


MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY



QK
1
M183
BOT

CONTENTS

- RECONSIDERATION OF THE TAXONOMIC STATUS OF MASON'S LILAEOPSIS – A STATE-PROTECTED RARE SPECIES IN CALIFORNIA
Peggy L. Fiedler, Esa K. Crumb, and A. Kate Knox..... 131
- A COMPARISON OF THE EFFECTS OF Na_2SO_4 AND NaCl ON THE GROWTH OF *HELIANTHUS PARADOXUS* AND *HELIANTHUS ANNUUS* (ASTERACEAE)
M. O. Mendez and O. W. Van Auken..... 145
- THE DIVERSITY AND BIOGEOGRAPHY OF THE ALPINE FLORA OF THE SIERRA NEVADA, CALIFORNIA
Philip W. Rundel..... 153

NEW SPECIES

- A NEW SPECIES OF *ASTRAGALUS* (FABACEAE) FROM THE WASATCH MOUNTAINS OF UTAH
Beth Lowe Corbin..... 185
- GRIMMIA VAGINULATA**, (BRYOPSIDA, GRIMMIACEAE) A NEW SPECIES FROM THE CENTRAL COAST OF CALIFORNIA
Kenneth Kellman..... 190

BOOK REVIEWS

- INTRODUCTION TO CALIFORNIA CHAPARRAL
Christopher Blaylock..... 199

NOTEWORTHY COLLECTIONS

- CALIFORNIA 201
COLORADO..... 204
MEXICO 205

MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbaria, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription information on inside back cover. Established 1916. Periodicals postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to MADROÑO, Kim Kersh, Membership Chair, University and Jepson Herbarium, University of California, Berkeley, CA 94720-2465. kersh@berkeley.edu.

Corresponding Editor—TIMOTHY LOWREY
Museum of Southwestern Biology
MSC03 2020
University of New Mexico
Albuquerque, NM 87131-0001
madrono@unm.edu

Copy Editor—RICHARD WHITKUS
Department of Biology
Sonoma State University
1801 E. Cotati Avenue
Rohnert Park, CA 94928-3609
whitkus@sonoma.edu

Book Editor—JON E. KEELEY
Noteworthy Collections Editors—DIETER WILKEN, MARGRIET WETHERWAX

Board of Editors
Class of:

- 2011—JAMIE KNEITEL, California State University, Sacramento, CA
KEVIN RICE, University of California, Davis, CA
2012—GRETCHEN LEBUHN, San Francisco State University, CA
ROBERT PATTERSON, San Francisco State University, CA
2013—ERIC ROALSON, Washington State University, WA
KRISTINA SCHIERENBECK, California State University, Chico, CA
2014—BRANDON PRATT, California State University, Bakersfield, CA
TOM WENDT, University of Texas, Austin, TX

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 2011–2012

- President*: V. Thomas Parker, Department of Biology, San Francisco State University, San Francisco, CA 94132, parker@sfsu.edu
First Vice President: Andrew Doran, University and Jepson Herbaria, University of California, Berkeley, CA 94720, andrewdoran@berkeley.edu
Second Vice President: Marc Los Huertos, Division of Science & Environmental Policy, California State University, Monterey Bay, Seaside, CA 93955, mloshuertos@csumb.edu
Recording Secretary: Mike Vasey, Department of Biology, San Francisco State University, San Francisco, CA 94132, mvasey@sfsu.edu
Corresponding Secretary: Heather Driscoll, University Herbarium, University of California, Berkeley, CA 94720, hdriscoll@berkeley.edu
Treasurer: Thomas Schweich, California Botanical Society, Jepson Herbarium, University of California, Berkeley, CA 94720, tomas@schweich.com

