

MORPHOLOGICAL VARIATION IN THE RARE IDAHO ENDEMIC, *LEPIDIUM PAPILLIFERUM* (BRASSICACEAE) AND SEGREGATION OF OWYHEE COUNTY POPULATIONS AS A NEW VARIETY OF *LEPIDIUM MONTANUM*

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ABSTRACT

Lepidium papilliferum (L.F. Hend.) Nelson & Macbr. (Brassicaceae) is a rare annual or biennial endemic to southwestern Idaho and listed as threatened by U.S. Fish and Wildlife Service under the Endangered Species Act. It comprises three main metapopulations: the Jarbidge, Boise Foothills (BF), and Snake River Plains (SRP) populations. This study investigates morphological relationships among these populations of *L. papilliferum* and the closely related *Lepidium montanum* Nutt. var. *montanum*, to determine if there is sufficient evidence to taxonomically segregate the Jarbidge populations currently considered *L. papilliferum* from the other *L. papilliferum* populations. We measured 22 morphological characteristics on 61 herbarium specimens and conducted a Principal Components Analysis to assess the range of variability for these characters across the full range of *L. papilliferum* populations in southwestern Idaho. Jarbidge and SRP (including BF) populations were distinguishable by the first three principal component axes, which represented 56.4% of the variation among sampled populations. Six morphological characters (relating mainly to trichomes and leaf division) differed significantly between Jarbidge and SRP *L. papilliferum* populations. The Jarbidge populations are morphologically and geographically distinct from the others and can be supported as a distinct variety — ***L. montanum* var. *owyheense*** Barbour & Mansfield, **var. nov.** The absence of papillae on the filaments of Jarbidge plants supports closer affinity to *L. montanum* than to *L. papilliferum*. Current genetic data support the current taxonomy and this proposed taxonomy equally-- with *L. montanum* as paraphyletic and *L. papilliferum* as monophyletic in both cases.

Lepidium papilliferum (L.F. Hend.) Nelson & Macbr. (Brassicaceae) (slickspot peppergrass) is a rare polyploid species endemic to southwestern Idaho (Smith et al. 2009). *Lepidium papilliferum* is specifically endemic to small slickspot microhabitats within sagebrush-steppe ecosystems, hence its patchy distribution (Moseley 1994; Stillman 2006). The history of its classification is inconsistent, and uncertainty remains about relationships among *L. papilliferum* and closely related species, particularly as variation within the closely-related, more widely distributed *L. montanum* Nutt. is widespread (Moseley 1994; Al-Shehbaz & Gaskin 2010; Larson et al. 2010). While *L. papilliferum* was first described as a variety of *L. montanum* (Henderson 1900), recent revisions have treated *L. papilliferum* as a distinct species (Al-Shehbaz & Gaskin 2010; Holmgren 2005). Henderson's name refers to the distinctive feature of clavate trichomes — notably on the staminate filaments (Henderson 1900). According to Rollins (1993), two morphological characters in addition to the filament papillae distinguish *L. papilliferum* from *L. montanum* var. *montanum*, the only other currently recognized non-perennial variety of *L. montanum* — while all leaves of *L. papilliferum* are divided, *L. montanum* specimens have some entire leaves, and, unlike *L. montanum*, *L. papilliferum* has siliques that are broadly ovate to nearly orbicular, not tapered near the apices, and have no wing vestiges at the apices. Based on these criteria southwest Idaho populations in slickspots with leaf divisions similar to the type of *L. papilliferum* have been treated as that species. Widespread variation in and among the taxa of these species makes relationships difficult to quantify (Al-Shehbaz & Gaskin 2010).

Populations of *Lepidium papilliferum* fall into three broad geographical divisions: A “Snake River Plains” (SRP) population set in Ada, Canyon, and Elmore counties, an adjacent “Boise Foothills” (BF) population set in Ada, Gem and Payette counties, and a 70 km distant “Jarbidge” population set in Owyhee County (Fig. 1). Some differences in morphological characteristics among these metapopulations have been noted in the field (Colket 2006), raising the possibility that one or more of these metapopulations may constitute distinct taxa. Indeed, Jarbidge *L. papilliferum* individuals apparently lack one of the diagnostic morphological characters used to distinguish *L. papilliferum* from *L. montanum*—trichomes on the filaments (Al-Shehbaz & Gaskin 2010; Moseley 1994; Smith et al. 2009). SRP and BF populations are less obviously distinct and previous studies have treated the BF populations as a subset of the broader SRP population (Larson et al. 2010; Smith et al. 2009; Stillman 2006).

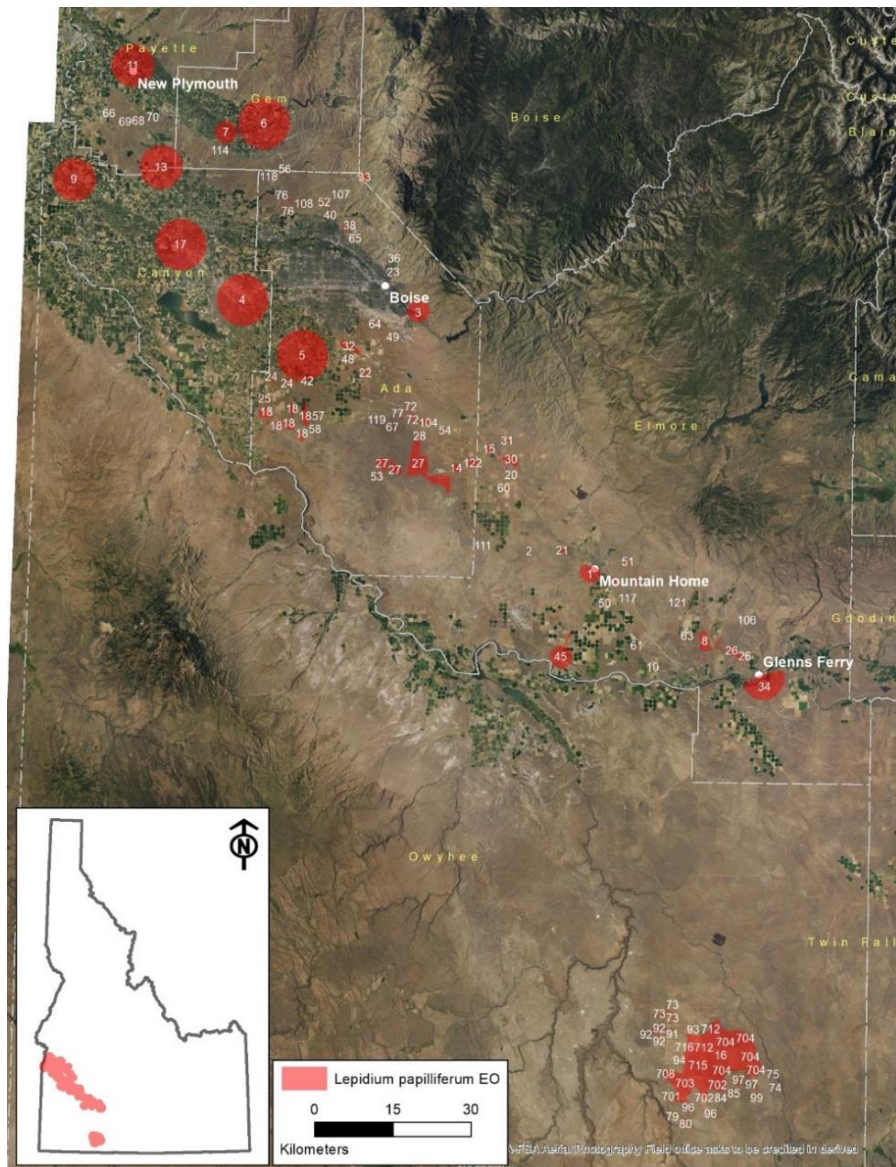


Figure 1. Distribution of *Lepidium papilliferum* populations: Jarbidge (in bottom right--Owyhee Co.); SRP (Elmore, southern Ada and eastern Canyon Cos.); BF (southern Gem, southern Payette, and northern Ada Cos.); historical (Canyon, Gem, and Payette Cos.). Size of red circles indicates area of uncertainty. Map courtesy of U.S. Fish & Wildlife Service (2021).

