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STIPITATE AND NON-STIPITATE FORMS OF *ERICAMERIA GREENEI* (ASTERACEAE)

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ABSTRACT

Leaves of typical *Ericameria greenei* have sunken glands, while those in the northeastern part of the range (central Idaho, northeastern Oregon and northern Washington) have raised, stipitate glands. The two forms are distinctly allopatric in Idaho and Washington, dividing the overall distribution of *E. greenei* into two segments, but stipitate-glandular forms occur sporadically, probably as populational variants, in the range of the non-stipitate populations (typical *E. greenei*). Two taxa might be formally recognized among the *E. greenei* populations, but a principal components analysis indicates that both gland forms are reasonably included within the single species, distinguishable from the closely related *E. bloomeri*, which is consistently non-stipitate. The presence of stipitate glands is an unreliable character to distinguish *E. greenei* from *E. bloomeri*. *E. bloomeri* does not occur in Idaho.

Ericameria greenei (A. Gray) Nesom and *Ericameria bloomeri* (A. Gray) J.F. Macbr. are small shrubs in Asteraceae with several to many heads per branch. Most authors now treat *E. greenei* and *E. bloomeri* as separate species (Urbatsch 2012; Legler et al. 2018; Urbatsch et al. 2006; Jaster et al. 2017), but the two are morphologically similar, both placed in sect. *Macronema* (Hall 1928; Nesom 1990). Both are positioned within the same clade by analysis of nuclear ribosomal 3' ETS and ITS sequences (Roberts & Urbatsch 2003). *Ericameria suffruticosa* (Nutt.) Nesom is the only species more closely related to *E. greenei* than *E. bloomeri* (Roberts & Urbatsch 2003).

Different sources distinguish *Ericameria greenei* and *E. bloomeri* using different characters. Urbatsch et al. (2006) differentiate *E. greenei* from *E. bloomeri* by the presence or absence of stipitate glands on their leaves, claiming that *E. greenei* possesses stipitate glands (Figure 2) and *E. bloomeri* non-stipitate, resinous glands (Figure 3). Hall (1928), however, noted that foliage of *E. greenei* has glands that are "minutely stalked in rare cases." Furthermore, the lectotype of Greene's collection of *E. greenei* from northern California lacks stipitate glands (Nesom, personal communication) as do all collections of *E. bloomeri*. Cronquist (1994) considered *E. greenei* as a variety of *Haplopappus bloomeri* A. Gray—*H. bloomeri* var. *greenei* (A. Gray) Cronquist. Cronquist noted that "both varieties embrace glandular and tomentose-puberulent phases that often grow intermingled." Legler et al. (2018) recognize *E. greenei* first by its shorter, wider, and more oblanceolate or spatulate leaves—compared to *E. bloomeri*'s longer, narrower, and more filiform to linear-oblong leaves—secondly by less pronounced difference in outer and inner phyllary length, and lastly in its more compact inflorescence.

The confusion surrounding the relationship of glandularity to other morphological characters in *Ericameria greenei* and *E. bloomeri* led to our study. Our recent collections of *Ericameria* from the Owyhee Mountains of southern Idaho consistently lack stipitate glands (Figure 1) placing them with the type of *E. greenei*, while collections elsewhere in Idaho consistently possess stipitate glands. Ambiguity in current floristic treatments result in different interpretations of specimens from the Owyhee Mountains and Idaho north of the Snake River Plain. Furthermore, in lacking stipitate glands it seemed plausible that Owyhee Mountains specimens may best be classified as *E. bloomeri* despite having wider and shorter leaf dimensions that would otherwise place them in *E. greenei*. If they are to be classified as *E. greenei*, then should there be varietal distinction between the non-stipitate forms in the Owyhee Mountains and those with stipitate glands in the rest of Idaho north of the Snake River? This study investigates the taxonomy of plants identified as *E. greenei* using the criteria of Legler et al. (2018), which include both stipitate and non-stipitate forms. Our goal is to understand the morphological relationship of glandular characteristics to other morphological characters in both *E. greenei* and *E. bloomeri* in relationship to their geographic ranges, and to determine the identities of Idaho plants.

Specimens of *Ericameria suffruticosa* were also examined in our preliminary investigations. These plants have wider and oblanceolate leaves similar to *E. greenei* (Legler et al. 2018; Urbatsch et al. 2006; Urbatsch 2012). But unlike *E. greenei*, *E. bloomeri*, and the Owyhee collections, *E. suffruticosa* has fewer heads (1–3 per branch), more flowers per head, and even more pronounced glandular stipes (Urbatsch et al. 2006; Legler et al. 2018; Hall 1928). Based on these criteria and our preliminary results, we chose not to include *E. suffruticosa* in our study despite its obvious close relationship to the other two species. *Ericameria suffruticosa* has never been found in the Owyhee Mountains.

Understanding the taxonomy of the Owyhee Mountains plants has implications for their conservation status. If treated as *E. bloomeri*, these plants would represent a significant range extension for that species and also be the only populations of *E. bloomeri* in Idaho. If all Idaho populations are treated as *E. greenei*, then *E. bloomeri* would otherwise be absent from Idaho. Alternatively, if significant morphological and coherent geographic variation exists among stipitate and non-stipitate populations of *E. greenei*, then regarding the two as separate taxa might be justified.