The Council of the California Botanical Society comprises the officers listed above plus the immediate *Past President*, Dean Kelch, Jepson Herbarium, University of California, Berkeley, CA 94720, dkelch@berkeley.edu; the *Membership Chair*, Kim Kersh, University and Jepson Herbaria, University of California, Berkeley, CA 94720, kersh@berkeley.edu; the *Editor of Madroño*; and three elected *Council Members*: Chelsea Specht, Department of Plant and Microbial Biology, University of California, Berkeley, CA 94720-2465, cdspecht@berkeley.edu; Ellen Simms, Department of Integrative Biology, 3060 Valley Life Sciences Bldg., #3140, University of California, Berkeley, CA 94720, esimms@berkeley.edu. Staci Markos, University and Jepson Herbaria, University of California, Berkeley, CA 94720, smarkos@berkeley.edu. *Graduate Student Representatives*: Ben Carter, Department of Integrative Biology and University Herbarium, University of California, Berkeley, CA 94720, bcarter@berkeley.edu. *Webmaster*: Susan Bainbridge, Jepson Herbarium, University of California, Berkeley, CA 94720-2465, sjbainbridge@berkeley.edu.



RECONSIDERATION OF THE TAXONOMIC STATUS OF MASON'S LILAEOPSIS – A STATE-PROTECTED RARE SPECIES IN CALIFORNIA

PEGGY L. FIEDLER

Natural Reserve System, UC Office of the President, Office of Research and
Graduate Studies, 1111 Franklin Street, 6th Floor, Oakland, CA 94607
peggy.fiedler@ucop.edu

ESA K. CRUMB

Wetlands and Water Resources, 818 Fifth Ave, STE 208, San Rafael, CA 94901

A. KATE KNOX

7730 19th Avenue NE, Seattle, WA 98115

ABSTRACT

Lilaeopsis masonii is a California state-listed rare species with a wide range of morphologies observed in the field throughout its range, and in herbaria collections. This extensive variation confounds reliable taxonomic identification, particularly for those specimens intermediate between *L. masonii* and its sister taxon, *L. occidentalis*. To investigate the genetic basis of this morphological variation, we examined two portions of the *Lilaeopsis* genome in seven species. Specifically we sought to determine whether *L. masonii* is sufficiently distinct from its closely related, widespread congener to continue to warrant specific status. DNA sequence analysis of ITS1, 5.8S, and ITS2 nuclear ribosomal DNA revealed no differences between *L. occidentalis* and *L. masonii* California collections, and minimal differences between these samples and *L. occidentalis* collected from the state of Washington, suggesting strongly that these two species form a single clade. A combination of fragment data from three AFLP primers yielded 274 fragments from 29 samples. Genetic Manhattan distance values calculated from the AFLP matrix within species ranged from a low of 1.4 to a high of 6.6, reflecting minor differences among all samples. UPGMA cluster phenograms support the results of the PCA analysis, illustrating a cluster of *L. occidentalis* + *masonii* samples distinct from other *Lilaeopsis* species. Because conservation dollars should protect unique evolutionary entities, we suggest that *L. masonii* be subsumed under *L. occidentalis* and therefore no longer receive formal state protection.

Key Words: AFLP, Apiaceae, California endangered species Act, goldilocks conundrum, ITS, *lilaeopsis masonii*, *lilaeopsis occidentalis*, UPGMA.

Lilaeopsis masonii Mathias & Constance (Mason's *lilaeopsis*) is one of 15 wetland or aquatic species of the widespread genus *Lilaeopsis* Greene within the Apiaceae. The genus *Lilaeopsis* is comprised of perennial herbs characterized by a horizontal stem with leaves commonly in clusters ("ramets") borne directly from the stem, although rarely leaves occur individually. *Lilaeopsis* is notable in its morphologic simplicity—entire, generally linear leaves; simple umbels; absence of a carpophore; and, a strongly reduced habit (Petersen et al. 2002; Downie et al. 2000; Downie et al. 2008). Such simple morphology has led to a long history of taxonomic uncertainties and difficulty in the reconstruction of its phylogeny.