Smith et al. (2009) conducted phylogenetic analysis of two nuclear and two chloroplast DNA sequences of *Lepidium papilliferum* and closely related species. Though they found *L. papilliferum* (Jarbidge and SRP/BF populations) to be monophyletic within paraphyletic *L. montanum*, they did not find sufficient evidence to conclude that the Jarbidge and SRP *L. papilliferum* populations were genetically distinct. However, other studies have suggested more pronounced divergence between SRP and Jarbidge *L. papilliferum* populations (Larson et al. 2010; Stillman 2006). Stillman (2006) analyzed allozymes and found that *L. papilliferum* populations from the Jarbidge and SRP regions were less similar to each other than among populations within each region, suggesting that as the isolation of the two metapopulations has increased, gene flow among populations has been unable to counter genetic drift. Similarly, using amplified restriction fragment length polymorphisms (AFLPs), Larson et al. (2010) resolved *L. papilliferum* into distinct Jarbidge and SRP subgroups. In phylogenetic analyses of the same two chloroplast genes and two different nuclear genes, the latter authors also found monophyletic *L. papilliferum* within paraphyletic *L. montanum* but sister to *L. montanum* var. *montanum*, instead of to *Lepidium fremontii* S. Wats. as suggested by Smith et al. (2010).

The three populations of *Lepidium papilliferum* appear to occupy similar ecological niches. They all occur in slickspot microenvironments within the broader sagebrush-steppe ecosystem (Moseley 1994; Colket 2006). Slickspots are small depressions that over time accumulate fine soil particles (clay) and relatively high salt content due to pooling rainwater (Colket 2006). However, due to the different geological histories of each region, plants from the three populations may experience distinct edaphic environments (Colket 2006; Barbour & Mansfield unpublished data). Boise Foothills populations are also at higher elevations than populations from the Snake River Plain (Colket 2006). Threats to *L. papilliferum* include habitat loss through agricultural conversion or urban expansion as well as damage to microenvironment sites through wildfire and trampling by livestock (Moseley 1994). Additionally, large-scale invasions of exotic annuals in sagebrush-steppe environments may lead to the decline of native plant species and drastically alter the ecology of the invaded regions (Moseley 1994).

Because of its sensitivity to disturbance, Moseley (1994) considered *Lepidium papilliferum* to be a good indicator species for monitoring the health and stability of Snake River Plain sagebrush-steppe habitats in Idaho. He also noted that since the discovery of the species in 1892, 21 known populations have disappeared (Moseley 1994), a rate (approximately two populations lost per decade since 1892) that is higher than the documented extirpation rate for any Idaho rare plant species (Moseley 1994). Moseley argues that the actual rate of decline for *L. papilliferum* has been much higher than the documented rate due to progressive degradation of the sagebrush-steppe ecosystem as a whole (1994). Increased habitat fragmentation may make *L. papilliferum* populations increasingly isolated and vulnerable as habitat loss continues (Moseley 1994). There are currently fewer than 80 populations of *L. papilliferum* remaining (Fig. 1 — from U.S. Fish & Wildlife Service 2021).

Treated as *Lepidium montanum* var. *papilliferum*, this taxon was first listed in 1990 for protection as a threatened taxon under the Endangered Species Act of 1973 (ESA--US Fish and Wildlife Service 1990). In 2002 the taxon was listed as an endangered species as *L. papilliferum* (U.S. Fish & Wildlife Service 2002). In 2007 a decision was made to withdraw the proposals to continue to list *L. papilliferum* because of the taxonomic uncertainty surrounding the taxon (U.S. Fish & Wildlife Service 2007). In 2012, an Idaho District Court decision reverted the taxon to “proposed” status. In 2016 *L. papilliferum* was reinstated with “threatened” status (U.S. Fish & Wildlife Service 2016). Because *L. papilliferum* is recognized by the U.S. Fish & Wildlife Service as a threatened species under the ESA and worthy of protection, clarification of the morphological differentiation within this species in relation to *L. montanum* will impact management priorities.

Morphological analyses have been used successfully in the past to elucidate variation among closely-related taxa and to define species in Brassicaceae. Heenan et al. (2007) used a combination of Principal Components Analysis (PCA) on morphological data and genetic analysis to describe variation

in two endemic New Zealand *Lepidium* species. Khalik (2005) conducted morphological studies on the trichomes of many Brassicaceae genera, including *Lepidium* species and found trichomes to be useful morphological characters for the identification of taxonomic units, including tribes, genera, species, subspecies, and varieties. Significantly, the main characteristic noted in casual field observation to distinguish the Jarbidge from SRP *L. papilliferum* populations relates to the presence or absence of trichomes on the filaments. The primary objective of this paper is to clarify the degree of morphological divergence among the three *L. papilliferum* population systems. We also investigate morphological relationships between *L. papilliferum* and the closely-related taxon *L. montanum* var. *montanum*. Morphological information on this group will inform the forthcoming monograph on *Lepidium montanum* (Al-Shehbaz pers. comm.).

Methods

We measured 22 morphological characters (Table 1) from a sample of 61 herbarium specimens (Fig. 2, Table 2) including *Lepidium montanum* var. *montanum* (8 collections), SRP *L. papilliferum* (29 collections), BF *L. papilliferum* (3 collections) and Jarbidge (15 collections), as well as six “historical” collections referred to as *L. philonitrum* (discussed below).

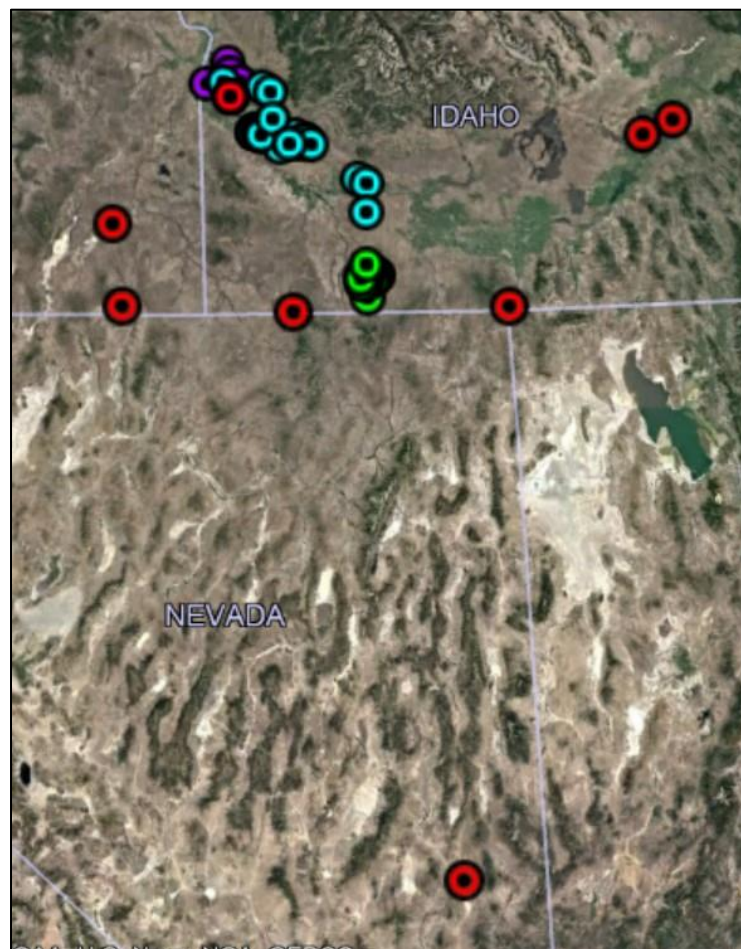


Figure 2. Populations used in this study (see Table 2). *Lepidium papilliferum* including SRP and BF (blue), *L. montanum* var. *montanum* (red), *L. montanum* var. *owyheense* (green), *L. philonitrum* (purple) Table 1. Morphological characters measured and their definitions. Upper cauline leaves were measured approximately 1/3 of the way from their branch tip to the branch connection with the main stem. Lower cauline leaves were approximately 1/3 of the way up from the stem base.

