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VARIATION IN *LEWISIA KELLOGGII* (PORTULACACEAE) WITH DESCRIPTION OF A NEW SPECIES ENDEMIC TO IDAHO

Barbara L. Wilson[1], Valerie D. Hipkins[2], Edna Rey-Vizgirdas[3], and Thomas N. Kaye[1]

ABSTRACT.—*Lewisia kelloggii* has been understood as a rare plant with a disjunct range in California and Idaho. Examination of herbarium specimens and analysis of isozymes in 6 Idaho and 7 California populations revealed consistent differences between plants of the 2 states. Fixed differences in alleles at 2 loci (AAT2 and PGI1) distinguished Idaho from California plants. Genetic identities based on isozymes between Idaho and California populations averaged 0.58, lower than the average for congeneric plant species. Idaho plants were smaller than most California plants, but California plants were variable. The most consistent morphological difference between Idaho and California specimens was the difference in the number of glands on the margins of bracts and sepals. Idaho plants had 0 (–5) pink glands on each margin of these organs, all on teeth near the tips. In California plants these organs had 12–25 glands on each margin, the distal ones elevated on teeth and the proximal ones sessile. We recognize the Idaho plants as a new species, *L. sacajaweana,* and retain the name *L. kelloggii* for the California populations.

Key words: Lewisia kelloggii, Lewisia sacajaweana *sp. nov., Portulacaceae, taxonomy, isozymes, endemic, Idaho, California.*

Lewisia kelloggii K. Brandegee *sensu lato* is a small rare plant found on ridgelines in open areas on excessively drained, coarse-textured, granitic and volcanic soils. It has been understood as having a disjunct range, occurring in the Sierra Nevada of California (from Plumas County south to Fresno County) and in Idaho (in Butte, Custer, Elmore, and Valley Counties). Small morphological differences between the Idaho and California populations have raised the possibility that they should be considered separate species.

Lewisia kelloggii populations in California and Idaho appear reproductively isolated because they have no mechanism of primary seed dispersal likely to cross the 540 km between them (Mathew 1989). Geographic isolation and consequent reproductive isolation alone are not sufficient to justify treating the Idaho and California populations as members of 2 distinct species. Separate species status would be justified if isolation has led to genetic differentiation expressed as consistent morphological differences between the species, fixed differences in the alleles studied in isozyme analysis, and low genetic identities.

We examined *L. kelloggii* specimens from California and Idaho to learn whether morphological traits consistently distinguish them. We performed an isozyme analysis of 7 California and 6 Idaho populations to assess genetic variability, compare alleles occurring in different populations, and measure genetic identity (Nei 1973). We selected isozyme analysis for this study because the results can be compared with large databases of similar results from other species (Hamrick and Godt 1989) and because isozymes had worked well to distinguish species in an earlier study of California *L. kelloggii* (Foster et al. 1997). We used the morphological and isozyme information to assess the species status of populations from the 2 states. Anticipating results, we refer to the Idaho populations as *L. sacajaweana* throughout this paper.

METHODS

Morphology

We borrowed *L. kelloggii* specimens from herbaria at University of California, Berkeley (UC and JEPS); California Academy of Science (CAS and DS); and California State University, Chico (CHSC). Additional specimens were collected in Idaho during 2001 and deposited at Oregon State University (OSC). The

[1]Institute for Applied Ecology, 563 SW Jefferson Street, Corvallis, OR 97333.
[2]USDA Forest Service, National Forest Genetic Electrophoresis Laboratory (NFGEL), 2480 Carson Road, Placerville, CA 95667.
[3]USDA Forest Service, Boise National Forest, 1249 S. Vinnell Way, Suite 200, Boise, ID 83709.

TABLE 1. Collection locations for *Lewisia kelloggii* samples used in the isozyme study. *N* = sample size.

State	National forest	Population	Latitude/Longitude	*N*	Collector	Date collected
CA	Eldorado	Brown Rock	38.66°N 120.26°W	32	Robert C. Saich	28-Jun-99
CA	Eldorado	Pack Saddle Pass	38.76°N 120.17°W	32	Robert C. Saich	28-Jun-99
CA	Plumas	Plumas A	39.75°N 120.86°W	28	Molly Hunter	27-Jul-99
CA	Plumas	Plumas B	39.79°N 120.90°W	18	Molly Hunter	27-Jul-99
CA	Sierra	Shuteye Peak	37.35°N 119.42°W	30	Robert C. Saich	28-Jun-00
CA	Tahoe	Soda Springs #1	39.31°N 120.43°W	30	Robert C. Saich	22-Jun-00
CA	Tahoe	Soda Springs #2	39.31°N 120.41°W	30	Robert C. Saich	22-Jun-00
ID	Boise	Burnt Creek	43.31°N 115.28°W	30	Amanda Dabbs	22-Jun-99
ID	Boise	Greencreek Lake	43.34°N 115.20°W	28	Amanda Dabbs	15-Jun-99
ID	Boise	Miller Mountain	44.08°N 115.30°W	30	Amanda Dabbs	07-Jul-99
ID	Boise	No Name Creek	43.31°N 115.28°W	30	Amanda Dabbs	22-Jun-99
ID	Boise	Road 409	44.37°N 115.44°W	30	Amanda Dabbs	17-Jun-99
ID	Boise	Whitehawk Summit	44.23°N 115.53°W	30	Amanda Dabbs	08-Jul-99

herbaria at the Rancho Santa Ana Botanic Garden (RSA); the Rocky Mountain Herbarium, Laramie, Wyoming (RM); and Humboldt State University (HSC) did not have specimens of this plant (acronyms from Holmgren et al. 1990). For the purpose of describing the species, we measured or counted plant parts on all plants for which measurements or counts were possible. A list of all specimens examined is found in the Appendix.

For morphometric analysis, we quantified 7 morphological traits (Table 2). Specimens included in this analysis were all those that had petals that dried flat (so that they could be measured) and bracts and sepals with margins exposed: 7 of *L. kelloggii* ssp. *kelloggii,* including 2 of *Kellogg s.n.;* 8 of *L. kelloggii* ssp. *hutchisonii* Dempster; and 7 of *L. sacajaweana,* including 2 of *Hitchcock & Muhlick 8690* (Appendix). The ratio of longest leaf length to widest leaf width was log-transformed, and other values were used untransformed because their distribution did not differ significantly from normal. We used discriminant analysis to test for significant differences among Idaho specimens and California specimens identified as *L. kelloggii* ssp. *kelloggii* and *L. kelloggii* ssp. *hutchisonii,* to determine which traits were most useful for distinguishing taxa. We used principal components analysis to evaluate patterns of morphological variation in the specimens, including morphological discontinuities or overlap among taxa, and factor analysis to evaluate the importance of individual traits to the observed pattern of variation. All 3 analyses were performed using NCSS (Hintz 2001).