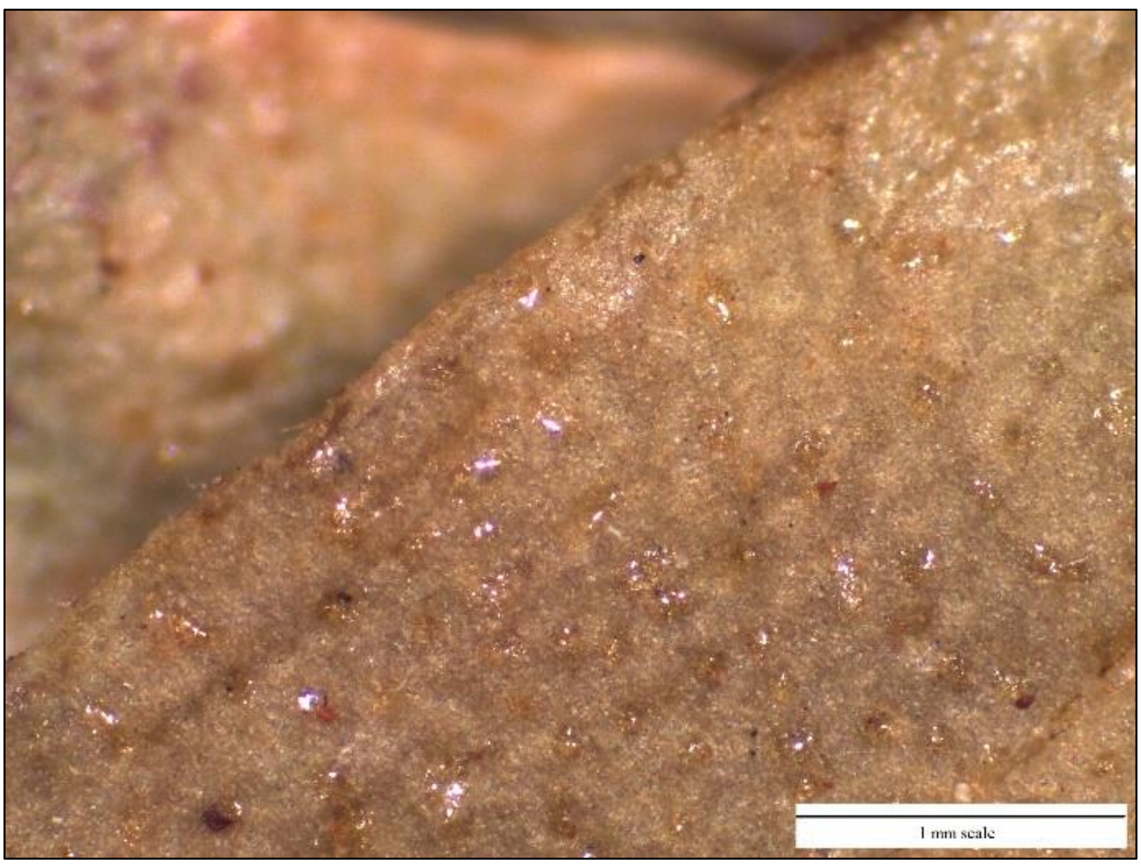

Figure 1. Non-stipitate *Ericameria greenei* from Owyhee Mountains of southern Idaho. Glands are present as "resin dots" in shallow pits at the leaf surface. Compare *E. bloomeri* in Figure 3.

Figure 2. *Ericameria greenei* leaf with stipitate-glands, typical of northern Idaho collections.

Figure 3. *Ericameria bloomeri* — leaf glands ("resin dots") lack stipes.

Methods

We examined all specimens of *Ericameria bloomeri* and *E. greenei* identified as such using the criteria of Legler et al. (2018) from The College of Idaho (CIC), Boise State University (SRP), University of Nevada (RENO), Washington State University (WTU), and Oregon State University (OSC, WILLU). We then selected 130 specimens representing the full range of morphologic and geographic variation described in literature (Table 1; Urbatsch 2012; Legler et al. 2018; Urbatsch et al. 2006; Jaster et al. 2017). We measured the 24 characters listed in Table 2 on these specimens and performed a One Way ANOVA on a subset of 62 specimens. Using the 16 characters found to be significant (Table 2), we performed a Principal Components Analysis (PCA) on a subset of 93 specimens chosen to include all non-stipitate forms of *E. greenei* from the Owyhee Mountains, 22 non-stipitate *E. greenei* from elsewhere, 31 stipitate forms of *E. greenei*, and 31 specimens of *E. bloomeri*. Sigma Plot 3.0 was used for all statistical analyses. We created a map of the geographic range of the 130 specimens selected based on the latitude and longitude noted by the collector. If a Public Land Survey System township and range was given instead, we converted it to latitude and longitude using Earth Point <http://www.earthpoint.us/Townships.aspx>. If only the name of a location was given, Google Earth Pro 2019 was used to georeference that location. The latitude and longitude data were compiled and the website Copy Paste Map < http://copypastemap.com/> was used to produce a map from the data.

Table 1. Specimens used in this study. Stipitate forms of *E. greenei* are referred to as *E. greenei*.

Accession #	State	County	Latitude, Longitude	Collector	Coll. #	Taxon	Included in
CIC 044862	ID	Owyhee	43.0047, -115.7003	C. Davidson	12106	Nonstip. E. greenei	ANOVA, PCA
CIC 045731	CA	Plumas	40.06, -121.24	B. Corbin	1535	E. bloomeri	ANOVA, PCA
CIC 018526	ID	Valley	45.14, -115.92	L. Smithman	895	E. greenei	ANOVA, PCA
CIC 023469	OR	Harney	42.71, -118.63	D. Mansfield	90-586	E. greenei	ANOVA, PCA
CIC 017844	ID	Idaho	43.76, -114.31	B. Ertter	3996	E. suffruticosa	ANOVA, PCA
CIC 050434	ID	Owyhee	43.00211, -116.70383	D. Mansfield	15-374	Nonstip. E. greenei	ANOVA, PCA
CIC 038738	ID	Lemhi	45.12, -114.60	B. Ertter	9511	E. greenei	ANOVA, PCA
CIC 024062	OR	Harney	42.63, -118.59	D. Mansfield	92-206	E. greenei	ANOVA, PCA
CIC 037070	ID	Owyhee	42.9862, -116.6922	D. Mansfield	9407	Nonstip. E. greenei	ANOVA, PCA
CIC 025875	ID	Owyhee	43.0609, -116.8579	A. DeBolt	1523	Nonstip. E. greenei	ANOVA, PCA
CIC 044027	ID	Owyhee	42.67063, -116.43857	E. George	445	Nonstip. E. greenei	ANOVA, PCA
CIC 019416	ID	Owyhee	42.6849, -116.7943	R. Rosentrater	3252	Nonstip. E. greenei	ANOVA, PCA
CIC 016288	ID	Owyhee	42.9511, -116.6357	W. Baker	8198	Nonstip. E. greenei	ANOVA, PCA
CIC 050436	ID	Owyhee	42.97638, -116.71542	D. Mansfield	15-379	Nonstip. E. greenei	ANOVA, PCA
CIC 021002	ID	Owyhee	43.0173, -116.7785	L. Smithman	1970	Nonstip. E. greenei	ANOVA, PCA
CIC 017695	ID	Idaho	45.26, -116.14	L. Smithman	537	E. greenei	ANOVA, PCA
CIC 017975	ID	Adams	45.10, -116.20	N. Tobias	sn	E. greenei	ANOVA, PCA
CIC 044632	ID	Idaho	45.225, -115.977	B. Ertter	21200	E. greenei	ANOVA, PCA
CIC 020914	ID	Valley	44.95, -115.96	L. Smithman	776	E. greenei	ANOVA, PCA
CIC 016287	ID	Boise	43.97, -114.99	P. Packard	73-226	E. greenei	ANOVA, PCA
CIC 016285	ID	Custer	44.00, -114.95	P. Packard	73-254	E. greenei	ANOVA, PCA
CIC 051057	ID	Elmore	43.61172, -115.42118	D. Mansfield	16393	E. greenei	ANOVA, PCA
CIC 052520	ID	Custer	43.814645, -114.13373	D. Mansfield	17382	E. greenei	ANOVA, PCA
CIC 013273	ID	Valley	45.03, -115.92	L. Smithman	439	E. greenei	ANOVA, PCA
CIC 022923	ID	Valley	44.39, -115.53	H. Clouser	91-150	E. greenei	ANOVA, PCA
CIC 002995	ID	Valley	44.85, -115.95	B. Ertter	7405	E. greenei	ANOVA, PCA
CIC 020924	ID	Valley	45.01, -115.88	L. Smithman	737	E. greenei	ANOVA, PCA
CIC 013276	ID	Valley	45.09, -115.90	L. Smithman	453	E. greenei	ANOVA, PCA
CIC 016286	ID	Valley	44.99, -116.11	B. Ertter	422/2	E. greenei	ANOVA, PCA