Table 1. Morphological characters measured and their definitions. Upper cauline leaves were measured approximately 1/3 of the way from their branch tip to the branch connection with the main stem. Lower cauline leaves were approximately 1/3 of the way up from the stem base.

	Character	Definition
1.	Main stem presence	0-3; 0=1 main stem, 1=2-3, 2=4-5, 3=6+
2.	Upper cauline leaf division	Leaflets/side (excluding tip)
3.	Upper cauline leaf division depth	Depth (mm) of deepest leaflet division
4.	Upper cauline leaf length:width ratio	(mm), width measured at leaf midpoint
5.	Lower cauline leaf division	Leaflets/side (excluding tip)
6.	Lower cauline leaf division depth	Depth (mm) of deepest leaflet division
7.	Lower cauline leaf length:width ratio	(mm), width measured at leaf midpoint
8.	Trichomes on filaments	0 vs. 1; 0 if absent, 1 if present
9.	Plant height	(mm)
10.	Length of lowest branch	(mm)
11.	Leaf tip shape	0-3; 0=most rounded
12.	Mature fruit length:width ratio	(mm)
13.	Mature fruit shape	0-3; 0=most rounded
14.	Stem trichome density	Number trichomes/mm, upper stems
15.	Stem trichome length	0-3; 0=shortest
16.	Stem trichome homogeneity	0-3; 0=most homogenous in terms of length, shape
17.	Stem trichome shape (clavate vs. cylindric)	0-3; 0=most cylindric
18.	Leaf division overall	0-3; 0=all leaves entire, 1=some leaves entire, 2=all leaves divided, 3=some leaflets divided
19.	Upper cauline leaf length	(mm)
20.	Lower cauline leaf length	(mm)
21.	Fruit length	(mm)
22.	Fruit width	(mm)

Specimens used in this study were selected from herbaria at Utah State University (UTC), Idaho State University (IDS), Boise State University (SRP), Idaho Department of Fish and Game, Boise District Bureau of Land Management (BBLM), the College of Idaho (CIC), New York Botanical Garden Herbarium (NY) and Harvard University (GH; Table 2). Biennial forms were excluded from the analysis to avoid confounding the study results, and only mature plants were included. We found five collections, made before 1950, from Canyon, Payette, and Gem counties and annotated variously as either *Lepidium papilliferum* or *L. montanum* var. *montanum*, which did not fall within the range of morphological variation for either taxon (Table 2). Suspecting that these “pre-1950,” hereafter referred to as “historical” collections, may correspond to a separate, possibly extinct, variety of *Lepidium montanum*, we included the type specimen of *Lepidium philonitrum* Nelson & Macbr. (currently considered a synonym of *L. montanum* var. *montanum* — Al-Shehbaz & Gaskin 2010), from Payette County, in the historical set for our morphological analysis, and we refer to the “historical” group as *L. philonitrum*.

Table 2. Sample specimens. Boise Foothills populations are included as with Snake River Plain (SRP—see text.)

	Accession	Collector	Coll. #	Latitude Longitude	Study Designation	Date Collected	Name resulting from this study
1	CIC036329	N. Otting	1576	42.6827 -117.9126	<i>L. montanum</i>	2008 May	<i>L. montanum</i> var. <i>montanum</i>
2	CIC017976	G. Ralston	sn	42.0086 -113.9976	<i>L. montanum</i>	1990 July	<i>L. montanum</i> var. <i>montanum</i>
3	CIC017813	L.C. Smithman	667	43.42083 -112.0978	<i>L. montanum</i>	1981 June	<i>L. montanum</i> var. <i>montanum</i>
4	CIC007607	R. Rosentreter	6142	43.3112 -112.4386	<i>L. montanum</i>	1989 June	<i>L. montanum</i> var. <i>montanum</i>
5	CIC020376	R. Rosentreter	3621	41.9999 -114.0001	<i>L. montanum</i>	1985 June	<i>L. montanum</i> var. <i>montanum</i>
6	CIC006317	G. Schiemer	sn	43.68 -116.70	<i>L. montanum</i>	1954 May	<i>L. montanum</i> var. <i>montanum</i>
7	CIC006103	P.L. Packard	79- 231	42.0535 -117.8182	<i>L. montanum</i>	1979 June	<i>L. montanum</i> var. <i>montanum</i>
8	CIC063009	A. Tiehm	16359	37.9018 -114.7860	<i>L. montanum</i>	2011 Jun	<i>L. montanum</i> var. <i>montanum</i>
9	UTC00246280	B. Schweigert	54	42.2835 -115.3416	Jarbidge	2006 June	<i>L. montanum</i> var. <i>owyheense</i>
10	UTC00246265	B. Schweigert	39	42.3539 -115.393	Jarbidge	2006 May	<i>L. montanum</i> var. <i>owyheense</i>
11	UTC00246264	B. Schweigert	38	42.2469 -115.4565	Jarbidge	2006 May	<i>L. montanum</i>

							var. <i>owyheense</i>
12	BBLM002093	J. Klott	sn	42.2089 -115.4488	Jarbidge	1993 Aug	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>
13	BBLM002101	A. DeBolt	2197	42.1 -115.4	Jarbidge	1996 June	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>
14	UTC00246278	B. Schweigert	52	42.2496 -115.408	Jarbidge	2006 June	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>
15	NYBG00076423	N.H. Holmgren	5805	42.23 -115.35	Jarbidge	1972 June	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>
16	UTC00246261	B. Schweigert	35	42.2744 -115.2935	Jarbidge	2006 May	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>
17	BBLM002106	S. Popovich .	6356	42.2815 -115.4327	Jarbidge	2001 June	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>
18	UTC00246259	B. Schweigert	33	42.2384 -115.4259	Jarbidge	2006 May	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>
19	UTC00246279	B. Schweigert	53	42.2595 -115.3052	Jarbidge	2006 June	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>
20	UTC00246263	B. Schweigert	37	42.3039 -115.3706	Jarbidge	2006 May	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>
21	UTC00246277	B. Schweigert	51	42.2777 -115.4251	Jarbidge	2006 June	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>
22	UTC00246262	B. Schweigert	36	42.2716 -115.2971	Jarbidge	2006 May	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>
23	UTC00246260	B. Schweigert	34	42.2029 -115.4187	Jarbidge	2006 May	<i>L.</i> <i>montanum</i> var. <i>owyheense</i>