Isozyme Study

SAMPLING.—Two to 3 leaves per plant were collected from each of approximately 30 plants per population in 7 California and 6 Idaho populations (Table 1). Leaves from each individual were bagged separately from those of other individuals, and stored and shipped on ice within 2 days of collection to the National Forest Genetic Electrophoresis Laboratory (NFGEL), where they arrived still cold and alive. Collection locations were reported in terms of legal descriptions (township / range / section) and converted to latitude/longitude using the program TRS2LL (Wefald 2001). Idaho populations sampled the entire known range of the species. California collection localities were chosen to sample most heavily the central and northern parts of the range, where both named subspecies grow. One southern population, from Shuteye Peak, was included. Three pairs of populations were very close together. The Burnt Creek and No Name Creek populations were within 0.6 mile on Red Mountain, Idaho. The 2 Soda Springs populations were within 2 miles of each other. The 2 populations from the Plumas National Forest were a few hundred feet apart.

TISSUE PREPARATION.—We refrigerated samples until they could be processed, within 3 days of arrival. One 7-mm-diameter leaf disk per individual was submerged in 100 µL of a 0.1 M Tris-HCl (pH 8.0) extraction buffer, with 10% (w/v) polyvinylpyrrolidone-40, 10% sucrose, 0.17% EDTA (Na_2 salt), 0.15% dithiothreitol, 0.02% ascorbic acid, 0.10% bovine albumin, 0.05% NAD, 0.035% NADP, and

TABLE 2. Variables used in morphometric analysis of *Lewisia kelloggii* and *L. sacajaweana.* Factor weights for the first 2 axes of discriminant analysis (DA) and principal components analysis (PCA) for *Lewisia.* Values for the DA axes are correlations between variables and variates (axes). Values for PCA are factor loadings on axes. * = log transformed.

Variable	Units	*L. kelloggii* ssp. *kelloggii* mean (*s*)	*L. kelloggii* ssp. *hutchisonii* mean (*s*)	*L. sacajaweana* mean (*s*)	Canonical variate 1 DA	Canonical variate 2 DA	PCA axis 1 PCA	PCA axis 2 PCA
N		8	7	7				
Leaf length	cm	2.89 (1.09)	5.21 (2.03)	4.51 (1.66)	–0.00862	–0.4-634	0.150738	0.901428
Petal length	cm	1.69 (0.16)	2.62 (0.43)	1.58 (0.24)	–0.24104	–0.67651	0.823643	0.353622
Sepal length	cm	0.86 (0.12)	1.14 (0.18)	0.63 (0.13)	–0.27269	–0.32193	0.910429	0.231352
Bract length	cm	0.81 (0.16)	1.01 (0.30)	0.68 (0.25)	–0.10518	–0.14850	0.671260	0.324558
Glands on sepals	count	14.43 (2.15)	18.12 (2.59)	2.14 (2.12)	–0.58909	0.07020	0.879224	–0.271780
Glands on bracts	count	18.43 (2.78)	19.12 (5.05)	0.43 (1.13)	–0.47703	0.38120	0.830819	–0.273720
Leaf length/width ratio*	—	1.50 (0.31)	1.56 (0.40)	2.05 (0.27)	0.13455	–0.17284	–0.576400	0.675336

0.005% pyridoxal-5-phosphate (USDA Forest Service 2000). Samples were then frozen at –70°C. On the day of electrophoresis, samples were thawed and ground and the extracts absorbed onto 3-mm-wide wicks prepared from Whatman 3MM chromatography paper.

ELECTROPHORESIS.—Methods of electrophoresis followed the general methodology of Conkle et al. (1982), with some modifications (USDA Forest Service 2000). All enzymes were resolved on 11% starch gels. We used a lithium borate electrode buffer (pH 8.3) with a Tris citrate gel buffer (pH 8.3; Conkle et al. 1982) to resolve alcohol dehydrogenase (ADH), fluorescent esterase (FEST), leucine aminopeptidase (LAP), phosphoglucomutase (PGM), and phosphoglucose isomerase (PGI). We used a sodium borate electrode buffer (pH 8.0) with a Tris citrate gel buffer (pH 8.8; Conkle et al. 1982) to resolve glucose-6-phosphate dehydrogenase (G6PDH), glutamate-oxaloacetate transaminase (GOT), triosephosphate isomerase (TPI), and uridine diphosphoglucose pyrophosphorylase (UGPP). A morpholine citrate electrode and gel buffer (pH 6.1; USDA Forest Service 2000) was used to resolve isocitrate dehydrogenase (IDH), phosphogluconate dehydrogenase (6PGD), and malate dehydrogenase (MDH). Enzyme stain recipes follow USDA Forest Service (2000). Ten percent of individuals were run and scored twice.

ISOZYME INTERPRETATION.—We inferred genetic interpretations directly from isozyme phenotypes based on knowledge of the generally conserved enzyme substructure, compartmentalization, and isozyme number in higher plants (Gottlieb 1981, 1982,Weeden and Wendel 1989). We are unaware of a chromosome count for *L. kelloggii* (Moldenke 1973, Mathew 1989, Dempster 1993, Goldblatt 2001). One diploid locus each was scored for ADH, FEST, and PGM1. Two loci (i.e., a pair of homoeologous loci) were scored for G6PDH, GOT2, IDH1, LAP2, MDH1, MDH2, MDH4, PGI2, PGM2, TPI1, TPI2, UGPP1, UGPP2, 6PGD1, and 6PGD2. PGI1 was also scored and used to distinguish populations but was not included in statistical analysis. For enzymes scored as pairs of loci, an isozyme band pattern comprising a single band was considered to represent 2 homoeologous loci. For analysis as an allotetraploid, we assumed that 1 locus of each pair was invariant and assigned all uncommon alleles to the other unless the observed band combinations or intensities suggested otherwise.

Assuming that the plants were allotetraploid, we analyzed 33 loci using Popgene, version 1.21 (Yeh et al. 1997). A locus was considered polymorphic if an alternate allele occurred even once. We calculated unbiased genetic distances (Nei 1978), expected heterozygosity (Nei 1973), and gene flow [Nm (the effective number of migrants per year) = 0.25(1 – Fst)/Fst; (Slatkin and Barton 1989)]. The fixation indices for populations (F) were calculated in Popgene (Yeh et al. 1997) following Hartl and Clark (1989), but F-statistics for the hierarchy of regions within the species (Fpt), populations within the species (Fst), populations within regions (Fsp), and individuals within the species (Fit), regions (Fip), and populations (Fis) were calculated by the method of Weir (1990). The 2 methods produced slightly different values for F. Dendrograms based on