Evidence for monophyly of *Lilaeopsis* is strong (Petersen et al. 2002). However, recent research based on molecular evidence from nuclear and chloroplast genes suggests that the genus is best placed in the Oenantheae tribe within the Apioideae (Downie et al. 2008) and that *Lilaeopsis* is sister to the clade comprising *Ptilimnium*, *Limnosciadium*, *Daucosma*, *Cynosciadium* and rachis-leaved species of *Oxypolis*, not the Mexi-

can genus *Neogoezia* as suggested by Petersen et al. (2002). The New World endemics clade of tribe Oenantheae is native to North America and comprises a monophyletic group that appears to be evolving much faster than any other major clade recognized in the tribe (Hardway et al. 2004).

Early taxonomic work on the genus in California by Hill (1927) and Mason (1957) included mention of comparatively smaller and narrower leaves in *Lilaeopsis* specimens occurring away from the coast, in contrast to a relatively more robust coastal form. Professor Herbert Mason, an early expert on the wetland flora of California, first collected a relatively smaller *Lilaeopsis* from Brannan Island of the San Francisco Bay/Sacramento-San Joaquin Delta (Bay-Delta). He referred to the smaller form as the "San Francisco Bay and river-mouth" form (Mason 1957: 631). This specimen, according to Mason (unpublished) was "definitely distinct from the coastal *L. occidentalis*." Western *lilaeopsis* (*Lilaeopsis occidentalis* J. M. Coulter & Rose) is a widespread, common species,

ranging from the Queen Charlotte Islands of British Columbia, Canada to Marin County, California (Affolter 1985). Considered to be a coastal species confined to salt water or brackish water intertidal habitats, collections of *L. occidentalis* from inland fresh water lentic and lotic habitats are known, but considered “uncharacteristic” (Affolter 1985).

Lilaeopsis masonii was not described as a distinct taxon for two decades after the smaller form in the Bay-Delta was first observed. In 1977, Mathias and Constance formally recognized the diminutive nature of a specimen obtained from Twitchell Island in the Bay-Delta as *L. masonii* (Mathias and Constance 1977). Mathias and Constance described *L. masonii* as distinct from *L. occidentalis* based upon the former (rare) taxon bearing narrower, typically shorter, and more or less terete leaves, and an inland distribution. They honored Herbert Mason’s expertise in the wetland flora of the State with the specific epithet.

Mason’s *lilaeopsis* was one of the first vascular plant species to be protected as “rare” under the California Endangered Species Act (CESA) (California Fish & Game Code §§2050, *et seq.*). At the time of its listing in November 1979, only seven population occurrences were known (CNDDDB 2009). Since formal protection, the documented extent of geographic distribution and population abundance of *L. masonii* has increased nearly three-fold, primarily as a result of concentrated field survey efforts conducted in the early 1990’s by Golden, Fiedler, and Zebell (Golden and Fiedler 1991; Golden 1992; Fiedler and Zebell 1993; Zebell and Fiedler 1996). Today, Mason’s *lilaeopsis* is known to occur within 24 USGS quadrangles and seven counties (CNPS 2008), spanning across roughly 690 square miles. One hundred eighty-six documented occurrences are on record with the state (CNDDDB 2009), although most, but not all are extant.

A History of Taxonomic Uncertainty

Confusion over the taxonomic limits of this rare species existed from the beginning of its description. Two examples are relevant. First, a long-controversial *Lilaeopsis* specimen collected by Schreiber (#2266 UC, 28 June 1936) from Chicken Ranch Beach in Marin County derives from outside the circumscribed geographic range of the endemic inland taxon. Leaf lengths from this specimen range between 15 to 42 mm, a morphological range characteristic of comparatively larger leaf lengths for *L. masonii*. However, it is possible to key these larger leaved Chicken Ranch Beach specimens to *L. occidentalis* in every relevant flora (e.g., Hickman 1993).

Affolter (1985) examined this specimen in his monograph of *Lilaeopsis*, and accepted it as *L.*

masonii, but noted that it was a geographical outlier for the rare, Bay-Delta endemic species. Today, CNPS (Tibor 2001) acknowledges that this specimen is likely to be *L. occidentalis*, not the rare *L. masonii*, but provides no explanation. Several attempts to relocate this *Lilaeopsis* material at Chicken Ranch Beach by the authors have failed as the population appears to be extirpated, thereby making an independent species corroboration impossible.