Accession #	State	County	Latitude, Longitude	Collector	Coll. #	Taxon	Included in
CIC 002994	ID	Adams	45.09, -116.21	B. Ertter	7347	E. greenei	ANOVA, PCA
CIC 027197	ID	Valley	44.42, -116.14	C. Baun	20	E. greenei	ANOVA, PCA
CIC 017693	ID	Idaho	45.25, -116.15	L. Smithman	539	E. greenei	ANOVA, PCA
CIC 020924	ID	Idaho	45.22, -115.98	L. Smithman	767	E. greenei	ANOVA, PCA
CIC 045832	ID	Idaho	45.246, -116.132	B. Ertter	21606	E. greenei	ANOVA, PCA
CIC 024959	ID	Harney	42.75, -118.60	H. Sheldon	11	E. greenei	ANOVA, PCA
CIC 28812	ID	Clearwater	46.52, -116.30	J. Duft	1345	E. greenei	ANOVA, PCA
CIC 045827	ID	Idaho	45.246, -116.132	B. Ertter	21607	E. greenei	ANOVA, PCA
CIC 27610	ID	Boise	44.00, -115.34	J. Duft	58	E. greenei	ANOVA, PCA
CIC 036675	ID	Valley	44.56, -116.18	B. Ertter	9593	E. greenei	ANOVA, PCA
CIC 036676	ID	Valley	44.56, -116.18	B. Ertter	9592	E. greenei	ANOVA, PCA
CIC 025468	OR	Harney	42.63, -118.58	D. Mansfield	94-47	E. greenei	ANOVA, PCA
CIC 023471	OR	Harney	42.71, -118.57	D. Mansfield	90-450	E. greenei	ANOVA, PCA
RENO 37395	NV	Ormsby	39.15, -119.88	A. Tiehm	2840	E. bloomeri	ANOVA, PCA
RENO 32050	NV	Washoe	39.59, -119.93	M. Williams	72-70-4	E. bloomeri	ANOVA, PCA
RENO 29709	NV	Washoe	39.95, -119.80	R. Evans	sn	E. bloomeri	ANOVA, PCA
RENO 11105	CA	Alpine	38.69, -119.83	C. Saulisberry	31	E. bloomeri	ANOVA, PCA
RENO 62107	CA	Modoc	41.80, -120.21	M. Williams	83-154-1	E. bloomeri	ANOVA, PCA
RENO 59125	CA	Siskiyou	41.58, -121.58	M. Williams	85-69-1	E. bloomeri	ANOVA, PCA
RENO 52926	CA	El Dorado	38.8697, -120.0297	E. Dean	4490	E. bloomeri	ANOVA, PCA
RENO 11353	NV	Washoe	39.59, -119.93	W. Billings	1454	E. bloomeri	ANOVA, PCA
SRP 27898	ID	Klamath	38.0856, -121.9517	R. Halse	6676	E. bloomeri	ANOVA, PCA
SRP 051496	CA	Plumas	39.99, -121.24	F. Oswald	8876	E. bloomeri	ANOVA, PCA
SRP 018278	OR	Deschutes	43.96, -121.22	R. Halse	2747	E. bloomeri	ANOVA, PCA
RENO 53012	OR	Jackson	42.08, -122.72	S. Sundberg	2638	Nonstip. E. greenei	PCA
SRP 018274	OR	Josephine	42.09, -123.36	W. Baker	638	Nonstip. E. greenei	PCA
SRP 018273	OR	Wallowa	45.24, -117.29	G. Mason	1713	Nonstip. E. greenei	PCA
SRP 018272	OR	Klamath	43.16, -121.78	J. Leiberg	sn	Nonstip. E. greenei	PCA
SRP 023967	OR	Linn	44.41, -121.88	M. Thompson	95121	Nonstip. E. greenei	PCA
OSC 32846	OR	Hood River	45.37, -121.70	H. Gilkey	sn	Nonstip. E. greenei	PCA
OSC 178811	OR	Douglas	43.15, -122.45	J. Fosback	699	Nonstip. E. greenei	PCA
ORE 107517	OR	Linn	44.46, -121.90	J. Hickman	497-3	Nonstip. E. greenei	PCA
OSC 22191	OR	Klamath	43.03, -122.12	R. Pendleton	sn	Nonstip. E. greenei	PCA
OSC 35873	OR	Klamath	42.90, -122.08	Scullen	sn	Nonstip. E. greenei	PCA
OSC 31531	OR	Lake	43.13, -120.16	E. Anderson	sn	Nonstip. E. greenei	PCA
OSC 130583	OR	Lane	44.10, -121.77	G. Vecten	58-221	Nonstip. E. greenei	PCA
OSC 11955	OR	Siskiyou	41.41, -122.19	A. Heller	14438	Nonstip. E. greenei	PCA
OSC 73699	OR	Harney	42.64, -118.58	K. Dahle	122	Nonstip. E. greenei	PCA
ORE 09191	NV	Clark	35.97, -114.77	I. Clokey	8570	Nonstip. E. greenei	PCA
RENO 52909	NV	Washoe	39.59, -119.93	M. Williams	7185	Nonstip. E. greenei	PCA
ORE 94123	NV	Lake	42.22, -120.10	D. Yiagst	sn	Nonstip. E. greenei	PCA
ORE 76799	OR	Linn	44.42, -121.95	A. Roach	sn	Nonstip. E. greenei	PCA
OSC 10974	OR	Lake	42.70, -120.55	J. Elder	sn	Nonstip. E. greenei	PCA
OSC 213401	OR	Jackson	42.08, -122.72	S. Sundberg	2638	Nonstip. E. greenei	PCA
OSC 74849	OR	Klamath	42.95, -122.10	W. Baker	sn	Nonstip. E. greenei	PCA
OSC 168921	OR	Jackson	42.03, -123.83	M. Paetzl	sn	Nonstip. E. greenei	PCA
RENO 52927	NV	Douglas	39.09, -120.04	F. Hillman	sn	E. bloomeri	PCA
RENO 52922	NV	Aspen	39.46, -119.91	N. Peterson	432	E. bloomeri	PCA
RENO 52921	NV	Storey	39.31, -119.67	B. Larson	118	E. bloomeri	PCA