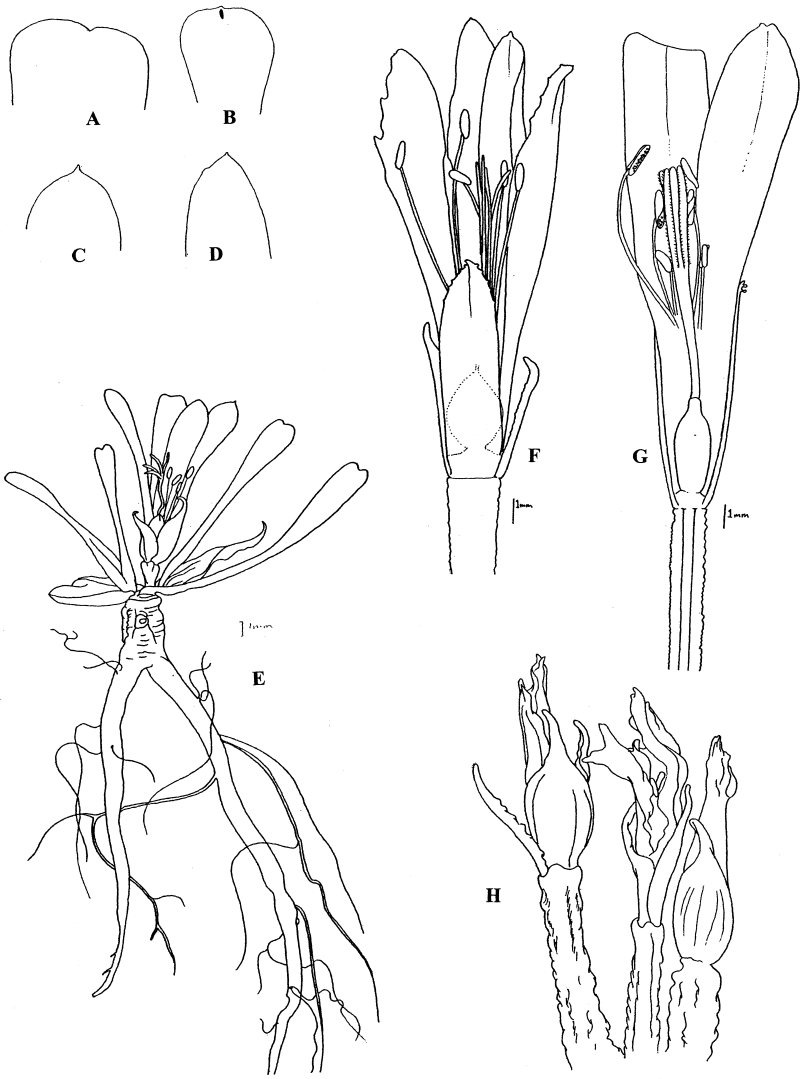

Fig. 1. *Lewisia sacajaweana.* A–D, petal tips; E, habit; F, flower, with location of ovary behind sepal indicated; G, flower, cut open; H, flowers after anthesis. Note that withered petals remain in flower, sepals expand around growing ovary, and peduncle shrinks. Scale bars = 1 mm.

unbiased genetic distances (Nei 1978) were generated using UPGMA.

RESULTS

Morphology

The Idaho plants are small, succulent, scapose plants with white flowers (Figs. 1, 2). The peduncle is relatively narrow and elongate during flowering but becomes shorter and thicker after flowering, bringing the capsule back to or near the ground (Fig. 1). Petal tip shape is variable and petals are often more or less damaged or misshapen (Fig. 1). Idaho plants had a smaller range of variation than California plants (Table 2). Idaho plants had small petals like *Lewisia kelloggii* ssp. *kelloggii,* but they tended to have proportionately narrower leaves than either California subspecies. The most consistent difference between the plants of the 2 states was in number of teeth and/or glands on the margins of the

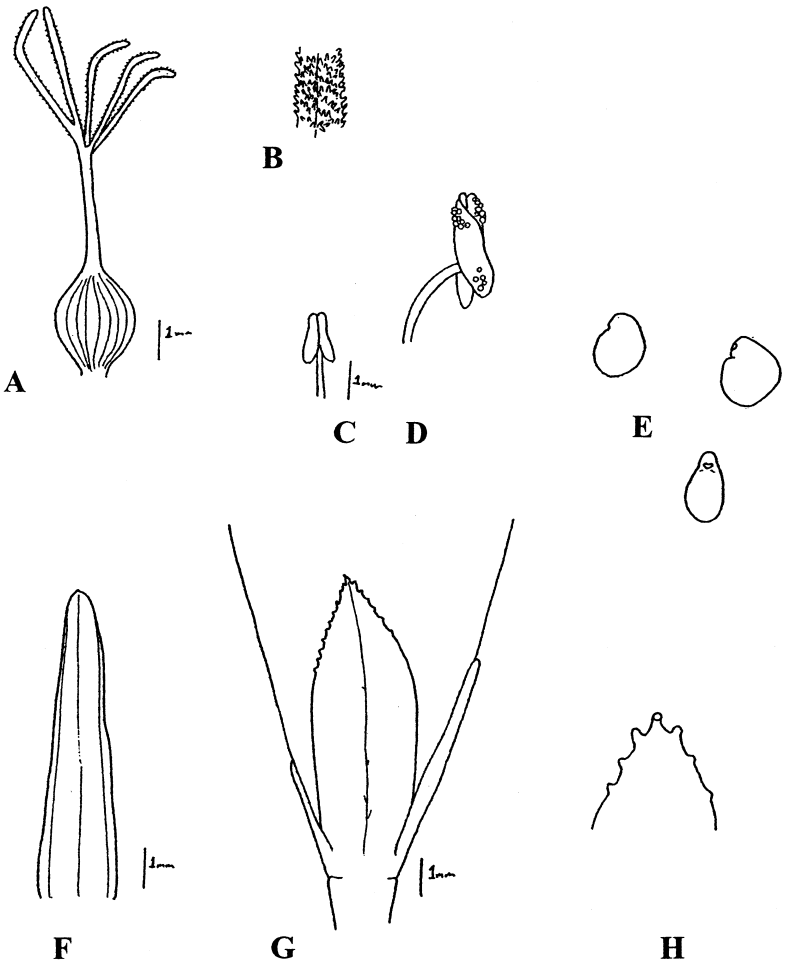

Fig. 2. Flower parts of *Lewisia sacajaweana.* A, pistil (note bend in stigmas); B, section of stigma; C and D, anthers; E, seeds; F, bract with hyaline margins; G, flower base showing sepal; H, sepal tip with teeth and gland-tipped mucro.

bracts and sepals (Table 3). Idaho plants usually lacked pink glands along these margins (though they might have up to 5), whereas California plants had 12–25 pink glands (compare Fig. 3 with Figs. 1E, 1H, and 2H).

Discriminant analysis of morphological traits indicated that all 3 *Lewisia* taxa were significantly different from each another ($P < 0.0001$). However, the 2 California subspecies (*L. kelloggii* ssp. *hutchisonii* and *L. kelloggii* ssp. *kelloggii*) were similar enough that there was a slight chance ($P < 0.02$) that 4 specimens were misclassified between them, 2 because they combined the large flower size of *L. kelloggii* ssp. *hutchisonii* with the small leaves of *L. kelloggii* ssp. *kelloggii,* and 2 because their measurements were mostly intermediate. Numbers of glands on sepals and bracts were the variables most highly correlated with the 1st discriminant axis ($r = –0.59$ and –0.48, respectively), which separated Idaho from California specimens (Table 2). Length of leaves and petals were the 2 variables most highly correlated with the 2nd discriminant axis ($r = –0.41$ and –0.68, respectively), which distinguished the larger *L. kelloggii* ssp. *hutchisonii* specimens from the smaller *L. kelloggii* ssp. *kelloggii* and *L. sacajaweana.* When the analysis was rerun without using gland number (results not shown), only 1 specimen each of *L. kelloggii*

TABLE 3. Selected morphological traits in *Lewisia* populations in Idaho and California. * = excluding the usually gland-tipped mucro at the tip.