It is important to note that (1) numerous collections of *L. occidentalis* from the beaches of Marin and Sonoma counties exist, (2) leaf lengths range by an order of magnitude or more within and between adjacent populations of *L. occidentalis*, (3) the number and clarity of internal crosswalls considered important diagnostic characters are more likely a function of relative plant size, exposure, or both, and (4) inland collections of the common species are known from the state of Washington (e.g., UC 1594452; 4 September 1962). Also noteworthy, *L. masonii* has never again been collected on the Pacific coast of North America beyond Schreiber’s Marin Co. collection in 1936.

Further, Affolter (1985) remarked that leaves from a collection of *L. masonii* (derived from Sherman Island immediately down river of Twitchell and Brannan islands) cultivated for his greenhouse comparisons were “remarkably longer than any of the herbarium material” (Affolter 1985:70). He suggested the observed overall larger and more robust greenhouse material was evidence of how difficult it is to understand vegetative plasticity from herbarium material alone. However, the relatively robust response of Mason’s *lilaeopsis* to the mild conditions of a greenhouse suggests strongly that strict morphological distinctions between the two taxa are problematic.

Additional morphological characters further support the assertion that *L. masonii* is not distinctly different from *L. occidentalis*. Affolter (1985:70) noted that the “two taxa are similar in several respects,” including similar (1) leaf shapes (linear), (2) rhizome branching architecture, (3) fruit shapes, (4) fruit cell types, (5) fruit venation patterns, (6) habitats, and they have (7) overlapping geographic distributions. Despite all these similarities, Affolter (1985:71) supported their separate specific status, primarily because “when grown under a common-garden environment in the greenhouse, the two species retained the vegetative characteristics that distinguish them in the field.”

Subsequent laboratory studies conducted by the principal author and her students (Golden and Fiedler 1991; Golden 1992; Fiedler and Zebell 1993; Zebell and Fiedler 1996) have provided little clarity. Most importantly, no nucleotide variation was found among nine

populations of *L. masonii* or between *L. occidentalis* and *L. masonii* when the 204 nucleotides of the ITS2 nuclear genome were ascertained (Fiedler and Zebell 1993). Fiedler and her colleagues thus concluded tentatively that the rare species was most likely an inland ecotype not clearly distinct from its widespread congener.

Field Observations

Decades of field observations of *Lilaeopsis* throughout the Bay-Delta, Suisun Marsh, and Napa River ecosystems do not reinforce many of the conclusions offered by Hill (1927), Mason (1957, unpublished), Mathias and Constance (1977), and Affolter (1985) supporting the recognition of two distinct taxa. Rather, the few vegetative characteristics that typify this genus are highly variable both within and between populations throughout this region. Occurrences of *L. masonii* in the lower Napa River, studied since 2001 (WSP 2007, unpublished; Blasland, Bouck, & L, Inc. unpublished; Entrix unpublished; L.C. Lee & Associates unpublished; Stillwater Sciences and Fiedler unpublished) include a full spectrum of individual ramet sizes. Often, both large and small forms of *Lilaeopsis* species, easily identifiable to the two different species, can be found growing in the same location. Often the plant stature/leaf length size gradient runs perpendicular to the shoreline, where the small “*masonii*” form (approx. 1.5–4.5 cm in height) grows relatively close to the water’s edge, while increasing larger and more robust “*occidentalis*” (approx. ≥ 11 cm in height) can be found further from the water. “Intermediate” or medium-sized *Lilaeopsis* material (approx. >6.25 and <11 cm in height) is common throughout this shoreline/river bank habitat and geographic range, and keys to either (or both) the rare or the common species. We call this phenomenon—i.e., range in size of a critical morphological character, with significant overlap between taxa—the “Goldilocks Conundrum” to highlight the problem that the intermediate-sized material is not “just right,” but rather, highly problematic.

