THE LOMATIUM GRAYI COMPLEX (APIACEAE) OF THE WESTERN UNITED STATES: A TAXONOMIC REVISION BASED ON MORPHOMETRIC, ESSENTIAL OIL COMPOSITION, AND LARVA-HOST COEVOLUTION STUDIES

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ABSTRACT

The *Lomatium grayi* complex is morphologically diverse across it range. The type species of this complex, *Lomatium grayi* s.s., has been found to not be a host of the larvae of *Papilio indra*, while the other three morphotypes are larval-hosts. A fifteen character, morphometric analysis was conducted on 390 herbarium specimens from throughout the range of this species. PCA, MANOVA, CDA, and Tukey tests revealed that the majority of the characters in this dataset were significantly different between four regional morphotypes. As a result of the morphometric analysis, the morphotypes are herein proposed as four species. Two new species are proposed for populations of *L. grayi* in the Pacific Northwest. **Lomatium papilioniferum** is proposed for plants in California, western Idaho, northern Nevada, Oregon, and Washington. **Lomatium klickitatense** is proposed for populations of robust plants from western Klickitat County, Washington, and northern Hood River County, Oregon. **Lomatium grayi** var. **depauperatum** is elevated to a species. This leaves no infraspecific taxa within *L. grayi* s.s. A presence/absence phenetic analysis of combined essential oil data was inconclusive regarding the composition of *L. grayi* s.s., which was found to be more similar to *Lomatium klickitatense* and *Lomatium depauperatum* than other species of *Lomatium*. Taxonomic treatments for each of the four species in this complex are provided. A key to these species and the multiple species that have been commonly mistaken for *L. grayi* is also included.

RESUMEN

El complejo *Lomatium grayi* es morfológicamente diverso en todo su rango. Se ha descubierto que la especie tipo de este complejo, *Lomatium grayi* s.s., no es un huésped de las larvas de *Papilio indra*, mientras que los otros tres morfotipos son hospedadores de larvas. Se realizó un análisis morfométrico de quince caracteres en 390 especímenes de herbario de todo el rango de esta especie. Las pruebas PCA, MANOVA, CDA y Tukey revelaron que la mayoría de los caracteres en este conjunto de datos eran significativamente diferentes entre cuatro morfotipos regionales. Como resultado del análisis morfométrico, los morfotipos se proponen aquí como cuatro especies. Se proponen dos nuevas especies para poblaciones de *L. grayi* en el noroeste del Pacífico. **Lomatium papilioniferum** se propone para plantas de California, el oeste de Idaho, el norte de Nevada, Oregón y Washington. **Lomatium klickitatense** se propone para una pequeña población de plantas robustas del oeste del Condado de Klickitat, Washington y el norte del Condado de Hood River, Oregón. **Lomatium grayi** var. **depauperatum** se eleva a especie. Esto no deja taxa infraespecíficos dentro de *L. grayi* s.s. Un análisis fenético de los datos combinados de aceites esenciales no fue concluyente con respecto a la composición de *L. grayi*, que resultó ser más similar a *Lomatium klickitatense y Lomatium depauperatum* que otras especies de *Lomatium.* Se proporcionan tratamientos taxonómicos para cada una de las cuatro especies en este complejo. También se incluye una clave para estas especies y las múltiples especies que comúnmente se han confundido con *L. grayi*.

INTRODUCTION

Sereno Watson was the first to recognize the distinctiveness of the species that would later be known as *Lomatium grayi*. This taxon was first described as *Peucedanum millefolium* S. Watson in the Botany volume of the United States Geological Exploration of the Fortieth Parallel (Watson 1871). *Peucedanum millefolium* was widely used until a new combination, *Peucedanum grayi* J.M. Coult. & Rose, was proposed as the legitimate replacement by J.F. Coulter and J.N. Rose (1888). Watson's name was found to be illegitimate since *Peucedanum millefolium* (Eckl. & Zeyh.) Sond. was published first in 1861 based on a species from South Africa.

After 1900, taxonomists split the North American members of Apiaceae into several genera, separate from the European and Asian taxa (Coulter & Rose 1900; Jones 1908; Coulter & Rose 1909). In their comprehensive monograph, Coulter and Rose (1900), placed the North American species of *Peucedanum* into the genus *Lomatium* Raf., (published in 1819). However, Marcus Jones (1908) interpreted *Lomatium* Raf. to be a

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homonym of the genus *Lomatia* R. Br. (Proteaceae), which was published 9 years earlier. He proposed the genus *Cogswellia* Spreng. to be the legitimate genus. He transferred all of Coulter and Rose's (1900) *Lomatium* taxa into *Cogswellia*. Jones made the new combination *Cogswellia millefolia* (S. Watson) M.E. Jones based on Watson's original name, not Coulter and Rose's replacement. Jones' decision is another example of his persistent pattern of ignoring the rule of priority in his floristic treatments (Barneby 1964). A year later, Coulter and Rose (1909) published a comprehensive update to their 1900 monograph which recognized many of Jones' nomenclatural revisions. However, they did not accept Jones' name, *Cogswellia millefolia*, and made the new combination, *Cogswellia grayi* (J.M. Coult. & Rose) J.M. Coult. & Rose. Both names were used interchangeably for around a decade before further changes in botanical nomenclature forced *C. millefolia* into synonymy.

Despite the first binding rules of nomenclature being published by the Vienna International Botanical Congress in 1905, the status of the genus *Lomatium* was not reviewed until 1918. James F. MacBride concluded that *Lomatium* Raf. and *Lomatia* R. Br. are not homonyms because the differences in spelling between the two names lies only within the termination, based on Article 57 of the Vienna Code (Mathias 1938). He concluded that these names are distinct and *Lomatium* has priority over *Cogswellia*. MacBride's interpretation was later accepted by Mildred Mathias in her 1938 monograph, where she recognized the name, *Lomatium grayi*. Mathias' monograph has since become a standard reference for *Lomatium* nomenclature.

Since first described by Watson, only two new varieties have been proposed within this taxon, and both were described by Marcus Jones. The first, *Peucedanum grayi* var. *aberrans* M.E. Jones, was published in 1902 prior to Jones' adoption of *Cogswellia*. According to Jones, this variety was restricted to the Snake River drainage east and south of Weiser in Washington & Payette Counties, Idaho. Jones never made the new combinations necessary to recognize this taxon within his later concept of *Cogswellia millefolia*. Mathias relegated it to synonymy and it has never since been recognized as a variety within *L. grayi*. The second, *Cogswellia millefolia* var. *depauperata* M.E. Jones, was based on populations in desert mountain ranges south of the Great Salt Lake in Tooele County, Utah. This taxon was recognized by Mathias as *L. grayi* var. *depauperatum* (M.E. Jones) Mathias. Since her monograph, it has remained the only variety recognized within this otherwise wide-spread and ecologically diverse species. As most recently delimited in floras, *Lomatium grayi* is a complex of morphotypes, spread across 3 major floristic regions: the Pacific Northwest, the Intermountain Region, and the southern Rocky Mountains. The many populations of *L. grayi* are highly variable, such that taxonomists have never delimited this complex into more than the two varieties proposed by Mathias (1938).

From 1995 to 2005, Dr. Wayne Whaley mapped and studied the distribution of *Lomatium* species as a secondary aspect of another study involving the essential oil compositions of larval hosts of *Papilio indra* Reakirt (Indra swallowtail butterfly) (Dev et al. 2007; Beauchamp et al. 2009; Dev et al. 2010). Populations of two *P. indra* subspecies are found across the entire range of *L. grayi*. In Utah, Wyoming and Colorado, *P. indra* subsp. *indra* larvae use high elevation *Lomatium graveolens* (S. Watson) Dorn & R.L. Hartm., *Cymopterus hendersonii* (J.M. Coult. & Rose) Cronquist, and *Cymopterus terebinthinus* (Hook.) Torr. & A. Gray as hosts. Across the southern portion of the range of *L. grayi* in Utah and Colorado, *P. indra* subsp. *minori* Cross utilizes host plants *C. terebinthinus*, *C. hendersonii* and *Lomatium parryi* (S. Watson) J.F. Macbride. In Mesa and Garfield counties, Colorado it also uses *Lomatium eastwoodiae* (J.M. Coult. & Rose) J.F. Macbride. It is not unusual to see *L. grayi* growing sympatric with *C. terebinthinus* throughout this region, however, the butterfly larvae have never been observed using *L. grayi* in these regions. Instead, both butterfly subspecies preferentially choose *C. terebinthinus* (or one of the other species as indicated above) when present in mixed populations with *L. grayi*.

In contrast, butterfly-host investigations in the Pacific Northwest found that *P. indra* subsp. *indra* prefers *L. grayi* in this ecoregion as well as *C. terebinthinus* and other *Lomatium* species. Whaley first observed *P. indra* subsp. *indra* using plants of a robust morphotype as larval hosts in populations along the Klickitat River (Klickitat Co, Washington) in June of 2002. Whaley in Dev. et al 2007 proposed that these robust populations of *L. grayi* were a putative new variety, morphologically different than the Great Basin desert populations of *L.*

grayi var. *depauperatum* and the Intermountain and Rocky Mountain populations of *L. grayi* var. *grayi*. However, this proposal was not intended as a formal publication, since a name and the required documentation to describe this new taxon was not included.

For this study, a comprehensive, population level morphometric and statistical analysis was performed on *L. grayi* populations within the major ecoregions throughout its range from British Columbia south to northern New Mexico. These studies are used in conjunction with butterfly-host field investigations completed by Whaley from 1987 to 2011 and a combined analysis of three essential oil chemical studies (Dev et al. 2007; Beauchamp et al. 2009; Dev et al. 2010) to determine if there are discreet species boundaries within this morphologically complex taxon.

MATERIALS AND METHODS

Field observations and voucher specimens of *P. indra* and *Lomatium* populations made by Whaley from 1987 to 2010 throughout the western United States formed the basis for the more selective field surveys and morphological analyses performed in this study. Herbarium specimens of *L. grayi* s.l. were examined from BRY, CIC, IDS, OSC, ORE, SRP, POM, RENO, RM, RSA, WILLU, WS, and WTU from throughout the range of the species. To supplement the herbarium specimens in the morphological analyses, additional vouchers were collected of the putative morphotypes in the spring of 2014 and 2015 from multiple populations in Idaho, Oregon, Utah, and Washington. Vouchers for this study are deposited at OSC, UNLV, UVU, RENO, and UC. The field surveys focused on sampling the majority of all observed morphological variants found in preliminary morphological analyses of loaned herbarium specimens in this group. Ecoregion names used in the habitat descriptions of the taxonomic treatment and in GIS layer maps are level four ecoregions for the western United States developed by the Environmental Protection Agency (U.S. Environmental Protection Agency 2013; Omernik & Griffith 2014).

From an initial set of over 600 specimens loaned for this study, a total of 390 specimens of *L. grayi* s.l. were measured for the morphometric analysis (see Appendix 1 for the localities of the specimens). Many loaned specimens could not be analyzed due to the poor quality of the specimens or the immature growth stage of the individuals on the sheet (plants in early-season flowering stages, plants with not fully expanded leaves, plants in late fruiting stages with dry, fragmented leaves).

Of the characters examined for the taxonomic treatment, only quantitative characters were selected for this study. Due to the difficulty of measuring floral characters of pressed specimens and the immaturity of leaves on these flowering specimens, only characters from specimens in fruiting stage with fully expressed leaves were selected for measurement. Fifteen characters were selected for the morphometric study (Table 1). Morphological characters were measured with an Olympus SZ10 stereo-microscope, a ring-light illuminator, and a DP72 digital camera using a micrometer scale with an accuracy to the nearest tenth of a millimeter at a magnification of 0.6x to 6.3x. Measurements of larger characters (BLeaf1, BLeaf2, BLeaf4, Umb1, Umb2d, Umb3) were made using metric ruler and with an accuracy to the nearest millimeter. Leaf measurements were selected from the basal 1–3 leaves on a specimen proximal to the apex of the caudex. Figure 1 is a composite image showing the central primary leaflets of the four morphotypes in this study. The leaflet and pinnule lobe morphology has been more explicitly defined in this project than in any other previous study of *L. grayi* (and perhaps *Lomatium* in general). This figure has been provided to further illustrate the differences in the leaflet and pinnule morphology described in the multivariate study and taxonomic treatment.

Other qualitative, distinguishing characters, such as the weathering pattern of fibers present on the caudex, the outline of the leaf cross section (dorsi-ventrally flattened or elliptic to round), or the presence of cauline leaves and peduncles were excluded, instead of being coded as binary characters. Cauline leaves were not used for leaf measurement to avoid bias and variance due to leaf position. Only mature leaves arising from nodes nearest to the caudex were measured. The taxa in this study always have basal leaves and peduncles, even if there are cauline ones present. Additionally, whether a taxon is caulescent (having cauline leaves and/ or peduncles) or acaulescent (without cauline leaves or peduncles) is a primary distinguishing character.

TABLE 1. Quantitative characters included in the morphometric analyses.

Morphological Character Description	Units	Code
Leaf central rachis length-(basal-most; from lowest leaflet pair to node of the terminal leaflet)	mm	BLeaf1
Petiole sheath length-(basal-most; distance from the lowest leaflet node to apex of the membranous petiolular sheath)	mm	Bleaf2
Petiole sheath width-(basal-most; from the central petiole vein to the edge of the membrane)	mm	BLeaf4
Fruit wing width (mature only)	mm	Frt2
Fruit length \times width ratio (mature only)	ratio	Frt4
Flower stalk width-(just below the umbel; in fruit)	mm	Stem1
Ultimate pinnule intercostal area length at base - (average; first or second lateral pinnules below the terminal leaflet; measured from the base to 1st lobe along the rachillae)	mm	ULeaf2
Ultimate pinnule intercostal area length at mid-rachillae (first or second lateral pinnules below the terminal leaflet; measured from the 1st lobe to 2nd lobe base along the rachillae)	mm	ULeaf3
Ultimate apical pinnule lobe length- (average)	mm	Uleaf5
Ultimate apical pinnule lobe width-(average; width measured at leaflet midpoint)	mm	Uleaf7
Umbel peduncle length-(basal-most; in fruit)	mm	Umb1
Umbel primary ray length (only outer rays measured, in fruit)	mm	Umb2d
Umbel primary ray number- (in fruit)	count	Umb3
Umbel secondary ray length-average (flower stalks, in fruit)	mm	Umb4
Umbel secondary ray number- (in fruit)	count	Umb5

These characters were used to sort *L*. *grayi* into the initial morphotypic groups. They were excluded based on Marhold (2011), who recommended that distinguishing characters should be excluded in discriminant analyses.

For most morphological characters, 3–5 replicates of each character were measured on each specimen. Fruiting peduncle length and mature leaf rachis length were the exception. Due to the size of this species, only 1 or 2 full leaves or peduncles are typically preserved on a herbarium sheet. Duplicate sheets were examined, when available, to add replicate measurements for each voucher. Where possible, multiple vouchers were selected for each of the ecoregions listed in the taxonomic treatment.

Data Analysis.—All univariate and multivariate analyses were calculated using PAST 3.16 (Hammer et al. 2001). Missing values were substituted with the averages calculated from values for specimens within the same ecoregion and state. A Principal Components Analysis (PCA) was performed in order to determine which of the 15 characters contributed the most to the percent variation. A multivariate analysis of variance (MANOVA) was used to determine if morphological characters were significantly differentiated among the morphologically-assigned, morphotypic groups. Next, a Canonical Discriminant Analysis (CDA) was performed using the morphotypes as groups (each a putative species or OTU) in order to test how many of specimens in each of the groups were correctly classified. Tukey's pairwise post-hoc tests were performed using characters that showed significant inequality in the means (p >0.05) in order to determine what characters contributed to differences between the morphotypes resulting from the multivariate analyses.

An initial statistical, PCA, and CDA (not shown) was conducted using a 153 specimen dataset. For this initial study, the specimens were identified based on qualitative morphological characters into three morphotypic groups: the Pacific Northwest "*papilioniferum*" morphotype, the eastern Great Basin "*depauperatum*" morphotype (delimited by Mathias as *L. grayi* var. *depauperatum*), and the Intermountain-Rocky Mountain typical morphotype (referred to herein as *L. grayi* s.s.).

Within the Pacific Northwest "*papilioniferum*" morphotype, specimens were selected from throughout Oregon, western Idaho, northern Nevada, and Washington. Among the few specimens that have been collected from the population in Canada, only a single collection had the requisite morphological characters to be measured for this study. No specimens from the Modoc County, California population were used due to the poor quality of the few specimens that have been collected. Within *Lomatium grayi* s.s., specimens were



FiG. 1. Central primary leaflet morphological variation between species. Lomatium depauperatum (A: Alexander & Whaley 3324; B: Alexander & Whaley 3326; C: Alexander & Badeau 3360), L. grayi (D: Alexander & Whaley 3360; E: Alexander 3134), L. papilioniferum (F: Alexander 3300; G: Alexander & Whaley 3084; H: Alexander & Whaley 3096; J: Alexander & Badeau 3312). The landmarks for measuring characters Uleaf2 (Ultimate pinnule intercostal area length at base; labeled bar 2) and Uleaf 3 (Ultimate pinnule intercostal area length at mid-rachillae; labeled bar 1) can be found identified on specimen I. The scale bar in the lower left-hand corner is 15 mm long.

selected from throughout Colorado, southeastern Idaho, northern Utah, and southwestern Wyoming. Only a single collection from the populations in Northwestern New Mexico had the requisite morphological characters to be measured for this study. Within the Great Basin desert "*depauperatum*" morphotype, forty specimens were selected from this region in northeastern Nevada (8) and western Utah (32). Fewer specimens from Nevada were selected for this study than ones from Utah due to the condition of the specimens and the high prevalence of duplicate collections in herbaria.

Lastly, the initial PCA, CDA, and the box-and-whisker plots of the means showed that two specimens from the Klickitat River Canyon (Klickitat County, Washington) were outliers and significantly different morphologically from the "*papilioniferum*" morphotype (not shown). To test if this "*klickitatense*" morphotype was significantly different morphologically from the remaining morphotypes, the final PCA and CDA analysis was performed on an expanded 390 specimen dataset, including 24 specimens assigned to the "*klickitatense*" morphotype. This new morphotype can be distinguished from the other three based on caudex morphology, presence of cauline leaves and peduncles, and the greater overall leaf size. Additional specimens from the 2014–2015 field surveys within the four regional groups were selected for this expanded analysis.

Chemical Analysis.—An aggregate matrix of the essential oil components extracted from the leaves across the majority of hosts of *P. indra* has not been published. Each of the prior published studies, co-authored by Whaley, has concentrated on a small subsample of species. A cumulative analysis of the essential oil components data from previous studies was conducted for this analysis to determine if the samples of *L. grayi* analyzed in Dev et al. (2007) are more similar, chemically, to each other than they are to the other host species reported in the other studies. A table of essential oil components in 17 host species in Apiaceae (see Appendix 2; 1 of each species excluding *L. grayi*, 3 samples, *Lomatium howellii* (S. Watson) Jeps., 2 samples, and *C. hendersonii*, 2 samples) was aggregated from the results of Dev et al. (2007, 2010) and Beauchamp et al. (2009; see Table 2). Essential oil composition and Kovats retention indices (RI) were obtained by gas chromatography (GC) using a Hewlett Packard 6890 fitted with a flame ionization detector (FID).

A total of 319 compounds were found to be present in the host species among these studies. The data from these studies were scored as binary (presence or absence). Trace components were scored as present. Percent concentrations of compounds were not used in NJ and PCA due to the differences in treatment of trace compounds. Trace compounds were labeled differently across the two studies. Non-host species of *P. indra* from these studies were not added to the matrix. The essential oil component table was used in PAST for a cluster analysis to create a neighbor-joining dendrogram (Fig. 2; Saitou & Nei 1987) and a Principal Components Analysis (PCA; Fig. 3) of the presence/absence data matrix.

The morphological and essential oil analyses were used to address the following questions:

- 1) Are the four morphotypes of Lomatium grayi s.l. significantly different morphologically?
- 2) Which morphological characters contribute to these regional morphotypes?
- 3) If significantly different morphotypes are detected, do they warrant taxonomic recognition?

RESULTS

None of the 15 characters examined for this study were found to be normally distributed in the statistical analysis. For the morphological PCA and CDA, the data were log transformed to meet the assumptions of the multivariate analyses and standardized by subtracting by the mean and dividing by the standard deviation to account for the differences in units of the various data types in this dataset (see Table 1). The first component of the PCA explained 38.85% of the total variance (not shown). Of the 12 largest loadings in component one, the greatest correlations were from Stem1 and Umb2d (0.35 and 0.33). The second component of the PCA explained 11.62% of the total variance. The greatest correlations to the second axis were from Frt2 (the highest positive loading of 0.46) and ULeaf7 and ULeaf2 (the lowest, negative loadings, -0.45 and 0.42). Of these, Frt2, Frt4 (0.22), and ULeaf7 did not significantly contribute to the variation in component one. All other components of the PCA explained less than 10% of the total variance.

MANOVA revealed that the four groups were significantly different morphologically (Wilks' lambda =

TABLE 2. List of Apiaceae taxa and the Papilio indra subspecies that utilize them as larval hosts. * = taxon examined for the combined chemical analysis.

Larval Host Species	Papilio indra subspecies
Aletes acaulis*	subsp. indra
Cymopterus panamintensis*	subsp. fordii, subsp. parvindra
Cymopterus petraeus	subsp. <i>minori</i>
Cymopterus hendersonii*	subsp. <i>indra</i> , subsp. <i>minori</i>
Cymopterus terebinthinus	subsp. <i>indra</i> , subsp. <i>minori</i>
Lomatium brandegeei*	subsp. indra
Lomatium californicum	subsp. <i>shastensis</i>
Lomatium depauperatum*	"bonnevillensis" (undescribed)
Lomatium eastwoodiae*	subsp. <i>minori</i>
Lomatium graveolens*	subsp. indra
Lomatium grayi*	none
Lomatium howellii*	subsp. <i>shastensis</i>
Lomatium junceum*	subsp. <i>minori</i>
Lomatium klickitatense*	subsp. indra
Lomatium papilioniferum	subsp. indra
Lomatium parryi *	subsp. minori, subsp. nevadensis, subsp. martini, subsp. panamintensis
Lomatium rigidum*	cf. subsp. <i>phyllisae</i>
Lomatium scabrum*	subsp. <i>calcicola</i>
Musineon tenuifolium*	subsp. indra
Sphenosciadium capitellatum*	subsp. <i>indra</i>
Tauschia arguta*	subsp. <i>pergamus</i>
Tauschia parishii*	subsp. pergamus, subsp. phyllisae

0.025; F=60.07; df1 = 45, df2 = 1106; p<<0.0001). The CDA correctly classified 95.6% of the specimens into the four morphotypic groups. The scatterplot (Fig. 4) was similar to the distribution of groups in the morphological PCA (not shown). Table 3 shows a matrix of the results of the classification tests applied to the 390 specimen dataset during the CDA. Discriminant axis one accounted for 80% of the variation. The loadings indicate that five characters were the largest contributors: ULeaf2 (0.29), Uleaf3 (0.23), Umb5 (0.21), Stem1 (0.20), and Umb2d (0.19). Discriminant axis two accounted for 14% of the variation. The loadings indicate that seven characters were the largest contributors: ULeaf5 (0.33), BLeaf4 (0.32), Stem1 (0.30), Frt2 (0.25), Bleaf 2 (0.25), Umb3 (0.25), and Umb1 (0.22). Box-and-whisker plots of the means (Fig. 5) were calculated to help graphically display these differences.

Of the 129 specimens determined as *Lomatium grayi* s.s., 8 were classified into other morphotypes in the CDA. All 15 characters were significantly different between the "*papilioniferum*" morphotype and *L. grayi* s.s. (p = 0.00–0.01) in the Tukey tests. Six specimens (ID: *Holmgren & Marttala* 5494 BRY, IDS, *Holmgren & Holmgren* 15540 BRY; CO: *Vanderhorst* 264 RM, Sigstedt & O'Kane 82-381 RM, Goodding Sel-28-41 RM) were classified as the "*depauperatum*" morphotype, mostly due to having a measurable intercostal region between the rachilla and the basal-most pinnule lobe (ULeaf3). These specimens were the outliers in the mean box plots (Fig. 5D). Despite these outliers, the Tukey test showed a significant difference between these two species (p<<0.0001). Overall, the presence of a measurable intercostal area between the rachilla and the basal-most pinnule lobes are rare in *L. grayi*. The leaves are highly complex and it is certainly possible that a few pinnules per plant may have a measurable basal intercostal region. One pair of duplicates (*Holmgren & Martalla* 5494 BRY and IDS) had different average measurements for this character (0.05 vs. 0.31 mm). The BRY duplicate was much closer to the *L. grayi* cluster in the scatterplot.

The last two specimens, classified as the "*papilioniferum*" morphotype (WY: *Nelson & Cramer 34745*, RM; ID: *Davis s.n.* 30 Apr 1932, IDS), were a result of similar, potential measurement error. A duplicate from RM of the IDS specimen was also measured, however, it was classified as *L. grayi* in the CDA. This discrepancy is likely a result of the differences in the measurement of ULeaf2 (RM dup. = 0.0 mm vs IDS dup. = 0.4 mm). More measurements need to be taken on these individuals to be sure that this is an average result and not from atypical pinnules or as a result of measurement error.