Trait	Idaho (*L. sacajaweana*)	California (*L. kelloggii*)
Flower placement	nestled in rosette	nestled in rosette or held above it
Peduncle	jointed at base	jointed at base or above, the segment below base often equal to that above
Placement of marginal teeth and/or glands	often only near tip; always in upper half	extending to near base
Marginal teeth on sepals and bracts*	eglandular (or upper 1–5/ side with glands)	glandular
Number of marginal teeth and/or glands on each side*	0 (–9)	(5–) 8–25
Petal color	white	white to pink or lavender
Petal number	5 (–7)	(5–) 7–9
Petal length	10–20 mm	15–30 mm
Stamen number	8 (12)	8–26
Anther color	cream to yellow	cream, yellow, or pink
Style branches	4 (–5)	3–6

ssp. *kelloggii* and *L. kelloggii* ssp. *hutchisonii* were misclassified as *L. sacajaweana.*

Principal components analysis of morphometric data clearly separated *L. sacajaweana* from *L. kelloggii* along axis 1, but the California specimens identified as *L. kelloggii* ssp. *hutchisonii* and *L. kelloggii* ssp. *kelloggii* did not form separate clusters; some specimens were intermediate (Fig. 4). The 1st axis accounted for 54% of the morphological variation, and the first 2 axes together accounted for 75%. Factor loadings for this analysis suggested that the 1st axis was strongly associated with flower traits (glands on sepals and bracts, as well as sepal and petal length), and the 2nd reflected the length and shape of leaves (Table 2). Two sheets for each of 2 collections (*Kellogg s.n.* and *Hitchcock and Muhlick 8680*) were included in the analysis. These sheets contained different individual plants. Sheets from the same collection did not cluster together, indicating considerable within-population variation.

Lewisia kelloggii ssp. *hutchisonii* specimens examined were mostly from the northern part of the species' California range (Plumas, Sierra, and Butte Counties) with 1 from the central part of the range (Placer County). Most *L. kelloggii* ssp. *kelloggii* specimens examined came from the southern part (Mariposa County) and central part (Placer and Nevada Counties), with only 1 from the north part (Plumas County) of the range, where *L. kelloggii* ssp. *hutchisonii* predominates.

Polyploidy

Evidence for polyploidy in *Lewisia kelloggii* included multiband patterns in 3 pairs of homoeologous loci: PGI2 (7 populations), PGM2 (1 population), and TPI1 (3 populations). We also observed unbalanced heterozygosity in 10 loci and high levels of heterozygosity, including 8 pairs of homoeologous loci in which all individuals of at least 1 population were heterozygous. However, 3 enzymes (ADH, FEST, and PGM1) appeared diploid because they exhibited high levels of homozygosity, 2 classes of homozygotes occurred in some populations, and all heterozygotes appeared balanced. Variable numbers of gene copies have been observed before in polyploids (Stebbins 1947) and might be expected in a genus characterized by an aneuploid series of chromosome numbers (Table 4).

Evidence about the mode of inheritance in homoeologous loci was mixed. The fixed heterozygosity characteristic of polyploids with disomic inheritance was observed in at least 1 population in each of 7 homoeologous pairs of loci. All populations exhibited fixed heterozygosity for 6PGD2. On the other hand, some enzymes in some populations gave evidence for tetrasomic inheritance (Soltis and Rieseberg 1986). Two different classes of unbalanced heterozygotes (1112 and 1222) were observed in 8 populations for 6 loci. In 5 loci that had other evidence of polyploidy, 8 populations exhibited 2 alternate homozygous conditions.

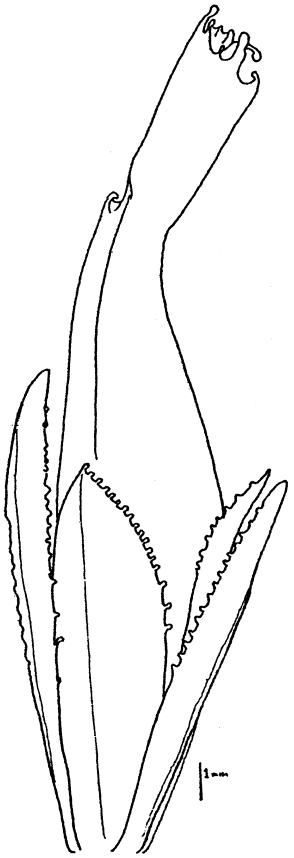

Fig. 3. Flower of *Lewisia kelloggii* after anthesis. Note toothed bracts and sepals.

Genetic Variation and Differentiation

Lewisia kelloggii was highly variable, with 85% of the loci polymorphic, averaging more than 3 alleles per locus (Table 5). In *L. kelloggii* populations, 39%–58% of the loci were polymorphic in each population, but in Idaho, 5 of the 6 populations had less than 20% polymorphic loci.

Genetic variation was strongly structured by geography. About half the isozyme variation detected in this study was variation between states (Fst = 0.525; Table 6). Fixed differences between states were detected in 1 pair of homeologous loci (AAT-2) and in the PGI1 locus. Nearly fixed differences were detected in 3 pairs of homoeologous loci. In 6PGD1, Idaho samples always had allele 2, with variants 4 and (rarely) 1, while California plants never had allele 2, but had 3 alleles never observed in Idaho and (rarely) allele 1. In MDH2, Idaho individuals had alleles 1, 2, and occasionally 6. Plants from northern and central California had alleles 3, 7, and rarely 4, but the southern Shuteye Peak population had 2, 7, and rarely 4. In TPI1, all Idaho individuals had allele 1 and a few were heterozygotes with 1 and 2, while California populations nearly all had allele 4, none had allele 2, and allele 1 was rare. Twelve alleles at 8 pairs of homoeologous loci were unique to Idaho, and 29 alleles at 14 pairs of homoeologous loci were unique to California. The mean genetic identity between California and Idaho populations was 0.58. When these genetic identities were expressed diagrammatically, the populations fell easily into 2 groups, 1 from California and 1 from Idaho (Fig. 4).

Geographic structuring of isozyme variation also existed within states. Intrastate populations were highly differentiated, with Fst of 0.43 in California and 0.62 in Idaho (Table 6). Genetic identity among California populations varied from 0.69 to 0.99, and within Idaho varied from 0.76 to 0.99. Populations within 2 miles of each other were similar (0.965 for Plumas A and B and 0.998 for Soda Springs 1 and 2 in California; 0.992 for Burnt Creek and No Name Creek in Idaho). Inferred gene flow was very low, especially among Idaho populations (Nm = 0.324 in California, 0.155 in Idaho.)

Samples from the Plumas National Forest (Table 1) came from populations previously identified as *L. kelloggii* ssp. *hutchisonii.* Genetic identities of these samples with other northern California populations averaged 0.873 (range 0.835–0.909).

The California population from Shuteye Peak, located over 100 km south of the other populations included in this analysis, was particularly distinct. Genetic identities between the Shuteye Peak population and other California populations were low, averaging 0.73. Of the 42 alleles detected in this population, 48% were widespread (occurring in both California and Idaho), 33% were shared with other California populations, 7% were shared only with Idaho populations, and 12% were unique.