Accession #	State	County	Latitude, Longitude	Collector	Coll. #	Taxon	Included in
RENO 52918	CA	Nevada	39.39, -120.09	P. Pabaubaue	sn	E. bloomeri	PCA
RENO 52903	CA	Nevada	39.17, -120.14	P. A. L.	3078	E. bloomeri	PCA
RENO 52905	CA	Mono	37.73, -118.95	M. Williams	86-80-1	E. bloomeri	PCA
RENO 52904	OR	Klamath	43.495, -121.923	R. Halse	6326	E. bloomeri	PCA
RENO 61937	NV	Douglas	39, -119.9	A. Tiehm	17218	E. bloomeri	PCA
RENO 52910	NV	Humboldt	41.64, -119.26	J. Nachlinger	2153	E. bloomeri	PCA
RENO 52920	CA	Siskiyou	41.58, -121.58	M. Williams	85-69-1	E. bloomeri	PCA
RENO 52931	NV	Washoe	39.61, -119.98	M. Williams	86-74-1	E. bloomeri	PCA
RENO 52924	NV	Douglas	39.09, -120.04	P. Kennedy	sn	E. bloomeri	PCA
RENO 56401	CA	Mono	38.25, -119.09	W. Billings	2189	E. bloomeri	PCA
RENO 52929	NV	Washoe	39.59, -119.93	M. Williams	7180	E. bloomeri	PCA
RENO 52923	NV	Carson City	39.16, -119.89	J. Sulman	sn	E. bloomeri	PCA
RENO 52928	CA	Siskiyou	42.68, -124.44	G. Butler	1823	E. bloomeri	PCA
RENO 52913	NV	Washoe	39.46, -119.91	A. Heller	sn	E. bloomeri	PCA
RENO 52917	NV	Washoe	39.34, -119.92	L. Asche	sn	E. bloomeri	PCA
RENO 52915	NV	Washoe	39.95, -119.80	A. Heller	sn	E. bloomeri	PCA
OSC 10973	CA	Siskiyou	41.32, -122.48	H. Heller	sn	E. greenei	
WTU 364983	WA	Kittitas	47.38, -120.88	D. Knoke	972	Nonstip. E. greenei	
WTU 373866	WA	Kittitas	47.52, -121.03	D. Knoke	1682	Nonstip. E. greenei	
WTU 334369	WA	Kittitas	47.06, -121.04	C. Bjork	2807	Nonstip. E. greenei	
WTU 395933	OR	Harney	42.63, -118.58	J. Smith	6967	Nonstip. E. greenei	
WTU 75200	WA	Okanogan	48.44, -120.47	C. Hitchcock	8096	E. greenei	
WTU 273003	WA	Chelan	47.43, -120.76	A. Kruckeberg	6393	Nonstip. E. greenei	
WTU 6447	WA	Chelan	47.43, -120.76	S. Blake	sn	Nonstip. E. greenei	
WTU 190538	WA	Chelan	48.09, -120.33	G. Ward	37	E. greenei	
WTU 232779	WA	Klickitat	45.97, -122.86	W. Suksdorf	sn	E. bloomeri	
WTU 129467	WA	Yakima	46.23, -120.82	V. Heidenreich	sn	E. bloomeri	
WTU 6728	WA	Yakima	46.2, -121.49	S. Blake	sn	E. bloomeri	
WTU 6485	WA	Chelan	47.83, -120.57	G. Morrill	298	E. bloomeri	
WTU 397473	OR	Harney	43.59, -119.06	N. Otting	3045	E. bloomeri	
WTU 131415	OR	Klamath	42.95, -122.1	W. Baker	6237	Nonstip. E. greenei	
WTU 278580	OR	Baker	44.78, -117.83	B. Bafus	405	Nonstip. E. greenei	
WTU 223789	OR	Jackson	42.04, -122.89	K. Chambers	2307	Nonstip. E. greenei	
WTU 217980	WA	Klickitat	46.2, -121.49	A. Kruckeberg	sn	E. bloomeri	
WTU 7201	WA	Okanogen	48.45, -119.63	C. Fiker	459	E. bloomeri	
WTU 271120	WA	Yakima	46.45, -120.86	E. Hunn	735	E. bloomeri	
WTU 6864	WA	Yakima	46.46, -120.74	J. Thompson	11 130	E. bloomeri	
WTU 417256	WA	Kittitas	43.3007, -120.7612	R. Olmstead	sn	Nonstip. E. greenei	
WillU 21706	OR	Hood River	45.5, -121.6	M. Peck	20129	E. greenei	
WillU 18176A	OR	Wallowa	45.23, -117.27	M. Peck	18516	E. greenei	
WTU V051856	OR	Klamath	42.95, -122.1	J. Thomson	135	E. greenei	
WTU V051855	OR	Klamath	42.95, -122.1	W. Baker	62312	E. greenei	
WTU V051863	WA	Kittitas	47.24, -120.56	J. Thomson	9752	E. greenei	

Results

Of the characters measured, 16 were found to be statistically significant (One Way ANOVA, $P<0.05$) between the groups (Table 2). Of the 16 significant characters, 7 distinguish non-stipitate *Ericameria greenei* from *E. bloomeri*: leaf apical width, leaf basal width, leaf length/apical width ratio, leaf length/basal width ratio, midnerve angle, heads per branch, and inflorescence length. Six characters are significantly different between stipitate *E. greenei* and other non-stipitate forms: involucre length, involucre width, outer phyllary length, phyllary length/basal width ratio, inflorescence length, and heads per branch. Only involucre length differs significantly between stipitate and non-stipitate *E. greenei*. Three characters that distinguish stipitate *E. greenei* from *E. bloomeri* are not significantly different between *E. bloomeri* and non-stipitate *E. greenei*: involucre length/width ratio, outer/inner phyllary length ratio, and peduncle length (Table 2).