Fi6. 2. Neighbor joining dendrogram of the combined chemical data based on the results of Dev et al. (2007, 2010) and Beauchamp et al. (2009). The numbers refer to host-butterfly species groups discussed in the text and Figure 3. **AA** = Aletes acaulis; **CH1** = population 1 of *Cymopterus hendersonii*; **CH2** = population 2 of *Cymopterus hendersonii*; **CP** = *Cymopterus panamintensis*; **LGA** = *Lomatium gravi*; **LD** = *Lomatium depauperatum*; **LK** = *Lomatium klickitatense*; **LB** = *Lomatium howellii*; **LJ** = *Lomatium nowellii*; **LH** = population 1 of *Lomatium howellii*; **LH** = population 2 of *Lomatium howellii*; **LJ** = *Lomatium junceum*; **LP** = *Lomatium paryi*; **LR** = *Lomatium rigidum*; **LS** = *Lomatium scabrum*; **MT** = *Musineon tenuifolium*; **SC** = *Sphenosciadium capitellatum*; **TA** = *Tauschia arguta*; **TP** = *Taushia parishii*. Abbreviations of the subspecies of *Papilio indra* that use the taxon as a larval host is labeled above the line: **IND** = *P. indra* subsp. *indra*; **IND** "**B**" = *P. indra* subsp. *nevadensis*; **PAR** = *P. indra* subsp. *panamintensis*; **PAR** = *P. indra* subsp. *panamintensis*; **PAR** = *P. indra* subsp. *panamintensis*; **PAR** = *P. indra* subsp. *shastensis*.



Fi6. 3. Scatterplot of the principal components analysis using the combined chemical data based on the results of Dev et al. (2007; 2010) and Beauchamp et al. (2009). The first two components comprise 12% of the total variation. The taxa to the right of the dotted line correspond to group 3 in the NJ dendrogram (Fig. 2). The taxa above the solid line correspond to group 2 and the taxa below the line corresponds to group 1 in the dendrogram. *Lomatium parryi* (LP) is an outlier that is grouped with group 3 in the dendrogram. **AA** = *Aletes acaulis*; **CH1** = population 1 of *Cymopterus hendersonii*; **CH2** = population 2 of *Cymopterus hendersonii*; **CP** = *Cymopterus panamintensis*; **LGA** = *Lomatium grayi*; **LD** = *Lomatium depauperatum*; **LK** = *Lomatium klickitatense*; **LB** = *Lomatium howellii*; **LJ** = *Lomatium junceum*; **LP** = *Lomatium parryi*; **LR** = *Lomatium rigidum*; **LS** = *Lomatium scabrum*; **MT** = *Musineon tenuifolium*; **SC** = *Sphenosciadium capitellatum*; **TA** = *Tauschia arquta*; **TP** = *Taushia parishii*.

Six of the 40 specimens placed within the "depauperatum" morphotype were classified as Lomatium grayi s.s. in the CDA (ID: Holmgren & Marttala 5494 BRY, IDS, Holmgren & Holmgren 15540 BRY; CO: Vanderhorst 264 RM, Sigstedt & O'Kane 82-381 RM, Goodding Sel-28-41 RM). In the Tukey tests, seven characters were not significantly different between the "depauperatum" morphotype and L. grayi s.s. (BLeaf1, BLeaf2, Frt4, Uleaf3, ULeaf5, Umb1, Umb5; p = 0.18–0.99), and the other eight were significantly different (BLeaf4, Frt2, Stem1, ULeaf2, ULeaf7, Umb2d, Umb3, Umb4; p<<0.0001; see also Figs. 4A–41). All 15 characters were significantly different between the "depauperatum" morphotype and the "klickitatense" morphotype (p = 0.00–0.01).

Out of 197 specimens that were placed within the "*papilioniferum*" morphotype, two were classified as "*klickitatense*" morphotype (ID: Alexander & Whaley 3084 UVSC; Suksdorf 6420 WS) and one was classified as "*depauperatum*" morphotype (OR: *Peck* 15973 WILLU) in the CDA. In the Tukey tests, five characters were not significantly different between "*klickitatense*" morphotype and the "*papilioniferum*" morphotype (Frt4, Uleaf2, Umb2d, Umb4, Umb5; p = 0.36–0.99), and the other eleven were significantly different (BLeaf1, BLeaf2, BLeaf4, Frt2, Stem1, Uleaf3, ULeaf5, ULeaf7, Umb1, Umb3, Umb5; p<=0.002; see also Figs. 4A–4I). In addition, one character (ULeaf5; p = 0.92; see also Fig. 5E) was not significantly different between "*papilioniferum*" morphotype and the "*depauperatum*" morphotype. The other fourteen were significantly different (p=0.000–0.002).

One pair of duplicates placed within the "*papilioniferum*" morphotype (*Suksdorf 6420*, Jun 1909; *Suksdorf 6420*, Mar 1909; both on the same sheet at WS) was classified into two different morphotypes in the CDA. Both





had different average measurements for leaf and umbel characters. The duplicate collected in March is typical of early season flowering forms of these taxa. The leaves are not as fully expanded and the peduncles are not as long and robust as later season plants. The other duplicate was collected in June in fruit. Both specimens were collected in the vicinity of Bingen (Klickitat County, Washington), along the western edge of the range of the *"klickitatense"* morphotype. Although both of these were initially determined as the *"papilioniferum"* morphotype, the CDA reveals that this may be a specimen of the *"klickitatense"* morphotype. These results reaffirm that early-season flowering forms of these two morphotypes cannot be reliably identified.

In contrast to the other groups, the "*klickitatense*" morphotype was the most cohesive. None of the 24 specimens placed within this morphotype was classified as another in the CDA. All of the characters were significantly different from those of the other groups in the Tukey tests, except for four in the "*papilioniferum*" morphotype (see above). The apical leaf lobe is very narrow and rounded in "*klickitatense*" morphotype and not noticeably dorsi-ventrally compressed, which distinguishes it from all but the most robust forms of the "*papilioniferum*" morphotype. In cross section and width (ULeaf7; Fig. 5F), the apical pinnule lobes are identical to the dimensions found in *L. grayi*. The only difference is in the length of the ultimate apical lobes (ULeaf5; Fig. 5E), which are up to 15 mm (versus up to 5 mm in *L. grayi* s.s.).

In the chemical PCA analysis (Fig. 3; only components 1 and 2 are shown), the first six components had eigenvalues greater than two and accounted for 66% of the variance. *Lomatium grayi* s.s. (LGA) is not more similar chemically to other species of *Lomatium* than it is to the other two morphotypes sampled (Fig. 2 and 3). It is also not more similar to the outgroup, non-host, *Lomatium* species included in Dev et al. (2010; not shown). *Lomatium howellii* (LH), which is host to *P. indra* subsp. *shastensis* J. Emmel and T. Emmel, is the only outlier in the PCA. It is placed outside the 95% confidence ellipse (not shown).

	k	р	g	d	Total	
k	24	0	0	0	24	
р	2	194	0	1	197	
g	0	2	121	6	129	
d	0	0	6	34	40	
Total	26	196	127	41	390	

TABLE 3. Classification Matrix for the 390 specimens Canonical Discriminant Analysis. 95.64% of the specimens were correctly classified. The rows are the assigned groups in the analysis and the columns are the groups predicted by the CDA. The groups are coded as "g" (*L. grayi* s.s.), "d" (*L. depauperatum* or "depauperatum" morphotype), "p" (*L. papilioniferum* or "papilioniferum" morphotype), and "k" (*L. klickitatense* or "klickitatense" morphotype).

Neither the host genera nor the subspecies of *P. indra* form completely cohesive clusters in the NJ dendrogram (Fig. 2) nor the PCA (Fig. 3) analyses of the essential oil data. In the dendrogram, group 1 is composed of the majority of taxa that are host to *P. indra* subsp. *calcicola* J. Emmel & Griffin, *P. indra* subsp. *fordii* J. A. Comstock & Martin, *P. indra* subsp. *parvindra* J. Emmel, T. Emmel, & Griffin, *P. indra* subsp. *pergamus* Hy. Edwards, and *P. indra* subsp. *phyllisae* J. Emmel. Group 2 is composed of the majority of taxa that are host to *P. indra* subsp. *indra* subsp. *minori*. Group 3 is the outlier species, *Lomatium howellii* (LH) which is host to *P. indra* subsp. *shastensis*. *Lomatium parryi* (LP) falls between group 2 and group 3 in the PCA and NJ dendrogram. It is unique among the sampled taxa due to being the only species that is host to *P. indra* subsp. *minori* and three other subspecies not present elsewhere in the dendrogram.

DISCUSSION

The PCA, MANOVA, CDA, and Tukey tests revealed that the majority of the characters in this dataset were significantly different between the morphotypes. That 95 percent of the specimens were correctly classified in the CDA is significant evidence of the morphological distinctiveness of these morphotypes. Additionally, none of the mis-classified specimens had the qualitative characters states of the morphotype classified by the CDA. As a result of these significant quantitative differences, the distinguishing qualitative characters, and the mostly disjunct geographic distributions, a species-level delimitation was made for these four morphotypes in the taxonomic treatment.

Based on the results of the original chemical analyses (Dev et al. 2007; Beauchamp et al. 2009; Dev et al. 2010), the primary attractant compounds for *P. indra* are hypothesized to be a combination of pinenes, terpinenes, phellandrnes and limonenes, all of which contribute to the citrus-like and pine-like odors of the host species. In addition, myrcene, p-cymene, two forms of ocimene, terpinene, terpinolene, and terpineol were found to be present in the majority of host species (the exceptions are: terpineol was not detected in *Lomatium brandegeei* (J.M. Coult. & Rose) J.F. Macbr.; terpinene was not detected in *L. parryi*; terpinolene was not detected in *Lomatium junceum* Barneby & N.H. Holmgren and *L. parryi*; Beauchamp et al. 2009). Unlike other swallowtail species, the necessary laboratory studies using live *P. indra* females and purified essential oil compounds have not been completed. These studies are needed to determine which of these compounds are the key attractants (Dev et al. 2010).

The result of the PCA and NJ dendrogram of the combined essential oil data show that the neither the host genera nor the *P. indra* subspecies form completely cohesive groups based solely on presence of compounds (Appendix 3). All but four *Lomatium* species are more similar to one another than they are to other host genera. *Cymopterus hendersonii* (CH) and *Tauschia arguta* (Torr. & A. Gray) J.F. Macbr. (TA) are more similar to species in other genera in the dendrogram (*Aletes acaulis* (Torr.) J.M. Coult. & Rose, AA, and *Sphenosciadium capitellatum* A. Gray, SC, respectively) than they are to the other members of their own genus (*Cymopterus panamintensis J.M. Coult. & Rose*, CP, and *Tauschia parishii* (J.M. Coult. & Rose) J.F. Macbr., TP, respectively). The other genera, *Aletes, Musineon*, and *Sphenosciadium* were represented by a single species. All of these taxa form three species groups in the NJ dendrogram (Fig. 2), which are labeled in the PCA (Fig. 3).



Fi6. 5. Box plots of the means and standard deviations of the 390 specimen analysis. The taxa are coded along the X axis as "g" (Lomatium grayis.s.), "d" (L. depauperatum or "depauperatum" morphotype), "p" (L. papilioniferum or "papilioniferum" morphotype), and "k" (L. klickitatense or "klickitatense" morphotype). Box plots for nine of the fifteen characters are shown: **5A**–Fruit wing width, Frt 2; **5B**–Flower stalk width, Stem1; **5C**–ULeaf2, Ultimate pinnule intercostal area length at base, Uleaf2; **5D**–Ultimate pinnule intercostal area length at mid-rachillae, ULeaf3; **5E**–Ultimate apical pinnule lobe length, ULeaf5; **5F**–Ultimate apical pinnule lobe width, ULeaf7; **5G**–Umbel peduncle length, Umb1; **5H**–Umbel primary ray length, Umb2d; **5I**–Umbel primary ray number, Umb3.



Fig. 5. (continued).

Two species fall outside the expected groups based on larval-host taxonomy. The first exception is *Musineon tenuifolium* Nutt. ex Torr. & A. Gray (MT). This taxon is placed within group one, but is host to *P. indra* subsp. *indra*. The second is *T. arguta* (TA) which is placed within group two, but is host to *P. indra* subsp. *pergamus*. The grouping of these taxa as more similar to groups with other *P. indra* subspecies is mostly due to the presence of the divergent suites of compounds that differentiate the two groups in the dendrogram. Most of these compounds are present at low levels and few are suspected attractants to *P. indra*.

Group 3 is composed of samples of *L. howellii* (LH), which is host to *P. indra* subsp. *shastensis*. It is the only outlier in the PCA. Since only one host of this butterfly subspecies was sampled, it is not known if the other hosts have similar compositions. Several compounds present only in *L. howellii* contributed to this result. Most were present at levels less than 1%. Most notably, octyl acetate was present at the highest concentration of all oils in this species (23.5–24.8%; Beauchamp et al. 2009). This compound was only found in *L. brandegeei*, *L. grayi* s.s. and the "*klickitatense*" morphotype at levels less than 0.1% (Dev et al. 2007; Beauchamp et al. 2009). Octyl acetate is also present at high concentrations in several species of the genus *Heracleum* (Apiaceae; Iscan et al. 2004) which is also known as a larval host to the old-world swallowtail species, *Papilio machaon* L. (Prudic et al. 2007).

Although it does not fall outside the 95% confidence ellipse, the two samples of *C. hendersonii* fall in a cluster disjunct from the remainder of group two (Fig. 3). This taxon is unique among these host species, having methyl chavicol and (E)-anethole contribute 63.8% of the total oil composition. The anise aroma typical of this species is caused by the high percent composition of these two compounds in the leaves. The suspected attractants for *P. indra* are still present, but at lower levels than the other taxa of group 1 (Beauchamp et al. 2009).

Lomatium brandegeei (LB), *L. eastwoodiae* (LE), and *L. parryi* (LP) are more similar to *L. howellii* (LH; group 3) in the dendrogram than they are to other *Lomatium* species. This similarity is primarily a result of the presence of a suite of compounds common to all four species. *Lomatium brandegeei* is the only one of the hosts that does not contain limonene. However, it has the highest percent composition of beta-phellandrene (60.9%) of all sampled host species. All three sampled morphotypes of *L. grayi* (LGA, LD, LK) and *L. brandegeei* (LB) share a higher percent composition of gamma-terpinene (4.4–16.1%) than the other *Lomatium* host species sampled (0–1.8%). The only other host species sampled to have a high percent composition of gamma-terpinene is *S. capitellatum* (6.9%; SC). The presence of germacrene D is also a characteristic shared among *L. brandegeei*, *L. eastwoodiae*, *L. howellii*, *L. parryi*, and the three morphotypes of *L. grayi* (LGA, LD, LK). It is missing in all other host species except for *C. panamintensis* (CP), *Lomatium scabrum* (J.M. Coult. & Rose) Mathias (LS), and *M. tenuifolium* (MT). It is possible that one or more of these compounds could be contributing to the host preference of the *P. indra* subspecies between these plant taxa.

Lastly, the three sampled morphotypes of *L. grayi* (LGA, LD, LK) are differentiated from the other sampled hosts by the presence of senkyunolide and (**Z**)-ligustilide. The celery aroma of the leaves of these morphotypes are a result of high concentrations of these compounds in the leaves (Dev. et al 2007). Senkyunolide is a major component in the leaves of *Apium graveolens* L. (cultivated celery; Van Wassenhove et al. 1990) and variants of ligustilde are a major component in the roots of species of *Ligusticum* (Collin et al. 2014). Various swallowtail butterfly utilize *Ligusticum* species as a larval-host. *Papilio zelicaon* Lucas is known to oviposit on *Ligusticum grayi* J.M. Coult. & Rose in the Pacific Northwest (Prudic et al. 2007). Both of these species are sympatric with the "*papilioniferum*" morphotype. During his previous studies, Whaley (unpub. data) observed larvae of *P. zelicaon* utilizing plants of the "*papilioniferum*" morphotype. *Papilio zelicaon* utilizes a far broader range of host species compared to *P. indra* and *Lomatium grayi* is listed as a host to *P. zelicaon* (Prudic et al. 2007)—a determination which would include all the morphotypes studied herein. However, it is not known if *L. grayi* s.s. is a common larval host.

The essential oil analysis in this study provides little additional evidence for the differentiation between the morphotypes of *L. grayi*. It is not apparent by the percent composition of the essential oils why *P. indra* does not oviposit on *L. grayi* s.s. By "drumming" their fortarsi against the leaf surface, female butterflies use chemo-tactile receptors to detect the presence of these compounds (Beauchamp et al. 2009). The presence of these compounds indicates to the female that this host is acceptable as a food source for the larvae (Nishida 2005). These receptors can also detect the presence of deterrent compounds, but none of the potential deterrent compounds present in the non-host taxa from Dev. et al. (2010) are present in *L. grayi* s.s at a concentration above 0.05%. The results of the combined PCA and NJ dendrogram further support the conclusions conclusion of Dev et al. (2007) that a characteristic other than the presence of a suite of essential oils is driving the larval-host specificity between *L. grayi* s.s. and the other morphotypes (LP, LD, LK).

Despite the chemical data being inconclusive, recent molecular systematic studies have shown that there is support for the differentiation of the "papilioniferum" morphotype from *L. grayi s.s.* and *L. grayi var. depauperatum* (Smith et. al., unpublished data) at the species-level. Distribution maps show the localities of specimens of *L. depauperatum* ("depauperatum" morphotype; Fig. 6), *L. grayi s.s.* (Fig. 6), *L. klickitatense* ("klickitatense" morphotype; Fig. 7), and *L. papilioniferum* ("papilioniferum" morphotype; Fig. 8) examined for this study. A detailed list of the vouchers examined can be found in Appendix 1. Further discussions of these four taxa can be found in the taxonomic treatment below.

TAXONOMIC TREATMENT

KEY TO SPECIES COMMONLY MIS-IDENTIFIED AS LOMATIUM GRAYI S.S.

DUE TO SIMILAR LEAF MORPHOLOGY

L. minus	 Peduncle and stems stout and inflated; petals purple or reddish purple, anthers purple
	1. Peduncle and stems slender or stout, but not inflated; petals white, ochroleucous, or yellow (petals purple in L.
	tuberosum), anthers ochroleucous, yellow, or purple.
	2. Petals purple (rare yellow forms were reported by Mastroguiseppe et al. 1985), bladeless basal sheaths present, up to
L. tuberosum	
	2. Petals white, ochroleucous, or yellow, bladeless basal sheaths absent (or sometimes only appearing bladeless due to
	the fragmentation of the early-season, depauperate leaflet)
	3. Ultimate pinnule lobes congested, obscuring the short intercostal areas along the rachillae, apical 2–3 pinnule pairs
	of the secondary leaflets without a naked intercostal region between the rachilla and the basal-most pinnule lobes,
Insfeldianum	appearing sessile. 4. Plants caulescent L. bru
Insteidianum	
	4. Plants acaulescent.
	5. Sheathing basal leaflets divided into 4–6 primary rachises, the largest 2 lateral primaries similar in size and
	shape to the central primary, the additional, 1–3 smaller, lateral primaries identical to secondaries in length
L. quintuplex	and shape, restricted to Washington5. Sheathing based leaded in the same of the same
	central primary, small lateral primaries absent. Long-disjunct from the range of the prior species; widespread
L. grayi	in SE Idaho, E Utah, SW Wyoming, W Colorado, and NW New Mexico
L. grayi	3. Ultimate pinnule lobes diffuse, not obscuring the elongate intercostal areas along the rachillae; apical 2–3 pinnule
	pairs of the secondary leaflets with a naked intercostal region between the rachilla and the basal-most pinnule
	lobes, the leaflets appearing short-stalked or petiolulate.
	6. Basal leaf sheaths short and narrow, papery or leathery, the scarious margin obscure or absent, the thatch at the
	apex of the caudex composed primarily of numerous, weathered, gray stalks formed from the previous year's
	long-persistent peduncles, the sheaths from previous years absent or weathering into a few loose fibers.
	7. Calyx teeth present, 0.5–1 mm long, narrowly deltoid in shape; fruit winged laterally and dorsally, the dorsal
erebinthinus	wings obscuring developing even in immature stagesCymopterus t
	7. Calyx teeth absent or nearly obsolete, less than 0.2 mm long, broadly deltoid in shape, when present; fruit
pauperatum	
	6. Basal leaf sheaths long and broad, papery, the scarious margin broad and conspicuous, the sheaths from previ-
	ous years weathering into a dense thatch of fibers and chaffy or chartaceous scales at the apex of the caudex,
	the previous year's peduncles present in the thatch as a few, grey stalks; peduncles stout, 7–60 cm long.
	8. Peduncles 6–8 mm wide (1 cm below the apex); ultimate apical and lateral pinnules of the secondary and
	tertiary leaflets with a naked intercostal region (4.5)5–8 mm long (the naked intercostal region is located be-
	tween the rachilla and the basal-most pinnule lobes, and appears like a petiolule), ultimate apical lobes in X-
klickitatense	
	8. Peduncles 2–6 mm wide (1 cm below the apex); ultimate apical and lateral pinnules of the secondary and
	tertiary leaflets with a naked intercostal region 1–5(6) mm long (appears like a short petiolule), ultimate apical
pilioniferum	lobes in X-section flat or subterete, 1–7 (9) mm long
pilioniferum	5 () 5(11) 1 /

 Lomatium grayi (J.M. Coult. & Rose) J.M. Coult. & Rose, Contr. U.S. Natl. Herb. 7(1):229. 1900. BASIONYM: Peucedanum millefolium S. Watson, Botany (Fortieth Parallel) 129. 1871, nom. illeg., not Sond. 1862; Peucedanum grayi J.M. Coult. & Rose, Bot. Gaz. 13(8):209. 1888. PROTOLOGUE: Antelope Island, Salt Lake. Type: U.S.A. UTAH. Davis Co.: Antelope Island, Jun 1869, Sereno Watson 466 (HOLOTYPE: US127479; ISOTYPES: GH76984, YU [not seen]).

Cogswellia millefolia (S. Watson) M.E. Jones, Contr. W. Bot.12:35. 1908 Cogswellia grayi (J.M. Coult. & Rose) J.M. Coult. & Rose, Contr. U.S. Natl. Herb. 12(10):450. 1909 Lomatium millefolium (S. Watson) J.F. Macbr., Contr. Gray Herb. 53:15. 1918.

Note.—There is some confusion in floristic treatments as to where the holotype or lectotypes of specimens from the Clarence King expedition (Watson 1871) should be designated. For types of taxa designated by Sereno Watson, Tiehm (1985) recommends that the specimen from US be designated as the holotype or lectotype if present. Tiehm did not designate the type material of *Peucedanum millefolium* at US or YU as the holotype and did not see the specimen at GH. There does not appear to the senior author to be any special circumstance to indicate that the US specimen should not be designated as the type, therefore Tiehm's recommendation is followed herein.

Plants: acaulescent. **Roots:** a stout, irregularly thickened taproot. **Caudices:** simple or multicipital; the thatch at the apex dense, composed of the previous year's basal leaf sheaths and peduncles weathering into numerous fibers and chaffy scales, the previous year's peduncles readily weathering and not persistent in the thatch as



Fi6. 6. Regional distribution map of *Lomatium grayi* (circles) and *L. depauperatum* (triangles) in Intermountain and Rocky Mountain regions of the western United States. For reference, the map also shows adjacent vouchers of *L. papilioniferum* (squares) in Idaho and Nevada. Marker 1 is the type locality of *L. depauperatum*. Marker 2 is the type locality of *L. grayi*. Marker 3 indicates specimens in the mixed population of *L. depauperatum* and *L. grayi* in the Canyon Mountains of Juab Co., Utah. Due to the map scale, the circles representing specimens of *L. grayi* are obscured.



Fi6. 7. Close-up distribution map of *Lomatium klickitatense* (stars) in Klickitat County, Washington and neighboring Hood River and Wasco County Oregon showing adjacent vouchers of *L. papilioniferum* (squares). The state boundary line bisects the Columbia River Gorge. Marker 1 is the type locality of *L. klickitatense*. Marker 2 indicates specimens (squares) initially determined as *L. papilioniferum* that were classified as *L. klickitatense* in the CDA. For a region-wide map, see Figure 8.



Fi6. 8. Regional distribution map of *Lomatium papilioniferum* (squares) in the Pacific Northwest of the western United States. The long-disjunct population on islands adjacent to Vancouver Island in British Columbia, Canada is not shown, far to the upper left of the left-hand corner of the map. For reference, the populations of L. klickitatense (stars) are shown on the left and in the lower right had corner are disjunct populations of *L. grayi* (circles) and *L. depauperatum* (triangles). Marker 1 is the type locality of *L. papilioniferum*. Marker 2 is indicated the location of the distribution map of *L. klickitatense* (see Fig. 7). Marker 3 is the location of the long-disjunct population of *L. papilioniferum* in the valleys east of the Warner Mountains, Modoc County, California (mapped but not included in the morphometric analyses).

grey stalks. **Stems:** glabrous, 0.8-2 dm. **Leaves:** cauline leaves absent; basal leaves glabrous, primary leaflets pinnate, 5-8 secondary leaflet pairs along each rachis, the lateral leaflets at least half to subequal to the central primary in length, secondary leaflets pinnate, tertiaries pinnate, the quaternaries entire or pinnatifid (3–20 lobed), ultimate leaflet pinnules leafy to the base, intercostal regions obscured by densely clustered pinnule lobes, the intercostal region between the rachilla and the basal-most pinnule lobe 0-0.1 mm, appearing sessile; ultimate apical lobes linear, in X-section sub-terete, $0.8-4.8 \times 0.1-0.4$ mm, apex acute or acuminate. **Inflorescences:** peduncles 1–5, glabrous, slender, 0.6-3.5 (6) mm wide (1 cm below the apex), 8-40 cm long; involucre 0; umbels 5–20-rayed, rays glabrous, 0.5-8 cm; involucellar bracts absent or 2–10, linear or lanceolate, narrowly scarious margined, $2-10 \times 0.1-0.6$ mm. **Flowers** 10–40 per umbellet; petals yellow; anthers yellow or ochroleucous. **Fruit** oblong or elliptic, glabrous, 5-18 mm long, body 1.5–5 mm wide, wings thin, 0.4-2 mm wide, vittae 1–2 in the intervals, 2–6 on the commissure; pedicels 2–18 mm.