DISCUSSION

Distinctions Between Idaho and California Populations

The *Lewisia kelloggii* specimens from Idaho can be distinguished from all the varied populations of *L. kelloggii* from California. The

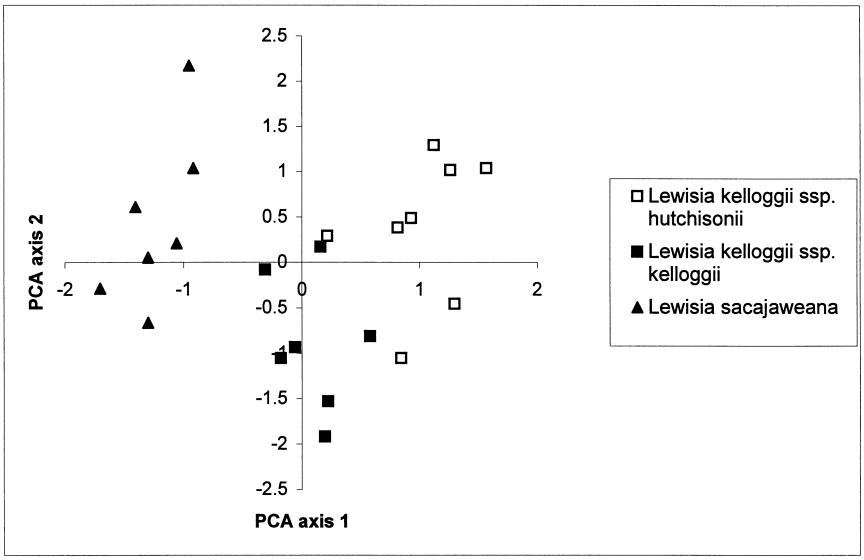

Fig. 4. Principal components analysis (components 1 and 2) of 7 morphological traits scored for *Lewisia kelloggii* ssp. *kelloggii, L. kelloggii* ssp. *hutchisonii,* and *L. sacajaweana.*

most consistent morphological trait separating them is the number of glands on the bracts and sepals, the most strongly weighted canonical variates in our discriminant analysis and with factor weights exceeding 0.8 in principal components analysis. In *L. kelloggii* these organs are fringed with teeth bearing many (12–25) glands, but in *L. sacajaweana* they typically lack glands, except 1 at the very tip. This trait can be difficult to assess in dried specimens because the bracts and sepals tend to roll up longitudinally, concealing the margins. The 2 species also tend to differ in size of flower parts (smaller in *L. sacajaweana*); sepal length was the most strongly weighted factor for principal components analysis axis 1, and petal length was almost as heavily weighted (Table 2). In addition, *L. sacajaweana* had proportionally narrower leaves than *L. kelloggii.*

Lewisia sacajaweana and *L. kelloggii* are also clearly distinguished by isozymes. Fixed differences in 2 enzyme systems differentiate them. Genetic identities between Idaho and California populations average 0.58. In general, plant populations within the same species (and subspecies) have genetic identities greater than 0.90, and populations of different congeneric species have genetic identities (Nei 1973) averaging 0.68, though varying from 0.25 to 1.00 (Crawford 1990). The Idaho plants have not previously been recognized as a species. However, the Idaho populations are amply distinct from the California plants and should be recognized as a separate species.

Lewisia brachycalyx A. Gray, *L. kelloggii,* and *L. sacajaweana* share the traits of solitary flowers having the 2 bracts so close below the sepals that they appear to be 2 more sepals. All 3 species belong in the *Lewisia* section *Brachycalyx* (Mathew 1989). *Lewisia brachycalyx* has a disjunct distribution extending from Baja California to Arizona, and perhaps also New Mexico and southern Utah (Davidson 2000). *Lewisia sacajaweana* resembles *L. brachycalyx* in that both have narrower leaves than *L. kelloggii* and both typically lack glands on the edges of the bracts and sepals. However, *L. sacajaweana* has blunt to notched leaf tips like *L. kelloggii* and unlike the tapered tips of *L. brachycalyx.*

We name the small bitterroot from Idaho *Lewisia sacajaweana* in honor of Sacajawea (alternate spelling Sacagawea), the Shoshone woman who participated in the Lewis and Clark Expedition, traveling through the limited range of *L. sacajaweana* 2 centuries ago. Bitterroot was valued by numerous tribes in the Rocky Mountain region for food and medicinal uses.

TABLE 4. Published chromosome numbers of *Lewisia.* * = recently moved to a different genus: *Cistanthe tweedyi* (Hershkovitz 1990).

Chromosome number	Species	Reference
2n = 20	*L. brachycalyx* G. Engelmann ex A. Gray	M. Daker in Elliott 1966
2n = 22	*L. longipetala* (Piper) Clay	Dempster 1993
2n = about 24	*L. congdonii* (Rydberg) S. Clay	M. Johnson in Mathew 1989
2n = 28	*L. cantelovii* J. T. Howell	Hohn 1975
	L. cotyledon (S. Watson) B. L. Robinson	Hohn 1975, M. Johnson in Mathew 1989
	L. leeana (T. C. Porter) B. L. Robinson	Hohn 1975, M. Johnson in Mathew 1989
	L. rediviva Pursh	M. Johnson in Mathew 1989
2n = 30	*L. columbiana* (T. J. Howell ex A. Gray) B. L. Robinson	Hohn 1975
2n = about 56	*L. nevadensis* (A. Gray) B. L. Robinson	M. Johnson in Mathew 1989
2n = about 66	*L. pygmaea* (A. Gray) B. L. Robinson	Weins and Halleck 1962
2n = 92	*L. tweedyi* (A. Gray) B. L. Robinson*	Kruckeberg 1957, Hohn 1975

Sacajawea harvested various food plants for the Corps of Discovery, probably including roots of *L. rediviva*, and she may well have known this obscure species.

Description of *Lewisia sacajaweana*

Lewisia sacajaweana B.L. Wilson and E. Rey-Vizgirdas **sp. nov.** (Fig. 4)

TYPE: USA: IDAHO: Boise County: Boise National Forest, Pilot Peak, on slopes east and west of road 380, at intersection with spur road to Pilot Peak Lookout, west of lookout, T07N R06E S01, 43°57.81′N, 115°41.8′W, elevation 3276 m. 13 July 2002. *J. J. Schenk and Edna Vizgirdas 527*. (Holotype: ID; isotypes, CAS, MO, OSC).

Herba pusilla; perennis, scaposa, succulenta, glabra, radice palari. Folia rosulata, integra spathulata 4.8–8 cm longa, brunneola vel olivacea apice rotundato aut emarginato, mucronato. Scapus articulatus prope basin, 15–30 mm longus sub anthesi. Bracteae 2, subulatae, 5.5–8 mm longae, proxime infra sepala, sepalis similes sed sepalis dimidia parte angustiores. Sepala 2, rosea, plerumque brunneola vel olivacea, anguste ovata, 5–8 mm longa, 1.75–3 mm lata, mucrone roseo, glandifero, et dentibus 0–3 (–7) in quoque marginem eglandulatis vel raro glande rosea. Petala alba, 5 (–7), 10–20 mm longa, integra vel dentibus paucis, apice rotundato, obtuso AUT emarginato, mucrone roseo saepe. Stamina 8 (12), 314 mm longa, antheris 1–1.5 mm longis, flavis. Pistillum stigmatibus 4 (–5), albis, 3–5 mm longis. Semina 1.3–1.6 mm × 1.4–2.0 × 1 mm, testa nigra, nitida, minute tuberculata.