In the PCA, *Ericameria bloomeri* is easy to distinguish from the other groups. Neither stipitate nor non-stipitate forms of *E. greenei* overlap with *E. bloomeri* (Figure 4). This is also observed when PCA Axis 1 is plotted vs. Axis 3 (data not shown). Furthermore, non-stipitate forms of *E. greenei* from the Owyhee Mountains and from other geographic locations have greater overlap with *E. greenei* than with *E. bloomeri*. Though there is overlap between the two groups of non-stipitate *E. greenei*, these groups fall mostly into the ordination space occupied by stipitate *E. greenei* (Figure 4).

In Idaho non-stipitate *E. greenei* is limited to the Owyhee Mountains and is allopatric with stipitate *E. greenei* north of the Snake River Plain. In Washington the stipitate forms are parapatric to non-stipitate forms of *E. greenei* in Chelan and Kittitas Counties. Only stipitate forms of *E. greenei* are evident in the Wallowa Mountains of northeastern Oregon. Throughout the rest of Oregon and northern California, including the type locality on Mt. Eddy of the Scott Mountains, non-stipitate forms predominate, but stipitate forms regularly occur (near Mt. Hood, on Steens Mountain, in Klamath County and in the Scott Mountains). Only non-stipitate forms are evident in the disjunct population from the Charleston Mountains of southern Nevada. (Table 1, Figure 5).

Table 2. Ranges of the characters measured for each group of plants and their significance. All 130 samples examined are included within the ranges given. Of the 24 characters measured 16 were found to be statistically significant (One Way ANOVA, $P < 0.05$). The final column shows which categories, if any, have statistically significant differences in the given character. *E. greenei* refers to stipitate forms of *E. greenei*

Character	*E. bloomeri*	*E. greenei*	Nonstip. *E. greenei*	Significance	Distinguishes
Gland Stipe Length	None	0-18 µm	None	P = <0.001	E. greenei from others
Leaf Apical 1/3 Width	0.5-4 mm	2-8 mm	2-6 mm	P = <0.001	E. bloomeri from others
Leaf Basal 1/3 Width	0.5-3 mm	1-5 mm	1-5 mm	P = <0.001	E. bloomeri from others
Leaf Apical Length/Width Ratio	9-60.	3.3-15	3-14.	P = <0.001	E. bloomeri from others
Leaf Basal Length/Width Ratio	9-60.	5.2-16.7	4-25.	P = <0.001	E. bloomeri from others
Midnerve Angle	10-45˚	20-90˚	14-85˚	P = <0.001	E. bloomeri from others
Involucre Width	3-10 mm	5-20 mm	4-8 mm	P = <0.001	E. greenei from others
Involucre Length/Width Ratio	1-3.8	0.9-2.1	0.75-2.2	P = <0.001	E. bloomeri from E. greenei
Outer Phyllary Length	2-10 mm	2-17 mm	2-11 mm	P = <0.001	E. greenei from others
Phyllary Basal Length/Width Ratio	2-10.	2-17.	1-11.	P = <0.001	E. greenei from others
Average Heads Per Branch	1-7.1	1-4.	1.3-7.5	P = <0.001	Nonstip. From others
Phyllary Apical 1/3 Width	0.5-1.5 mm	0.5-2 mm	0.5-1.5 mm	P = <0.001	E. greenei from others
Outer/Inner Phyllary Length Ratio	0.31-1.3	0.42-1.7	0.3-2	P = 0.003	E. bloomeri from E. greenei
Involucre Length	5-13 mm	7-17 mm	3-11 mm	P = 0.016	E. greenei from Nonstip.
Peduncle Length	0.5-16 mm	1-15 mm	1-11 mm	P = 0.022	E. bloomeri from E. greenei
Inflorescene Length	9-20 mm	12-20 mm	7-19 mm	P = 0.023	Nonstip. From others
Inner Phyllary Length	5-13 mm	4-15 mm	5-11 mm	P = 0.052	N/A
Gland Diameter	0-14 µm	2-92 µm	9-23 µm	P = 0.052	N/A
Phyllary Apical Length/Width Ratio	2-10.	2-11.	3-16.	P = 0.063	N/A
Number of Phyllary Series	2-3.	2-3.	1-3.	P = 0.087	N/A
Leaf Length	19-45 mm	8-40 mm	20-27 mm	P = 0.094	N/A
Glands	Absent or Presen	Absent or Presen	Present	P = 0.156	N/A
Angle of Branches	90-155˚	90-153˚	120-155˚	P = 0.238	N/A
Basal 1/3 Phyllary Width	1-2 mm	0.5-2 mm	1-1.5 mm	P = 0.689	N/A