Range.—Colorado: Archuleta, Delta, Dolores, Garfield, La Plata, Mesa, Moffat, Montezuma, Rio Blanco, and San Miguel counties; Idaho: Bannock, Bear Lake, Bonneville, Franklin, Caribou, and Oneida counties; New Mexico: Rio Arriba and San Juan counties; Utah: Cache, Daggett, Davis, Juab, Millard, Utah, Rich, San Juan, Sanpete, Sevier, Summit, Tooele, and Uintah counties; Wyoming: Lincoln, Sublette, Sweetwater, and Uinta counties (Fig. 6).

Ecology.—Central Basin and Range: Malad and Cache Valleys, Sagebrush Basins and Slopes, Woodlandand Shrub-Covered Low Mountains; Colorado Plateaus: Escarpments, Monticello-Cortez Uplands, Northern Uinta Basin Slopes, Semiarid Benchlands and Canyonlands; Middle Rockies: High Elevation Valleys, Midelevation Sedimentary Mountains, Partly Forested Mountains; Northern Basin and Range: Semiarid Hills and Low Mountains; Southern Rockies: Crystalline Mid-Elevation Forests, Sedimentary Mid-Elevation Forests; Wasatch and Uinta Mountains: Mid-Elevation Uinta Mountains, Semiarid Foothills; Wyoming Basin: Foothill Shrublands and Low Mountains, Rolling Sagebrush Steppe, Sub-Irrigated High Valleys.

Discussion.—In all previous treatments, the range of *L. grayi* var. *grayi* was composed of all populations throughout the Pacific Northwest and eastward to Colorado, New Mexico, Utah, and Wyoming. In this study, the range of *L. grayi* s.s. was found to be disjunct from the range of the Pacific Northwest populations, delimited herein as *L. papilioniferum*. In Idaho, *L. papilioniferum* is found in western and central Idaho while *L. grayi* is found only in southeastern Idaho. The disjunction between these two taxa lies primarily within the eastern Snake River Plains and the central portion of the Northern Basin and Range ecoregions (Bingham, southeastern Blaine, Cassia, Jerome, Minidoka, Power, and Twin Falls counties), where no vouchers from field investigations, herbarium loans or online databases were found during this study.

In the vicinity of the type locality, around the edge of the Great Salt Lake eastward to the foothills and canyons of the Wasatch Range (Davis and Salt Lake county, Utah), Lomatium grayi populations are mostly average-sized individuals mixed with some much taller, more robust individuals, especially in years with abundant moisture. These robust plants attain a size that is comparable to plants of average size in Oregon and western Idaho populations of L. papilioniferum. The type collection is average sized for L. grayi and does not represent one of these robust individuals. The robust plants of L. grayi, however, have the characteristic dense fibrous thatch composed of rapidly weathered basal leaf sheaths and peduncles. Only the largest individuals have a few persistent peduncles. In contrast, individuals of L. papilioniferum have a dense fibrous thatch of weathered basal leaf sheaths intermixed with many, grayish, long-persistent, basal stalks of the peduncles. Although the sizes of the pinnule lobes in these northwestern populations are longer than those found throughout the remainder of the range of L. grayi, the lobes are crowded along the primary and secondary leaflets such that the rachillas are obscured. Although the lobe length could be evidence of past introgression, the environment could be contributing to this size difference. The populations along the western foothills of the Wasatch Range and Bear River Ranges are mostly below 4500 feet in elevation. The remainder of the populations in eastern Utah, southeastern Idaho, western Colorado and southwestern Wyoming are found mostly between 5000 and 10,000 feet in elevation. The longer growing season at the lower elevation populations in northern Utah are likely one reason for the presence of these larger, more robust individuals. In many years,

these lower elevation populations are in flower when the populations in the canyons in the Bear River Range, Uinta Mountains, and Wasatch Range eastward to Wyoming and Colorado are in an early stage of growth, with only their first pairs of basal leaves. The leaves of most of the higher elevation populations in Colorado, eastern Utah, and Wyoming are nearly indistinguishable from those of the central Washington species, *L. quintuplex*.

Populations of *P. indra* subsp. *indra* and *P. indra* subsp. *minori* are found within the range of *L. grayi* s.s., but neither subspecies uses it as a larval host. Due to the lower elevation range of most populations, individuals of *L. grayi* in the Wasatch and Bear River Ranges are already past the fruiting stage by the time *P. indra* subsp. *indra* females are laying eggs on other *Lomatium* and *Cymopterus* species. In western Colorado, where mixed populations of *L. grayi* and *C. terebinthinus* are common, *P. indra* subsp. *minori* preferentially lays eggs on *C. terebinthina* and *L. eastwoodiae*. Throughout its range, both butterfly subspecies appear to exclude *L. grayi* as a suitable host plant (Whaley, unpub. data). This suggests that *P. indra* has switched hosts at some point after the speciation event that gave rise to *L. papilioniferum*.

The physiological or chemical basis for this case of butterfly-host switching is not known. In the laboratory *Papilio indra* subsp. *indra* which used *L. graveolens* at high elevations (8000–10,000 ft) in the Wasatch Range of Utah can be successfully reared on *L. grayi* s.s. with no observable harmful effects (Whaley, unpublished data). Likewise the "bonnevillensis" race of *Papilio indra* (an undescribed subspecies, Whaley, in prep.) from the Great Basin desert ranges in Utah uses *L. depauperatum* and can be successfully reared using *L. grayi s.s.* This implies that essential oil composition of *L. grayi* does not prompt female attraction even though essential nutrients are available (see Appendix 2; Dev et al. 2007).

2. Lomatium depauperatum (M.E. Jones) J.A. Alexander & W. Whaley, comb. nov. BASIONYM: Cogswellia millefolia var. depauperata M.E. Jones, Contr. W. Bot. 12:38. 1908. PROTOLOGUE: Dugway, Dutch Mountain, Granite Mountains, Cove Creek, Detroit, Fish Springs, etc., western Utah. TYPE: U.S.A. UTAH. Tooele Co.: Dugway, 2 Jun 1891, M.E. Jones s.n. (LECTOTYPE designated by Mathias (1938:271) as "Jones, Dugway, Utah, 2 Jun 1891 (Po [sic] 78055)"); POM78055; ISOLECTOTYPEs: none).

Lomatium grayi var. depauperatum (M.E. Jones) Mathias, Ann. Missouri Bot. Gard. 25:270. 1937.

Note.—The original type publication by Jones included multiple syntypes and did not specify a type, which has been overlooked by all previous floristic and monographic treatments of this genus. Mathias did not state why she selected the specimen dated "2 June 1891" as the type. POM78055 is mostly likely Jones' original type material because the specimen at POM was labeled as "new variety material" in Jones' hand and determined by him to "var. depauperata." Mathias' (1938:271) citation is an effective lectotypification of this taxon. The type citation by Welsh (1982:165) is an effective second-step lectotypification. He designated the type as "Dugway, Jones sn [sic], 1891 (US!; POM!; NY!)." Welsh essentially recognized all of the 1891 collections from Dugway as type material by including the syntypes at US [dated 26 May 1891] and NY [dated 28 May 1891]. However, since he did not include accession numbers or dates, his type citation does not select which of the 1891 specimens at POM are the lectotype. The type citation by Cronquist et al. (1997:404) is an effective third-step lectotypification, changing the lectotype from the Dugway syntype dated 28 May 1891 (see list below). Neither Welsh nor Cronquist et al. include justifications for their re-lectotypifications. Since it seems clear that Jones intended POM70855 to be the type through his annotations on the specimen, Mathias' original lectotypification is kept herein and the Welsh second-step and Cronquist et al. third-step re-lectotypifications are rejected. The type material determined as "isotypes" at NY and US are isosyntypes and not isolectotypes (see below). The holotype appears to be a unicate.

As it is often difficult to determine which specimens are types from Jones' publications, the syntypes found during this study are listed herein (Juab Co.: Detroit [Detroit Mining District, Drum Mountains], 25 May 1891, *Marcus E. Jones s.n.*, [POM78054]; Millard Co.: Cove Creek, 16 Jun 1898, *Marcus E. Jones s.n.*, [POM78157]; Tooele Co.: Dugway, 26 May 1891, *Marcus E. Jones s.n.* [US57855, may be just a transposition error for May 28 as the label is typed and not in Jones' hand]; Dugway, 28 May 1891, *Marcus E. Jones s.n.* [POM78053; NY405809]; Dutch Mountain, 12 Jun 1899, *Marcus E. Jones s.n.* [POM78051]; Granite Mountains [Granite Peak, N of the Dugway Range], 07 Jun 1900, *Marcus E. Jones s.n.*, [POM78158]). The Fish Springs syntype was not found at RSA and may have been mistakenly distributed as a duplicate to DS. It should be looked for at CAS.

Plants: acaulescent. **Roots:** a stout, irregularly thickened taproot. **Caudices:** simple or multicipital; the thatch at the apex dense, composed primarily of the previous year's peduncles weathering into numerous, long-persistent, gray stalks, the basal leaf sheaths from previous years absent or weathering into a few loose fibers. **Stems:** 2–6 dm, glabrous. **Leaves:** cauline leaves absent; basal leaves glabrous, primary leaflets pinnate, 5–8 secondary leaflet pairs along each rachis, the laterals at least half to subequal to the central primary in length,

secondary leaflets pinnate, tertiaries pinnate, quaternaries entire or pinnatifid (3–6 lobed), ultimate leaflet pinnules leafy to the base, sparsely lobed, appearing sessile, or with a naked intercostal region between the rachilla and the basal-most pinnule lobes (appearing short-petiolulate) 0.1-0.8 mm, the intercostal areas not obscured by pinnule lobes; ultimate apical lobes linear, in ×-section dorsi-ventrally compressed (appearing flat), $1.0-4.5 \times 0.3-0.7$ mm, apex acuminate. **Inflorescences:** peduncles 1 to 10+, glabrous, slender, 1-2 mm wide (1 cm below the apex), 9-33 cm long; involucer 0; umbels 5-15-rayed, rays glabrous, 0.5-6 cm; involucellar bracts absent or 2-10, linear or lanceolate, narrowly scarious margined, $2-5 \times 0.1-0.6$ mm. **Flowers:** 10-20 per umbellet; petals yellow; anthers yellow or ochroleucous. **Fruit:** oblong or elliptic, glabrous, 5-9 mm long, body 1-3 mm wide, wings thin, 0.3-1.5 mm wide, vittae 1-2 in the intervals, 2-6 on the commissure; pedicels 2-16 mm.

Range.—Nevada: Elko and White Pine counties; Utah: Beaver, Box Elder, Juab, Millard, and Tooele counties (Fig. 6).

Ecology.—Central Basin and Range: Carbonate Sagebrush Valleys, High Elevation Carbonate Mountains, Salt Deserts, Sagebrush Basins and Slopes, Shadscale-Dominated Saline Basins, Woodland- and Shrub-Covered Low Mountains; Northern Basin and Range: Dissected High Lava Plateau, Saltbush-Dominated Valleys.

Discussion.—This taxon has long been considered a variety of *L. grayi*. It was first comprehensively delimited by Mildred Mathias (1938). She restricted its range to the *L. grayi* populations in the desert mountain ranges of the eastern Great Basin of Nevada and Utah and populations from the mountain ranges west of the Wasatch Front that are sympatric with the typical variety. Mathias stated that *L. grayi* var. *depauperatum* is "similar to the species [*L. grayi* var. *grayi*] but usually lower [with] leaves dissected into few remote small linear pinnae." Her statement was similar to that of Jones in his type description. All later floristic treatments have followed Mathias (1938) with little deviation and no additional support for the delimitation of these two taxa as varieties. There have been no prior published analyses that have investigated the morphological similarity of these two taxa.

Morphological studies and field surveys for this study have found that the populations proposed by other authors as being intergradient with typical *L. grayi*, are morphologically distinct and mostly disjunct (see Fig. 6). In mountain ranges where these two taxa are growing in mixed populations, *L. depauperatum* can be distinguished vegetatively by its flat, dorsi-ventrally compressed ultimate pinnule lobes and the thick thatch composed mostly of persistent inflorescence peduncles on the caudex branches. The sheaths of the basal leaves are narrow and leathery without the broad scarious margins characteristic of *L. grayi*. These narrower sheaths are not readily weathered and produce only a few loose, broad, chartaceous fibers on each caudex branch. In contrast, the ultimate leaflet segments of *L. grayi* are oval in cross section, with only a slight dorsi-ventrally compressed surfaces. The caudex branches are covered in a dense fibrous thatch formed from the easily weathered, broad, scarious basal leaf sheaths. The microhabitat of these two taxa are most commonly collected together), *L. grayi* is found mostly on the talus slopes and under shaded understories of oak and juniper thickets at the bottom of the canyons while *L. depauperatum* is found growing in rock crevices and on exposed talus slopes at the base of cliff faces.

Furthermore, individuals with long pinnule lobes have been identified during this study in mountain ranges scattered throughout the range of *L. depauperatum*, not just those mountains that overlap with the range of *L. grayi*. Specifically, long-lobed forms have been found at higher elevations in mountain ranges with greater annual precipitation (Deep Creek Range [Holmgren & Holmgren 10819 NY, RENO; Whaley & Moses s.n. 15 May 2013 SRP, UVSC]; Pilot Range [Holmgren & Holmgren 11110 BRY, RSA, NY) than the population in lower elevation, dry, desert mountain ranges. These vouchers are intergradient with those of *L. grayi* in the morphometric analysis (Fig. 4). In the dry desert mountain ranges of western Utah, plants from the same populations during drought have exceptionally small leaflets compared to other individuals collected in the

same vicinity during wet years. These data suggest that the long leaflet forms arise as a result of precipitation and other local microhabitat effects and not as a result of intergradation or hybridization.

Although herbarium collections of *L. depauperatum* often appear to be smaller plants than *L. grayi*, this species is often found with short leaves and many peduncles in broad, many branched clumps growing in rock crevices. Only a few younger individuals are ever collected without a branched caudex. The pinnule lobes in *L. depauperatum* are linear in cross section and dorsi-ventrally flattened. The pinnule lobes range from a millimeter in length to the length found in *L. grayi*. This has led to a confusion between these two species when found in mixed populations in central Utah, with the longer leaflet individuals being interpreted as intergradient forms. On average, the short-pinnule lobes of typical *L. depauperatum* are nearly indistinguishable from some morphotypes of *C. terebinthinus*. The leaflet pinnules are so similar in shape that occasionally some Washington and Oregon plants of *C. terebinthinus* are misidentified as *L. depauperatum* in herbarium and research vouchers.

The range of *L. depauperatum* lies exclusively within the drainage basin of the Pleistocene Lake Bonneville. Whereas *Papilio indra* subsp. *indra* uses only higher elevation *Lomatium* and *Cymopterus* species as hosts in northern Utah, the lower elevation populations west of the Wasatch Range have switched to using *L. depauperatum* almost exclusively. The lower elevation desert populations of *P. indra* have been suggested to be a new "*bonnevillensis*" subspecies, but it has not been formally described. Apparently, both the "*bonnevillensis*" race of *P. indra* and *L. depauperatum* have evolved in concert, differentiating from their nearest relatives and adapting to desert habitats as the former Lake Bonneville receded.

Although the "bonnevillensis" race of *P. indra* has only been observed to use *L. depauperatum* as a larval host, other species at higher elevations in this region may also be used. For example, this race uses *L. depauperatum* in the foothills of the Stansbury Range (Tooele County, Utah) and Raft River Mountains (Box Elder County, Utah) while at high elevation in these mountains *Papilio indra* subsp. *indra* uses *L. graveolens* and *C. hendersonii*, respectively. In the House (Millard County, Utah), and Deep Creek Ranges (Juab County, Utah), "bonnevillensis" uses *L. depauperatum* growing in canyons between 5000 and 7000 ft in elevation. In these ranges *L. graveolens* and *C. hendersonii* occur above 8,000 feet, but due to remoteness there are few *P. indra* records and no documentations of larval hosts. Both *L. graveolens* and *C. hendersonii* are hosts for *P. indra* subsp. *indra* subsp. *indra* subsp. *indra* subsp. *minori* respectively (see discussion of *L. gravi*).

- 3. Lomatium klickitatense J.A. Alexander & W. Whaley, sp. nov. Type: U.S.A. Washington. Klickitat Co.: Klickitat-Appleton Road, 2.5 km W of the junction with Washington Highway 142, on a mid-level bench of the Klickitat River Canyon, 25 May 2014, J.A. Alexander & W. Whaley 3096 (HOLOTYPE: OSC255194 [sheet 1 of 2], OSC255195 [sheet 2 of 2; Fig. 9]; ISOTYPES: RENO, UVSC, WTU, UC).
 - *Note.*—In the senior authors' experience, the majority of the hand-drawn illustrations for *Lomatium* species with finely divided leaves are not useful for illustrating the differences between the species. An image of the holotype for this species and *L. papilioniferum* has been substituted for the traditional illustration with the goal of providing a more detailed presentation of the morphology. This taxon differs from *L. grayi* in having diffuse ultimate pinnule lobes, the lobes not obscuring the elongate intercostal areas along the rachillae (vs. the lobes, the previous year's peduncles long-persistent in the thatch as grey stalks (vs. the previous year's peduncles readily weathering into thatch at the base of the stem and not long-persistent in the thatch as grey stalks), and a disjunct distribution west of the range of *L. grayi*; differs from *L. depauperatum* in having stout fruiting peduncles, 30–60 cm long and 6–8 mm wide (vs. 9–33 cm long and 1–2 mm wide), the thatch at the apex of the caudex composed a dense thatch of fibers and chaffy or chartaceous scales from previous years basal leaf sheaths, the previous year's peduncles long-persistent in the thatch as grey stalks (vs. thatch at the apex of the caudex composed of numerous gray stalks formed from the previous year's long-persistent peduncles, the sheaths from previous years absent or weathering into a few loose fibers), and a disjunct distribution north and west of the range of *L. depauperatum*; differs from *L. papilioniferum* in having fruiting peduncles 6–8 mm wide (vs. 2–6 mm wide), ultimate apical and lateral pinnules of the secondary and tertiary leaflets with a naked intercostal region between the rachilla and the basal-most pinnule lobes 5–8 mm long (vs. 1–5 mm long), and ultimate apical pinnule lobes 7–15 mm long (vs. 1–7 mm long).

Plants: subacaulescent or caulescent. **Roots:** stout, irregularly thickened taproots. **Caudices:** simple or multicipital; the thatch at the apex dense, composed of the previous year's basal leaf sheaths weathering into numerous fibers and chaffy scales, the previous year's peduncles long-persistent in the thatch as grey stalks. **Stems:** 4–15 dm, glabrous. **Leaves:** cauline leaves 1–2, similar to the basal; basal leaves glabrous, primary



Fig. 9. Image of sheet 2 of the holotype of Lomatium klickitatense, J.A. Alexander & W. Whaley 3096 (0SC255195). Sheet 1 is not shown (0SC255194).

leaflets pinnate, 5–8 secondary leaflet pairs along each rachis, lateral leaflets at least half to subequal to the central primary in length, the secondary leaflets pinnate, tertiaries pinnate, quaternaries entire or pinnatifid (3–20 lobed), ultimate leaflet pinnules not leafy to the base, with a naked intercostal region between the rachilla and the basal-most pinnule (appearing like a petiolule) (4.5) 5–8 mm; ultimate apical lobes linear, in X-section sub-terete, (6.5) 7–15 × 0.1–0.4 mm, apex acuminate. **Inflorescences:** peduncles 1 to 10+, glabrous, stout, 30–60 cm long, 6–8 mm wide (1 cm below the apex); involuce 0; umbels 16–30-rayed, rays 4–12 cm, glabrous; involucel bractlets absent or 2–10, linear or lanceolate, 2–10 × 0.1–0.6 mm, narrowly scarious margined. **Flowers:** 10–40 per umbellet; petals yellow; anthers yellow or ochroleucous. **Fruits:** oblong or elliptic, glabrous, 9–16 mm long, body 3–6 mm wide; wings thin, 1–2 mm wide, vittae 1–2 in the intervals, 2–6 on the commissure, pedicels 9–15 mm.

Range.-Washington: Klickitat County; Oregon: Hood River and Wasco counties. (Fig. 7).

Ecology.—**Eastern Cascades Slopes and Foothills:** Oak/Conifer Foothills, Yakima Plateau and Slopes. *Etymology.*—The epithet "klickitatense" ("of the Klickitat region") refers to the distribution of this taxon being mainly from Klickitat County, Washington.

Discussion.—The robust populations from the Klickitat River Valley have long been associated with *Lomatium grayi* var. *grayi* in regional floras. However, the distinctiveness of the morphology of these plants has been unrecognized mostly due to collecting habits of herbarium botanists. In general, the average individual of this taxon is larger than a herbarium sheet, with peduncle lengths, leaf widths, and individual canopy diameters closer to the size of *Lomatium columbianum* Mathias & Constance than to average individuals of *L. grayi* or *L. papilioniferum*. As such, herbarium botanists have commonly collected depauperate or early-season flowering individuals of this taxon, which fit on a sheet but have below average-sized, immature leaflets and umbels. Of the few times this species has been collected in fruit, herbarium botanists have tended to collect the late season fruiting peduncles, which at that stage stand out from the landscape as remarkably large compared to other *Lomatium* species. The fruiting peduncles are often almost as large as those of *L. columbianum* and are identical in size to those of *L. papilioniferum*. Unfortunately, the leaves at this late fruiting stage have begun to wither and fragment or are absent entirely on the sheet, further obscuring the distinctive leaf morphology of this taxon.

The range of this taxon is limited to the Eastern Cascades Slopes and Foothills ecoregion immediately north and south of the Columbia River Gorge. The majority of the populations of this taxon are restricted to the Oak-Conifer Foothills sub-region with a few populations along the upper Klickitat River drainage east of Glenwood in the Yakima Plateau and Slopes sub-region.

Examinations of herbarium specimens and additional field surveys in the spring of 2015 indicated that the populations of this taxon extend from the slopes of the foothills of the lower Klickitat River drainage westward to the slopes east of the White Salmon River Canyon in the vicinity Bingen and White Salmon. In Oregon, this taxon is limited to the Hood River drainage along the slopes of the Columbia River Gorge from the vicinity of Hood River (Hood River County) westward to just east of Mitchell Point and eastward to the cliffs west of Mosier (northwestern Wasco County). These surveys also found that the only point of contact for this species and *L. papilioniferum* are along the northeastern boundary of the Oak-Confer Foothill sub-region along the Little Klickitat River and on rocky slopes of the Oak-Confer Foothill sub-region along the rock.

Throughout the range of *L. klickitatense*, *P. indra* subsp. *indra* uses this species as a host plant. However it does not seem to distinguish between *L. klickitatense* and neighboring populations of *L. papilioniferum*. Both species appear to be equally suitable host plants for this butterfly subspecies.

Cymopterus terebinthinus is the only other host plant for this butterfly subspecies in this region (Whaley, unpublished data). Populations of *C. terebinthinus* are found in Washington along the western boundary of the range of *L. klickitatense* between the city of Cook and Little Huckleberry Mountain (Skamania Co.: *Fishbien & Greer 5786* [originally misidentified as *L. grayi*], north of Grassy Knoll about 3 mi SE of Big Huckleberry

Mountain, HPSU; *Suksdorf 11480*, Dog Creek near Cooks, WS) northward to the base of Mount Adams (Yakima County: near top of Crofton Butte, *Slichter 50*, WTU; *Suksdorf 4107*, Mount Paddo, WS).

- 4. Lomatium papilioniferum J.A. Alexander & W. Whaley, sp. nov. Type: U.S.A. OREGON. Baker Co.: Burnt River, 1 km W of the mouth, along the Snake River Road, E of Huntington, 14 Apr 2015, J.A. Alexander 3300 (HOLOTYPE: OSC255196 [sheet 1 of 2; Fig. 10], OSC255197 [sheet 2 of 2]; ISOTYPES: NY, UNLV, UVSC, WTU, UC).
 - Peucedanum grayi var. aberrans M.E. Jones, Contr. W. Bot. 10:55–56. 1902. PROTOLOGUE: Monroe Creek, 20 Apr 1900, Middle Fork of the Weiser River, 14 Jul 1899, Cuddy Mts., 11 Jul 1899 [Jones 6341], Snake River below Weiser, 28 Apr 1900, all in southern Idaho. TYPE: U.S.A. Idaho. Washington Co.: Monroe Creek, 20 Apr 1900, Marcus E. Jones 6342 (LECTOTYPE [first step] partially designated by Cronquist et al. (1997:404); LECTOTYPE [second step] designated here as the "Monroe Creek" syntype from Jones' herbarium, the POM lectotype is not stamped with Jones' collection number); POM77496; ISOLECTOTYPES: ORE64184; WTU243850 [not seen]; US127459 [internet image]; NY2912678 [internet image]).
 - Note.—Neither Coulter and Rose (1909) nor Mathias (1938) listed a type for this taxon in the synonymy of their respective monographs. Jones, himself, did not name a new combination for this taxon when he transferred species of *Peucedanum* to *Cogswellia*. Apparently, the first publication to mention types of this taxon was Cronquist et al. (1997), who stated only that the types were from Idaho and no type had been designated to date. Jones (1902) described this variety as having "leaf segments filiform, oil tubes interrupted and variable in length except the central one in each interval normally 2, rarely 1 or 3 in each interval" (55–56). Presumably the oil tube characters came from the two syntypes from July. Jones does not discuss how his taxon differed from typical *L. grayi*. The oil tube characters are not described in detail enough to differentiate them from typical *L. grayi*. I can find no evidence that any syntypes were marked as type material by Jones (loaned specimens from RSA). All of the types were collected in the same meta-population in the foothills and rivers east and south of Weiser, Washington Co., Idaho. All of the syntypes are similar morphologically, although the two specimens collected in July are in fruit and have dry and highly fragmented leaves. In lieu of other evidence, the first syntype is selected herein as the lectotype, being the material with best well-developed leaves showing the filiform leaf segments described by Jones in the type publication.