Planta rara in solo sterili granitico montium in Idaho.

A *Lewisia kelloggii* sepalis et bractis integris vel dentibus eglandulatis distinguenda.

A *Lewisia brachycalyx* foliis spathulatis distinguenda.

A low, scapose, succulent, glabrous perennial herb with a taproot, 3–7 cm tall. (All measurements taken from dried specimens.) Taproot single or often with 2 main branches, the fleshy portion 3–8 mm wide and 4–10 cm long; surface of root reddish brown or brown, cortex white, surface of stele pale yellow to pink or orange, especially toward the top. Caudex very short, 1.5–5 cm wide, subterranean. Leaves in a rosette, ascending, entire, with stomata on both sides, often dying and rolling up at or before anthesis; the outermost (oldest) leaves of the year papery and 1.3–3 cm long, 3–5 mm wide, rounded at tip, mucronate, sometimes fleshy and pink distally; the inner (younger) leaves succulent, (1.9) 4.8–8 cm long and (3.5) 4–7 mm wide, dull green to reddish brown (but with the lower 2–4 cm typically whitish), narrowly oblanceolate or spatulate, very gradually tapering to the petiole, which shrinks and becomes wrinkled when dry; the leaf surface covered with a cuticle 1.5 μm thick topped with waxy ridges and flakes which may give the appearance of minute pubescence; leaf tips rounded and slightly notched. Scape jointed at the base but not disarticulating, the portion above the joint 15–30 mm long and 1.0–1.6 mm wide at anthesis, but shrinking to 5–7 mm long and 1.7–2.0 mm wide after anthesis and pulling the flower back to the ground. Bracts 2, lanceolate, awl-shaped, 5.5–8 mm long and 0.9–1.6 mm wide at half length, located immediately below the sepals and similar to them in color and length but about half as wide, with scarious margins 0.3 mm wide near the base and tapering in width upwards; tipped by a usually glandular mucro and with

TABLE 5. Genetic variation in *Lewisia kelloggii* populations: *n* = average number of samples per locus, P = percent polymorphic loci, A = average number of alleles per locus, Ae = effective number of alleles per locus (Kimura and Crow 1964), Ho = observed heterozygosity, He = expected heterozygosity, SW = Shannon's information index (Lewontin 1972). Standard deviation in parentheses.

Forest: Population	*n*	P	A	Ae	Ho	He	SW
Total	370	85	3.36 (1.60)	1.72 (0.57)	0.06 (0.07)	0.35 (0.22)	0.61 (0.39)
California (*L. kelloggii*)	196	82	2.85 (1.37)	1.56 (0.63)	0.09 (0.13)	0.28 (0.23)	0.49 (0.40)
Eldorado: Brown Rock	32	52	1.76 (0.90)	1.39 (0.52)	0.11 (0.18)	0.20 (0.24)	0.32 (0.38)
Eldorado: Pack Saddle Pass	32	58	1.94 (1.00)	1.45 (0.62)	0.13 (0.20)	0.22 (0.25)	0.35 (0.41)
Plumas: Plumas A	27	39	1.64 (0.93)	1.27 (0.49)	0.04 (0.07)	0.14 (0.22)	0.23 (0.35)
Plumas: Plumas B	18	42	1.58 (0.79)	1.28 (0.46)	0.08 (0.15)	0.15 (0.22)	0.24 (0.34)
Sierra: Shuteye Peak	30	45	1.61 (0.75)	1.18 (0.30)	0.07 (0.13)	0.12 (0.17)	0.20 (0.27)
Tahoe: Soda Springs 1	30	48	1.67 (0.82)	1.28 (0.49)	0.10 (0.19)	0.14 (0.21)	0.24 (0.34)
Tahoe: Soda Springs 2	30	39	1.58 (0.83)	1.26 (0.45)	0.08 (0.16)	0.14 (0.21)	0.22 (0.34)
Idaho (*L. sacajaweana*)	174	58	1.88 (0.93)	1.26 (0.40)	0.02 (0.05)	0.15 (0.20)	0.24 (0.31)
Boise: Burnt Creek	30	12	1.12 (0.33)	1.04 (0.14)	0.02 (0.08)	0.03 (0.09)	0.04 (0.14)
Boise: Greencreek Lake	27	48	1.70 (0.85)	1.29 (0.53)	0.07 (0.14)	0.14 (0.22)	0.24 (0.34)
Boise: Miller Mountain	30	18	1.18 (0.39)	1.07 (0.18)	0.01 (0.01)	0.05 (0.12)	0.08 (0.18)
Boise: No Name Creek	30	15	1.15 (0.36)	1.08 (0.24)	0.02 (0.06)	0.05 (0.13)	0.07 (0.19)
Boise: Road 409	29	18	1.21 (0.48)	1.09 (0.23)	0.03 (0.07)	0.06 (0.14)	0.09 (0.21)
Boise: Whitehawk Summit	30	9	1.09 (0.29)	1.04 (0.16)	0.01 (0.04)	0.02 (0.09)	0.04 (0.13)

TABLE 6. F-statistics (fixation indices) for *Lewisia kelloggii* for a 3-level sampling hierarchy (individuals within populations within states within total), assuming that the plants are allotetraploids with disomic inheritance.

Comparison	F
individual within population	Fip = 0.483
individual within state	Fis = 0.755
individual within total	Fit = 0.884
population within state	Fps = 0.526
population within total	Fpt = 0.775
state within total	Fst = 0.525

0 (–5) teeth on each side in the upper half, these teeth eglandular or less often tipped with a pink gland. Sepals 2, ovate-lanceolate, 5–8 mm long and 1.75–3 mm wide, sometimes pink but usually dull green or brown and becoming pink in the upper half with age; sepals tipped by a usually glandular mucro and with 0–3 (–9) teeth on each side in the upper half, these teeth eglandular or less often tipped with a pink gland; sepal base fitting tightly around the growing capsule. Petals white, 5 (–7), entire or with a few widely and irregularly spaced teeth, which may be pink and gland-tipped, near the tip; petals 10–20 mm long and 1.5–5 mm wide, widest near the tip (or near the center in unusually small petals), the tip rounded, obtuse, or emarginate, often with a tiny mucro which may be pink. Withered petals remain in the flower after anthesis, covering the capsule. Stamens 8 (–12), in 2 (–3) series that differ in length, 3–14 mm long, the anthers pale yellow, 1–1.5 mm long. Ovary superior, pink, 2–3 mm long at anthesis; undivided style white or pink, topped by 4 (–5) white style branches each 3–5 mm long; style branches minutely hairy and apparently stigmatic their entire length, at anthesis spreading horizontally and bending horizontally at nearly 90°, 0.5–1 mm from the tip, forming a swastika-like shape. Capsule often persisting below ground and releasing seeds by decomposition. Seeds thickly disk-shaped, 1.3–1.6 × 1.4–2.0 × 1 mm, shiny black, the surface cells swelling outward between the anticlinal walls, producing a finely tuberculate surface.

