRP	CA		MK178385	MK178336	MK178410	MK178460	MK178484	MK178435	MK178361
	RH3 = Mason 127	OSC	CA		MK178386	MK178337	MK178411	MK178461	MK178485	MK178436	MK178362
L. engelmannii	K. Mason 147	SRP	CA	Trinity	MK178387	NA	MK178412	MK178462	MK178486	MK178437	MK178363
	K. Mason 148	OSC	CA	Trinity	MK178388	MK178338	MK178413	MK178463	MK178487	MK178438	MK178364
	MP sn = Paetzel s.n.	OSC	OR	Josephine	MK178389	MK178339	MK178414	MK178464	MK178488	MK178439	NA
	R. P. McNeill sn	CIC	CA	Siskiyou	MK178390	MK178340	MK178415	MK178465	MK178489	MK178440	NA
	VS sn = Stansell s.n.	OSC	OR	Curry / Josephine	MK178391	MK178341	MK178416	MK178466	NA	MK178441	MK178365
L. marginatum	DF = French 2864	OSC	CA	Lake	MK17	NA	NA	NA	NA	NA	MK17

					8392						8366
	LC = Constance 3289	OSC	CA	Shasta	MK17 8393	MK17 8342	MK17 8417	NA	NA	MK17 8442	MK17 8367
	RH 9011 = Halse 9011	OSC	CA	Glenn	MK17 8394	MK17 8343	MK17 8418	MK17 8467	NA	MK17 8443	MK17 8368
L. kogholiine	RM1 = Mason 120	OSC	CA	Mendocino	MK17 8374	MK17 8324	MK17 8399	MK17 8449	MK17 8473	MK17 8424	MK17 8349
	RMA, Mason		CA	Mendocino	MK17 8375	MK17 8325	MK17 8400	MK17 8450	MK17 8474	MK17 8425	MK17 8350
	RMB, Mason		CA	Mendocino	MK17 8376	MK17 8326	MK17 8401	MK17 8451	MK17 8475	MK17 8426	MK17 8351
	RMC, Mason		CA	Mendocino	MK17 8377	MK17 8327	MK17 8402	MK17 8452	MK17 8476	MK17 8427	MK17 8352
	RMD, Mason		CA	Mendocino	MK17 8378	MK17 8328	MK17 8403	MK17 8453	MK17 8477	MK17 8428	MK17 8353
	RME = Mason		CA	Mendocino	MK17 8379	MK17 8329	MK17 8404	MK17 8454	MK17 8478	MK17 8429	MK17 8354
L. tracyi	KLC = Chambers 5517	OSC	CA	Humboldt	MK17 8396	MK17 8345	MK17 8420	MK17 8469	MK17 8490	MK17 8445	MK17 8370
	BGB 2907 = Brehm 2907	OSC	CA	Shasta	MK17 8395	MK17 8344	MK17 8419	MK17 8468	NA	MK17 8444	MK17 8369
	T1 = Mason 137	SRP	CA		MK17 8397	MK17 8346	MK17 8421	MK17 8470	MK17 8491	MK17 8446	MK17 8371
	T2 = Mason 138A	SRP	CA		MK17 8398	MK17 8347	MK17 8422	MK17 8471	MK17 8492	MK17 8447	MK17 8372
	T3 = Mason 146	OSC	CA		NA	MK17 8348	MK17 8423	MK17 8472	MK17 8493	MK17 8448	MK17 8373

Appendix 3. Geolithology and geocomposition of ultramafic bedrock in the areas where four *Lomatium* grow in northern California, from USGS (2018). The age of the ultramafic rock can have an influence on the proportion of serpentine plant endemics, perhaps due to time periods for weathering to occur and for adaptation to ultramafic soils (Brooks 1985). KM = Klamath Mountains. CR = Coast Range and western Klamath Mountains.

	Lomatium kogholiini	***Lomatium tracyi***	***Lomatium engelmannii***	***Lomatium congdonii***
Geologic unit	3 (southern region)	2 (and 3?)	1	2
Major Rock	Serpentinite	Serpentinite amd Peridotite	Peridotite	Serpentinite and Peridotite
Minor Rock	Peridotite	Pyroxenite	Serpentinite and Pyroxenite	Pyroxenite
Ultramafic Zone (Range and Age)	Coast Ranges and Western Klamath Mountains	Western Sierra Nevada and KM and possibly CR	Trinity Ophiolite	Western Sierra Nevada and Klamath Mountains
Age	Middle to late Jurassic (youngest)	KM: Late Proterozoic (?) to early Jurassic CR: Middle to late Jurassic	Ordovician (oldest)	Later Proterozoic (?) to early Jurassic