As it is often difficult to determine which specimens are types from Jones' publications, the syntypes found during this study are listed herein (Payette Co.: 18 mi below Weiser [Payette vicinity], 28 Apr 1900 [*Marcus E. Jones s.n.*, POM77943]; Washington Co.: Cuddy Mountains, 15 Jul 1899, [*Marcus E. Jones s.n.*, POM78066; *Marcus E. Jones 6341*, NY1141482]; Middle Fork of the Weiser River, 15 Jul 1899 [*Marcus E. Jones s.n.*, POM78065]).

Lomatium papilioniferum differs from *L. grayi* in having diffuse ultimate pinnule lobes, the lobes not obscuring the elongate intercostal areas along the rachillae, the previous year's peduncles long-persistent in the thatch as grey stalks (vs. the previous year's peduncles readily weathering into thatch at the base of the stem and not long-persistent in the thatch as grey stalks), and a disjunct distribution west of the range of *L. grayi*; differs from *L. depauperatum* in having stout fruiting peduncles, 7–60 cm long and 2–6 mm wide (vs 9–33 cm long and 1–2 mm wide), the thatch at the apex of the caudex composed a dense thatch of fibers and chaffy or chartaceous scales from previous years basal leaf sheaths, the previous year's peduncles long-persistent in the thatch as grey stalks (vs thatch at the apex of the caudex composed of numerous gray stalks formed from the previous year's long-persistent peduncles, the sheaths from previous years absent or weathering into a few loose fibers), and a disjunct distribution north and west of the range of *L. depauperatum*; differs from *L. klickitatense* in having fruiting peduncles 2–6 mm wide (vs 6–8 mm wide), ultimate apical and lateral pinnules of the secondary and tertiary leaflets with a naked intercostal region between the rachilla and the basal-most pinnule lobes, appearing like a petiolule, 1–5 mm long (vs. 5–8 mm long), and ultimate apical pinnule lobes 1–7 mm long (vs. 7–15 mm long).

Plants: acaulescent, subacaulescent, caulescent. **Roots:** stout, irregularly thickened taproots. **Caudices:** simple or multicipital; the thatch at the apex dense, composed of the previous year's basal leaf sheaths weathering into numerous fibers and chaffy scales, the previous year's peduncles long-persistent in the thatch as grey stalks. **Stems:** 4–8 dm, glabrous. **Leaves:** cauline leaves 1–2, similar to the basal; basal leaves 2–4 pinnate, glabrous, glabrescent, or sparsely scaberulous (rarely); primary leaflets pinnate with 5–8 secondary leaflet pairs along each rachis, laterals at least half to subequal to the central primary in length, the secondary leaflets pinnate, tertiaries pinnate, quaternaries entire or pinnatifid (3–30 lobed), ultimate leaflet pinnules not leafy to the base, with a naked intercostal region between the rachilla and the basal-most pinnule (appearing like a petiolule) 1–5 (6) mm, the intercostal areas not obscured by pinnule lobes; ultimate apical lobes linear, lanceolate, deltoid, in X-section dorsi-ventrally compressed (appearing flat) or sub-terete, 1–7 (9) × 0.1–0.6 mm, apex acute or acuminate. **Inflorescences:** peduncles 1 to 10+, slender to stout, not inflated, 7–60 cm long, 2–6 mm wide (1 cm below the apex), glabrous; involucre 0; umbels 6–40-rayed, rays 1 to 20 cm, glabrous;



Fig. 10. Image of sheet 1 of the holotype of Lomatium papilioniferum, J.A. Alexander 3300 (0SC255196). Sheet 2 is not shown (0SC255197).

This document is intended for digital-device reading only. Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org. involucel bractlets absent or 2–10, linear or lanceolate, $2-8 \times 0.1-0.6$ mm, narrowly scarious margined. **Flowers:** 10–40 per umbellet; petals yellow; anthers yellow or ochroleucous. **Fruits:** oblong or elliptic, glabrous, 6–13 mm long, body 2–6 mm wide, wings thin, 0.5–2 mm wide, vittae 1–2 in the intervals, 2–6 on the commissure, pedicels 6–15 mm.

Range.—Canada. British Columbia; United States. California: Modoc County; Idaho: Ada, Adams, Blaine, Boise, Elmore, Gem, Gooding, Idaho, Nez Perce, Owyhee, Payette, Valley, and Washington counties; Nevada: Elko County; Oregon: Baker, Crook, Gilliam, Grant, Hood River, Jefferson, Malheur, Morrow, Multnomah, Sherman, Umatilla, Union, Wallowa, Wasco, and Wheeler counties; Washington: Asotin, Benton, Chelan, Columbia, Douglas, Franklin, Garfield, Grant, Kittitas, Klickitat, Okanogan, Skamania, Spokane, Stevens, Walla Walla, Whitman, and Yakima counties (Fig. 8).

Ecology.—**Blue Mountains:** Canyons and Dissected Highlands, Continental Zone Foothills, Deschutes River Valley, John Day/Clarno Highlands, John Day/Clarno Uplands, Maritime-Influenced Zone, Melange, Mesic Forest Zone, Subalpine-Alpine Zone, Wallowa/Seven Devils Mountains; **Cascades:** Western Cascades Lowlands and Valleys; **Central Basin and Range:** Upper Humboldt Plains; **Columbia Plateau:** Channeled Scablands, Deep Loess Foothills, Loess Islands, Lower Snake and Clearwater Canyons, Okanogan Drift Hills, Palouse Hills, Pleistocene Lake Basins, Umatilla Dissected Uplands, Umatilla Plateau, Yakima Folds; **Eastern Cascades Slopes and Foothills:** Grand Fir Mixed Forest, Oak/Conifer Foothills, Yakima Plateau and Slopes; **Idaho Batholith:** Dry Partly Wooded Mountains, Hot Dry Canyons, Southern Forested Mountains; **Northern Basin and Range:** Owyhee Uplands and Canyons, Pluvial Lake Basins, Semiarid Uplands; **Northern Rockies:** Okanogan-Colville Xeric Valleys and Foothills, Spokane Valley Outwash Plains; **Snake River Plain:** Mountain Home Uplands, Semiarid Foothills, Treasure Valley, Unwooded Alkaline Foothills; **Willamette Valley:** Valley Foothills; **Vancouver Island** (Canada).

Etymology.—The epithet "*papilioniferum*" ("butterfly bearing") acknowledges that *L. papilioniferum* is a host to *Papilio indra* where *L. grayi* s.s. is not. This difference was first observed by Whaley during his *Papilio indra* field studies (see Dev et al. 2007).

Discussion.—The primary distribution of *L. papilioniferum* ranges across a greater diversity of ecoregions than the other three species. This taxon spans Washington and Oregon eastward into Idaho across five ecoregions (the Columbia Plateau, Blue Mountains, Northern Basin and Range, the southern Idaho Batholith, and the western Snake River Plains). Scattered populations along the edge of its primary range are found in six additional ecoregions: the Cascades, Northern Rockies Ecoregion, southern part of the Northern Basin and Range Ecoregion, Eastern Cascades Slopes and Foothills Ecoregion (but conspicuously absent from Deschutes and Lake counties, Oregon), Willamette Valley Ecoregion, and long-disjunct populations on islands around Vancouver Island, British Columbia, Canada (but conspicuously absent in the adjacent San Juan Islands of the Puget Lowlands Ecoregion of Washington).

Throughout most of the range of *L. papilioniferum*, *P. indra* subsp. *indra* utilizes it as a larval host. The largest populations of this butterfly are found along the Columbia River Gorge in the vicinity of The Dalles and the John Day Dam on the Oregon and Washington sides of the river. It has also been found using *L. papilioniferum* as a host in the Snake River drainage with the largest populations found in Washington between Wawawai County Park (Whitman County, Washington) eastward to the cliffs around Clarkston (Asotin and Whitman counties) and in Oregon along Brownlee Reservoir in the Snake River Canyon from the Spring Recreation Site southward to the mouth of the Burnt River east of Huntington (Baker County; the type locality). In Idaho, the butterfly has also been found in numerous populations in the mountains north and east of the Snake River and in the Owyhee Mountains (Silver City Range, Owyhee County). Among the three, long-disjunct populations of *L. papilioniferum*, only the populations in the Independence Mountains of Elko County Nevada have been confirmed to have populations of *P. indra* subsp. *indra* using it as a larval host. It is not known if *P. indra* is present in the other long-disjunct populations of *L. papilioniferum* in the Surprise Valley of California (Modoc County) or on islands in the vicinity of Vancouver Island, British Columbia, Canada. The

status of the identification of a specimen for the sole report of this taxon from the Crater Lake vicinity in Klamath County (Applegate 4774a, WILLU 14942) is unresolved, but it may be misidentified.

Papilio indra subsp. indra has also been found to use two other species of Lomatium and Cymopterus as host plants in the Pacific Northwest (see Table 2). In Oregon and western Idaho, *P. indra* uses both *L. papilioniferum* and *C. terebinthinus* as larval hosts. Both of the hosts and the butterflies can be found at low elevation sites along river drainages and on talus slopes at higher elevations. In Washington, populations of *P. indra* subsp. *indra* use exclusively *L. brandegeei* as a larval host at higher elevation sites in the Cascade Range (Chelan, Kittitas, Okanogan and Yakima counties), while the low elevation populations east of the Cascade Range along the upper Columbia River drainage use *L. papilioniferum* and *C. terebinthinus*. Unlike the pattern of host preference in the Wasatch Range of Utah, *P. indra* subsp. *indra* has not switched hosts exclusively in favor of higher elevation host plants in the Pacific Northwest (Whaley, unpub. data).

One of the notable results of this study is the quantification of the high levels of variation in pinnule lobe morphology and observed levels of plant biomass variation between *L. klickitatense*, *L. papilioniferum*, and *L. grayi*. The largest species, *L. klickitatense*, has the longest pinnule lobes of any of the three taxa and the largest plant biomass. The pinnule lobes in this species are round to oval in cross section with very little dorsi-ventral compression. These long, oval pinnule lobes have also been observed even at the first-year seedling stage. The leaflet pinnules of *L. grayi* s.s. are similar those of in *L. klickitatense* (round to oval in cross section with very little dorsi-ventral compression) but are on average much shorter, more numerous, and highly clustered along the leaflet rachillas. Individuals of *L. grayi* have a smaller biomass on average than the other three species. The smallest plants in this complex are individuals with an unbranched caudex and only 1 or 2 peduncles in populations at or above 9000 ft elevation in eastern Utah and western Colorado.

Comparatively, populations of *L. papilioniferum* express a combination of the features of *C. terebinthinus*, *L. depauperatum*, *L. klickitatense*, and *L. grayi*. In scattered populations throughout the range of *L. papilioniferum*, individuals can be found that are similar in size to average plants of *L. grayi*. However, these plants have short, dorsi-ventrally flattened leaflet lobes that are nearly identical to *L. depauperatum* and *C. terebinthinus* (an example of this morphotype is shown in Figure 1H). In this study, 10–25% of loaned specimens were misidentified in folders of *L. grayi* and *C. terebinthinus*. The confusion between these two species is mostly due to the shorter and flat pinnule-lobe morphotype of *L. papilioniferum* being similar to that found in forms of *C. terebinthinus*. Other individuals have long leaflets and a larger, many branched caudex, resembling the smallest individuals of *L. klickitatense*. At sites examined for this study, the variation appears to be continuous with these two morphotypes growing adjacent to average sized individuals with intermediate length pinnule lobes which are oval in cross section.

This morphological diversity may also have an ecological component. Another flat pinnule lobe morphotype that has lobes even shorter and more deltoid-shaped that the morphotype in Figure 1H has been commonly collected in low-elevation sites along the Columbia River between the mouth of Willow Creek (Gilliam County, Oregon), Hat Rock State Park (Umatilla County, Oregon), and the mouth of the Snake River (Franklin and Walla Walla counties, Washington) in the Pleistocene Lake Basins and Yakima Folds subregions. *Cymopterus terebinthinus* is sympatric with *L. papilioniferum in this region*. As a result, vouchers of *L. papilioniferum* from this area are often misidentified as *C. terebinthinus* when collected in early-season flowering stages. In contrast, at the highest elevation populations in the Blue Mountains Ecoregion of Idaho, Oregon and Washington and in the southern mountains and foothills of the Idaho Batholith Ecoregion, the long pinnule morphotype has been more commonly collected. These observations suggest that both at a local population level and an ecoregional level, the biomass and leaf size of plants may be dependent on levels of moisture in the soil during the growing season. However, other factors may be contributing to the levels of morphological diversity expressed in populations of *L. papilioniferum*.

This study was not the first to observe a difference between biomass among individuals in populations of *L. papilioniferum*. Richard Ellison and John Thompson of Washington State University first observed a difference in plant biomass and seed size between individuals of *L. grayi* at four study site populations in

southeastern Washington (populations considered *L. papilioniferum* in this treatment). However, it was found that larvae of two species of weevils and one species of moth were a likely cause. Through field and greenhouse experiments on individuals from these populations, it was found that the larvae of two natively-occurring species of weevils (*Apion oedorhychum* Le Conte and *Smicronyx* Schönherr) were both acting as parasites and seed predators in *Lomatium* populations. Both adult and larval predation of seeds in umbels affected the mass and germinability of maturing seeds. The adults are proliferous, laying eggs in a majority of flowers in an umbel. An entire plant may be infected, leaving few seeds undamaged. Ellison and Thompson's study found that even the seeds that were undamaged tended to have a reduced mass and germinability compared to control individuals. Seedling biomass from larval damage). Furthermore, in greenhouse experiments testing the levels of environmental competition (lower light, reduced pot size, competition with *Bromus tectorum* seedlings), 24–31% of the overall plant biomass variance was explained by seed mass (Ellison & Thompson 1987).

During this study, most of the observed populations of L. papilioniferum were infected with the larvae of these seed weevils. Infestations appear to be more common in northern populations than in populations in southeastern Oregon and southern Idaho. The characteristically rotund, globose seeds on infected umbels are diagnostic both in the field and in herbarium specimens (Alexander & Whaley 3094 OSC; Otting 4541 SRP). No individuals of L. gravi or L. depauperatum in the field or on herbarium specimens were observed to have these seed predators. They likely exist, but at a rate low enough that infected individuals are rare. Individuals of L. klickitatense were also observed to have these rotund seeds, indicating the presence of a seed weevil. However, the number of infected seeds per umbel were low and most individuals observed were undamaged. Additionally, the larval instars of various stages of *P. indra* subsp. indra are also impacting individuals by defoliating the leaves. The impact on individuals is high in small Lomatium populations with many butterflies competing for egg laying sites. In large Lomatium populations, such as those along the Columbia River, the competition for egg laving sites is much lower and the effects of defoliation by larvae is likely negligible. Based on these data, a major contributing factor to the biomass and leaf diversity of *L. papilioniferum* is likely the impacts of variable environmental conditions (light, precipitation, competition for root space, competition from non-natives) at the microhabitat and ecoregional level combined with the variable effects of adult and larval herbivory, seed predation and parasitism on each individual in a population. These factors may be contributing to the observed variability of plant size, seed size, and leaf morphology in populations of L. papilioniferum. Further division of this species into varieties based on leaf or seed size characters is unjustifiable at this time.

Jones originally described this taxon as *Peucedanum grayi* var. *aberrans* M.E. Jones. Jones' name has priority at the varietal level if this taxon is delimited as a variety within *L. grayi*. This name was never used by him (annotations on specimens at RSA) nor are any of the syntypes determined with this varietal name. No specimens in the loan from RSA were identified in his hand as "type material" like most of his other types. Jones never made use of this varietal name when he completed his transfer of *Lomatium* species into *Cogswellia*. In addition, no subsequent authority recognized this taxon as anything other than a synonym of typical *L. grayi*. Jones' name required lectotypification herein in order to determine if the name should remain a synonym of *L. grayi* or be transferred as a synonym of *L. papilioniferum*.

APPENDIX 1

List of vouchers examined in this study for the morphometric analysis.

Lomatium depauperatum

U.S.A. Nevada. Elko Co.: Goshute Mountains, N of Spring Gulch, Holmgren & Holmgren 10347, -114.1982, 40.6011, (BRY, (IDS); Antelope Range, N side, Tiehm 9511, -114.4052, 40.1358, (BRY,IDS,RM); Pilot Peak, W side, Tiehm 10735, -114.0989, 41.0337, (BRY,IDS,RM); Utah. Beaver Co.: Wah Wah Mountains, Pine Grove, E of Pine Grove Reservoir, Goodrich & Hart 11200, -113.643, 38.341, (BRY); Wah Wah Mountains, E of head of Pine Grove, W head of Quartz Creek, Welsh 20518, -113.5743, 38.3353, (BRY). Box Elder Co.: Curlew Valley, Alderson s.n., 6 Jun 1964, -112.9836, 41.966, (WS); Camels Back Ridge, E side, Clark 5373, -112.945, 40.115, (BRY); Grouse Creek Mountains, eastern foothills, W of Bovine Spring, Dixon & Crabtree 113, -113.66, 41.5829, (BRY); Bovine Mountains, Devils Playground, Dixon 717, -113.66, 41.518, (BRY); Pilot Range, W side, S of Cove Springs, Fale s.n., June 13, 1973, -114.0332, 41.1094, (BRY); Pilot Range, Pilot Peak, E side, NW of Willow Canyon, Harper s.n., July 3, 1972, -114.0697, 41.0209, (BRY); Bovine Mountains, Holmgren & Holmgren 9225, -113.662, 41.4872, (BRY, RM);

Pilot Range, Patterson Pass, Holmgren & Holmgen 11110, -114.0124, 41.19, (BRY); Hansel Mountains, Lone Rock, S of Monument Point, *Johnson & Nufer 3694*, -112.8427, 41.6992, (BRY); Black Pine Mountains, southern foothills, Green Canyon, Cedar Creek Substation, *Neese 11585*, -113.1579, 41.9774, (BRY). **Juab Co.:** Canyon Mountains, Lyman Canyon, *Alexander & Whaley 3324*, -112.2105, 39.3534, (UVSC); Glison Mountains, mouth of Long Canyon, *Goodrich 15335*, -112.3002, 39.6081, (BRY); Desert Mountain, Desert Mountain Pass, *Goodrich 15335*, -112.5856, 39.7792, (BRY); Canyon Mountains, Leamington Canyon, E of Uisco Cement Plant, *Goodrich 15358*, -112.1859, 39.5633, (BRY); Drum Mountains, Black Boy Mine, *Goodrich 18388*, -113.0361, 39.571, (BRY); Canyon Mountains, Lyman Canyon, *Whaley & Mosess.n.*, 20 May 2004, -112.2105, 39.3534, (UVSC). **Millard Co.:** Drum Mountains, Black Boy Mine, *Alexander & Whaley 3326*, -113.0328, 39.5687, (UVSC); Pavant Valley, The Cinders, W of Flowell, *Atwood 10896*, -112.4612, 38.9812, (BRY); Cricket Mountains, N of Johnson Pass, *Atwood 23563*, -112.8681, 39.1026, (BRY); House Range, Sawtooth Canyon, E of Notch Peak, *Baird & Franklin 3269*, -113.3869, 39.1439, (BRY); Confusion Range, King Top, *Goodrich 12425*, -113.5338, 38.9879, (RM, 2 sheets); Canyon Mountains, Oak Creek Campground, *Goodrich 15325*, -112.2672, 39.3482, (BRY); Canyon Mountains, Buck Hollow, *Goodrich 15590*, -112.2268, 39.4011, (BRY); Leamington Canyon, Gilson Mountains, Jones s.n., 8 May 1911, -112.261, 39.5458, (RM); Wah Wah Mountains, Lawson Cove, W of Lawson Cove Reservoir, *Welsh & Chatterley 19523*, -113.4429, 38.6956, (BRY); Canyon Mountains, Leamington Pass, *Welsh 16598*, -112.2091, 39.5076, (BRY). **Tooele Co:** Grassy Mountain, *Alexander & Badeau 3360*, -113.15, 40.77, (OSC); Dugway Pass, Dugway Mountains, Jones s.n., 28 May 1891, -113.0834, 39.8557, (RM).