To resolve our conundrum and determine whether *L. masonii* is a discrete species distinct from *L. occidentalis*, we initiated a genetic analysis of seven species of this genus. We hypothesized that there were no significant differences between diagnostic portions of the genome selected for this study of the two species, *L. masonii* and *L. occidentalis*. Based on these analyses, we then explored whether *L. masonii* warrants continued recognition as a distinct species or rather, should be subsumed under the widespread and common *L. occidentalis*. If no significant differences were shown to exist between diagnostic portions of the *L. occidentalis* and *L. masonii* genomes, then *L. masonii* should

be subsumed within *L. occidentalis*, and continued protection under the California Endangered Species Act for *L. masonii* should be reconsidered.

Fallon (2007) noted that genetic information is being used increasingly to resolve taxonomic issues for protection at the federal level under the U.S. Endangered Species Act of 1973 (ESA). She conducted a review of listing decisions made by the U.S. Fish & Wildlife Service and the National Marine Fisheries of species, subspecies, or distinct population segments (DPSs) proposed for protection under the ESA. Fallon determined that the listing fate of a DPS based upon data from more than one genetic marker resulted in a higher probability of protection than candidate taxon or population segment whose discreteness was determined by a single genetic marker. With the cautionary tale of Fallon’s findings in mind, we examined the ITS region of the nuclear genome and, to corroborate our ITS findings, conducted an amplified fragment length polymorphism (AFLP) analysis on a similar suite of taxa.

We chose the ITS region in large part because Hardway et al. (2004) found evidence for particularly rapid evolution in the *Oenanthe* clade that includes *Lilaeopsis* when compared to the rest of the taxa. Sequence divergences in this clade averaged 6–7 times higher (approx. 17%) than between species in *Oenanthe* (approx. 2.8%) or *Cicuta* (approx. 2.4%) (Hardway et al. 2004). AFLP analysis was selected as a secondary marker system based on the increasing popularity of this form of DNA fingerprinting as a complementary system in phylogenetic studies (Holland et al. 2008). Additionally, AFLP fingerprinting offers a reliable, robust, and genomically comprehensive method of genetic analysis for taxa lacking complex nuclear and organellar markers (Vos et al. 1995).

MATERIALS AND METHODS

Field Collection

Lilaeopsis masonii specimens were collected in the spring of 2007 from locations along the Napa River and in the Sacramento/San Joaquin Delta. *Lilaeopsis occidentalis* was collected from Bodega Head, California, and Mason and Lawrence lakes in Washington State (Fig. 1). Leaf material to be used in DNA extraction was preserved in silica gel at the time of collection. Vouchers were deposited at the herbarium at San Francisco State University (SFSU) (Table 1). Material for *L. brasiliensis* (Glaz.) Affolter and *L. mauritiana* G. Petersen & J. Affolter was obtained from a commercial aquarium supplier (freshwateraquariumplants.com). The dataset is composed of 35 nrDNA ITS sequences representing seven taxa, including three sequences