Key to Selected *Lewisia* section *Brachycalyx*

1. Bracts more than 2, or distinctly separated from the 2 sepals . . . . . other sections
1. Bracts 2 and located immediately below the sepals, so sepals apparently 4 2
   2. Leaves oblanceolate, the tips tapered; flowers 3–6 cm in diameter, sepals and bracts entire) . . . . . *Lewisia brachycalyx*
   2. Leaves spatulate, the tips rounded to emarginate; flowers usually 2–3 cm in diameter; sepals and bracts entire or toothed) 3
      3. Teeth on each side of the sepals and bracts 0–5 (–7), usually lacking pink glands, located in only upper half . . . . . *Lewisia sacajaweana*
      3. Teeth on each side of sepals and bracts (5–) 8–25, glandular, the teeth and/or

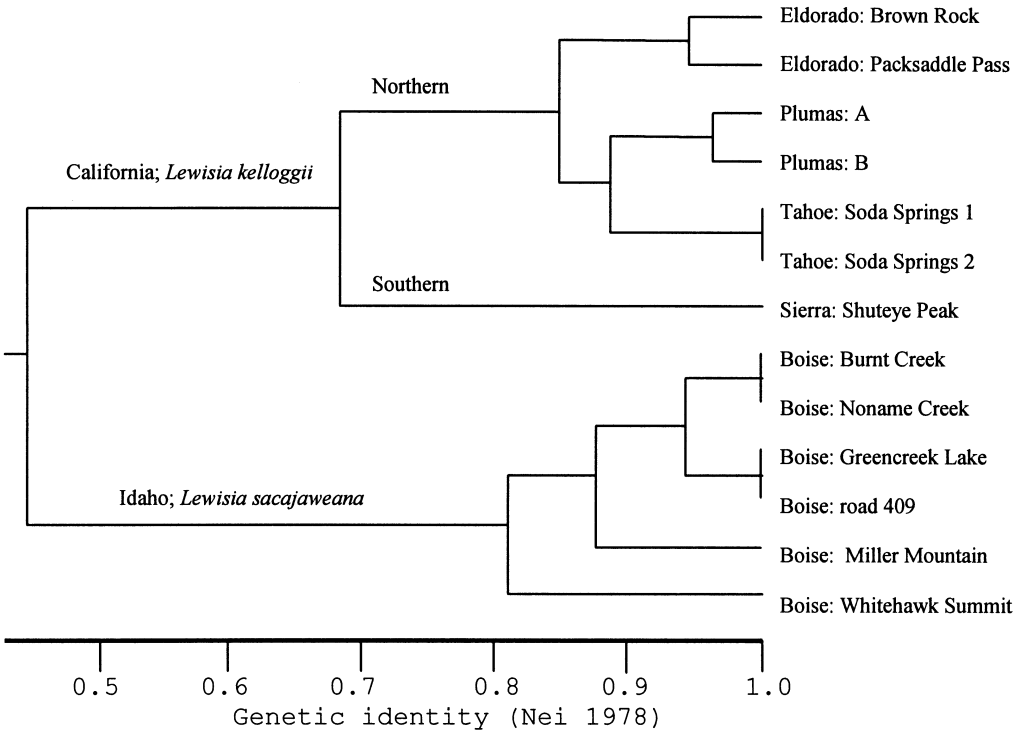

Fig. 5. Similarities among *Lewisia kelloggii* populations, based on Nei's (1978) unbiased genetic distances.

glands extending well below the middle . . . . . *Lewisia kelloggii*

4. Longest leaves usually >4.5 cm (–10 cm) long, >1 cm wide; petals 2 or >2 cm long; range Placer County and north . . . . . *L. kelloggii* ssp. *hutchisonii*

4. Longest leaves usually <4.5 cm long, <1 cm wide; petals usually <2 cm long; throughout range of the species . . . . . *L. kelloggii* ssp. *kelloggii*

Variation and Taxonomy Within California

Distinguishing *Lewisia sacajaweana* from *L. kelloggii* is complicated by variation among *L. kelloggii* populations. The morphological variation has been noticed and treated taxonomically. *Lewisia kelloggii* was published based on a specimen from Placer County, California (Brandegee 1894), near the center of the plant's California range. The holotype remains at CAS (Howell 1949) and an isotype is at UC (Appendix). Plants growing farther south in California, particularly in Yosemite National Park, are similar in size to those at the center of the range but may have more flower parts. The southern plants have been named *L. yosemitana* (Jepson 1923) and are distinguished from *L. kelloggii* because *L. yosemitana* has 16–26 stamens, versus 10–15 for *L. kelloggii,* but that distinction did not win wide acceptance in this morphologically variable species. In our morphometric analysis, plants from Yosemite National Park cluster with other *L. kelloggii* from farther north (Fig. 4), but the analysis did not include counts of flower parts because "*Lewisia* is fiendishly hard to describe adequately from pressed material. . . . The number and shade of petals, stamens, and stigmas defies the most careful dissection" [letter from Lauramay Dempster to Paul Hutchison, 2 March 1989, in a fragment packet on *Hutchison and Bacigalupi 8105* (JEPS)]. Isoyzme analysis suggests that the southern populations may be differentiated from their more northern relatives. The 1 southern population included in the isozyme study, from Shuteye Peak south of Yosemite, has 3 alleles found elsewhere only in the Idaho populations plus 5 unique alleles.

Its genetic identities with other California populations average 0.71 (range 0.66–0.74), lower than average for populations of different subspecies (Crawford 1990).

Plants twice the size of typical *L. kelloggii* were described as *L. kelloggii* ssp. *hutchisonii* from a single specimen collected on Saddleback Mountain in Sierra County, near the north edge of the species' California range (Dempster 1996). The 2 populations sampled from the Plumas National Forest came from populations previously identified as *L. kelloggii* ssp. *hutchisonii* (Janeway 1998), and inspection of specimens at CHSC supports this identification. Genetic identities with other northern California populations average 0.873. In the context of the highly differentiated California populations, these plants did not exhibit isozyme patterns distinct from the typical populations (Fig. 5). When Dempster (1996) described *L. kelloggii* ssp. *hutchisonii,* she commented on the lack of intermediates between the holotype, the only plant of this taxon she had seen, and *L. kelloggii* ssp. *kelloggii.* Collections at CHSC fill the gap between the 2 taxa, morphologically and geographically (Appendix), and principal component analysis showed that some specimens are intermediate (Fig. 4). Discriminant analysis suggests that petal length could be useful in distinguishing the California taxa (*L. kelloggii* ssp. *hutchisonii* has longer petals).

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Appendix on the following page.

APPENDIX

Taxonomic Citations

Lewisia kelloggii K. Brandegee, Proc. Calif. Acad. Sci. Ser. II. 4: 1494; *Oreobroma kelloggii* (K. Brandegee) Rydb., N. Am. Fl. 21: 326. 1932. CA: Sierra Nevada, Camp Yuba (Cisco), 27 June 1870, Kellogg s.n. (HT: CAS; IT: UC).