Lomatium grayi

U.S.A. Colorado. Archuleta Co.: Dry Gulch, E of the San Juan River, Weddle 13, -106.9549, 37.2994, (FS). Delta Co.: Youngs Peak, N of Crawford, Hartman & Taylor 56640, -107.6016, 38.7094, (RM); N of Youngs Peak, N of Crawford, Taylor 5102, -107.6119, 38.7249, (RM); Stevens Gulch, E of Fry Mesa, Taylor 6032, -107.6198, 38.8956, (RM). Dolores Co.: Dolores Canyon Overlook, Nelson 1451, -108.7912, 37.8093, (RM). Garfield Co.: Grand Hogback, Main Elk Creek, NW of New Castle, Hartman & Vanderhorst 24530, -107.5846, 39.6093, (RM); Willow Peak, E side, N of Glenwood Canyon, Hartman 24882, -107.115, 39.6674, (RM); Grand Hogback, Main Elk Creek, N of mouth of Deep Creek, Hartman 25868, -107.585, 39.697, (RM); Grand Hogback, Monument Peak, Hartman et al. 24655, -107.9266, 39.7169, (RM); Grand Hogback, West Rifle Creek, E of Monument Peak, N of Harris Reservoir, Hartman et al. 24705, -107.8855, 39.7209, (RM); Willow Peak, Willow Spring, Johnston & Lucas 1755, -107.154, 39.6501, (RM, 2 sheets); Glenwood Canyon, E of Glenwood Springs, Osterhout 4578, -107.3094, 39.5626, (RM); Glenwood Canyon, E of Glenwood Springs, Osterhout s.n., 23 Jun 1912, -107.3094, 39.5626, (RM); No Name Creek, N of Glenwood Canyon, Vanderhorst 264, -107.2869, 39.5714, (RM); Mitchell Creek, N of Glenwood Canyon, Vanderhorst 2700, -107.3572, 39.59, (RM); Roan Cliffs, S of Rio Blanco, Weber 3345, -107.956, 39.712, (RM). La Plata Co.: Los Pinos River, Bayfield, Baker 507, -107.6138, 37.2312, (RM); Los Pinos River, Ignacio, Goodding Sel 28-41, -107.6229, 37.1157, (RM). Mesa Co.: Book Cliffs, Cocoran Wash, W of Cocoran Peak, O Kane & Anderson 2352, -108.522, 39.323, (RM); Coon Hollow, SW of De Beque, W of the Colorado River, Peterson et al. 82-53, -108.2766, 39.3077, (RM). Moffat Co.: Douglas Mountain, Zenobia Peak, Ginter 1034, -108.8602, 40.6035, (FS); Wymore Gulch, E of Fortification Creek, Hartman 70521, -107.4408, 40.5934, (RM); Wymore Gulch, E of Fortification Creek, Hartman 70555, -107.4408, 40.5934, (RM); hill E of Fortification Creek, NE of Fortification Rocks, Hartman 70620, -107.5467, 40.7814, (RM); Dry Woman Canyon, S of the Yampa River, Neely 3979, -108.7412, 40.4576, (RM); Indian Water Canyon, S of East Cactus Flat, Neely 4051, -108.5749, 40.4321, (RM); Zenobia Basin, S of Douglas Mountain, Neely 4364, -108.8796, 40.6326, (RM); Blue Mountain, NE of Tanks Peak, O Kane 2732, -108.7549, 40.4385, (RM); Douglas Mountain, NW of Zenobia Basin, O'Kane 3095, -108.896, 40.6418, (RM); Douglas Mountain, S of Greystone, Peterson 491, -108.6713, 40.5683, (RM); Cold Spring Mountain, Beaver Basin, Porter 3918, -108.958, 40.9458, (RM); Blue Mountain Plateau, W of Stuntz Reservoir, Porter 4474, -109.0476, 40.4348, (RM). Montezuma Co.: Mancos River, E of Mancos, Baker et al. 80, -108.2705, 37.3515, (RM); Mancos Valley, W of Mancos, Osterhout 1887, -108.3085, 37.3483, (RM); Mesa Verde, ridge between Soda Canyon and East Fork of Little Soda Canyon, NE of the Far View Visitor Center, Schmoll 1578, -108.4728, 37.2728, (RM). Rio Blanco Co.: White River, Meeker, Osterhout 2719, -107.9326, 40.0347, (RM); SE of Dark Canyon Spring, SW of Segar Mountain, Sigstedt & O Kane 82-381, -108.1201, 39.881, (RM); Barcus Creek, Sigstedt & Popp 82-108, -108.4708, 40.0552, (RM); White River, NW of Burro Mountain, Vanderhorst 2485, -107.7009, 39.9497, (RM). San Miguel Co.: Bishop Canyon, NW of Egnar, Moore 4497, -108.9882, 37.9611, (RM). Idaho. Bannock Co.: Marsh Valley, W of the Portneuf River, S of Inkom, Atwood 9919, -112.2226, 42.7555, (BRY); Marsh Creek, W of McCammon, Davis 198, -112.2292, 42.6588, (IDS); Portneuf River, mouth of Rapid Creek, Davis s.n., 30 Apr 1932, -112.239, 42.8008, (IDS,RM). Bonneville Co.: Caribou Range, head of Peterson Creek, Holmgren & Holmgren 15540, -111.5705, 43.3708, (BRY); Caribou Range, Flatiron Hollow, NW of Palisades Reservoir, Holte et al. TNF-557, -111.3023, 43.38, (FS); Bridge Creek, E of Grays Lake, Phinney 42, -111.3453, 43.0267, (FS). Caribou Co.: Webster Range, Crow Creek, mouth of Camel Hollow, Holmgren & Holmgren 14878, -111.1322, 42.5861, (BRY); Grays Range, Henry Peak, E side, Holmgren & Marttala 5494, -111.379, 42.9297, (BRY, IDS); Blackfoot River, Enoch Valley, Holte & Glennon 5437, -111.4572, 42.9207, (IDS); Blackfoot River, Enoch Valley, Holte & Glennon 5454, -111.4572, 42.9207, (IDS). Onieda Co.: Malad Range, mouth of Twomile Creek, S of Malad City, Atwood & Corwin 9852, -112.2139, 42.16, (BRY); New Mexico. Rio Arriba Co. Carracas Rim, S of San Juan River, NW of Tio Quinto Canyon, Wilken & Painter 14718, -107.2751, 36.9845, (RM). Utah. Cache Co.: Bear River Valley, Richmond, Alderson s.n., 7 Jun 1964, -111.8121, 41.9545, (WS); Cache Valley, Logan, W of the mouth of Logan Canyon, C.P. Smith 1525, -111.7877, 41.7448, (RM); Cache Valley, Logan, W of the mouth of Logan Canyon, C.P. Smith 1553, -111.7877, 41.7448, (RM); Cache Valley, Logan, W of the mouth of Logan Canyon, C.P. Smith 1658, -111.7877, 41.7448, (RM); Cache Valley, N of Logan, Cronquist 536, -111.8264, 41.7667, (IDS); Cache Valley, N of Logan, Hart & Hunter 472, -111.8264, 41.7667, (WS); Cache Valley, N of Avon, Julander 105, -111.8136, 41.5351, (FS). Daggett Co.: Uinta Mountains, S of Tolivers Canyon, foothills SW of Browns Park, Thorne & Zupan 6290, -109.2086, 40.8648, (BRY). Davis Co.: Antelope Island, Alexander 3134, -112.23, 41.05, (UVSC); Antelope Island, Harms 448, -112.2229, 41.0291, (WS). Juab Co.: Wasatch Range, E of Mount Nebo, Salt Creek, N of the mouth of Red Creek, Goodrich 18740, -111.7144, 39.7725, (BRY); Wasatch Range, E of Mount Nebo, Salt Creek, N of the mouth of Red Creek, Goodrich 18740C, -111.7144, 39.7725, (BRY); East Tintic Mountains, Robinson [Lower Mammoth], W of Mammoth, Jones s.n., 26 Jun 1909, -112.1166, 39.9279, (RM); San Pitch Mountains, Chicken Creek, E of the mouth, Lewis 5236, -111.8178, 39.55, (BRY); Wasatch Range, E of Mount Nebo, Salt Creek, N of the mouth of Lunt Hollow, Thorne & Thorne 2466, -111.7104, 39.7589, (BRY). Millard Co.: Canyon Mountains, Lyman Canyon, Alexander & Whaley 3327, -112.2, 39.35, (UVSC); Church Mountains, E of Eightmile Canyon, Goodrich 13976, -112.2282, 39.1984, (BRY); Pavant Range, Big Hollow, Goodrich 16868, -112.2481, 38.7424, (BRY). Rich Co.: Bear River, E of Sage Creek Junction, Dorn 8632, -111.07, 41.7761, (RM); Sage Creek, W of Sage Creek Junction, Hartman 3095, -111.175, 41.7734, (RM); Crawford Mountains, S side, NE of Woodruff, Refsdal & Nelson 5082, -111.1056, 41.5465, (RM); Bear Lake, NE of Meadowville, Thorne & Thorne 1247, -111.3675, 41.8586, (BRY). San Juan Co.: La

Sal Mountains, Slaughter Flats, Slaughter Spring, Atwood & Thompson 8808, -109.3458, 38.4021, (BRY0132494); Pine Ridge, E of La Sal, Franklin 1682, -109.2013, 38.3316, (BRY); East Canyon, N of Piute Knoll, Heil & Porter 21808, -109.1547, 37.9491, (BRY); La Sal Mountains, South Mountian, Deer Creek, E of Pole Canyon trailhead, Schwan 6, -109.2223, 38.3661, (FS); La Sal Mountains, Hop Creek, E of Trough Draw, W of Trinity Canyon, Thompson s.n., early July 1981, -109.0983, 38.3784, (BRY). Sanpete Co.: Sanpete Valley, NE of Fairview, Jones 5548, 30 Jun 1894, -111.4119, 39.6437, (RM, 2 sheets); Wasatch Plateau, Diary Fork, S of VABM Sky High, Van Boskirk 45587, -111.3854, 39.9336, (FS). Sevier Co.: Pavant Range, Three Creeks Reservoir, Robinette 108, -112.4291, 38.621, (FS); Pavant Range, Meadow Creek, Miller & Leidig 207, -112.3052, 38.878, (FS). Summit Co.: West Fork Bear River, S of confluence with the Bear River, Goodman & Hitchcock 1556, -110.8579, 40.8526, (RM); Mill Creek, N of Lone Mountain, Goodman 394, -110.8459, 40.9942, (RM). Tooele Co.: Sheeprock Mountains, Vernon Creek, N of J Hill, Atwood 10699, -112.3476, 39.931, (RM); Rush Valley, E of Benmore, W of Vernon Creek, Frischknecht 8, -112.4018, 40.015, (FS); Oquirrh Mountains, Lake Point, Jones 1728, 20 May 1880, -112.2464, 40.6865, (RM, 2 sheets); Oquirrh Mountains, Lake Point, Jones s.n., 20 May 1880, -112.2464, 40.6865, (RM159743); Salt Mountain, W of Stansbury Mountains, Lewis 1122, -112.7143, 40.5486, (FS); Stansbury Mountains, West Canyon Trailhead, Schoemaker 3, -112.5725, 40.5915, (FS); Stansbury Mountains, Deadman Canyon, SW of the first main fork, Taye 927, -112.6236, 40.3789, (BRY). Uintah Co.: Mosby Mountain, E of Chicken Spring, W of Mosby Creek, Goodrich 14274, -109.8398, 40.6004, (BRY); Whiterocks River Canyon, mouth of Ralphs Canyon, Goodrich 4398, -109.9227, 40.5846, (BRY); Uinta Mountains, Whiterocks River Canyon, mouth of Ralphs Canyon, Graham 7805, -109.9227, 40.5846, (RM); Uinta Mountains, Deep Creek, SW of Pine Ridge, Neese 14115A, -109.7315, 40.555, (BRY); Uinta Mountains, Pine Ridge, W of Dry Fork, Neese et al. 14036, -109.7332, 40.5725, (BRY). Utah Co.: Provo Canyon, Davis 5136, -111.5584, 40.3645, (WS). Wyoming. Lincoln Co.: Sublette Range, S of Salt Canyon, Cramer et al. 6048, -111.0231, 42.3867, (RM); Bridger Creek, outcrop S of WY Highway 89, Dorn 3732, -111.0394, 41.7799, (RM); Salt River Range, S side of Anderson Canyon, NE of Afton, Fertig 14101, -110.905, 42.7453, (RM); Star Valley, 0.5 miles E of US 89 along Strawberry Creek, Harrison 157, -110.9825, 42.8863, (RM); Star Valley, 0.5 miles E of US 89 along Strawberry Creek, Harrison 546, -110.9823, 42.8865, (RM); Oyster Ridge, between Wheat Creek and Windy Gap, Hartman & Cramer 45630, -110.5226, 41.9865, (RM); Bridger Creek, W of Eli Hill, Nelson & Cramer 34745, -111.034, 41.7776, (RM); Hogsback Ridge, lower slopes on the SE end, E of Buckman Hollow, Nelson & Nelson 26326, -110.31, 42.2678, (RM); Sublette Range, confluence of Mill Creek and the South Fork of Mill Creek, Nelson 35768, -110.9372, 42.2045, (RM); Salt River Range/ Tunp Range, Smiths Fork, mouth of Hobble Creek, Nelson 35928, -110.855, 42.3794, (RM); Salt River Range, E of Afton, Payson & Armstrong 3328, -110.905, 42.7308, (RM); Oyster Ridge, Hams Fork, Refsdal & Refsdal 4791, -110.5286, 41.7531, (RM); Tunp Range, Grade Creek Road, 2 miles S of Nugent Park, Shultz & Shultz 2596, -110.7969444, 42.2013889, (RM). Sublette Co.: Bald Mountain, 21 air miles WNW of Big Piney, Cramer & Kellett 8975, -110.4618, 42.6728, (RM); North Cottonwood Creek, 7 air miles W of Halfway, Cramer 1168, -110.4792, 42.8006, (RM). Sweetwater Co.: Cedar mountain, 7 air miles N of McKinnon, Aldrich 170, -109.9326, 41.1219, (RM); Cedar Mountain, 11 air miles NNE of Burntfork, Dueholm 10309, -109.9528, 41.18, (RM); Upper Red Creek, 24 air miles E of Flaming Gorge Reservoir, Fertig & Studenmund 13586, -109.0722, 41.0642, (RM). Uinta Co.: Hickey Mountain, Dorn 3751, -110.2091, 41.0914, (RM); Evanston, Nelson 2979, -110.9794, 41.2628, (RM); Evanston, Nelson 4556, -110.9539, 41.2596, (RM); Bear River, Payson & Payson 4824, -111.02, 41.37, (WS); Evans Creek, W of the Blacks Fork, E of Bigelow Bench, Refsdal & Lathrop 795, -110.5358, 41.1633, (RM); Mill Creek, N of Utah State Line, Refsdal 289, -110.8602, 41.0048, (RM); Hinshaw Creek, Refsdal 4458, -110.7361, 41.3322, (RM); 3 miles S of Lonetree, Rollins 2301, -110.1516, 41.0193, (RM).

Lomatium klickitatense

U.S.A. Oregon. Hood River Co.: Columbia River, Hood River, *Alexander & Badeau 3312*, -121.513, 45.71, (OSC); Columbia River, W of mouth of Starvation Creek, Historic Columbia River Highway State Trail, *French 1891*, -121.6853, 45.6916, (OSC); Columbia River, Hood River, *Gilkey s.n.*, Apr 1939, -121.5542, 45.71, (OSC). Wasco Co.: Columbia River, Rock Creek, SW of Mosier, *Powne 201*, -121.4078, 45.682, (OSC); Columbia River, W of Mosier, *Soltis & Soltis 2208*, -121.4118, 45.6872, (WS3); **Washington. Klickitat Co.:** Klickitat River Canyon, Klickitat-Appleton Road, *Alexander & Whaley 3096*, -121.198, 45.8, (OSC); Klickitat River Canyon, SE of mouth of Sheep Canyon, *Brehm 2676*, -121.0769, 45.9244, (BRY,WS); Columbia River, turnoff to Horse Thief State Park, *Camp 3364*, -121.113, 45.64, (WTU); Columbia River, E of Bingen, W of Look Lake, *French & Brehm 1894*, -121.414, 45.6996, (BRY); Columbia River, 2 mi. east of Bingen, *French & Brehm 2342B*, -121.43, 45.7, (SRP); Klickitat River, along Glenwood Highway, *Giblin & Hahn 2617*, -121.114, 45.9463, (WTU); Little Klickitat River Canyon, W of mouth of Blockhouse Creek, *Grable 8643*, -120.9921, 45.8161, (WS); Little Klickitat River Canyon, mouth of Blockhouse Creek, *Grable 8661*, -120.9783, 45.819, (WS); Columbia River, E of Bingen, *Halse 3275*, -121.4982, 45.7256, (IDS,WS); Columbia River, White Salmon, Dock Grade, *Halse 3383*, -121.431, 45.7237, (RM); Klickitat River Canyon, N of Klickitat, *Hart 1068.1A*, -121.1051, 45.8751, (WS); Klickitat River Canyon, Stimpson Flats, *Simmons & Gilmartin 82-170*, -121.1103, 45.9286, (WS); Little Klickitat River Canyon, *Simmons et al. 84-302*, -121.0266, 45.8402, (WS); Columbia River, near Bingen, *Thompson 8156*, -121.4633, 45.715, (WTU8324).

Lomatium papilioniferum

British Columbia. Vancouver Island, Janszen s.n., 23 Aug 1984, -123.8, 49.07, (WS). U.S.A. Idaho. Ada Co.: Boise Valley, Davis s.n., 10 May 1936, -116.074, 43.509, (IDS); north tributary of Currant Creek along Cartwright Road, Boise Foothills, *Ertter & Shaffer 21722*, -116.231, 43.73, (SRP); empty flat, Idaho Fairgrounds, Boise, Hunnicutt 96-26, -116.233, 43.667, (SRP). Adams Co.: Blue Mountains, Rocky Comfort Flat, *Bent 11-20*, -116.7108, 44.9633, (BRY); Weiser River, Evergreen Campground, *Davis 4501*, -116.3872, 44.8927, (IDS, 2 sheets); Blue Mountains, Cuddy Mountains, Placer Creek, *Goff 11-45*, -116.7061, 44.816, (BRY); Blue Mountains, Snake River, N of mouth of Limepoint Creek, *Mansfield 11-432*, -116.7788, 45.0812, (BRY). Boise Co.: Idaho Highway 52, Payette River Canyon, W of Horseshoe Bend, *Alexander & Whaley 3084*, -116.2566, 43.9, (UVSC); Pleasant Valley, Sand Creek on Pleasant Valley Rd., *Ertter & Smithman 4233*, -116.2349, 43.3748, (CIC); Payette River, Grandjean, *Johnson 89*, -115.1692, 44.1614, (IDS). Canyon Co.: Big Willow, *Macbride 124*, -116.6778, 44.0438, (WS).
Elmore Co.: Boise Mountains, mouth of Little Rattlesnake Creek, *Pearse 190*, -115.6997, 43.5896, (FS); Boulder Mountains, Big Wood River, *Woods 50a*, -114.417, 43.789, (RM). Gem Co.: Sucker Creek, W of Squaw Butte, *Ertter 5694*, -116.488, 44.038, (RM); Jackass Gulch, SE of Emmett, *Ertter et al. 5851*, -116.469, 43.833, (RM); Bennett Hills, City of Rocks, Fourmile Creek, *Smith 6621*, -114.7699, 43.1285, (BRY); Black Canyon Reservoir, *Yensen & Tarifa 12-12*, -116.3783, 43.9416, (CIC). Gooding Co.: West Mountains, Second Fork, W of Sage Hen Reservoir, *Smith 4497*, -116.2584, 44.3188, (BRY); Jadabo Co.: mear American Bar, 0.5 miles below

Rice Creek Bridge over Salmon River, 14 air miles W of Grangeville, Riley 2062, -116.4061, 45.9043, (WS). Lincoln Co.: Timber Gulch, Mount Bennett Hills, Lewicki 75-17, -114.56, 43.13, (SRP). Nez Perce Co.: Spalding, Mastrogiuseppe 436, -116.8187, 46.4476, (WS); Clearwater River, 5 miles E of Lewiston, Meyer 1427, -116.8899, 46.4451, (WS); Clearwater River, mouth of Potlach Creek, Ownbey 2384, -116.7666, 46.4814, (WS). Owyhee Co.: Sawpit Creek, 1 mile south of Silver City, Baker 7870, -116.732, 43.002, (SRP); Owyhee Mountains, Jordan Valley-Silver City road, 19 km E of Jordan, Holmgren 10496, -116.6492, 43.0496, (WS). Valley Co.: Ponderosa State Park, Duft 1060, -116.0769, 44.9321, (CIC); Fourmile Creek, Fourmile Campground, Gray 9, -115.6727, 44.8558, (FS); E of Meadows, Mains 245, -116.206, 44.96, (RM); Ecks Flat, Meadows Summit, Miles 245, -116.18745, 44.95095, (FS). Washington Co.: Dead Indian Ridge, NW of Weiser, Davis 4481, -117.1618, 44.3127, (IDS); Snake River, NW of Henley Basin, Hartman & Handley 64329, -117.2094, 44.41968, (BRY); Monroe Creek, Jones s.n., 20 Apr 1900, -116.96, 44.2425, (WTU); Windy Ridge, Kleinschmidt Grade, E of Hells Canyon, Lewis 1266, -116.78, 45.0582, (FS4); Highway 95, 5 miles S of Midvale, Reisentz 57660, -116.8109, 44.4401, (WS); Crane Creek Road, Smith 7287, -116.5399, 44.3831, (SRP). Nevada. Elko Co.: Independence Mountains, North Fork California Creek, Crane 60, -115.9477, 41.4144, (FS); eastern ridge of Porter Peak, south of California Gulch, Mansfield & Carlson 9211b, -116.1101, 41.679, (CIC); east of Maggie Summit, Bull Run Mountains, Mansfield & Markin 8273, -116.0499, 41.678, (CIC); Independence Mountains, Jack Creek, Smith 11868, -116.001, 41.5489, (CIC); Independence Mountains, W of Jack Creek Campground, Whaley & Moses s.n., 19 May 2004, -116.0921, 41.5069, (UVSC). Oregon. Baker Co.: Burnt River, along the Snake River Road, E of Huntington, Alexander 3300, -117.23, 44.36, (OSC); Blue Mountains, Paddy Creek, W of McBride Campground, French 5071, -117.2936, 44.9684, (OSC); Blue Mountains, Bradley Creek Mine, Ridge E of East Fork Eagle Creek, W of mouth of Sullivan Creek, Head 785, -117.3626, 45.005, (OSC). Crook Co.: Cabin Ranger Station [Cow Cabin Barn], Mill Creek, mouth of Evans Creek, Ingram 219, -120.6633, 44.3917, (FS); Ochoco Mountans, SW of Ochoco Pass, Kruckeberg 2152, -120.4092, 44.4761, (RM); Ochoco Mountans, SW of Ochoco Pass, Kruckeberg 2152, -120.4092, 44.4761, (WS); Ochoco Mountains, Hamilton Butte, Peck 15973, -120.4436, 44.4554, (WILLU); Ochoco Mountains, Winter Butte, SE of the Ochoco Guard Station, Peck 17121, -120.3388, 44.3509, (WILLU); Ochoco Mountains, Paulina Creek, W of Ruby Butte, Wilson et al. 12327, -120.0135, 44.2355, (OSC). Gilliam Co.: Columbia River, E of the mouth of Phillipi Canyon, E of Quinton Station, Detling 4178, -120.4683, 45.687, (ORE); Columbia River, mouth of the John Day River, Henderson 14323, -120.6521, 45.7273, (ORE). Grant Co.: Blue Mountains, Case Ridge, SE of Dale, Hartman & Bradtke 70788, -118.9334, 44.9638, (BRY); Blue Mountains, Squaw Creek, NE of the confluence with Little Malheur River, Henderson 5189b, -118.2365, 44.229, (ORE); Strawberry Range, Wildcat Basin, Hinchliff 1393, -118.7335, 44.28, (OSC); One mile above Fields Creek, Buck Cabin Creek Trail, Kruckeberg 5440, -119.3, 44.35, (WTU); Blue Mountains, Canyon City, Peck 10184, -118.9515, 44.39, (WILLU). Hood River Co.: Columbia River, E of Mitchell Point, Clarke s.n., 15 Apr 1944, -121.6014, 45.705, (OSC); Columbia River, Mitchell Point, W side, French 1876, -121.6183, 45.7023, (OSC). Jefferson Co.: Lyle Gap, NE of Madras, Peck 26155, -121.0037, 44.7662, (WILLU). Malheur Co.: Succor Creek, mouth of Trimbly Creek, Crosby 1193, -117.1197, 43.4529, (OSC); Succor Creek, 1.5 miles N of campground, Halse 1494, -117.1272, 43.4818, (IDS,WS); Owyhee River, Watson, E of the mouth of Blue Canyon, Henderson 9266, -117.4085, 43.3053, (ORE); Barren Valley, mouth of Couch Creek, W of Crowley Guard Station, Joyal 845, -117.99, 43.2266, (OSC); Freezeout Creek, S of Freezeout Spring, Otting et al. 759, -117.5176, 43.6053, (OSC). Morrow Co.: Willow Creek, 1.5 miles E of Heppner, Grable 4404, -119.5232, 45.345, (WS); Willow Creek, 1.5 miles E of Heppner, Grable 4463, -119.5232, 45.3435, (WS). Multnomah Co.: Columbia River, Crown Point State Park, E of Corbett Station, Mackaness 2737, -122.3, 45.5396, (OSC). Sherman Co.: Columbia River, mouth of the John Day River, Henderson 5189a, -120.6521, 45.7273, (ORE); John Day River, W side, near the mouth, Hitchcock 20440A, -120.6542, 45.7269, (WS). Umatilla Co.: Walla Walla River, E of the mouth of Couse Creek, Boyd 16, -118.3481, 45.9043, (WS); Umatilla River, 2 miles S of Umatilla, Cronquist 5699, -119.3277, 45.8849, (WS); Lincton Mountain, Cash Hollow, S of the Walla Walla River, Fletcher 38, -118.3281, 45.8837, (RM); East Birch Creek, 7 miles SE of Pilot Rock, Grable 6290, -118.7693, 45.4035, (WS); Walla Walla River, mouth of Cash Hollow, Hansen 69, -118.3333, 45.8965, (WS); Blue Mountains, Umatilla River, E of Thoru Hollow, W of Gibbon, Hanson s.n., 9 May 1971, -118.4266, 45.6917, (OSC); Umatilla River, Barnhart, W of Pendleton, Henderson 839, May 1886, -118.9314, 45.6543, (ORE); Walla Walla River, E of the mouth of Couse Creek, James 10, -118.3479, 45.9038, (WS); Walla Walla River, 4 mi. E of Milton-Freewater, Johnson 5, -118.306, 45.8977, (WS); Pendleton, Jones s.n., 15 May 1905, -118.7957, 45.6591, (RM); Walla Walla River, 5 mi. E of Milton-Freewater, Lathrop s.n., 27 Mar 1951, -118.2771, 45.8864, (WS); Blue Mountains, Hay Creek, E of Weston, Leach 2821, -118.4133, 45.8172, (ORE); Blue Mountains, South Fork of the Umatilla River, SE of mouth of North Fork of the Umatilla River, Markow 11844, -118.1869, 45.7252, (RM); Lincton Mountain, Cash Hollow, S of the Walla Walla River, Ness 86, -118.3282, 45.8842, (WS); Walla Walla River, 2 mi. E of Milton-Freewater, N of Lincton Mountain, Taylor 14, -118.3248, 45.8968, (WS); Walla Walla River, mouth of Couse Creek, Thulon 6, -118.3671, 45.9073, (WS). Union Co.: Grande Ronde River, W of La Grande, Anderson 31, 28 May 1949, -118.1271, 45.344, (OSC); Blue Mountains, Spout Springs, Peck 22353, -118.0489, 45.7527, (WILLU); Blue Mountains, Dark Canyon, Flat Lake Lookout Tower [historical], W of Tucker Spring, Reid & Peterson 439, -118.4166, 45.3625, (FS); Blue Mountains, Dark Canyon, Flat Lake Lookout Tower [historical], W of Tucker Spring, Reid & Peterson 450, -118.4166, 45.3625, (FS). Wallowa Co.: Big Creek, near the head, Summit Ridge, S slope Wallowa Mountains, Cusick 1915, -116.7047, 45.3976, (WS); Imnaha River, Evergreen Forest Camp, Kruckeberg 3113, -117.0001, 45.1188, (WS); Wallowa Mountains, Lostine River Canyon, Leach 69, -117.4268, 45.397, (ORE); Marble Point; Frances Lake Trail, Mason 5213, -117.3847, 45.2898, (OSC); Wallowa Mountains, Buckhorn Spring, Peck 17318, -116.8441, 45.7545, (WILLU). Wasco Co.: Tygh Ridge, Butler Canyon, N of mouth of Oak Canyon, French 2053, -121.1867, 45.2805, (OSC); Columbia River, E of Mosier, Leach 2610, -121.3884, 45.6872, ORE); Columbia River, The Dalles, Lunell s.n., 10 May 1906, -121.2151, 45.6355, (RM, 2 sheets); Blue Mountains, W of Clarno, N of Hastings Peak, McNeal 2507, -120.6154, 44.9032, (BRY); Columbia River, E of The Dalles, Peck 14568, -121.0691, 45.6453, (WILLU); Tygh Ridge, head of Butler Canyon, Peck 26185, -121.1475, 45.3055, (WILLU); Columbia River, The Dalles, Sheldon 12127, -121.2151, 45.6355, (ORE); Columbia River, The Dalles, Thompson 10376, -121.2151, 45.6355, (WILLU); Tygh Valley, mouth of Butler Canyon, Winegar s.n., 20 April 1966, -121.19, 45.2591, (OSC). Wheeler Co.: John Day River, 13 miles W of Spray, Cronquist 6432, -119.8958, 44.8167, (WS); Blue Mountains, ridge N of Pine Creek, Cove Creek, S of The Cove, Joyal & Halpern 327, -120.3742, 44.9378, (OSC); Blue Mountains, E of Wheeler Point, W of Wheeler Creek, Markow 11871, -119.8561, 44.9557, (RM); John Day Valley, Spray, Thompson 11345, -119.7959, 44.8371, (WS); Washington. Asotin Co.: Grande Ronde River, N of mouth of Grouse Creek, Gitzendanner 77, -117.3812, 46.0008, (WS356611); Snake River, W of mouth of Clearwater River, Hart 336, -117.0634, 46.4309, (RM,WS 2 sheets); Megginson Gulch, W of the Snake River, Hitchcock & Samuel 2582, -117.3811, 46.4417, (RM); Anatone Butte, Jones 1917, -117.2546, 46.1099, (WS). Benton Co.: Cold Creek Valley, N of the Yakima River, Baird 604, -119.4451, 46.3921, (BRY); Rattlesnake Hills, S of Snively Basin, Baird 787, -119.709, 46.412, (BRY); Cold Creek, NE of the Yakima Ridge, SW of McGee Well, Baird 968, -119.78, 46.57, (BRY); Columbia River, White