24	UTC00246268	B. Schweigert	42	43.7533 -116.3686	BF	2006 May	<i>L.</i> <i>papilliferum</i>
25	UTC00246271	B. Schweigert	45	43.2747 -116.2082	SRP	2006 May	<i>L.</i> <i>papilliferum</i>
26	UTC00246272	B. Schweigert	46	43.3002 -116.1099	SRP	2006 May	<i>L.</i> <i>papilliferum</i>
27	UTC00246266	B. Schweigert	40	43.8966 -116.872	SRP	2006 May	<i>L.</i> <i>papilliferum</i>
28	none	B. Colket	sn		SRP	2005 June	<i>L.</i> <i>papilliferum</i>
28	none	B. Colket	sn		SRP	2005 June	<i>L.</i> <i>papilliferum</i>
30	none	B. Colket	sn		SRP	2005 June	<i>L.</i> <i>papilliferum</i>
31	none	B. Colket	sn		SRP	2005 June	<i>L.</i> <i>papilliferum</i>
32	CIC19401	R. Rosentreter	3201	43.32 -115.94	SRP	1983 June	<i>L.</i> <i>papilliferum</i>
33	CIC31327	J. Grimes.	1611	43.0179 -115.4316	SRP	1980 May	<i>L.</i> <i>papilliferum</i>
34	CIC20628	J. Grimes	1609	43.2937 -115.8866	SRP	1980 May	<i>L.</i> <i>papilliferum</i>
35	CIC9951	A. DeBolt	669	43.3364 -115.9452	SRP	1987 May	<i>L.</i> <i>papilliferum</i>
36	UTC00246273	B. Schweigert	47	42.9816 -115.3447	SRP	2006 May	<i>L.</i> <i>papilliferum</i>
37	CIC31328	J. Grimes	1607	43.3682 -116.0504	SRP	1980 June	<i>L.</i> <i>papilliferum</i>
38	BBLM 002099	A. DeBolt	1678	42.7572 -115.3644	SRP	1993 May	<i>L.</i> <i>papilliferum</i>
39	NYBG00076585	A. DeBolt	1448	43.5 -116.27	SRP	1990 May	<i>L.</i> <i>papilliferum</i>
40	SRP011120	J.F. Smith	2716	43.372 -116.394	SRP	1993 July	<i>L.</i> <i>papilliferum</i>
41	CIC6320	A. Stanford	sn	43.3 -116.0	SRP	1975 May	<i>L.</i> <i>papilliferum</i>
42	CIC23937	A. DeBolt	1464a	43.3899 -116.3983	SRP	1990 June	<i>L.</i> <i>papilliferum</i>
43	SRP022024	J.H. Kaltenecker	50	43.4167 -116.4667	SRP	1994 April	<i>L.</i> <i>papilliferum</i>
44	SRP006333	H.D. Papenfuss	302	43.37 -116.40	SRP	1990 May	<i>L.</i> <i>papilliferum</i>
45	SRP010483	M. Mancuso	617b	43.7135 -116.2840	BF	1992 April	<i>L.</i> <i>papilliferum</i>
46	NYBG0076134	A. DeBolt	1145a	43.3901 -116.4738	SRP	1989 June	<i>L.</i> <i>papilliferum</i>
47	BBLM002105	A. DeBolt	1076a	43.3938 -116.4241	SRP	1989 April	<i>L.</i> <i>papilliferum</i>
48	BBLM002095	A. DeBolt	1145b	43.3901 -116.4738	SRP	1989 June	<i>L.</i> <i>papilliferum</i>

49	BBLM002098	A. DeBolt	1464b	43.3899 -116.3983	SRP	1990 June	<i>L.</i> <i>papilliferum</i>
50	BBLM002096	A. DeBolt	1145c	43.3901 -116.4738	SRP	1989 June	<i>L.</i> <i>papilliferum</i>
51	CIC021931	A. DeBolt	1076b	43.3938 -116.4241	SRP	1989 April	<i>L.</i> <i>papilliferum</i>
52	NYBG00076586	A. DeBolt	1464c	43.3899 -116.3983	SRP	1990 June	<i>L.</i> <i>papilliferum</i>
53	NYBG00076584	H.D. Papenfuss	302	43.3718 -116.3964	SRP	1990 May	<i>L.</i> <i>papilliferum</i>
54	NYBG00701819	N.H. Holmgren	13140	43.37 -116.39	SRP	1998 June	<i>L.</i> <i>papilliferum</i>
55	CIC6319	B. Ertter	8/4	43.7978 -116.7684	BF	1974 May	<i>L.</i> <i>papilliferum</i>
56	IDS0014424	H.W. Davis	sn	43.871 -116.699	Historical	1947 May	<i>L.</i> <i>philonitrum</i>
57	IDS0014423	R.J. Davis	115	43.7852 -116.9432	Historical	1938 May	<i>L.</i> <i>philonitrum</i>
58	NYBG00076208	J. F. Macbride	880	43.8 -116.6	Historical	1911 June	<i>L.</i> <i>philonitrum</i>
59	CIC007212	H.M. Tucker	sn	43.68 -116.69	Historical	1935 May	<i>L.</i> <i>philonitrum</i>
60	CIC004496	H.M. Tucker	sn	43.68 -116.69	Historical	1935 May	<i>L.</i> <i>philonitrum</i>
61	GH00019222	J.F. Macbride	32	43.9546 -116.7174	Historical	1910 May	<i>L.</i> <i>philonitrum</i> Type

The 22 characters measured included anther, leaf, stem, and fruit characteristics (Table 1). Qualitative characteristics, such as trichome presence, were coded (e.g. 0=absence, 1=presence), while quantitative characteristics were either counted (e.g. number of leaf divisions) or measured to the nearest 0.5 mm (e.g. cauline leaf length.) Characters were measured using a dissecting scope (Olympus CO11) as necessary. For characters where fewer than five observations (of the 61 samples) were missing, the missing data were filled in using the character mean (1.85% of analyzed observations). Where greater than five observations were missing, the character was excluded from the analysis (4 characters, all relating to fruit morphology).

All analyzed data were standardized by subtracting the character mean from each individual observation and then dividing by the standard deviation. The standardized data were analyzed using PCA to determine the degree of separation among taxa. PCA eigenvectors, each scaled to its standard deviation, were used to isolate the characters that load significantly on each PCA axis (Pearson's $r > 0.5$ or $r < -0.5$). Finally, for all characters analyzed, means or medians and standard deviations were compared among the relevant population centers and plant taxa to determine significance. Data were analyzed using PC-ORD 5.10 (McCune & Mefford 2011) and Statistix 9 statistical software (Analytical Software 2008).

Results

Principal Components Analysis resolves four groups — populations from Jarbidge (*Lepidium montanum* var. *owyheense*), *L. papilliferum* from SRP and BF, *L. montanum* var. *montanum*, and a historical group corresponding to *L. philonitrum* (Fig. 3). Preliminary PCA did not distinguish SRP

from BF populations, thus they are combined in Figure 3. Cumulatively, the first three principal component axes captured 56.41% of the sample variation: PCA1 represented 25.31%, PCA2 represented 17.68%, and PCA3 represented 13.24%.

Characters that load highly on PCA1 (Pearson's $r > 0.5$) are stem trichome density and stem trichome length. Cauline leaf length to width ratio, lower cauline leaf division depth, plant height, and branch length all correlate negatively ($r < -0.5$) with PCA1. Upper cauline leaf division (number of leaflets), upper cauline leaf division depth, lower cauline leaf division, stem hair shape, and overall leaf division correlate negatively with PCA2. Lower cauline leaf length to width ratio correlates positively (Pearson's $r > 0.5$) with PCA3. Trichome presence on the filaments, stem hair homogeneity, and stem hair shape are significantly negatively correlated with PCA3 ($r < -0.5$). PCA1 vs. PCA3 distinguishes primarily between Jarbidge populations (*Lepidium montanum* var. *owyheense*) and SRP *L. papilliferum* populations (Fig. 3c). BF populations cluster within the SRP populations. Figure 3 also shows the historical populations (*L. philonitrum*) separate from the other three groups. PCA1 vs. PCA2 and PCA2 vs. PCA3 demonstrate a distinct morphological separation between *L. montanum* and all of the other groups (Figs 3a and 3b, respectively).

Six of the morphological characters analyzed had means that differed significantly between the sample collections from the Jarbidge and SRP *Lepidium papilliferum* metapopulations (Table 3). Upper and lower cauline leaf division were significantly higher for the Jarbidge individuals on average ($p = 0.008$ and $p = 0.001$, respectively). Trichomes on the filaments were present in all SRP specimens and absent in all Jarbidge specimens ($p < 0.001$, expressivity 1.00). Jarbidge specimens also had denser stem trichomes ($p = 0.002$) and longer lower branches ($p = 0.008$). Stem trichomes were significantly longer in Jarbidge specimens ($p = 0.037$). A single additional Jarbidge specimen, not included in this analysis, has been found that contains some trichomes on the filaments, and this specimen also was the only one observed in which some upper leaves were completely entire, a character otherwise found only in *L. montanum*.