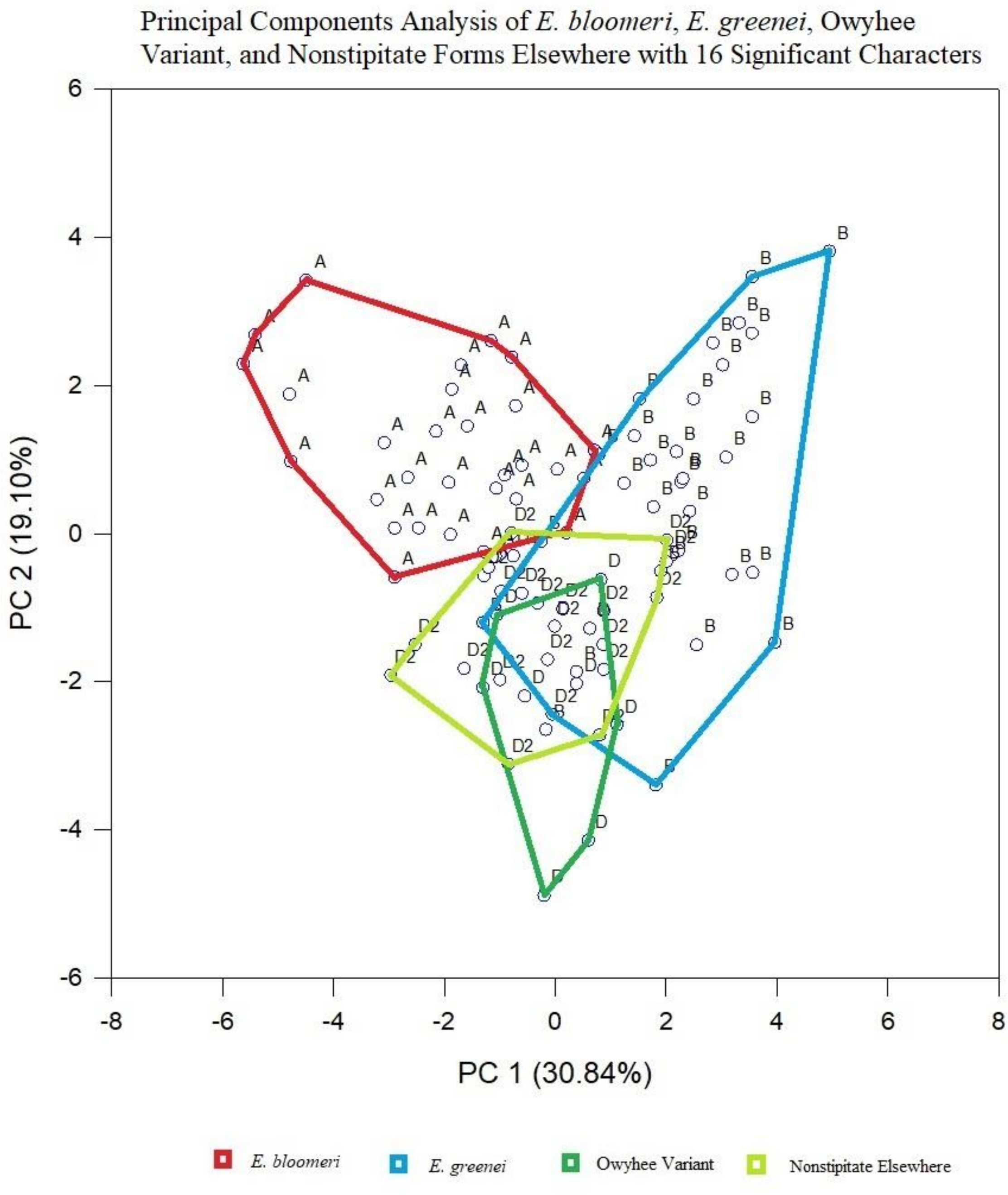

Figure 4. *E. bloomeri* is distinct from the other three population groups. *Ericameria greenei* (stipitate) has considerable overlap with both the Owyhee variant (non-stipitate) and the non-stipitate form found elsewhere. The ordination used the 16 characters shown to be significant (Table 2). The principal components 1 and 2 shown account for 49.94% of variation.

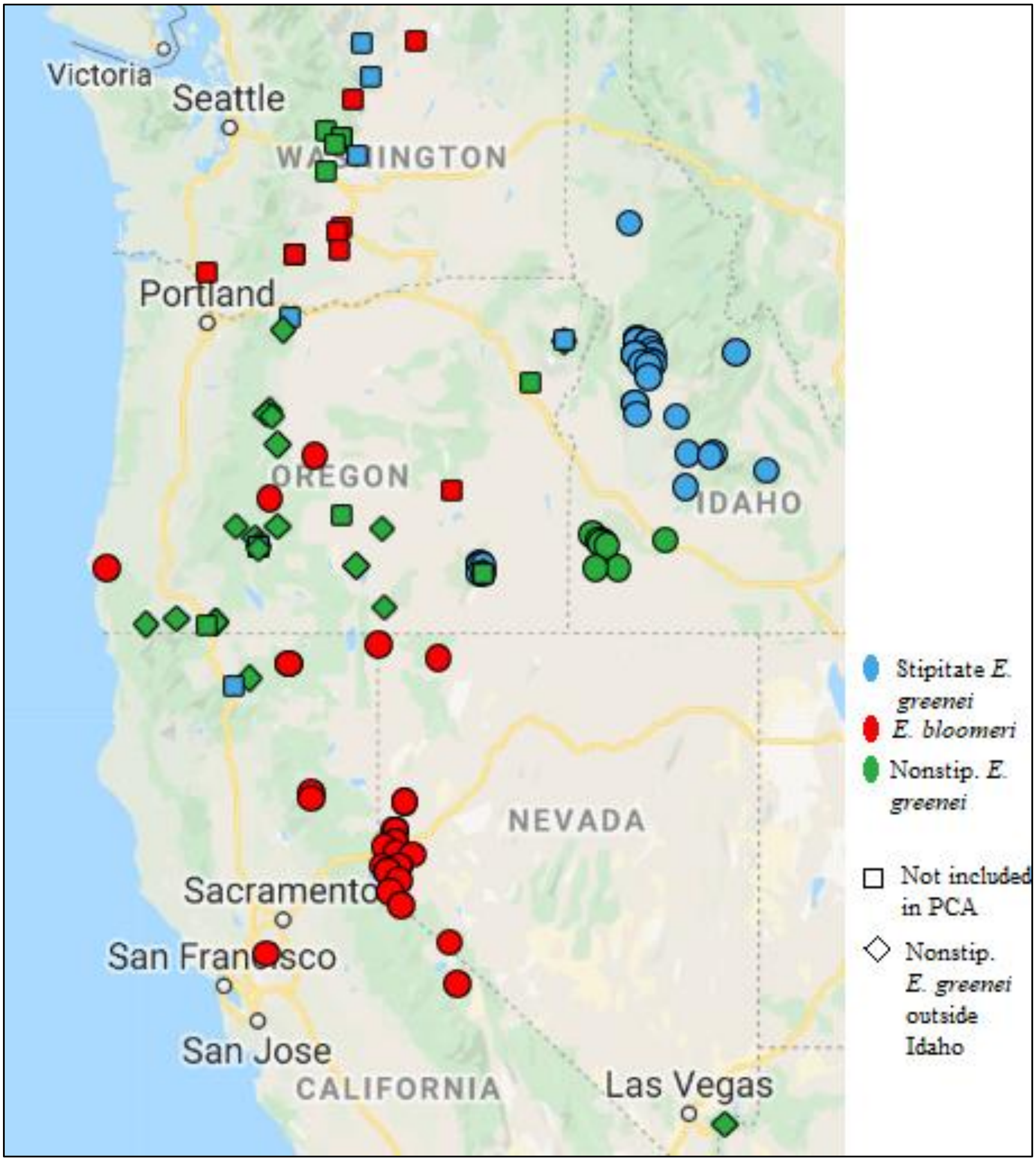

Figure 5. Geographic location of specimens.