Bluffs, Beattie 3960, -119.4785, 46.6647, (WS); Cold Creek Valley, N of Yakima River, Daubenmire 59102, -119.447, 46.3959, (WS); Cold Creek Valley, N of Yakima River, Daubenmire 59160, -119.447, 46.3959, (WS); Rattesnake Mountain, Hanford Site, Grable & Rickert 8704, -119.5694, 46.3779, (WS); Rattlesnake Creek, Hanford Site, O'Farrell & O'Farrell 71-1, -119.7166, 46.5, (WS); Columbia River, Hanford, St. John et al. 8118, -119.3871,46.5858, (WS). Chelan Co.: Columbia River, S of Chelan Falls, Ward 273, -120.003, 47.7832, (WS, WTU); Columbia River, Wenatchee, Whited s.n., 27 March 1900, -120.3287, 47.4539, (WS). Columbia Co.: Blue Mountains, Godman Spring, Constance et al. 1216, -117.784, 46.0987, (RM); Blue Mountains, between San Sousi Spring and Midway Spring, Kruckeberg 2500, -117.7588, 46.1762, (RM,WS); Blue Mountains, Table Rock, Kruckeberg 2527, -117.908, 46.031, (IDS,RM,WS). Douglas Co.: Columbia River, Badger Mountain, Thompson 14655, 1 June 1940, -120.2536, 47.5421, (WS). Franklin Co.: Columbia River, Taylor Flat, S of the mouth of Rankin Canyon, Baird 712, -119.2566, 46.4158, (BRY). Garfield Co.: Snake River, S side, E of Lower Granite Dam, Gitzendanner 51, -117.4253, 46.655, (WS); Huckleberry Butte vicinity, Pomeroy-Grouse Flat Road, Hitchcock & Muhlick 8316, -117.5844, 46.2371, (RM,WS). Grant Co.: Columbia River, Vernita Bridge, Schuler 42, -119.741, 46.6443, (WS); at junction of Crab and Wilson Creeks, Thompson 13709, -119.1207, 47.421, (WTU). Kittitas Co.: Columbia River, Vantage, Cook & Cook 364, -119.9891, 46.9446, (WS); Kittitas Valley, between Ellensburg and Kittitas, Eyerdam 1467, -120.4756, 46.9969, (WS); Kittitas Valley, Ellensburg, Thompson 11537, -120.5424, 46.9797, (WS); Bald Mountain, Thompson 14757, -120.95, 46.9666, (WS); Bald Mountain, Thompson 14824, -120.95, 46.9666, (WS); Kittitas Valley, Ellensburg, Whited 657, -120.5424, 46.9797, (WS). Klickitat Co.: Columbia River, mouth of Pine Creek, Cronquist 5663, -120.0889, 45.8014, (WS); Columbia Hills, W of Goodnoe Hills, Cronquist 5669, -120.5398, 45.7748, (WS); Columbia River, Maryhill, Cronquist 5676, -120.8271, 45.6875, (WS); Columbia Hills, Towal, Simmons 103, -120.6256, 45.7569, (WS); Columbia River, Bigen Gap, Bingen, Suksdorf 6420, 1 June 1909, -121.4586, 45.714, (WS); Columbia River, Bigen Gap, Bingen, Suksdorf 6420, 23 Mar 1909, -121.4586, 45.714, (WS); Columbia River, Bigen Gap, Bingen, Suksdorf 8140, 30 Mar 1899, -121.447, 45.706, (WS); Rock Creek, Thompson 17236, 12 April 1953, -120.4421, 45.7274, (WS230830). Okanogan Co.: Columbia River, N of Bridgeport, Fiker 2844, -119.6539, 48.003, (WS, 2 sheets). Skamania Co.: Columbia River, Cape Horn, Piper 5012, -122.1964, 45.5742, (WS). Spokane Co.: Riverside Park Cemetery, Spokane, Gage & Leyens 943, -117.458, 47.667, (WTU); Hangman Creek, Spokane, Sandberg & Leiberg 5, -117.4489, 47.6455, (WS). Stevens Co.: Columbia River, N of mouth of Spokane River, Rogers 395, -118.3367, 47.9193, (IDS,WS). Walla Walla Co.: Columbia River, mouth of Walla Walla River, Beattie 3915, -118.9091, 46.0533, (WS); Walla Walla Valley, College Place, Booth s.n., 9 April 1944, -118.3987, 46.0325, (WS); Walla Walla Valley, 2 miles S of Walla Walla, Hitchcock & Muhlick 8268, -118.3475, 46.0251, (WS); Walla Walla Valley, 7 miles E of Walla Walla, Lathrop s.n., 10 May 1951, -118.1769, 46.0793, (WS); Walla Walla Valley, 10 miles E of Walla Walla, Lathrop s.n., 10 May 1951, -118.1521, 46.0568, (WS, 3 sheets); Walla Walla Valley, NE of Walla Walla, Moore 20, -118.3025, 46.0887, (WS). Whitman Co.: Rock Lake, N of Ewan, Beattie & Lawrence 2370, -117.6261, 47.2216, (WS); Palouse River, Pullman, Cornwell s.n., 21 May 1975, -117.1903, 46.7328, (WS); Rock Creek, SW of Ewan, Cotton 957, -117.8389, 47.0829, (WS); Palouse River, Pullman, Elmer 77, -117.1903, 46.7328, (RM); Kamiak Butte, E of summit, Pine Ridge Trail, Fiely 107, -117.162, 46.864, (WS); Snake River, between Granite Point and Water Canyon, Huntley 850, -117.3086, 46.5829, (WS); Snake River, Granite Point, Karr 2, -117.3595, 46.6045, (WS); Snake River, E of Wilma, Keller 1, -117.1137, 46.4243, (WS); Snake River, MacMurry Canyon, N of Wawawai County Park, Kennedy s.n., 29 April 1981, -117.3783, 46.6454, (WS); Pullman, SE side, Magnuson 13, -117.1886, 46.7247, (WS); Snake River, 6 miles below Lewiston, Idaho, Parker 307, -117.1466, 46.4322, (WS); Snake River, SE of Granite Point, Phillips 1, -117.3541, 46.6017, (WS); Snake River, between VABM Truax and Granite Point, Pickett 220, -117.3382, 46.6019, (WS); Snake River, Wawawai, Piper s.n., 13 May 1893, -117.3755, 46.6368, (WS); Snake River, Wawawai County Park, Pubols 2, -117.3754, 46.6369, (RM); Wawawai Canyon, E of Wawawai County Park, Roeder 4, -117.3587, 46.6332, (WS); Palouse River, Pullman, Sharsmith 3957, -117.191, 46.7335, (WS); Palouse River, Palouse Falls, St. John & Pickett 6181, -118.2232, 46.6627, (WS); Wawawai Canyon, E of Wawawai County Park, Thompson s.n., 17 April 1981, -117.3428, 46.6288, (WS); Dry Creek, S of Steptoe, Vasey s.n., -117.3339, 46.9531, (WS, 2 sheets); Snake River, NE of Silcott Island, Wakefield 631, -117.1659, 46.4288, (WS). Yakima Co.: Yakima, Henderson s.n., 29 May 1892, -120.5631, 46.6173, (WS); Columbia River, SE of Priest Rapids, Mastrogiuseppe 1680, -119.908, 46.6341, (WS); American Ridge, Bumping River, Soda Springs Campground, Nielsen s.n., 17 July 1970, -121.2182, 46.9269, (WS); Toppenish Ridge, head of North Fork of Dry Creek, Thompson 17518, 22 May 1953, -120.88, 46.2218, (WS).

Other specimens cited but not included in the morphometric analysis.—U.S.A. California. Modoc Co.: east side of Surprise Valley, west of Sand Creek, *Bartholomew 2729*, -120.0482, 41.5774, (RENO,UC). Oregon. Gilliam Co.: Columbia River Gorge, S of the Philippi Canyon Exit of I-80, *Alexander & Whaley 3094*, (OSC). Wasco Co.: Columbia Basin, 6 air mi. NE of The Dalles, *Otting 4541*, -121.07, 45.64, (SRP).

APPENDIX 2

Essential oils found in each species examined in the combined chemical analyses. LGA = Lomatium grayi; LD= Lomatium depauperatum; LK = Lomatium klickitatense; LB = Lomatium brandegeei; LE = Lomatium eastwoodiae; LGR = Lomatium graveolens; LH1 = population 1 of Lomatium howellif; LH2 = population 2 of Lomatium howellif; LJ = Lomatium junceum; LP = Lomatium parryf; LR = Lomatium rigidum; LS = Lomatium scabrum. RI = Kovats retention indices. Codes by the numbered rows refer to the reference source that first reported the compound within the taxa. * = Dev et al. 2007; > = Beauchamp et al. 2009; ^ = Dev et al. 2010.

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ID#	Chemical	RI(obs)	LGA	LD	LK	LB	LE	LGR	LH1	LH2		LP	LR	LS
>*1	furfural	835-836	1	0	1	0	0	0	1	-	0	1	0	0
^2	ethyl 2-methyibutyrate	854	0	0	0	0	0	0	0	0	0	0	0	0
>*^3	(E)-2-hexenal	856-857	-	-	-	0	-	-	-	-	0	-	-	0
>4	(Z)-3-hexenol	859	0	0	0	0	0	0	0	0	0	1	0	0
>5	heptanal	904	0	0	0	0	0	0	1	-	0	0	0	0
9v*	isobutyl isobutyrate	921	1	1	1	0	0	0	0	0	0	0	0	0
>7	tricyclene	925	0	0	0	0	0	0	0	0	1	0	0	0
>*^8	alpha-thujene	931-932	1	1	-	-	0	1	-	0	-	0	1	0
6v*<	alpha-pinene	937-938	1	-	-	-	-	٦	-	-	-	-	1	-
>*^10	camphene	952-953	0	0	1	1	1	1	1	1	1	1	1	1
A11	benzaldehyde	963	0	0	0	0	0	0	0	0	0	0	0	0
>*^12	sabinene	976-978	1	1	-	-	1	0	0	0	1	-	1	0
>13	heptanol	977	0	0	0	0	0	0	0	-	0	0	0	0
>*^14	beta-pinene	978-979	-	-	-	-	-	-	-	-	-	-	1	-
>15	dehydro-1,8-cineole	066	0	0	0	0	-	0	0	0	0	0	0	0
>*^16	myrcene	992-993	-	-	-	-	-	-	-	-	-	-	1	-
>17	furfuryl methyl sulfide	1000	0	0	0	0	1	0	0	0	0	0	0	0
>*^18	al pha-phellandrene	1002	1	1	1	1	1	1	0	0	1	1	1	1
>*^19	isobutyl 2-methylbutyrate	1003-1005	-	0	0	0	0	-	0	0	0	0	1	-
>20	octanal	1004	0	0	0	0	0	0	-	-	-	0	0	0
>*21	isobutyl isovalerate	1007-1013	-	0	-	0	0	-	0	0	0	0	0	0
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5		(coo)ui	j,	j	Ĺ	;	;	5	;	LI 12	נ	1	i.]
^ 22	isobutyl 3-methylbutyrate	1009	0	0	0	0	0	0	0	0	0	0	0	0
>*23	isosylvestrene	1008-1009	1	1	-	0	-	0	0	0	0	0	0	0
^24	delta-3-carene	1010	0	0	0	0	0	0	0	0	0	0	0	-
^25	(E)-2-hexenyl acetate	1011	0	0	0	0	0	0	0	0	0	0	0	-
>*^26	alpha-terpinene	1015-1017	-	-	-	-	-	-	0	0	-	0	0	0
*^27	2-methylbutyl isobutyrate	1020-1021	-	-	0	0	0	0	0	0	0	0	0	0
>*^28	p-cymene	1025-1027	1	1	1	1	-	1	-	1	1	1	1	1
>*^29	beta-phellandrene	1031	1	1	-	-	-	-	-	1	1	1	1	1
>*^30	limonene	1031	1	1	1	0	-	-	1	1	1	1	1	1
^31	1,8-cineole	1034	0	0	0	0	0	0	0	0	0	0	0	0
>32	benzyl alcohol	1038	0	0	0	0	0	0	-	1	0	0	0	0
>*^33	(Z)-beta-ocimene	1042-1043	1	1	1	0	-	-	-	1	1	1	1	1
>*34	phenylacetaldehyde	1045-1046	0	0	1	0	0	-	1	1	0	0	0	0
*^35	butyl 2-methylbutyrate	1048	1	1	-	0	0	0	0	0	0	0	0	1
>*^36	(E)-beta-ocimene	1052-1054	1	1	-	1	-	1	1	1	1	1	1	1
>*^37	isobutyl angelate	1057-1058	1	0	0	0	0	1	0	0	0	0	1	0
>*^38	gamma-terpinene	1061-1062	1	1	-	1	1	1	1	1	1	0	1	1
*39	isoamyl butyrate	1064	1	0	0	0	0	0	0	0	0	0	0	0
>40	octanol	1068	0	0	0	0	0	0	-	1	0	0	0	0
^41	cis-sabinene hydrate	1070	0	0	0	0	0	0	0	0	0	0	0	0
^42	cis-linalool oxide (furanoid)	1076	0	0	0	0	0	0	0	0	0	0	0	0
>*43	trans-linalool oxide (furanoid)	1076	1	0	0	0	0	0	0	0	0	1	0	0
>44	p-cresol	1079	0	0	0	0	-	0	0	0	0	0	0	0

APPENDIX 2 cont.

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APPENDIX 2 cont.

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ID#	Chemical	RI(obs)	LGA	ΓD	LK	LB	LE	LGR	LH1	LH2		LP	LR	LS
>^45	m-cresol	1076-1081	0	0	0	1	0	0	0	0	0	-	0	0
*^46	butyl angelate (A)	1083	1	1	1	0	0	0	0	0	0	0	1	0
>47	p-mentha-2,4(8)-diene	1087	0	0	0	0	0	0	0	0	1	-	0	0
>48	p-cymenene	1088	0	0	0	0	0	0	1	1	0	0	0	0
>*^49	terpinolene	1088	1	1	1	1	1	1	1	1	0	0	1	1
>*50	isobutyl tiglate	1093-1094	1	0	0	-	0	0	0	0	0	0	0	0
>51	2-nonanone	1094	0	0	0	0	0	0	0	0	1	0	0	0
^52	6,7-epoxymyrcene	1094	0	0	0	0	0	0	0	0	0	0	0	0
>^53	6-camphenone	1095-1096	0	0	0	0	0	0	1	1	0	0	1	0
>*^54	linalool	1100	1	1	1	1	-	1	1	-	1	-	1	0
^55	3-methylbutyl 2-methylbutanoate	1102	0	0	0	0	0	0	0	0	0	0	1	0
>56	nonanal	1104	0	0	0	0	1	0	0	0	0	0	0	0
*57	2-methylbutyl 2-methylbutyrate	1105	1	1	1	0	0	0	0	0	0	0	0	0
>*58	isoamyl isovalerate	1105-1110	1	1	1	-	0	1	1	-	1	0	0	0
^59	2-methylbutyl 2-methylbutanoate	1106	0	0	0	0	0	0	0	0	0	0	-	1
√60	3-methylbutyl 3-methylbutanoate	1107	0	0	0	0	0	0	0	0	0	0	0	0
>61	p-mentha-1,3,8-triene	1107	0	0	0	0	1	0	0	0	1	0	0	0
>62	2-methylbutyl isovalerate	1111	0	0	0	0	0	-	0	0	0	0	0	0
√63	2-methylbutyl 3-methylbutanoate	1112	0	0	0	0	0	0	0	0	0	0	1	0
>64	heptyl acetate	1116	0	0	0	0	0	0	0	1	0	0	0	0
>*^65	dehydrosabina ketone	1122	1	-	-	-	1	1	0	0	0	-	-	-
*66	butyl-angelate (B)	1125	-	-	0	0	0	0	0	0	0	0	0	0
>67	trans-rose oxide	1130	0	0	0	0	0	0	0	0	1	0	0	0

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ID#	Chemical	RI(obs)	LGA	LD	LK	LB	ĽE	LGR	LH1	LH2	П	LP	LR	LS
>*68	(E,Z)-allo-ocimene (neo-alloocimene	1132-1136	0	1	0	0	0	0	0	0	0	1	0	1
>69	trans-pinovarveol	1137	0	0	0	0	0	0	0	0	Ļ	0	0	0
>*^70	(E,E)-allo-ocimene (alloocimene)	1132-1142	0	-	0	0	0	0	0	0	0	-	0	-
>^71	camphor	1144-1146	0	0	-	0		0	0	1	0	0	-	0
^72	3-methyl-2-buten-1-yl 2-methylbutyrate	1146	0	0	0	0	0	0	0	0	0	0	0	0
>73	neoisopulegol	1147	0	0	0	0	-	0	0	0	0	0	0	0
>74	trans-verbenol	1153	0	0	0	0	0	0	-	0	0	0	0	0
*^75	hexyl isobutyroate	1153	1	1	0	0	0	0	0	0	0	0	0	0
^76	isoamyl angelate	1154	0	0	0	0	0	0	0	0	0	0	1	0
>77	3-methyl-2-butenyl isovalerate	1154	0	0	0	0	0	-	0	0	0	0	0	0
^78	citronellal	1155-1157	0	0	0	0	-	0	0	1	0	0	1	1
۰79	2-methylbutyl angelate	1158	0	0	0	0	0	0	0	0	0	0	1	0
*80	pentylbenzene + 1-pentyl-1,3-cyclohexadiene	1160	-	0	1	0	0	0	0	0	0	0	0	0
>81	(E)-2-nonenal	1163	0	0	0	0	0	0	1	1	0	0	0	0
>82	pinocarvone	1164	0	0	0	0	0	1	0	0	1	0	0	0
>83	2-decanone isomer	1166	0	0	0	0	0	0	0	0	1	0	0	0
>84	1,4-dimethoxy-benzene	1166	0	0	0	0	0	0	0	0	0	-	0	0
>^85	borneol	1167-1168	0	0	0	0	1	0	0	1	0	1	1	0
>86	p-menth-1,5-dien-8-ol	1169	0	0	0	0	-	0	0	0	0	0	0	0
^87	lavandulol	1171	0	0	0	0	0	0	0	0	0	0	0	0
*^88	terpinen-4-ol (4-terpineol)	1176-1179		1	0	1	1	1	1	1	1	1	1	0
^89	viridine	1178	0	0	0	0	0	0	0	0	0	0	0	0
06v	naphthalene	1181	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 2 cont.

cont.	
PENDIX 2	
ΑF	

ID#	Chemical	RI(obs)	LGA	ΓD	LK	LB	LE	LGR	LH1	LH2		П	LR	LS
>91	p-methyl-acetophenone	1182	0	0	0	0	0	0	0	0	0	-	0	0
*92	thuj-3-en-10-al	1184	1	1	-	0	0	0	0	0	0	0	0	0
>^93	p-cymene-8-ol	1185-1186	0	0	0	0	0	0	-	-	0	-	0	0
>*^95	cryptone	1184-1188	-	-	-	0	-	-	0	0	0	-	-	-
96v*	amyl angelate (C)	1187-1190	-	-	0	0	0	0	0	0	0	0	-	0
>*^97	alpha-terpineol	1191-1192	-	-	-	0	-	-	-	-	-	-	-	-
>98	methyl salicylate	1192	0	0	0	0	0	0	0	0	0	1	0	0
>99	myrtenal	1194	0	0	0	0	0	0	0	0	-	0	0	0
>100	(Z)-4-decenal (cis-4-decenal)	1195	0	0	0	0	0	0	0	0	0	1	0	0
^101	(E)-4-decenal (trans-4-decenal)	1194	0	0	0	0	0	0	0	0	0	0	0	0
*^102	2-methylbutyl tiglate	1197-1200	1	0	0	0	0	1	0	0	0	0		0
>*^103	methyl chavicol	1196-1200	0	1	1	0	0	1	-	0	1	1	1	0
^104	(Z)-undecenal	1195	0	0	0	0	0	0	0	0	0	0	0	0
^105	4-methylpentyl 2-methylbutyrate	1201	0	0	0	0	0	0	0	0	0	0	-	0
^106	gamma-ter pineol	1202	0	0	0	0	0	0	0	0	0	0	0	0
>^107	decanal	1207	0	1	0	0	0	0	1	-	0	0	0	0
>*108	octyl acetate	1214	-	0	-	-	0	0	-	-	0	0	0	0
>109	trans-carveol	1220	0	0	0	0	-	0	0	0	0	0	0	0
>^110	citronellol	1228-1231	0	0	0	1	1	1	1	1	1	1	1	-
>*^111	methyl thymol (thymol methyl ether)	1236-1237	1	0	0	1	1	0	0	0	0	0	0	0
>*112	hexyl 2-methylbutyrate	1239-1240	-	-	0	0	0	0	-	-	0	0	0	0
^113	neral	1241	0	0	0	0	0	0	0	0	0	0	0	0
^114	cuminal	1242	0	0	0	0	0	0	0	0	0	0	-	0

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	Chemical	RI(obs)	LGA	D	LK	LB	LE	LGR	LH1	LH2	ב	Ч	LR	LS
*115	hexyl isovalerate	1244	1	-	0	0	0	0	0	0	0	0	0	0
>*^116	methyl carvacrol (carvacrol methyl ether)	1245	1	1	0	1	0	0	0	0	0	0	0	0
^117	hexyl 3-methylbutyrate	1247	0	0	0	0	0	0	0	0	0	0	0	0
>^118	carvone	1247	0	0	0	0	-	0	0	0	-	0	-	0
>*^119	piperitone	1254-1257	0	0	1	0	1	0	1	0	0	0	1	0
>120	linalyl acetate	1258	0	0	0	0	-	0	0	1	0	-	0	0
^121	geraneol	1258	0	0	0	0	0	0	0	0	0	0	0	1
^122	linalool acetate	1258	0	0	0	0	0	0	0	0	0	0	0	0
>123	(Z)-4-decenol	1260	0	0	0	0	0	0	0	0	0	1	0	0
>124	2-undecanone isomer	1261	0	0	0	0	0	-	0	0	1	0	0	0
>125	(E)-2-decenal	1264	0	0	0	0	0	0	0	Ļ	0	0	0	0
^126	methyl citronellate	1264	0	0	0	1	0	0	0	0	1	1	-	0
^127	geranial	1274	0	0	0	0	0	0	0	0	0	0	0	0
^128	citronelly formate	1275	0	0	0	0	0	0	0	0	0	0	0	0
>129	p-menth-1-en-7-al	1276	0	0	0	0	1	0	0	0	0	0	0	0
>130	decanol	1277	0	0	0	0	0	0	0	1	0	0	0	0
^131	dihydrolinalool acetate	1277	0	0	0	0	0	0	0	0	0	0	-	0
^132	p-menth-1-en-7-al	1277	0	0	0	0	0	0	0	0	0	0	0	1
>^133	alpha-terpinen-7-al	1283-1285	0	0	0	-	0	0	0	0	0	0	-	0
>*^135	(E) -an ethole	1286-1290	1	1	1	0	0	1	0	1	1	0	0	0
*136	indole	1287	0	0	1	0	0	0	0	0	0	0	0	0
>*^137	bornyl acetate	1288	1	1	1	0	0	1	0	1	0	1	-	-
^138	C6H11-angelate/tiglate	1289	0	0	0	0	0	0	0	0	0	0	-	0

APPENDIX 2 cont.

APPENDIX 2 cont.