Only one morphological character (trichome presence on the filaments) differed significantly between Jarbidge and BF *Lepidium papilliferum* specimens (Mann-Whitney $U = 0.00$, $p = 0.001$). No Jarbidge plants in our sample had trichomes on the filaments of their anthers, while all BF and SRP plants sampled had trichomes present on the filaments. Two morphological characters (lower cauline leaf division and upper cauline leaf length) differed significantly between SRP and BF plants (t-tests: $t = 2.48$, $p = 0.019$ and $t = 3.78$, $p = 0.002$, respectively). BF plants had more divisions on lower cauline leaves and longer upper cauline leaves.

SRP *Lepidium papilliferum* and *L. montanum* var. *montanum* differ significantly in 7 characters. SRP *L. papilliferum* collections had shorter lower branches than *L. montanum* (t-test, $t = 2.20$, $p = 0.034$). Additionally, SRP individuals had more deeply divided upper cauline leaves and a smaller upper cauline leaf length to width ratio (Mann-Whitney: $U = 17.0$, $p < 0.001$ and $U = 26.0$, $p < 0.001$, respectively). Stem trichome shape was more clavate for SRP specimens, while stem trichomes on *L. montanum* individuals were more cylindrical ($U = 0.0$, $p < 0.001$). *Lepidium montanum* plants were taller ($U = 57.5$, $p = 0.032$) and had less leaf division overall ($U = 11.0$, $p < 0.001$) compared to SRP *L. papilliferum* plants. Finally, SRP *L. papilliferum* specimens had trichomes on their filaments while *L. montanum* var. *montanum* individuals did not ($U = 0.0$, $p < 0.001$).

Figure 3. Principal Components Analysis of populations of *Lepidium montanum* var. *montanum* (red squares), Jarbidge *L. montanum* var. *owyheense* (green triangle), SRP (including BF) *L. papilliferum* (blue circles) and historical *L. papilliferum* (*L. philonitrum*--purple inverted triangles). PCA1 vs. PCA2 (Fig 3a) distinguishes *L. montanum* var. *montanum* and historical *L. papilliferum* (*L. philonitrum*) from extant *L. papilliferum*. PCA 2 vs. PCA 3 (Fig. 3b) distinguishes *L. montanum* from all of what is currently treated as *L. papilliferum*. PCA 1 vs. PCA 3 (Fig. 3c) distinguishes *L. montanum* from *L. papilliferum*. The 3-D plot (Fig. 3d) distinguishes among all 4 groups.

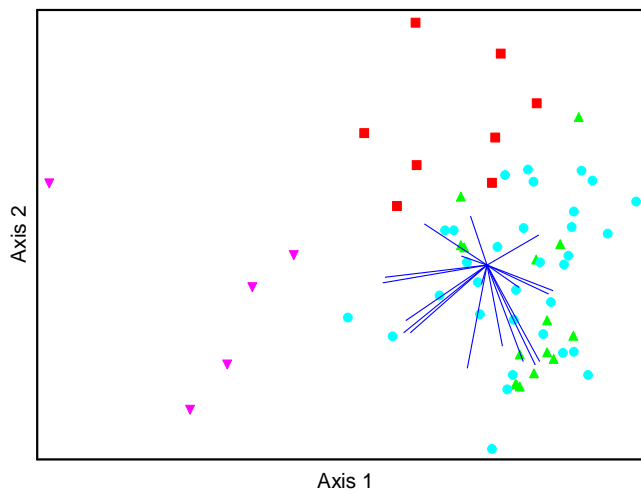
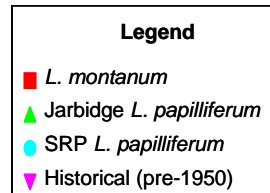


Figure 3a.

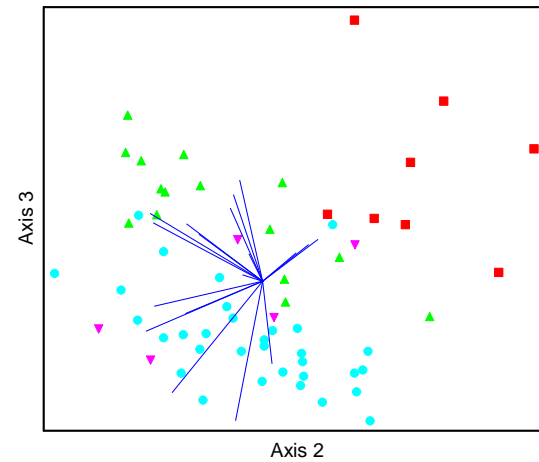


Figure 3b.

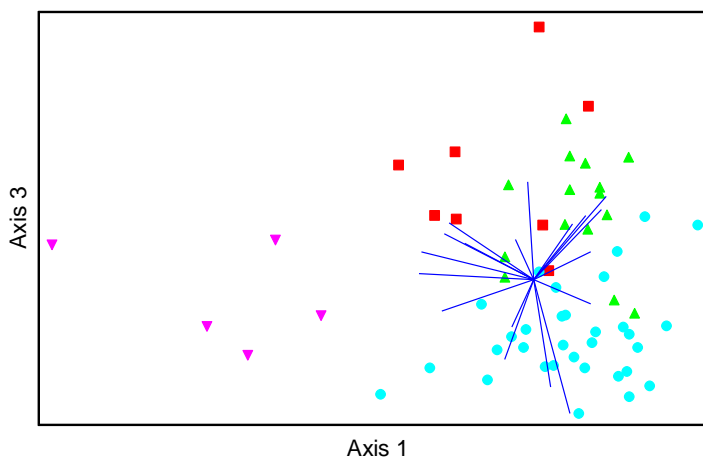


Figure 3c.

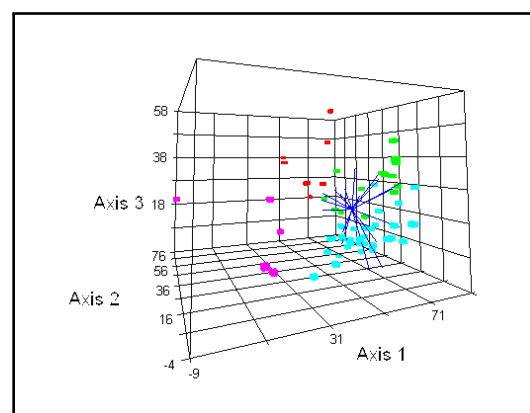


Figure 3d.

Table 3. Morphological character means and comparisons, by population set or taxa. Superscript letters represent statistically significant differences (comparisons containing the same number are not significantly different) at the $\alpha=0.05$ level. Means are listed above medians for each character. Due to a non-normal distribution of data, Mann-Whitney U-Tests were used to test differences except for in the following comparisons in which significant differences were measured using t-tests: SRP vs. *L. montanum* length of lowest branch; Boise Foothills vs. *Lepidium montanum* lower cauline leaf division; historical vs. *L. montanum* lower cauline leaf division depth, lower cauline leaf length, upper cauline leaf length, length of lowest branch, stem trichome shape, and leaf tip shape; Boise Foothills vs. historical upper cauline leaf length, stem trichome density, stem trichome length, plant height, and leaf division overall; and SRP vs. historical lower cauline leaf length, upper cauline leaf length, and stem trichome density.

* Denotes characters coded numerically (see Table 2).