Discussion

Ericameria populations from the Owyhee Mountains would be treated in Flora of North America by Urbatsch et al. (2006) as *E. bloomeri*, because they lack stipitate glands (Figures 1 and 3). However, the lectotype of *E greenei* also lacks stipitate glands. Thus, we examined a variety of morphological features to clarify the affinities of stipitate and non-stipitate *E. greenei* throughout the range of *E. bloomeri* and *E. greenei*. Three possible scenarios are evident. First, the Owyhee specimens may represent populations of *E. bloomeri* disjunct from the rest of *E. bloomeri* to the west. Second, the stipitate plants north of the Snake River Plain in Idaho may represent a different variety of *E. greenei* than the plants from the Owyhee Mountains. Finally, the stipitate and non-stipitate characteristics may be morphological variation insufficient to designate varietal distinction, despite the geographic allopatry of these two forms evident in Idaho.

Owyhee collections appear more like stipitate *Ericameria greenei* than *E. bloomeri,* with wider leaves, and smaller length/width ratios than *E. bloomeri* leaves (Table 2; Legler et al. 2018). The Owyhee variant resembles the non-stipitate form of *E. greenei* found throughout Oregon, Washington and northern California, with disjunct populations in southern Nevada, all, including the type, having leaves with a similar length to width ratio and the same non-stipitate resinous glands (Figure 4). A preliminary One Way ANOVA found only one significant difference among the characters measured between the Owyhee collections and non-stipitate *E. greenei* outside of Idaho, a difference in midnerve angles (data not shown). In the PCA the two groups of non-stipitate *E. greenei* overlap almost completely (Figure 4). This suggests that the Owyhee variant and non-stipitate *E. greenei* collected outside of Idaho represent the same taxonomic entity.

Our research suggests that the non-stipitate Owyhee collections should not be classified as *Ericameria bloomeri* despite having similar non-stipitate resinous glands (Figures 1 and 3). Rather, the non-stipitate *E. greenei* more closely resembles stipitate *E. greenei*, sharing a similar range of the following morphological characters with stipitate *E. greenei*: leaf apical width, leaf basal width, leaf length/apical width ratio, leaf length/basal width ratio, and midnerve angle (Table 2). This is also supported by the PCA of the 16 significant characters (Figure 4) and of all 24 characters (data not shown), in which the non-stipitate form of *E. greenei*, whether from the Owyhee region or elsewhere, overlap considerably with the stipitate form of *E. greenei*, while barely overlapping with *E. bloomeri*. Thus, we conclude that the Owyhee specimens are best classified as *E. greenei* and not as disjunct *E. bloomeri*. Furthermore, use of the "stipitate glands" to distinguish *E. greenei* from *E. bloomeri* (as in Urbatch et al. 2006) is unjustified.

To assess whether varietal distinction between stipitate and non-stipitate forms of *Ericameria greenei* is justifiable we asked first whether other morphological characters shared the same pattern of variation observed with gland form and then whether the forms exhibit consistent geographic variation. Involucre length was the only other character that differed between non-stipitate and stipitate *E. greenei*--the non-stipitate forms having shorter involucres (Table 2). In the PCA while the stipitate and non-stipitate forms of *E. greenei* showed different extremes in the ordination space, a significant degree of overlap was observed suggesting morphological continuity of stipitate and non-stipitate forms, as expected if they represent the same taxonomic entity (Figure 4). Furthermore, distinction between stipitate and non-stipitate samples can also sometimes be unclear in cases where the stipes may be especially small or when there are both stipitate and non-stipitate glands on the leaves of the same plant. WILLU 21706 and WILLU 18176A were scored as stipitate *E. greenei* and labeled in blue in Figure 5, but they produce non-stipitate glands as well as glands with stipes. Thus, stipitate glands may represent mere population variants within otherwise non-stipitate populations.

The two gland forms are clearly allopatric in Idaho with forms lacking stipitate glands occurring only in the Owyhee Mountains southwest of the Snake River Plain and those with stipitate glands north of the Snake River Plain. The stipitate form of *Ericameria greenei* extends through the Wallowa Mountains of northeastern Oregon and into the mountains of northern Washington. Stipitate forms of *E. greenei* also occur sympatrically with non-stipitate forms near Mt. Hood and in Steens Mountain in Oregon and in the Scott Mountains of northern California, where the non-stipitate type of *E. greenei* was collected (Figure 6). Thus, there appears to be allopatric differentiation of these two