			AFF	AFFENUIA Z CUTIL	cont.									
HD#	Chemical	RI(obs)	LGA	LD	LK	LB	LE	LGR	LH1	LH2	П	LP	LR	LS
^140	(Z,Z,Z)-3,6,9-tridecatriene	1291	0	0	0	0	0	0	0	0	0	0	1	0
>141	p-cymen-7-ol	1291	0	0	0	0	0	0	0	0	0	1	0	0
>*^142	lavandulyi acetate	1292-1294	0	-	0	0	1	1	1	0	0	1	0	1
*143	thymol	1293	0	0	1	0	0	0	0	0	0	0	0	0
>144	2-undecanone	1294	0	0	0	0	0	1	0	0	1	0	0	0
>145	benzyl isobutyrate	1296	0	0	0	0	0	0	0	0	0	1	0	0
>146	trans-pinocarvyl acetate	1298	0	0	0	0	0	0	0	0	0	1	0	0
*^147	carvacrol	1300-1302	0	0	1	0	0	0	0	0	0	0	0	0
^148	undecanal	1306	0	0	0	0	0	0	0	0	0	0	0	0
^149	4-methylhexyl 2-methylbutanoate	1307	0	0	0	0	0	0	0	0	0	0	1	0
>*150	2-methoxy-4-vinyl phenol	1312-1315	0	0	1	0	1	0	0	1	0	0	0	0
>151	nonyl acetate	1313	0	0	0	0	0	0	0	1	0	0	0	0
>152	cis-pinocarvyl acetate	1314	0	0	0	0	0	0	0	0	0	1	0	0
^153	neoiso-pulegyl acetate	1314	0	0	0	0	0	0	0	0	0	0	0	0
^154	p-vinyl guaiacol	1314	0	0	0	0	0	0	0	0	0	0	0	0
^155	(E,E)-2,4-decadienal	1322	0	0	0	0	0	0	0	0	0	0	0	0
*156	C6H13-angelate (D)	1322	1	1	0	0	0	0	0	0	0	0	0	0
^157	myrtenyl acetate	1334	0	0	0	0	0	0	0	0	0	0	0	0
^158	3-oxo-p-menth-1-en-7-al	1336	0	0	0	0	0	0	0	0	0	0	-	0
>159	heptyl 2-methylbutyrate	1337	0	0	0	0	0	0	0	1	0	0	0	0
>^160	trans-carvyl acetate	1339	0	0	0	0	1	0	0	0	0	0	0	0
^161	alpha-cubebene	1348	0	0	0	0	0	0	0	0	0	0	0	0
>162	alpha-longipinene	1352	0	0	0	0	0	0	0	-	0	0	0	0

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ID#	Chemical	RI(obs)	LGA	D	LK	LB	LE	LGR	LH1	LH2		LP	LR	LS
>163	citronellyl acetate	1354	0	0	0	1	1	1	1	1	0	1	0	0
^164	eugenol	1360	0	0	0	0	0	0	0	0	0	0	0	0
>165	2-dodecanone isomer	1367	0	0	0	0	0	0	0	0	1	0	0	0
^166	cyclosativene	1370	0	0	0	0	0	0	0	0	0	0	-	0
^167	longicyclene	1372	0	0	0	0	0	0	0	0	0	0	0	0
>168	methyl p-anisate	1374	0	0	0	1	0	0	0	0	0	0	0	0
>*^169	alpha-copaene	1376-1378	0	-	0	0	0	1	1	1	0	1	1	-
>^170	daucene	1380-1382	0	0	0	0	0	0	0	0	0	1	0	0
>^171	beta-bourbonene	1385-1388	0	0	0	1	1	0	0	-	0	-	-	-
*^172	beta-cubebene	1386-1388	0	-	0	0	0	0	0	0	0	0	0	0
>173	benzyl 2-methylbutyrate	1387	0	0	0	0	0	1	0	0	0	1	0	0
>174	benzyl isovalerate	1390	0	0	0	0	0	0	0	-	0	0	0	0
>*^175	beta-elemene	1391-1393	-	-	-	1	1	0	-	-	0	-	-	-
>176	2-dodecanone	1395	0	0	0	0	0	0	0	0	1	0	0	0
>177	2-phenyethyl isobutyrate	1395	0	0	0	0	0	0	0	0	0	1	0	0
>178	(Z)-jasmone	1397	0	0	0	0	0	0	0	0	0	1	0	0
>179	vanillin	1398	0	0	0	0	0	0	0	-	0	0	0	0
>^180	methyl eugenol	1400-1407	0	0	0	0	0	1	0	0	1	0	1	0
>181	italicene	1406	0	0	0	0	1	0	0	0	0	1	0	0
>182	longifolene	1406	0	0	0	0	0	0	0	0	0	0	0	0
>^183	dodecanal	1409	0	0	0	0	1	0	0	1	1	1	0	0
>184	decyl acetate	1411	0	0	0	0	0	0	-	-	0	0	0	0
>185	alpha-gujunene	1412	0	0	0	0	0	0	0	0	0	0	0	0

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APPENDIX 2 cont.

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APPENDIX 2 cont.

ID#	Chemical	RI(obs)	LGA	LD	LK	LB	LE	LGR	LH1	LH2		LP	LR	LS
^186	beta-ylangene	1419	0	0	0	0	0	0	0	0	0	0	0	0
>*^187	beta-caryophyllene	1420-1422	1	-	1	-	1	1	1	1	1	1	1	1
>188	lavandulyl isobutyrate	1428	0	0	0	0	-	0	0	0	0	0	0	0
>^189	beta-copaene	1430-1432	0	0	0	0	0	0	0	0	0	1	1	1
>190	beta-gurjunene	1431	0	0	0	0	0	0	0	-	0	0	0	0
>*191	gamma-elemene	1436-1441	0	0	-	-	0	0	0	-	-	-	0	0
^192	alpha-guaiene	1438	0	0	0	0	0	0	0	0	0	0	0	0
>193	trans-alpha-bergamotene	1435	0	0	0	0	0	1	0	1	0	0	0	0
*194	thujopsene	1436	0	0	1	0	0	0	0	0	0	0	0	0
>195	octyl 2-methylbutyrate	1437	0	0	0	0	0	0	1	1	0	0	0	0
>^196	2-methylbutyl benzoate	1439-1442	0	0	0	0	0	0	0	0	1	0	1	0
>^197	aromadendrene	1440-1448	0	0	0	-	0	0	0	0	0	0	0	0
>198	citronellyl propionate	1450	0	0	0	0	0	0	0	1	0	0	0	0
>*^199	alpha-humulene	1453-1457	-	-	-	-	-	-	-	-	-	-	1	1
>*^200	(E)-beta-farnesene	1459	0	1	0	0	0	0	-	1	0	1	1	0
>201	2-tridecanone isomer	1461	0	0	0	0	0	-	0	0	-	0	0	0
>202	dehydro-aromadendrane	1463	0	0	0	0	1	0	0	0	0	0	0	0
>^203	cis-muurola-4(14),5-diene	1466-1468	0	0	0	0	-	0	0	0	0	0	0	0
>*204	gamma-decalactone	1470-1471	0	1	1	1	0	0	0	0	0	0	0	0
>205	ethyl (E,Z)-2,4-decadienoate	1472	0	0	0	0	0	0	0	0	1	0	0	0
>206	7-epi-1,2-dehydrosesqui cineole	1474	0	0	0	-	0	0	0	0	0	-	0	0
^207	4,5-die pi-aristolochene	1474	0	0	0	0	0	0	0	0	0	0	0	0
^208	trans-cadina-1(6), 4-diene	1477	0	0	0	0	0	0	0	0	0	0	0	0

			APPE	APPENDIX 2 cont.	cont.									
ID#	Chemical	RI(obs)	LGA	ΓD	LK	LB	LE	LGR	LH1	LH2		LP	LR	LS
^ 209	beta-chamigrene	1477	0	0	0	0	0	0	0	0	0	0	0	0
>*^210	gamma-muurolene	1478-1480	0	1	1	1	1	1	1	1	0	1	1	1
^211	amorpha-4,7(11)-diene	1481	0	0	0	0	0	0	0	0	0	0	0	0
>*^212	germacrene D	1483-1484	1	1	1	1	1	0	1	1	0	1	0	1
^213	citronellyl isobutyrate	1484	0	0	0	0	0	0	0	0	0	0	0	0
>*^214	beta-selinene	1487-1488	0	0	-	1	1	0	0	0	1	0	0	0
>*^215	ar-curcumene	1484-1489	0	-	0	0	0	0	-	-	0	0	0	0
*^216	(E)-beta-ionone	1490	0	0	1	0	0	0	0	0	0	0	1	0
>217	trans-muurola-4(14),5-diene	1491	0	0	0	1	0	0	0	0	0	0	0	0
>^218	benzyl tiglate	1493	0	0	0	0	0	-	0	0	0	0	1	0
*219	delta-selinene	1493	0	0	1	0	0	0	0	0	0	0	0	0
^220	2-phenylethyl 3-methylbutanoate	1493	0	0	0	0	0	0	0	0	0	0	1	0
^221	valencene	1495	0	0	0	1	0	0	0	0	0	0	1	0
>^222	zingiberene (alpha-zingiberine)	1495-1496	0	0	0	0	0	0	0	1	0	0	0	0
>223	2-tridecanone	1496	0	0	0	0	0	1	0	0	1	0	0	0
>^224	al pha-selinene	1496	0	0	0	0	0	0	0	0	0	-	0	0
*226	delta-decalactone	1497	0	0	-	0	0	0	0	0	0	0	0	0
>^227	viridoflorene	1497-1500	0	0	0	0	0	0	0	-	0	0	0	0
>228	isodaucene	1500	0	0	0	0	0	0	0	0	0	-	0	0
>*^229	bicyclogermacrene	1498-1500	1	1	0	1	1	1	0	0	0	1	1	1
>^230	alpha-muurolene	1500-1501	0	0	0	-	-	0	0	0	0	-	-	-
*^231	alpha-cuprenene	1502-1510	0	-	0	0	0	0	0	0	0	0	0	0
>*^232	germacrene A	1505-1507	-	-	-	-	-	0	0	0	0	-	-	-

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ID#	Chemical	RI(obs)	LGA	LD	LK	LB	LE	LGR	LH1	LH2		LP	LR	LS
>*^233	(E,E)-alpha-farnesene	1507-1509	0	1	0	0	0	1	0	1	1	0	0	0
>234	beta-bisabolene	1508	0	0	0	0	0	0	1	0	0	1	0	0
>235	lavandulyl isovalerate	1510	0	0	0	0	-	0	0	0	0	0	0	0
>236	delta-amorphene	1510	0	0	0	-	0	0	0	0	0	0	0	0
>^237	lavandulyl 2-methylbutyrate	1512	0	0	0	0	-	0	0	0	0	0	0	0
>^238	gamma-cadinene	1515-1516	0	0	0	-	0	0	0	-	0	-	0	-
^239	(Z)-gamma-bisabolene	1516	0	0	0	0	0	0	0	0	0	0	0	0
*240	beta-sesquiphellandrene	1521	1	1	0	0	0	0	0	0	0	0	0	0
>*^241	delta-cadinene	1523-1526	1	1	0	1	1	1	1	1	0	1	1	1
^242	citronellyl butyrate	1532	0	0	0	1	0	0	1	0	0	0	0	0
^243	trans-cadina-1 (2),4-diene	1534	0	0	0	-	0	0	-	0	0	0	0	-
^244	kessane	1538	0	0	0	0	0	-	0	0	0	0	0	0
>^245	alpha-cadinene	1540-1541	0	0	0	1	1	0	0	1	0	1	0	1
>246	alpha-calacorene	1546	0	0	0	0	0	0	1	1	0	0	0	0
>247	elemol	1552	0	0	0	0	0	0	0	0	1	0	0	0
>*^248	germacrene B	1560-1561	1	1	1	1	1	0	1	1	1	1	0	1
>^249	(E)-nerolidol	1564-1566	0	0	0	0	0	0	1	1	0	0	0	0
>250	(E)-isoelemicin	1568	0	0	0	0	0	0	0	0	-	0	0	0
>251	2-tetradecanone isomer	1576	0	0	0	0	0	0	0	0	1	0	0	0
>^252	spathulenol	1579-1581	0	0	0	0	0	0	0	0	0	1	1	0
>253	globulol	1585	0	0	0	0	0	0	-	-	0	0	0	0
>254	caryophyllene oxide	1586	0	0	0	0	0	0	0	0	-	0	0	0
*255	lobulol	1587	0	-	0	0	0	0	0	0	0	0	0	0

			APPE	APPENDIX 2 cont.	cont.									
ID#	Chemical	RI(obs)	LGA	ΓD	LK	LB	LE	LGR	LH1	LH2		ΓЪ	LR	LS
>256	beta-copaen -4-alpha-ol	1592	0	0	0	0	-	0	0	0	0	0	0	0
>257	2-tetradecanone	1600	0	0	0	0	0	0	0	0	1	0	0	0
>^258	guaiol	1600	0	0	0	0	0	0	0	0	1	0	0	0
^259	5-epi-7-epi-alpha-eudesmol	1603	0	0	0	0	0	0	0	0	0	0	0	0
>*260	geranyl 2-methylbutyrate	1603-1604	0	0	1	0	0	0	0	1	0	0	0	0
>*^261	geranyl isovalerate	1606-1609	0	0	1	0	0	1	0	0	0	0	1	0
>262	beta-oplapenone	1609	0	0	0	0	0	0	0	0	0	0	0	-
>263	lauryl acetate	1609	0	0	0	0	0	0	1	1	0	1	0	0
>264	tetradecanal	1612	0	0	0	0	0	0	0	0	0	0	0	0
>265	10-epi-m-eudesmol	1625	0	0	0	0	0	0	0	0	0	0	0	0
>266	eremoligenol	1630	0	0	0	0	0	-	0	0	1	0	0	0
^267	1-epi-cubenol	1631	0	0	0	0	0	0	0	0	0	0	0	0
^268	gamma-eudesmol	1632-1634	0	0	0	0	0	0	0	0	-	0	0	0
>269	hinesol	1639	0	0	0	0	0	1	0	0	0	0	0	0
>270	epi-alpha-muurolol	1642	0	0	0	0	0	0	0	0	0	-	0	0
^271	6,6-dimethyl-6(3-methylphenyl)-heptan-3-one	1642	0	0	0	0	0	0	0	0	0	0	-	0
>^272	epi-gamma-cadinol	1644	0	0	0	1	1	0	0	0	0	0	0	0
*^273	3-butylphthalide	1646-1657	1	1	-	0	0	0	0	0	0	0	0	0
>*^274	alpha-muurolol	1646-1648	0	1	0	0	1	0	0	1	0	1	0	1
>275	beta-eudesmol	1651	0	0	0	0	0	-	0	0	1	0	0	0
>276	alpha-eudesmol	1653	0	0	0	0	0	-	0	0	1	0	0	0
>277	pogostol	1653	0	0	0	0	0	0	0	0	0	0	0	0
>^278	alpha-cadinol	1656	0	0	0	1	-	0	1	-	0	1	0	1

APPENDIX 2 cont.

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ID#	Chemical	RI(obs)	LGA	ΓD	LK	LB	LE	LGR	LH1	LH2	П	LP	LR	LS
>280	citronelly angelate	1664	0	0	0	0	0	1	0	0	0	0	0	0
>281	14-hydroxy-9-epi-beta-caryophyllene	1668	0	0	0	0	0	0	0	0	0	-	0	0
>^282	trans-calaminen-10-ol	1668	0	0	0	0	0	0	0	0	0	-	0	0
>283	cadalene	1675	0	0	0	0	0	0	-	0	0	0	0	0
>^284	tetradecanol	1674-1676	0	0	0	0	0	0	0	-	-	0	0	0
*285	(Z)-3-butylidene phthalide	1676	0	1	0	0	0	0	0	0	0	0	0	0
*286	gamma-dodecalactone	1682	-	0	-	0	0	0	0	0	0	0	0	0
>^287	alpha-bisabolol	1686-1687	0	0	0	1	0	0	0	0	0	1	0	0
>^288	eudesm-4(15),7-dien-1beta-ol	1686-1688	0	0	0	0	0	0	0	1	0	0	0	0
>289	2-pentadecanone	1689	0	0	0	0	0	1	0	0	1	0	0	0
*290	(E)-3-butylidene phthalide	1721	0	-	0	0	0	0	0	0	0	0	0	0
*^291	senkyunolide	1724-1729	1	1	1	0	0	0	0	0	0	0	0	0
*292	neocnidilide	1736	-	-	0	0	0	0	0	0	0	0	0	0
>^293	mint sulfide	1737-1741	0	0	0	1	1	1	0	1	1	1	0	-
>*295	(Z)-ligustilide	1744	1	1	1	1	0	0	0	1	0	0	0	0
>296	benzyl acetate	1760	0	0	0	0	1	0	0	1	0	0	0	0
^297	benzyl benzoate	1760	0	0	0	0	0	0	0	0	0	0	0	0
>298	psorolen	1771	0	0	0	0	0	1	0	0	0	0	0	0
*299	(E)-ligustilide	1800	0	1	0	0	0	0	0	0	0	0	0	0
>300	myristyl acetate	1809	0	0	0	0	0	0	1	1	0	0	0	0
>301	2,3,3'-trimethyl-2,3'-dihydroangelicin	1904	0	0	0	0	0	0	-	0	0	0	0	0
>*^302	methyl hexadecanoate	1924-1927	0	0	-	-	0	0	0	0	0	0	0	0
*^303	hexadecanoic acid	1958-1964	-	-	-	-	-	-	-	-	0	-	-	0

ID#	Chemical	RI(obs)	LGA	Ρ	ĸ	ΓB	ш	LGR	LH1	LH2		4	LR	LS
100	(T) falancial	2000	-	-	-	-		-			-	-	-	-
+000	(z/-1aicailii0i	0007	>	>	>	>	>	>	>	-	-	>	>	>
>*305	octadecanol	2078-2081	0	0	-	0	-	0	0	0	0	0	0	0
>306	methyl linoleate	2092	0	0	0	-	-	0	0	0	0	0	0	0
>307	methyl linolenate	2098	0	0	0	-	-	0	0	0	0	0	0	0
>*308	heneicosane	2100	1	0	1	0	0	1	0	1	1	0	0	0
>*^309	linoleic acid	2132-2134	1	1	1	0	-	0		-	0	1	0	0
>*^311	osthole	2134-2138	-	-	-	0	-	-	-	-	-	-	-	0
>*^312	linolenic acid	2139-2141	1	-	1	1	-	0	-	1	0	0	0	0
>313	docosane	2200	0	0	0	1	-	1		-	1	0	0	0
>314	retene	2218	0	0	0	0	0	0	0	0	0	-	0	0
>*315	tricosane	2300	-	0	1	1	-	-	-	-	-	-	0	0
>*316	tetracosane	2400	-	0	1	0	-	0	0	1	-	-	0	0
>*317	pentacosane	2500	-	0	1	0	1	0	0	-	1	-	0	0
>318	hexacosane	2600	0	0	0	0	1	0	0	0	0	0	0	0
>319	octacosane	2800	0	0	0	-	0	0	-	-	0	0	0	0

APPENDIX 2 cont.

APPENDIX 3

Essential oils found in each species examined in the combined chemical analyses (other genera in Apiaceae). AA = Aletes acaulis; CH1 = population 1 of*Cymopterus hendersonii;*CH2 = population 2 of*Cymopterus hendersonii;*CP =*Cymopterus panamintensi;*MT =*Musineon tenuifolium;*SC =*Sphenosciadium capitellatum;*TA =*Tauschia arguta;*TP =*Taushia parishii.* $RI = Kovats retention indices. Codes by the numbered rows refer to the reference source that first reported the compound within the taxa. * = Dev et al. 2007; > = Beauchamp et al. 2009; ^ = Dev et al. 2010.$

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ID#	Chemical	RI(obs)	AA	CH1	CH2	СР	MT	SC	TA	TP
>*1	furfural	835-836	0	0	0	0	0	0	0	0
^2	ethyl 2-methyibutyrate	854	0	0	1	1	0	0	0	0
>*^3	(E)-2-hexenal	856-857	0	0	0	1	1	1	0	1
>4	(Z)-3-hexenol	859	0	0	0	0	0	0	0	0
>5	heptanal	904	0	0	0	0	0	0	0	0
*^6	isobutyl isobutyrate	921	0	1	1	0	0	0	0	0
>7	tricyclene	925	0	0	0	0	0	0	0	0
>*^8	alpha-thujene	931-932	1	1	1	1	1	1	0	1
>*^9	alpha-pinene	937-938	1	1	1	1	1	1	1	1
>*^10	camphene	952-953	1	1	1	1	1	0	0	1
^11	benzaldehyde	963	0	0	1	0	0	0	0	0
>*^12	sabinene	976-978	0	1	1	1	1	1	1	1
>13	heptanol	977	0	0	0	0	0	0	0	0
>*^14	beta-pinene	978-979	1	1	1	1	1	1	1	1
>15	dehydro-1,8-cineole	990	0	0	0	0	0	0	0	0
>*^16	myrcene	992-993	1	1	1	1	1	1	1	1
>17	furfuryl methyl sulfide	1000	0	0	0	0	0	0	0	0
>*^18	alpha-phellandrene	1002	1	1	1	1	1	1	1	1
>*^19	isobutyl 2-methylbutyrate	1003-1005	0	1	1	0	1	0	0	0
>20	octanal	1004	0	0	0	0	0	0	0	0
>*21	isobutyl isovalerate	1007-1013	0	0	0	0	0	1	0	0
^22	isobutyl 3-methylbutyrate	1009	0	1	1	0	0	0	0	0
>*23	isosylvestrene	1008-1009	0	0	0	0	0	0	0	0
^24	delta-3-carene	1010	0	0	0	0	0	1	1	0
^25	(E)-2-hexenyl acetate	1011	0	0	0	0	0	0	0	0
>*^26	alpha-terpinene	1015-1017	1	1	1	1	0	1	1	1
*^27	2-methylbutyl isobutyrate	1020-1021	0	1	0	0	0	0	0	0
>*^28	p-cymene	1025-1027	1	1	0	1	1	1	1	1
>*^29	beta-phellandrene	1031	1	1	1	1	1	1	1	1
>*^30	limonene	1031	1	1	1	1	1	1	1	1
^31	1,8-cineole	1034	1	1	1	0	0	0	0	0
>32	benzyl alcohol	1038	0	0	0	0	0	0	0	0
>*^33	(Z)-beta-ocimene	1042-1043	1	1	1	1	1	1	1	1
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ID#	Chemical	RI(obs)	AA	CH1	CH2	СР	MT	SC	TA	TP
>*34	phenylacetaldehyde	1045-1046	0	0	0	0	0	0	0	0
*^35	butyl 2-methylbutyrate	1048	0	1	1	0	0	0	0	0
>*^36	(E)-beta-ocimene	1052-1054	1	1	1	1	1	1	1	1
>*^37	isobutyl angelate	1057-1058	0	0	0	0	0	0	0	0
>*^38	gamma-terpinene	1061-1062	1	1	1	01	1	1	1	1
*39	isoamyl butyrate	1064	0	0	0	0	0	0	0	0
>40	octanol	1068	0	0	0	0	0	0	0	0
^41	cis-sabinene hydrate	1070	0	1	0	0	0	0	0	0
^42	cis-linalool oxide (furanoid)	1076	0	0	0	1	0	0	0	0
>*43	trans-linalool oxide (furanoid)	1076	0	0	0	0	0	0	0	0
>44	p-cresol	1079	0	0	0	0	0	0	0	0
>^45	m-cresol	1076-1081	0	0	0	0	1	0	1	0
*^46	butyl angelate (A)	1083	0	0	0	0	1	0	0	0
>47	p-mentha-2,4(8)-diene	1087	0	0	0	0	0	0	0	0
>48	p-cymenene	1088	0	0	0	0	0	0	0	0
>*^49	terpinolene	1088	1	1	1	1	1	1	1	1
>*50	isobutyl tiglate	1093-1094	0	0	0	0	0	0	0	0
>51	2-nonanone	1094	0	0	0	0	0	0	0	0
^52	6,7-epoxymyrcene	1094	0	0	0	1	0	0	0	0
>^53	6-camphenone	1095-1096	0	0	0	0	0	0	0	0
>*^54	linalool	1100	1	1	0	1	1	1	0	0
^55	3-methylbutyl 2-methylbutanoate	1102	1	0	0	0	1	1	0	1
>56	nonanal	1104	0	0	0	0	0	0	0	0
*57	2-methylbutyl 2-methylbutyrate	1105	0	0	0	0	0	0	0	0
>*58	isoamyl isovalerate	1105-1110	0	0	0	0	0	0	0	0
^59	2-methylbutyl 2-methylbutanoate	1106	0	0	1	0	1	1	0	1
^60	3-methylbutyl 3-methylbutanoate	1107	0	1	1	0	1	1	0	1
>61	p-mentha-1,3,8-triene	1107	0	0	0	0	0	0	0	0
>62	2-methylbutyl isovalerate	1111	0	0	0	0	0	0	0	0
^63	2-methylbutyl 3-methylbutanoate	1112	1	0	1	0	0	1	0	1
>64	heptyl acetate	1116	0	0	0	0	0	0	0	0
>*^65	dehydrosabina ketone	1122	0	1	1	1	0	0	0	1
*66	butyl-angelate (B)	1125	0	0	0	0	0	0	0	0
>67	trans-rose oxide	1130	0	0	0	0	0	0	0	0
>*68	(E,Z)-allo-ocimene (neo-alloocimene	1132-1136	0	0	0	0	0	0	0	0
>69	trans-pinovarveol	1137	0	0	0	0	0	0	0	0

APPENDIX 3 cont.