Character	Boise Foothills <i>L. papilliferum</i> (n=3)		Jarbidge <i>L.</i> <i>montanum</i> var. <i>owyheense</i> (n=15)		SRP <i>L.</i> <i>papilliferum</i> (n=29)		<i>L. montanum</i> var. <i>montanum</i> (n=8)		Historical <i>L.</i> <i>philonitrum</i> (n=6)	
	Mean Median	SD	Mean Median	SD	Mean Media n	SD	Mean Media n	SD	Mean Media n	SD
Lower cauline leaf division	4.67 4.00 ^A	1.15	4.27 4.00 ^A	0.96	3.10 3.00 ^{BC}	1.03	2.38 2.50 ^B	1.41	2.33 2.00 ^C	0.82
Lower cauline leaf division depth	3.67 4.00 ^{AB}	0.58	3.23 3.00 ^A	0.92	3.41 3.50 ^A	1.35	2.44 2.25 ^A	1.59	6.00 6.00 ^B	2.00
Lower cauline leaf length	20.00 21.00 ^{AB}	4.58	16.00 15.00 ^A	6.79	14.25 15.00 ^A	5.13	16.19 16.00 ^A	7.15	24.50 22.50 ^B	5.65
Lower cauline leaf L:W ratio	2.60 2.63 ^A	0.09	2.51 2.55 ^A	0.85	2.28 2.08 ^A	0.72	2.86 2.70 ^A	1.08	2.34 2.23 ^A	0.60
Upper cauline leaf length	10.67 11.00 ^A	0.58	9.17 9.00 ^{AB}	2.05	8.40 8.00 ^B	2.69	9.69 8.75 ^{AB}	3.08	15.83 15.50 ^C	2.48
Length of lowest branch	91.67 95.00 ^{AB} C	50.0 8	114.33 115.00 A	37.5 8	77.59 65.00 ^B	46.2 4	116.29 124.65 A	33.5 3	225.83 260.00 C	91.55
Upper cauline leaf division	2.33 2.00 ^{ABC}	0.58	2.53 3.00 ^A	0.83	1.83 2.00 ^B	0.71	1.38 1.50 ^{BC}	0.74	1.17 1.00 ^C	0.75
Upper cauline leaf division depth	2.67 3.00 ^{AC}	0.58	2.07 2.00 ^{AC}	0.73	2.47 2.00 ^{AC}	1.04	0.88 0.75 ^B	0.64	3.38 3.00 ^C	1.83
Upper cauline leaf L:W ratio	2.32 2.20 ^{ABC}	0.39	2.03 2.00 ^A	0.46	2.00 1.83 ^A	0.39	3.32 3.10 ^B	1.34	4.90 2.76 ^{BC}	5.50

Stem trichome density	8.67 10.00 ^{AB}	2.31	12.80 12.00 ^A	4.44	8.63 8.00 ^B	2.81	8.88 7.50 ^{AB}	4.19	4.17 4.50 ^C	1.47
Stem trichome homogeneity *	2.00 2.00 ^A	0.50	1.30 1.50 ^A	0.53	1.55 1.50 ^A	0.63	1.19 1.50 ^A	0.59	1.75 1.75 ^A	0.52
Stem trichome length*	2.00 2.00 ^{AB}	0.50	1.93 2.00 ^A	0.68	1.47 1.50 ^B	0.69	1.25 1.00 ^{AB} C	0.89	0.83 1.00 ^C	0.26
Stem trichome shape*	2.50 2.50 ^{AC}	0.00	2.40 2.50 ^{AC}	0.21	2.49 2.50 ^A	0.06	0.81 1.00 ^B	0.59	2.33 2.50 ^C	0.26
Plant height	137.00 143.00 ^A B	29.4 6	127.50 135.00 AB	36.8 7	114.31 106.00 A	50.9 1	148.00 149.00 B	24.1 0	402.83 400.00 C	110.8 2
Leaf division overall*	2.33 2.00 ^A	0.58	2.43 3.00 ^A	0.73	2.22 2.00 ^A	0.41	1.13 1.00 ^{BC}	0.35	1.33 1.25 ^C	0.41
Leaf tip shape*	1.50 1.50 ^A	0.00	1.43 1.50 ^A	0.42	1.55 1.50 ^A	0.28	1.69 1.50 ^A	0.65	0.75 0.75 ^B	0.27
Main stem presence*	1.33 1.00 ^A	1.53	0.94 0.00 ^A	1.26	0.31 0.00 ^A	0.47	1.20 0.81 ^A	1.30	0.17 0.00 ^A	0.41
Trichomes on filaments*	0.84 1.00 ^A	0.28	0.00 0.00 ^B	0.00	0.97 1.00 ^A	0.12	0.00 0.00 ^B	0.00	0.17 0.00 ^B	0.41

Jarbidge *Lepidium papilliferum* and *L. montanum* var. *montanum* were separated by six significant morphological character comparisons. Jarbidge plants had significantly more leaflets (greater leaf division) on their lower cauline leaves (Mann-Whitney U=15.0, p=0.002), greater upper cauline leaf division (U=19.0, p=0.003), and more deeply divided upper cauline leaves (U=12.0, p=0.001). Upper cauline leaf length to width ratio was lower for Jarbidge individuals (U=16.5, p=0.003) and stem trichome shape was more clavate (U=0.0, p<0.001). Jarbidge plants had significantly greater leaf division overall compared to *L. montanum* var. *montanum* (U=11.0, p<0.001).

Five of the morphological characters included in our analysis differed significantly between BF *Lepidium papilliferum* and *L. montanum* var. *montanum*. Lower cauline leaf division and upper cauline leaf division depth were significantly greater in BF plants (t-test, t=2.5, p=0.034 and Mann-Whitney U=0.5, p=0.011, respectively). BF plants had stem trichomes with a more clavate shape (U=0.0, p=0.012). Additionally, BF plants exhibited greater leaf division overall (U=1.0, p=0.018) and BF plants had trichomes on their filaments while *L. montanum* var. *montanum* plants did not (U=0.0, p=0.006).

Historical (*Lepidium philonitrum*) populations differed from *L. montanum* var. *montanum* populations in nine characters. Leaf division depth (t-test, t=-3.72, p=0.003), lower cauline leaf length (t=-2.34, p=0.037), upper cauline leaf length (t=-4.0, p=0.002), lowest branch length (t=-2.79, p=0.031), upper cauline leaf division depth (Mann Whitney U=3.00, p=0.0040) and plant height (U=0.00, p=0.007) were all significantly greater in the historical populations. *L. montanum* var. *montanum* had denser (U=6.0, p=0.019) and more cylindrical (t=-6.7, p<0.001) stem trichomes. In historical plants, leaf tips were significantly rounder than in *L. montanum* var. *montanum* (t=3.66,

$p=0.004$). Historical collections also differed significantly from BF *L. papilliferum* in 8 characters, from SRP collections in 13 characters, and from Jarbidge collections in 12 characters (Table 3).

Discussion

Our results demonstrate morphological differentiation among four population systems of *Lepidium montanum* var. *montanum* and *L. papilliferum* in southwestern Idaho. Morphological divergence between Jarbidge and SRP/BF population systems is as pronounced as between *L. montanum* var. *montanum* and *L. papilliferum* (Fig. 3, Table 3). We therefore propose taxonomic distinction between the Jarbidge populations heretofore referred to as *L. papilliferum* and the remaining *L. papilliferum* populations in the Snake River Plain and Boise Foothills, referring to the former as *L. montanum* var. *owyheense*.

Boise Foothill populations, though more similar to Jarbidge than to SRP populations quantitatively in such characters as upper leaf lengths and lower leaf divisions, were like SRP populations in differing from Jarbidge populations qualitatively by possessing filament trichomes (Table 3). The papillae on the filaments — the feature that Henderson first pointed to as distinguishing the *papilliferum* type that he collected in what is today Nampa, Idaho, from *Lepidium montanum* — is the defining feature of *Lepidium papilliferum*, yet Jarbidge populations consistently lack them. Additionally, the Jarbidge populations have fruit apices that taper to a narrow, residual wing — a character that Rollins (1993) pointed out as distinguishing *L. montanum* from *L. papilliferum*. Though considerable variation exists within the SRP and BF populations (Table 3), they were not distinguishable by PCA, and filaments in all individuals observed possessed papillae. For these reasons, SRP and BF populations should be considered a single taxonomic unit, retaining the designation *L. papilliferum*, while the Jarbidge populations should be segregated as a variety of *L. montanum*.