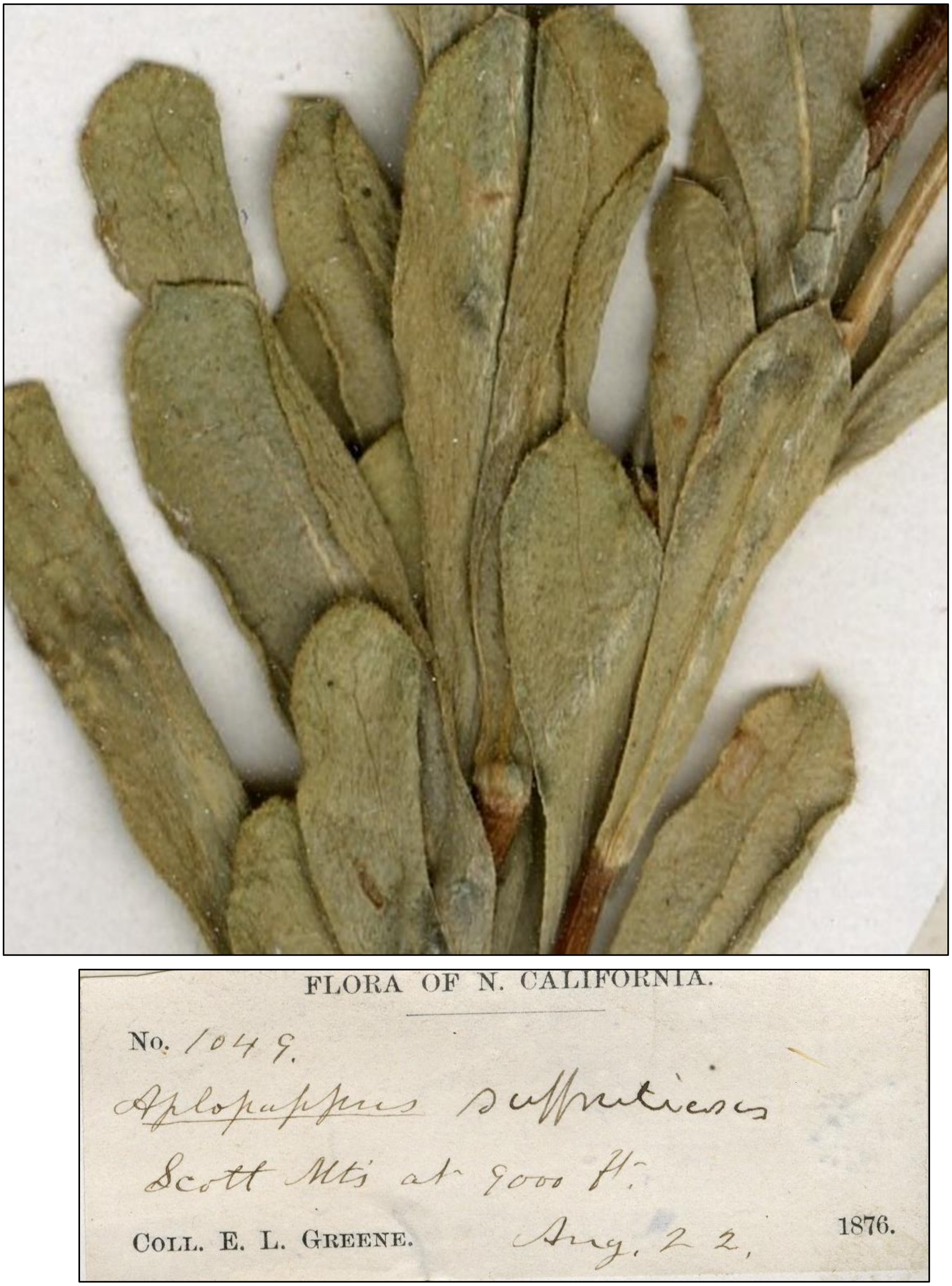

Figure 6. The lectotype collection by E.L. Greene from Mt. Eddy in the Scott Mountains in Siskiyou Co., California with non-stipitate glands.

forms along a border from central Washington to southern Idaho, but presence of both forms throughout much of Oregon and northern California. The Snake River Plain poses a significant barrier to distribution of other plant species (Ertter & Moseley 1992, Holmgren 1972) suggesting that this barrier may have facilitated evolutionary differentiation of varietal forms in *Ericameria* as well.

In his treatment of the Intermountain Flora Cronquist (1994) included *Ericameria greenei* as a variety of *E. bloomeri* under the synonym *Haplopappus bloomeri* var. *greenei* (A. Gray) Cronquist noting that "both varieties embrace glandular and tomentose-puberulent phases that often grow intermingled." Here we have demonstrated that while the glandular forms often "grow intermingled", they also are distinct in their distribution across a border from the Snake River Plain into northcentral Washington appearing as distinct varieties. In our study six of the 121 populations represented in Table 1 clearly exhibited a tomentose phase. Of those all were in stipitate *E. greenei* from northcentral Idaho and eastern Oregon. Hall (1928) recognized tomentose forms in both *E. greenei* and *E. bloomeri*, referring to the "finely tomentose" form of *E. greenei* under the name *Haplopappus mollis* A. Gray) ssp. *mollis* H.M. Hall. Our study sheds no light on whether these forms were "intermingled" with glabrous forms. Though we only observed tomentose forms in stipitate *E. greenei*, it is likely that Hall observed them in non-stipitate *E. greenei*, because he noted the occurrence of stipitate forms as "rare" and gave no indication of co-occurrence of stipitate glands and tomentose forms. These tomentose forms are represented with a variety of synonyms, including *Haplopappus greenei* var. *mollis* (A. Gray) A. Gray, *Hoorebekia greenei* ssp *mollis* (A. Gray) Piper and *Macronema greenei* var. *mollis* (A. Gray) Jeps. In Flora of North America Urbatsch et al. (2006) noted that "a tomentose entity that was recognized as *Haplopappus greenei* subsp. *mollis* differs also in other ways from typical *Ericameria greenei*. It may merit recognition at some level." Our study sheds no light on what those "other ways" might be. Though tomentose forms co-occur with stipitate glands in some instances, we observed many more instances in which stipitate glands occurred in otherwise glabrous plants. We were unable to detect any geographic patterns in tomentose forms, though our sample of tomentose forms was very limited.

We are reluctant to propose varietal rank to the populations of *Ericameria greenei* possessing stipitate glands. Though populations from northern Idaho, northeastern Oregon and northern Washington could easily be assigned to such a novel variety, many populations with stipitate glands throughout Oregon and northern California occurring in sympatry with otherwise non-stipitate forms (e.g. on Steens Mountain or Scott Mountains) would be wrongly assigned based on that single character. Furthermore, the paucity of other morphological distinction between the stipitate and non-stipitate forms (Table 2) argues against assigning varietal rank, as does the PCA (Figure 4), in which both gland forms fall within a single multivariate ordination space. Without a clearer understanding of the genetic basis of stipe formation of glands in *Ericameria* sect. Macronema, or additional morphological characters distinguishing stipitate and non-stipitate *E. greenei* (Figure 4) there remain unclear boundaries within *E. greenei*.

In this study we have rejected the use of stipitate glands as a taxonomic diagnostic for distinguishing *E. greenei* from *E. bloomeri*. The distinctions between *E. greenei* and *E. bloomeri* remain quantitative at best. Our research supports the classification of *Ericameria* specimens from the Owyhee Mountains as *E. greenei* not *E. bloomeri*. We demonstrate allopatric differentiation between stipitate and non-stipitate forms of *E. greenei*, but we hesitate to propose varietal status for the stipitate forms without further evidence. Thus, based on current records, *E. bloomeri* is absent from Idaho.

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