ID#	Chemical	RI(obs)	AA	CH1	CH2	СР	MT	SC	TA	TP
>*^70	(E,E)-allo-ocimene (alloocimene)	1132-1142	1	0	0	1	0	1	0	0
>^71	camphor	1144-1146	0	0	0	1	0	0	0	1
^72	3-methyl-2-buten-1-yl 2-methylbutyrate	1146	0	0	0	0	1	0	0	0
>73	neoisopulegol	1147	0	0	0	0	0	0	0	0
>74	trans-verbenol	1153	0	0	0	0	0	0	0	0
*^75	hexyl isobutyroate	1153	1	1	0	0	0	0	0	0
^76	isoamyl angelate	1154	0	0	0	0	0	0	0	0
>77	3-methyl-2-butenyl isovalerate	1154	0	0	0	0	0	0	0	0
^78	citronellal	1155-1157	0	1	1	1	1	0	0	0
^79	2-methylbutyl angelate	1158	0	0	0	0	0	0	0	1
*80	pentylbenzene + 1-pentyl-1,3- cyclohexadiene	1160	0	0	0	0	0	0	0	0
>81	(E)-2-nonenal	1163	0	0	0	0	0	0	0	0
>82	pinocarvone	1164	0	0	0	0	0	0	0	0
>83	2-decanone isomer	1166	0	0	0	0	0	0	0	0
>84	1,4-dimethoxy-benzene	1166	0	0	0	0	0	0	0	0
>^85	borneol	1167-1168	1	0	0	0	0	0	0	0
>86	p-menth-1,5-dien-8-ol	1169	0	0	0	0	0	0	0	0
^87	lavandulol	1171	0	0	0	1	0	1	0	0
*^88	terpinen-4-ol (4-terpineol)	1176-1179	1	1	1	1	1	0	0	1
^89	viridine	1178	0	0	0	0	0	1	0	0
^90	naphthalene	1181	0	0	0	0	0	0	1	0
>91	p-methyl-acetophenone	1182	0	0	0	0	0	0	0	0
*92	thuj-3-en-10-al	1184	0	0	0	0	0	0	0	0
>^93	p-cymene-8-ol	1185-1186	0	0	0	0	0	0	1	0
>*^95	cryptone	1184-1188	1	0	0	1	1	0	0	1
*^96	amyl angelate (C)	1187-1190	0	0	0	0	0	1	0	1
>*^97	alpha-terpineol	1191-1192	1	1	1	1	1	1	1	1
>98	methyl salicylate	1192	0	0	0	0	0	0	0	0
>99	myrtenal	1194	0	0	0	0	0	0	0	0
>100	(Z)-4-decenal (cis-4-decenal)	1195	0	0	0	0	0	0	0	0
^101	(E)-4-decenal (trans-4-decenal)	1194	0	0	0	0	1	0	0	0
*^102	2-methylbutyl tiglate	1197-1200	0	0	0	1	0	0	0	0
>*^103	methyl chavicol	1196-1200	1	1	1	1	0	0	0	1
^104	(Z)-undecenal	1195	0	0	0	1	0	0	0	0
^105	4-methylpentyl 2-methylbutyrate	1201	0	0	0	0	0	0	0	0

APPENDIX 3 cont.

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ID#	Chemical	RI(obs)	AA	CH1	CH2	СР	MT	SC	TA	TP
^106	gamma-terpineol	1202	0	0	1	0	0	0	0	0
>^107	decanal	1207	0	0	0	1	1	0	0	1
>*108	octyl acetate	1214	0	0	0	0	0	0	0	0
>109	trans-carveol	1220	0	0	0	0	0	0	0	0
>^110	citronellol	1228-1231	1	1	1	1	1	0	0	1
>*^111	methyl thymol (thymol methyl ether)	1236-1237	1	1	1	0	0	0	0	0
>*112	hexyl 2-methylbutyrate	1239-1240	0	0	0	0	0	0	0	0
^113	neral	1241	0	1	1	0	0	0	0	0
^114	cuminal	1242	0	0	0	0	0	0	0	1
*115	hexyl isovalerate	1244	0	0	0	0	0	0	0	0
>*^116	methyl carvacrol (carvacrol methyl ether)	1245	0	1	1	0	0	0	0	0
^117	hexyl 3-methylbutyrate	1247	0	1	1	0	0	0	0	0
>^118	carvone	1247	0	0	0	0	0	0	0	0
>*^119	piperitone	1254-1257	0	1	1	0	0	0	0	0
>120	linalyl acetate	1258	0	0	0	0	0	0	0	0
^121	geraneol	1258	0	0	0	0	1	0	0	0
^122	linalool acetate	1258	0	0	0	1	0	0	0	0
>123	(Z)-4-decenol	1260	0	0	0	0	0	0	0	0
>124	2-undecanone isomer	1261	0	0	0	0	0	0	0	0
>125	(E)-2-decenal	1264	0	0	0	0	0	0	0	0
^126	methyl citronellate	1264	0	0	0	0	0	0	0	1
^127	geranial	1274	0	0	1	0	0	0	0	0
^128	citronelly formate	1275	0	0	0	0	1	0	0	0
>129	p-menth-1-en-7-al	1276	0	0	0	0	0	0	0	0
>130	decanol	1277	0	0	0	0	0	0	0	0
^131	dihydrolinalool acetate	1277	0	0	0	1	0	0	0	1
^132	p-menth-1-en-7-al	1277	0	0	0	0	0	0	0	0
>^133	alpha-terpinen-7-al	1283-1285	0	0	0	0	0	0	0	0
>*^135	(E)-anethole	1286-1290	1	1	1	0	0	0	0	0
*136	indole	1287	0	0	0	0	0	0	0	0
>*^137	bornyl acetate	1288	0	0	0	1	1	0	1	1
^138	C6H11-angelate/tiglate	1289	0	0	0	0	0	0	0	0
^140	(Z,Z,Z)-3,6,9-tridecatriene	1291	0	0	0	0	0	0	0	1
>141	p-cymen-7-ol	1291	0	0	0	0	0	0	0	0
>*^142	lavandulyl acetate	1292-1294	0	0	0	0	1	1	0	0

APPENDIX 3 cont.

ID#	Chemical	RI(obs)	AA	CH1	CH2	СР	MT	SC	TA	TP
*143	thymol	1293	0	0	0	0	0	0	0	0
>144	2-undecanone	1294	0	0	0	0	0	0	0	0
>145	benzyl isobutyrate	1296	0	0	0	0	0	0	0	0
>146	trans-pinocarvyl acetate	1298	0	0	0	0	0	0	0	0
*^147	carvacrol	1300-1302	0	0	0	0	0	1	0	0
^148	undecanal	1306	0	0	0	0	1	0	0	0
^149	4-methylhexyl 2-methylbutanoate	1307	0	0	0	0	0	1	0	0
>*150	2-methoxy-4-vinyl phenol	1312-1315	0	0	0	0	0	0	0	0
>151	nonyl acetate	1313	0	0	0	0	0	0	0	0
>152	cis-pinocarvyl acetate	1314	0	0	0	0	0	0	0	0
^153	neoiso-pulegyl acetate	1314	0	0	0	0	1	0	0	0
^154	p-vinyl guaiacol	1314	0	1	1	0	0	0	0	0
^155	(E,E)-2,4-decadienal	1322	0	0	1	0	0	0	0	0
*156	C6H13-angelate (D)	1322	0	0	0	0	0	0	0	0
^157	myrtenyl acetate	1334	0	0	0	0	1	0	0	0
^158	3-oxo-p-menth-1-en-7-al	1336	0	0	0	1	0	0	0	0
>159	heptyl 2-methylbutyrate	1337	0	0	0	0	0	0	0	0
>^160	trans-carvyl acetate	1339	0	0	0	0	1	0	0	0
^161	alpha-cubebene	1348	0	0	0	0	1	0	1	1
>162	alpha-longipinene	1352	0	0	0	0	0	0	0	0
>163	citronellyl acetate	1354	0	0	0	0	0	0	0	0
^164	eugenol	1360	0	01	1	0	0	0	0	0
>165	2-dodecanone isomer	1367	0	0	0	0	0	0	0	0
^166	cyclosativene	1370	0	0	0	0	0	0	0	0
^167	longicyclene	1372	0	0	0	0	0	0	0	1
>168	methyl p-anisate	1374	0	0	0	0	0	0	0	0
>*^169	alpha-copaene	1376-1378	0	0	0	0	1	1	1	1
>^170	daucene	1380-1382	0	0	0	0	1	0	0	0
>^171	beta-bourbonene	1385-1388	1	0	0	1	1	1	1	1
*^172	beta-cubebene	1386-1388	0	0	0	0	0	0	1	0
>173	benzyl 2-methylbutyrate	1387	0	0	0	0	0	0	0	0
>174	benzyl isovalerate	1390	0	0	0	0	0	0	0	0
>*^175	beta-elemene	1391-1393	0	0	0	1	1	1	1	1
>176	2-dodecanone	1395	0	0	0	0	0	0	0	0
>177	2-phenyethyl isobutyrate	1395	0	0	0	0	0	0	0	0
>178	(Z)-jasmone	1397	0	0	0	0	0	0	0	0

APPENDIX 3 cont.

ID#	Chemical	RI(obs)	AA	CH1	CH2	СР	MT	SC	TA	TP
>179	vanillin	1398	0	0	0	0	0	0	0	0
>^180	methyl eugenol	1400-1407	1	1	1	0	0	0	01	00
>181	italicene	1406	0	0	0	0	0	0	0	0
>182	longifolene	1406	0	0	0	0	0	0	0	1
>^183	dodecanal	1409	0	0	0	0	1	1	0	0
>184	decyl acetate	1411	0	0	0	0	0	0	0	0
>185	alpha-gujunene	1412	0	0	0	0	0	0	0	1
^186	beta-ylangene	1419	0	0	0	0	1	0	0	0
>*^187	beta-caryophyllene	1420-1422	01	1	1	0	0	0	1	1
>188	lavandulyl isobutyrate	1428	0	0	0	0	0	0	0	0
>^189	beta-copaene	1430-1432	0	0	0	1	1	0	0	1
>190	beta-gurjunene	1431	0	0	0	0	0	0	0	0
>*191	gamma-elemene	1436-1441	0	0	0	0	0	0	0	0
^192	alpha-guaiene	1438	0	0	0	0	0	0	0	1
>193	trans-alpha-bergamotene	1435	0	0	0	0	0	0	0	0
*194	thujopsene	1436	0	0	0	0	0	0	0	0
>195	octyl 2-methylbutyrate	1437	0	0	0	0	0	0	0	0
>^196	2-methylbutyl benzoate	1439-1442	0	0	0	0	1	01	0	1
>^197	aromadendrene	1440-1448	0	0	0	0	1	0	0	0
>198	citronellyl propionate	1450	0	0	0	0	0	0	0	0
>*^199	alpha-humulene	1453-1457	0	0	01	1	1	1	1	1
>*^200	(E)-beta-farnesene	1459	01	0	01	0	0	1	1	1
>201	2-tridecanone isomer	1461	0	0	0	0	0	0	0	0
>202	dehydro-aromadendrane	1463	0	0	0	0	0	0	0	0
>^203	cis-muurola-4(14),5-diene	1466-1468	0	0	0	0	1	0	0	01
>*204	gamma-decalactone	1470-1471	0	0	0	0	0	0	0	0
>205	ethyl (E,Z)-2,4-decadienoate	1472	0	0	0	0	0	0	0	0
>206	7-epi-1,2-dehydrosesquicineole	1474	0	0	0	0	0	0	0	0
^207	4,5-diepi-aristolochene	1474	0	0	0	0	0	1	0	0
^208	trans-cadina-1(6),4-diene	1477	0	0	01	01	1	0	0	1
^209	beta-chamigrene	1477	0	0	0	0	0	0	1	0
>*^210	gamma-muurolene	1478-1480	1	0	0	1	1	1	01	1
^211	amorpha-4,7(11)-diene	1481	0	0	0	0	0	1	1	0
>*^212	germacrene D	1483-1484	0	0	0	1	1	0	0	0
^213	citronellyl isobutyrate	1484	1	1	01	0	1	0	0	0
>*^214	beta-selinene	1487-1488	0	0	0	1	0	1	1	0

APPENDIX 3 cont.

ID#	Chemical	RI(obs)	AA	CH1	CH2	СР	MT	SC	TA	TP
>*^215	ar-curcumene	1484-1489	0	0	0	0	0	0	0	1
*^216	(E)-beta-ionone	1490	0	0	0	0	0	0	0	0
>217	trans-muurola-4(14),5-diene	1491	0	0	0	0	0	0	0	0
>^218	benzyl tiglate	1493	0	0	0	0	0	0	0	0
*219	delta-selinene	1493	0	0	0	0	0	0	0	0
^220	2-phenylethyl 3-methylbutanoate	1493	0	01	0	0	0	1	0	0
^221	valencene	1495	0	0	0	0	0	0	0	0
>^222	zingiberene (alpha-zingiberine)	1495-1496	0	0	1	1	0	0	0	0
>223	2-tridecanone	1496	0	0	0	0	0	0	0	0
>^224	alpha-selinene	1496	0	0	0	0	0	1	0	0
*226	delta-decalactone	1497	0	0	0	0	0	0	0	0
>^227	viridoflorene	1497-1500	0	0	0	0	0	0	0	1
>228	isodaucene	1500	0	0	0	0	0	0	0	0
>*^229	bicyclogermacrene	1498-1500	1	1	0	0	1	1	1	1
>^230	alpha-muurolene	1500-1501	0	0	0	1	1	0	0	0
*^231	alpha-cuprenene	1502-1510	0	0	0	0	0	0	0	1
>*^232	germacrene A	1505-1507	0	0	0	1	0	1	1	0
>*^233	(E,E)-alpha-farnesene	1507-1509	1	1	1	0	0	0	0	1
>234	beta-bisabolene	1508	0	0	0	0	0	0	0	0
>235	lavandulyl isovalerate	1510	0	0	0	0	0	0	0	0
>236	delta-amorphene	1510	0	0	0	0	0	0	0	0
>^237	lavandulyl 2-methylbutyrate	1512	0	0	0	0	0	01	0	0
>^238	gamma-cadinene	1515-1516	0	0	0	1	1	0	01	0
^239	(Z)-gamma-bisabolene	1516	0	0	0	0	0	0	1	0
*240	beta-sesquiphellandrene	1521	0	0	0	0	0	0	0	0
>*^241	delta-cadinene	1523-1526	1	0	0	1	1	1	1	1
^242	citronellyl butyrate	1532	0	0	0	0	0	0	0	0
^243	trans-cadina-1 (2),4-diene	1534	0	0	0	0	1	1	1	0
^244	kessane	1538	0	0	0	0	0	0	0	0
>^245	alpha-cadinene	1540-1541	0	0	0	1	1	0	0	0
>246	alpha-calacorene	1546	0	0	0	0	0	0	0	0
>247	elemol	1552	0	0	0	0	0	0	0	0
>*^248	germacrene B	1560-1561	0	0	0	1	0	1	1	1
>^249	(E)-nerolidol	1564-1566	0	01	1	0	0	0	0	0
>250	(E)-isoelemicin	1568	0	0	0	0	0	0	0	0
>251	2-tetradecanone isomer	1576	0	0	0	0	0	0	0	0

APPENDIX 3 cont.

ID#	Chemical	RI(obs)	AA	CH1	CH2	СР	MT	SC	TA	TP
>^252	spathulenol	1579-1581	0	0	0	0	0	0	0	1
>253	globulol	1585	0	0	0	0	0	0	0	0
>254	caryophyllene oxide	1586	0	0	0	0	0	0	0	0
*255	lobulol	1587	0	0	0	0	0	0	0	0
>256	beta-copaen-4-alpha-ol	1592	0	0	0	0	0	0	0	0
>257	2-tetradecanone	1600	0	0	0	0	0	0	0	0
>^258	guaiol	1600	0	0	0	0	0	1	0	1
^259	5-epi-7-epi-alpha-eudesmol	1603	0	0	0	0	0	0	0	1
>*260	geranyl 2-methylbutyrate	1603-1604	0	0	0	0	0	0	0	0
>*^261	geranyl isovalerate	1606-1609	1	0	0	0	0	1	1	0
>262	beta-oplapenone	1609	0	0	0	0	1	0	0	0
>263	lauryl acetate	1609	0	0	0	0	0	0	0	0
>264	tetradecanal	1612	0	0	0	0	0	1	0	0
>265	10-epi-m-eudesmol	1625	0	0	0	0	0	0	0	1
>266	eremoligenol	1630	0	0	0	0	0	0	0	0
^267	1-epi-cubenol	1631	0	0	0	1	1	0	0	0
^268	gamma-eudesmol	1632-1634	0	0	0	0	0	1	0	0
>269	hinesol	1639	0	0	0	0	0	0	0	0
>270	epi-alpha-muurolol	1642	0	0	0	0	0	0	0	0
^271	6,6-dimethyl-6(3-methylphenyl)- heptan-3-one	1642	0	0	0	0	0	0	0	0
>^272	epi-gamma-cadinol	1644	0	0	0	0	1	0	0	1
*^273	3-butylphthalide	1646-1657	0	0	01	0	0	0	0	0
>*^274	alpha-muurolol	1646-1648	0	0	0	1	1	0	0	1
>275	beta-eudesmol	1651	0	0	0	0	0	0	0	0
>276	alpha-eudesmol	1653	0	0	0	0	0	0	0	0
>277	pogostol	1653	0	0	0	0	0	0	1	0
>^278	alpha-cadinol	1656	0	0	0	0	1	0	0	0
>280	citronelly angelate	1664	0	0	0	0	0	0	0	0
>281	14-hydroxy-9-epi-beta-caryophyllene	1668	0	0	0	0	0	0	0	0
>^282	trans-calaminen-10-ol	1668	0	0	0	0	0	1	0	0
>283	cadalene	1675	0	0	0	0	0	0	0	0
>^284	tetradecanol	1674-1676	0	0	0	0	0	1	0	0
*285	(Z)-3-butylidene phthalide	1676	0	0	0	0	0	0	0	0
*286	gamma-dodecalactone	1682	0	0	0	0	0	0	0	0
>^287	alpha-bisabolol	1686-1687	0	0	0	0	0	0	0	1

APPENDIX 3 cont.

ID#	Chemical	RI(obs)	AA	CH1	CH2	СР	MT	SC	TA	TP
>^288	eudesm-4(15),7-dien-1beta-ol	1686-1688	0	0	0	0	1	0	0	0
>289	2-pentadecanone	1689	0	0	0	0	0	0	0	0
*290	(E)-3-butylidene phthalide	1721	0	0	0	0	0	0	0	0
*^291	senkyunolide	1724-1729	0	01	01	0	0	0	0	0
*292	neocnidilide	1736	0	0	0	0	0	0	0	0
>^293	mint sulfide	1737-1741	0	0	0	01	01	0	0	1
>*295	(Z)-ligustilide	1744	0	0	0	0	0	0	0	0
>296	benzyl acetate	1760	0	0	0	0	0	0	0	0
^297	benzyl benzoate	1760	0	0	0	0	1	0	0	01
>298	psorolen	1771	0	0	0	0	0	0	0	0
*299	(E)-ligustilide	1800	0	0	0	0	0	0	0	0
>300	myristyl acetate	1809	0	0	0	0	0	0	0	0
>301	2',3',3'-trimethyl-2',3'-dihydroangelicin	1904	0	0	0	0	0	0	0	0
>*^302	methyl hexadecanoate	1924-1927	0	0	0	0	0	1	0	0
*^303	hexadecanoic acid	1958-1964	1	01	1	0	1	1	0	1
>304	(Z)-falcarinol	2036	0	0	0	0	0	0	0	0
>*305	octadecanol	2078-2081	0	0	0	0	0	0	0	0
>306	methyl linoleate	2092	0	0	0	0	0	0	0	0
>307	methyl linolenate	2098	0	0	0	0	0	0	0	0
>*308	heneicosane	2100	0	0	0	0	0	0	0	0
>*^309	linoleic acid	2132-2134	0	0	0	0	0	1	0	1
>*^311	osthole	2134-2138	0	0	01	0	0	1	0	1
>*^312	linolenic acid	2139-2141	0	0	01	0	0	1	0	0
>313	docosane	2200	0	0	0	0	0	0	0	0
>314	retene	2218	0	0	0	0	0	0	0	0
>*315	tricosane	2300	0	0	0	0	0	0	0	0
>*316	tetracosane	2400	0	0	0	0	0	0	0	0
>*317	pentacosane	2500	0	0	0	0	0	0	0	0
>318	hexacosane	2600	0	0	0	0	0	0	0	0
>319	octacosane	2800	0	0	0	0	0	0	0	0

APPENDIX 3 cont.

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REFERENCES

BARNEBY, R.C. 1964. Atlas of North American Astragalus. Mem. New York Bot. Gard. 13:1–1188.

BEAUCHAMP, P.S., E. CHEA, J.G. DIMAANO, V. DEV, B. LY, A.E. MIRANDA, & W.H. WHALEY. 2009. Essential oil composition of six Lomatium species attractive to indra swallowtail butterfly (*Papilio indra*): Principal component analysis against essential oil composition of Lomatium dissectum var. multifidum. J. Essent. Oil Res. 21:535–542.

COLLIN, G., H. GAGNON, A. ST.-GELAIS, & M. TURCOTTE. 2014. Composition of the essential oil and the hydrosol of the roots of *Ligusticum porteri*. Am. J. Essent. Oil. Nat. Prod. 3:4–10.

COULTER, J.M. & J.N. Rose. 1888. Revision of North American Umbelliferae. Wabash College, Crawfordsville, Indiana, U.S.A. COULTER, J.M. & J.N. Rose. 1900. Monograph of the North American Umbelliferae. Contr. U.S. Natl. Herb. 7:1–256.

- COULTER, J.M. & J.N. Rose. 1909. Supplement to the monograph of the North American Umbelliferae. Contr. U.S. Natl. Herb. 12:447–448.
- CRONQUIST A., N.H. HOLMGREN, & P.K. HOLMGREN. 1997. Subclass Rosidae (except Fabales). Intermountain flora: Vascular plants of the Intermountain West, U.S.A. 3A:1–446.

DEv, V., B. Ly, A.E. MIRANDA, & W. WHALEY. 2007. Composition of the essential oils of three varieties of *Lomatium grayi* (J.M. Coult & Rose) J.M. Coult & Rose. J. Essent. Oil Res. 19:244–248.

- DEV, V., W.H. WHALEY, S.R. BAILEY, E. CHEA, J.G. DIMAANO, D.K. JOGANI, B. LY, & D. EGGETT. 2010. Essential oil composition of nine Apiaceae species from western United States that attract female indra swallowtail butterfily (*Papilio indra*). Biochem. Syst. Ecol. 38:538–547.
- ELLISON, R.L. & J.N. THOMPSON. 1987. Variation in seed and seedling size: The effects of seed herbivores on *Lomatium grayi* (Umbelliferae). Oikos 49:269–280.
- JONES, M.E. 1902. Contributions to western botany, No. 10. Contr. W. Bot. 10:1-90 + figures.

JONES, M.E. 1908. Contributions to western botany: New species and notes. Contr. W. Bot. 12:1-81.

- HAMMER, Ø., D.A.T HARPER, & P.D. RYAN. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica, 4, 9 p. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
- ISCAN, G., T. OZEK, G. OZEK, A. DURAN, & K.H.C. BASER. 2004. Essential oils of three species of *Heracleum*: anticandidal activity. Chem. Nat. Compd. 40: 544–547.
- MARHOLD, K. 2011. Multivariate morphometrics and its application to monography at specific and infraspecific levels. In: T.F. Stuessy & H.W. Lack, eds. Monographic plant systematics: Fundamental assessment of plant biodiversity. A.R.G. Gantner Verlag K.G., Ruggell, Liechtenstein. Pp. 73–99.

MASTROGIUSEPPE, J.D., S.J. GILL, K.S. SIMMONS, & G.K. BROWN. 1985. Morphologic and cytotaxonomic evauluation of *Lomatium tuberosum* (Apaiceae). Brittonia 37:252–260.

MATHIAS, M.E. 1938. A revision of the genus Lomatium. Ann. Missouri Bot. Gard. 25:225.

NISHIDA, R. 2005. Chemosensory basis of host recognition in butterflies – multi-component system of oviposition, stimulants, and deterrents. Chem. Senses 30:i293–i294.

- OMERNIK, J.M. & G.E. GRIFFITH. 2014. Ecoregions of the conterminous United States Evolution of a hierarchical spatial framework. Environm. Managem. 54:1249–1266. doi:10.1007/s00267-014-0364-1
- PRUDIC, K.L., J.C. OLIVER, & F.A.H. SPERLING. 2007. The signal environment is more important than diet or chemical specialization in the evolution of warning coloration. Proc. Natl. Acad. Sci. U.S.A. 104:19381–19386; https://doi. org/10.1073/pnas.0705478104
- SAITOU, N. & M. NEI. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. Molec. Biol. Evol. 4:406–425.
- TIEHM, A. 1985. Vascular plant types of Clarence King's exploration of the fortieth parallel, 1867–1869. Brittonia 37:400–424.

- U.S. ENVIRONMENTAL PROTECTION AGENCY. 2013. Level III and IV ecoregions of the continental United States: Corvallis, Oregon, U.S. EPA, National Health and Environmental Effects Research Laboratory, map scale 1:3,000,000. www.epa.gov/ eco-research/level-iii-and-iv-ecoregions-continental-united-states.
- VAN WASSENHOVE, F., P. DIRINCK, G. VULSTEKE, & N. SCHAMP. 1990. Aromatic volatile composition of celery and celeriac cultivars. HortScience 25:556–559.
- WATSON, S. 1871. Botany. In: C. King. Report U.S. geological exploration of the fortieth parallel. 5:1–525. Government Printing Office, Washington, U.S.A.
- WELSH, S.L. 1982. Utah plant types—Historical perspective 1840 to 1981—Annotated list and bibliography. Great Basin Naturalist 42:129–195. www.jstor.org/stable/41711873.