This morphological conclusion is, to some degree, consistent with the genetic conclusions of both Stillman (2006) using allozymes and Larson *et al.* (2010) using AFLPs, in which samples from locations corresponding to both SRP and BF populations were all treated as “Snake River Plains” *Lepidium papilliferum* and genetically different than Jarbidge *L. papilliferum*. Likewise, Smith *et al.* (2009) suggested that the “genetic and morphologically unique characters of these two subgroups [sic Jarbidge and SRP metapopulations] is most likely the result of more recent isolation and perhaps indicative of genetic divergence and incipient speciation.” All three genetic studies (Smith *et al.* 2009, Stillman 2006, Larson *et al.* 2010) find *L. papilliferum* to be monophyletic within a paraphyletic *L. montanum* var. *montanum*. Yet there is disagreement regarding the sister to that monophyletic group. The taxonomic circumscription proposed here is consistent with *L. montanum* rather than *L. fremontii* as sister to the clade with *L. papilliferum* and *L. montanum* var. *owyheense*. *Lepidium fremontii* is a perennial subshrub from western Nevada to southern California and northern Arizona, disjunct from our region, yet *L. montanum* is contiguous with the *L. papilliferum*. Despite the need for additional genetic data to substantiate the claim that the Jarbidge populations are best circumscribed as a variety of *L. montanum*, rather than of *L. papilliferum* or *L. fremontii*, by lacking filament papillae Jarbidge populations have greater morphological affinity to *L. montanum* than to *L. papilliferum*.

Our study validated field observations of Colket (2006), in which she claimed *Lepidium papilliferum* from the Jarbidge metapopulations reliably lack the diagnostic trichomes on the filaments that distinguish *L. papilliferum* from *L. montanum*. Because trichome presence on the filaments is used as a diagnostic to segregate *L. papilliferum* from *L. montanum* (Al-Shehbaz & Gaskin 2010), the fact that Jarbidge individuals lack this distinguishing characteristic is a significant finding. Trichome characters are considered useful for distinguishing taxonomic units, for higher taxonomic levels as well as on the intraspecific level in Brassicaceae (Khalik 2005).

All of the *Lepidium montanum* populations sampled in our study correspond to the "western clade" of *L. montanum* var. *montanum* identified by Larson et al. (2010). Thus, the three distinct, extant morphological groups identified in our study — *L. montanum* var. *montanum*, SRP *L. papilliferum*, and Jarbidge *L. montanum* var. *owyheense* — correspond to the AFLP-based "western clade" of Larson et al. (2010). In that study, one anomalous sample in the "eastern clade" was found in Gem County. This sample is in the vicinity of old "Falks store" by "Falks bridge" in Payette County. The collection of Macbride (#32) in 1910 from Falks store (part of Canyon County in 1910 before county lines were changed) is the type specimen of *L. philonitrum* corresponding to our "historical" metapopulation. Thus, it is possible that the historical *L. papilliferum* may represent either a distinct incipient taxon as our morphological study suggests or an introduction of one or more *L. montanum* plants of the "eastern clade" of Larson et al. (2010) that were perhaps introduced in the 19th century with settlement in western Idaho. A similar scenario was suggested by Larson et al. (2010) to explain their Gem County anomaly.

Though both our morphologic study and the genetic studies of Larson et al. (2010) and Stillman (2006) all recognize three differentiated subgroups of Jarbidge *Lepidium papilliferum* (*L. montanum* var. *owyheense*), SRP *L. papilliferum*, and *L. montanum* var. *montanum*, the taxonomic implications are less clear. Though both Smith et al. (2009) and Larson et al. (2010) have recognized *L. papilliferum* as monophyletic within the paraphyletic *L. montanum*, Smith et al. (2009) suggested that the sister species to *L. papilliferum* is *L. fremontii*, a taxon not included in the study of Larson et al. (2010). The latter authors, however, place *L. papilliferum* sister to *L. montanum* var. *montanum* in the "western clade" of *L. montanum*. Based on existing data (Smith et al. 2009; Larson et al. 2010) the placement of Jarbidge populations in *L. montanum* as var. *owyheense* would maintain *L. montanum* as a paraphyletic taxon and *L. papilliferum*, in the narrower sense, as monophyletic. For *L. montanum* to be monophyletic it would also have to include *L. papilliferum*. However, until genetic results consistently support a single sister group to *L. papilliferum*, our proposed taxonomy must remain tentative.

How much insight morphological analysis provides into the true phylogenetic relationships at and below the species level for *Lepidium papilliferum* and closely-related taxa remains an open question. Bowman (2006) argues that one of the problematic aspects of basing phylogenetic relationships on morphology in Brassicaceae is that the developmental processes that contribute to characters such as fruit and leaf shapes are plastic. Morphology-based classification schemes specifically related to the genus *Lepidium* are often not supported by molecular data from more recent studies (Bowman 2006). Finer-resolution phylogenetic analyses are needed to clarify relationships within closely-related and problematic *Lepidium* species groupings, such as the *L. montanum* complex (Al-Shehbaz & Gaskin 2010). However, the Jarbidge metapopulation may be considered taxonomically distinct because it is "consistently and persistently distinct, and distinguishable by ordinary means" (Cronquist 1978; and in McDade 1995). The absence of reciprocal monophyly (Larson et al. 2010) argues against species level recognition of the Jarbidge populations, however. Thus, we propose recognition of the Jarbidge metapopulation as *L. montanum* var. *owyheense*.

Additionally, the "historical" collections (*Lepidium philonitrum*) differed from *L. papilliferum* populations by 8-13 morphological characters, including the absence of filament trichomes, and from *L. montanum* var. *montanum* by nine characters (Table 3). They were also distinguishable in the PCA (Fig. 3), suggesting that these historical collections represent a possibly extinct taxon distinct from *L. montanum* var. *montanum*, *L. montanum* var. *owyheense* and *L. papilliferum*, though our study did not examine the full range of variation in *L. montanum*, such as the "eastern clade" of Larson et al. (2010). Included within this set of historical populations is the *L. philonitrum* type specimen. Our results are consistent with resurrection of this taxon. To our knowledge, no populations of this historical group — *L. philonitrum*--have been relocated since 1950. The habitat of these populations — bottomlands in the Treasure Valley of Gem, Payette, and Canyon counties — is prime land for agriculture and development. In the same publication in which Nelson and Macbride elevated *L. montanum* var.

papilliferum to species rank, they described *L. philonitrum* distinguishing it in part from *L. papilliferum* by “habitat” without further explanation, possibly because it is less dependent on slickspots (Nelson & Macbride 1913). This group, compared to both *L. montanum* var. *montanum* and *L. papilliferum*, is taller, glabrate to sparsely covered by short hairs, with much longer branches and essentially unbranched in the lower stem. Understandably, it has been subsumed in *L. montanum* in recent treatments (Al-Shehbaz & Gaskin 2010; Holmgren 2005). Though further investigation of this likely extinct group would be desirable, it is likely that *L. philonitrum* has become extinct before such investigation is possible.

Lepidium papilliferum is currently listed as a threatened species under the Endangered Species Act (U.S. Fish & Wildlife Service 2016). It is considered highly vulnerable due to habitat loss — because of its specific habitat requirements (Colket 2006; U.S. Fish & Wildlife Service 2021). Threats persist for the species. Three of the five most stable management areas of the species are in the SRP/BF region while two are in the Jarbidge region (U.S. Fish & Wildlife Service 2021). Most *L. papilliferum* populations are small and fairly isolated populations within their larger metapopulations. Because of its small population size and highly fragmented distribution, it likely suffers due to inbreeding depression (Robertson & Ulappa 2004).

This study supports recognition of the Jarbidge metapopulation as a geographically and morphologically distinct entity — *Lepidium montanum* var. *owyheense*. This change in the taxonomy has implications for the status of populations currently identified as *L. papilliferum*. Our study supports increased conservation concern for *L. papilliferum*, with added concern for *L. montanum* var. *owyheense* and, if still extant, *L. philonitrum*.

LEPIDIUM MONTANUM Nutt. var. **OWYHEENSE** Barbour & Mansfield, **var. nov.** **TYPE:** **Idaho.** Owyhee Co.: Plains of Inside Desert, 7 km NW of Juniper Butte, 4930 ft, T13S R9E S20 SE (N 42.2815, W 115.4327), playettes of recently burned, unseeded island surrounded by large seeding, associates — *Poa sandbergii*, *Bromus tectorum*, *Ranunculus testiculatus*, 4 Jun 2001, S. Popovich 6356 (holotype: BBLM).