Lewisia yosemitana Jepson, Man. Fl. Pl. Calif. 352. 1923; *Oreobroma yosemitanum* (Jepson) Rydb., N. Am. Fl. 21: 326. 1932 [not *Lewisia rediviva* var. *yosemitana* K. Brandegee = *L. disepala* Rydb.]. CA: Mariposa County, Yosemite, El Capitan, Jepson 4357 (HT: JEPS).

Lewisia kelloggii ssp. *hutchisonii* Dempster, Madroño 43: 415. 1996. CA: Sierra Co., Saddleback Mountain, ca. 9 miles north of Downieville, July 1932, Hutchison & Bacigalupi 8105 (HT: JEPS; IT: CAS).

Specimens Examined
(* used in morphometric analysis)

Lewisia kelloggii* ssp. *kelloggii. **California: Eldorado Co.,** Cody Summit Ridge, southwest of Strawberry, T10N R16E S01, 7900 feet, 7 July 1971, *Stebbins 8039* (CAS); **Mariposa Co.,** on El Capitan, Yosemite Valley, 28 June 1917, *Buck & McCauley s.n.* (UC); El Capitan Trail, near type locality, 31 May 1940, *Howell 15551** (CAS); between Snow Creek and Mt. Watkins Ridge, 1 June 1940, *Howell 15574* (CAS); Gin Flat (2 miles east of), Crane Flat, 6300 feet, 30 May 1924, *Jepson 10514** (JEPS); Sierra Nevada, Yosemite Nat'l Park, Horse Ridge, 9500 feet, 6 July 1941, *Mason 12495* (JEPS, UC); on the top and slopes of a gravelly ridge near El Capitan, Yosemite, 4 July 1922, *Michaels s.n.** (CAS); Summit El Capitan, Yosemite National Park, 7640 feet, 21 June 1936, *Sharsmith 2154* (UC); Yosemite National Park, Mt. Watkins, 10921 feet, July 1916, *Sierra Club Members HMH 9071,* (UC); ridge top of Sentinel Dome, above Yosemite Valley, 28 June 1949, *Webber s.n.,* (CAS); **Nevada Co.,** Tahoe Nat'l Forest, Castle Peak, 9000 feet, 20 July 1932, Smith 2422* (CAS); **Placer Co.,** Camp Yuba (Cisco), Sierra Nevada, 27 June 1870, *[Kellogg s.n.]** (CAS); Camp Yuba (Cisco), Sierra Nevada, 27 June 1870, *Kellogg s.n.** (UC); **Plumas Co.,** Sierra Nevada, west shoulder of Mt. Elwell, trail to Mt. Elwell, Lakes Basin, 5 August 1974, *Williams & McPherson 74-P-14** (CAS); **no county,** American Valley, May 1877, *Austin s.n.* (UC); **locality data probably in error,** Siskiyou Mountains: Cook and Green Pass, July 1976, *Roderick s.n.*, (JEPS).

Lewisia kelloggii* ssp. *hutchisonii. **California: Butte Co.,** area of saddle between Coon Hollow and Chips Creek, near jeep trail, T25N R05E S10 SW1/4, 6300 feet, 22 July 1988, *Janeway & Schlising 3047** (CHSC); **Placer Co.,** Summit of Big Valley Bluff, about 7 air miles southeast of Emigrant Pass, 6350 feet, 17 June 1973, *Heckard & Stebbins 3444** (JEPS); **Plumas Co.,** Big Meadows, 1880, *Austin s.n.** (UC); USFS road 22N84X on the north side of Onion Valley at its junction with 22N43Y 0.8 mile east of La Porte–Quincy Rd., ca. 1 mile north of Pilot Peak, on the south edge of the road, 6750 feet, 8 August 1998, *Oswald & Pires 9460** (CHSC); **Plumas/Sierra Co. line,** in the center of the Pacific Crest Trail, on Bunker Hill Ridge, about 0.5 mile (air) southwest of Pilot Peak, T22N R10E S09 SW1/4, 6600 feet, 7 July 1994, *Ahart 7467** (CHSC); **Sierra Co.,** on the north side of Henness Pass Road, at Keystone Gap, east of Keystone Mountain, about 1.5 miles northeast of Middlewaters, about 11 miles (air) northeast of Allegheny, T19N R12E S06 SE1/4, 6600 feet, 1 July 1994, *Ahart 7446** (CHSC); Saddleback Mountain, forestry road ca. 9 miles north of Downieville, west of summit of junction with a side road to the northwest, on north-facing slopes within 100 feet from road, 1.8 miles north of side road to Excelsior Mine, 6000 feet, July 1982, *Hutchison & Bacigalupi 8105*** (CAS, JEPS); North Sierra Buttes Trail, ca. 1 mile south of Packer Saddle trailhead, 250 m, 27 June 1990, *Patterson 1958* (JEPS).

Lewisia sacajaweana. **Idaho: Boise Co.,** Miller Mountain Site #2, Lowman Ranger District, Boise Nat'l Forest, 44°08′40.18″N, 115°30′45.62″W, 7560 feet, 11 July 2002, *Potter & Beall s.n.* (OSC); Miller Mountain, near transects at site 3. Lowman Ranger District, Boise Nat'l Forest. 44°08′40.905″N, 115°30′45.361″W, 7650 feet, 11 July 2002, *Potter & Beall s.n.* (OSC); Miller Mountain, site 9, Lowman Ranger District, Boise Nat'l Forest, 44°08′41.073″N, 115°30′45.477″W, 7525 feet, 11 July 2002, *Potter & Beall s.n.** (OSC); Boise Nat'l Forest, Clear Creek Summit, on road 510, 100 feet east of the county line, 44°13.94′, 115°31.28′, 2362 m, 13 July 2002, *Schenk & Rey-Vizgirdas 525** (OSC); Boise Nat'l Forest, Scott Mt. road 555BC, 1.5 miles west of intersection with road 555, 44°10.43′, 115°42.62′, 2310 m, 13 July 2002, *Schenk & Rey-Vizgirdas 526** (OSC); Boise Nat'l Forest. Pilot Peak, on slopes east and west of road 380, at intersection with spur road to Pilot Peak Lookout, west of lookout. T07N R06E S01, 43°57.81′, 115°41.8′, 3276 m, 13 July 2002, *Schenk & Rey-Vizgirdas 527** (CAS, ID, MO, OSC); **Custer Co.,** Challis Nat'l Forest, Bench Creek Trail, west of Hwy 21, about 2 miles west of trailhead, on north side of trail, north of Bull Trout Lake, 44°19.95′, 115°15.74′, 13 July 2002, *Schenk & Rey-Vizgirdas 517* (OSC); **Elmore Co.,** ca. 4 miles north of Pine, Boise Nat'l Forest, 4 June 1944, *Hitchcock & Muhlick 8690*** (CAS, UC); **Valley Co.,** Boise Nat'l Forest, Whitehawk Mt. Summit, 150 feet north of outhouse, 44°17.5′, 115°31.89′, 2549 m, 13 July 2002, Schenk & Vizgirdas 520* (OSC).