This variety is similar to *Lepidium montanum* var. *montanum* in its annual to biennial habit, in having fruits tapered to wing vestiges at the apex, and in absence of papillae on the staminal filaments, different in having denser, longer and more clavate (less cylindrical) stem trichomes and highly divided leaves (never entire, except in rare case when filaments are papillate). This variety is similar to *Lepidium papilliferum* in its divided upper stem leaves and in having clavate (few cylindrical) stem hairs, different in having fruits that often taper to wing vestiges at the apex, no filament papillae, more divided upper stem leaves, and higher density of upper stem hairs (Fig. 4).

Annual or biennial herbs from taproot. **Stems** 1– several, erect to ascending, 4 - 15 cm tall, densely pubescent with some curved cylindrical hairs and more clavate hairs, internodes 5 – 25 mm, branched mostly above, lowest branches 4 – 10 (15) cm. **Basal leaves** pinnately lobed, both surfaces with straight or cylindrical hairs and clavate hairs, abaxial surfaces less densely so, withered by anthesis. **Cauline leaves** attenuate; obovate to oblanceolate in outline, 0.5 – 2 cm x 3 – 10 (18) mm; blades pinnatisect occasionally with an extra lobe on 1 (2) lobes, very rarely entire; lobes oblong. **Racemes** congested in flower, slightly elongated in fruit, dense; rachis with mostly clavate, but some cylindrical, straight or curved cylindrical trichomes. **Fruiting pedicels** divaricate, 3 – 5 x 0.1 – 0.2 mm, sparsely to densely puberulent with thin clavate hairs. **Flowers** sepals oblanceolate-obovate with scarious margins, glabrous, 1.5 – 2 x 0.8 – 1.5 mm; petals white, obovate to orbicular, 2.5 – 3.0 x 1.5 – 2.7 mm, claw 0.7 – 1.0 mm; stamens 6; filaments 1.5 – 2 mm, glabrous, very rarely with trichomes; anthers 0.4 – 0.6 mm. **Fruits** orbicular to ovate, widest below the middle, 2.4 – 2.6 x 1.8 – 2.6 mm, tapered to wing vestiges at the apex; valves smooth to veined, glabrous to slightly puberulent, notch 0.2 – 0.4 mm; valves smooth to veined; style 0.2 – 0.4 mm, equaling or slightly exserted beyond the apical notch. **Seeds** ovate, 1.2 – 1.8 x 0.9 – 1.1 mm.

**Key to *Lepidium montanum* and *L. papilliferum*
occurring or possibly occurring in southern Idaho**

1. Plants perennial or completely glabrous **L. montanum** varieties
(other than var. *owyheense* and var. *montanum*)
1. Plants annual or biennial and sparsely to densely pubescent.
 2. Filaments sparsely to densely puberulent; leaves all divided; plants of Ada, Canyon, Elmore, Gem, and Payette counties, elevation 700-1000 m **L. papilliferum**
 2. Filaments glabrous, if trichomes present, then some leaves entire.
 3. Plants 3–5 dm; lowest branch stem 2.2–4.2 dm; trichomes short and sparse, mostly clavate; Canyon, Gem, and Payette counties; likely extinct **L. philonitrum**
 3. Plants 0.5–2.5 (4) dm; lowest branch stem (0.3) 0.6–2.0 (2.3) dm; trichomes dense, either mostly cylindrical or mostly clavate; extant.
 4. At least some leaves entire; stem hairs mostly cylindrical, though often curved or crisped; plants widespread though not yet known from Owyhee County **L. montanum** var. **montanum**
 4. Leaves all divided (except in rare case when filaments have some papillae); stem hairs mostly clavate; plants of Owyhee County, elevation 1450-1700 m **L. montanum** var. **owyheense**

ACKNOWLEDGEMENTS

Dr. Ihsan Al-Shehbaz (Missouri Botanical Garden) gave initial support and advice on this project during a Brassicaceae workshop at The College of Idaho in 2008. He subsequently reviewed the manuscript and provided insight and helpful commentary. Thanks especially to Dr. Lynn Kinter (Idaho Department of Fish and Game) for guidance and help throughout the project. Further thanks to Beth Colket, Karen Colson, Jim and Karen Barbour, Emma George, and Dr. Chris Walser. This research was made possible thanks to the generosity of two Student Research Grants and an Environmental Leadership Program award through The College of Idaho.

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Figure 4. *Lepidium montanum* var. *montanum* differs from *L. papilliferum* (SRP/BF) and *L. montanum* var. *owyheense* in having fewer leaf divisions and more cylindrical (less clavate), less dense and shorter stem trichomes. *Lepidium montanum* var. *owyheense* differs from *L. papilliferum* in lacking filament papillae and in having more highly divided leaflets, and less dense.

Lepidium montanum var. *montanum* upper cauline leaves, showing fewer leaf divisions (with some leaves entire) than seen in *L. papilliferum* or *L. montanum* var. *owyheense*.



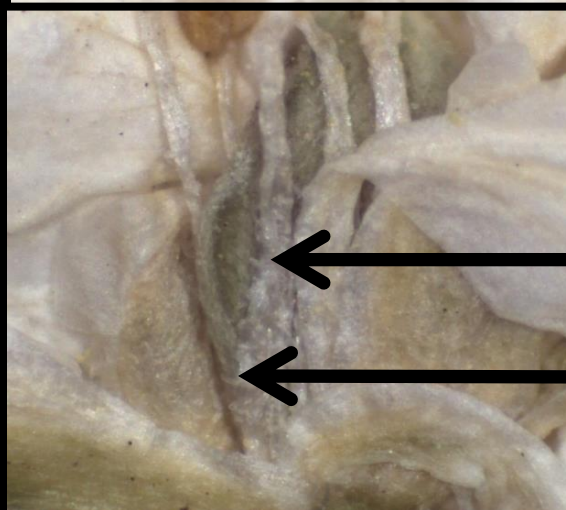
Lepidium montanum var. *montanum* upper stem hairs are significantly shorter and more cylindrical than those of *L. papilliferum* or *L. montanum* var. *owyheense*.



Lepidium montanum var. *owyheense* stamens, showing lack of trichomes on the filaments.



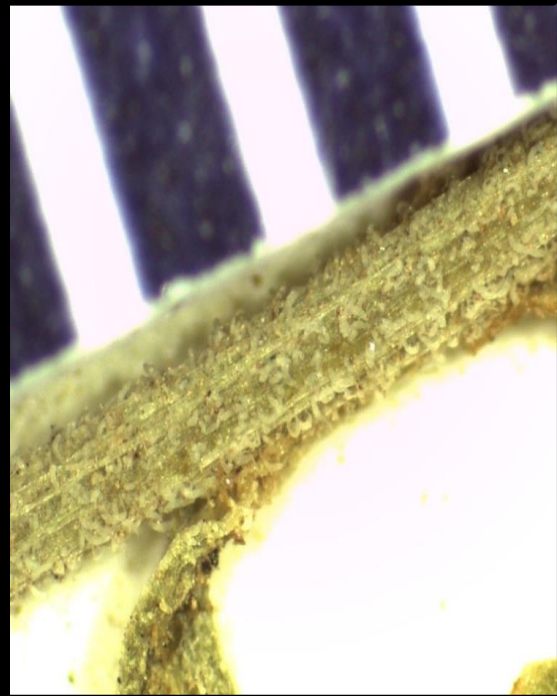
Lepidium papilliferum stamens, showing presence of trichomes on the filaments.



Lepidium montanum var. *owyheense* upper cauline leaves are significantly more divided on average than those of *L. papilliferum* (SRP/BF).



Lepidium montanum var. *owyheense* upper stem hairs are significantly denser than those of *L. papilliferum* (SRP/BF).



SRP/BF *Lepidium papilliferum* upper cauline leaves, are less divided than those of *L. montanum* var. *owyheense*.



SRP/BF *Lepidium papilliferum* upper stem hairs are significantly less dense than those of *L. montanum* var. *owyheense*.