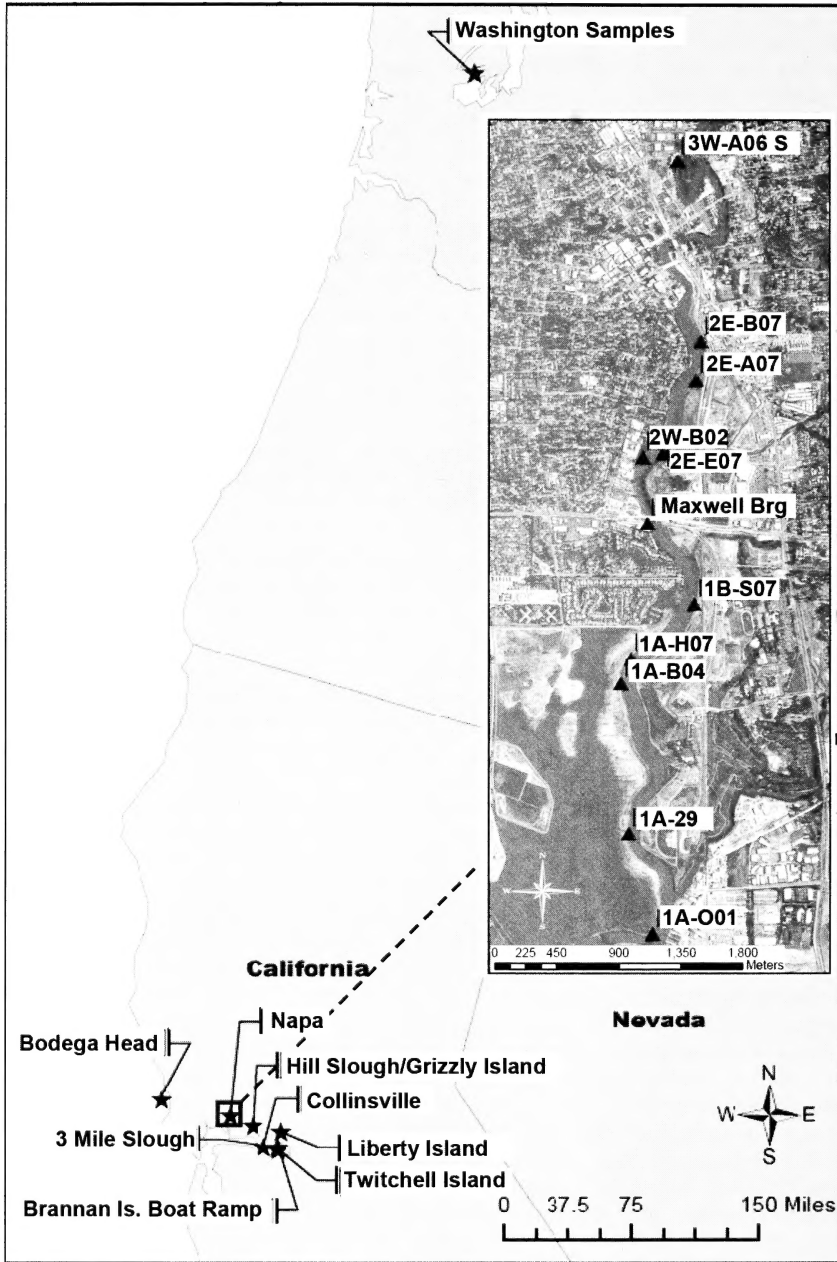


FIG. 1. Map of the geographic locations of *Lilaeopsis masonii* and *L. occidentalis* specimens collected for this study.

from Genbank (*L. carolinensis* J. M. Coulter & Rose, *L. novae-zelandiae* (Gand.) A. W. Hill, and *L. occidentalis*), two specimens from the aquarium trade labeled as *L. brasiliensis* and *L. mauritiana*, and two specimens of *L. schaffneriana* (Schltld.) J. M. Coulter & Rose subsp. *recurva* (A. W. Hill) Affolter courtesy of the Desert Botanical Garden staff. Comprehensive sampling was conducted for *L. masonii* and *L. occidentalis* as the purpose of this study was to resolve the taxonomic classification for these two species. A detailed systematic

study for *Lilaeopsis* is in preparation (S. Downie, Univ. of Illinois, Urbana-Champaign, personal communication).

ITS Methods

DNA from leaf tissue of five of the seven species was extracted using the Qiagen DNeasy Plant Mini Kit (QIAGEN, Inc., Valencia, CA), following the manufacturer's protocol with slight modifications. *Lilaeopsis carolinensis* and *L.*

TABLE 2. AFLP PRIMER AND ADAPTER SEQUENCES.

Primer	Sequence
Ad1EcoRI	5' -CTCGTAGACTGCGTACC- 3'
Ad1MseI	5' -GACGATGAGTCCTGAG- 3'
prampEcoRI	5' -GACTGCGTACCAATTCA- 3'
prampMseI	5' -GATGAGTCCTGAGTAAC- 3'
FAM-EcoRI	5' -GACTGCGTACCAATTCAAC- 3'
HEX-EcoRI	5' -GACTGCGTACCAATTCAACG- 3'
MseI + CAA	5' -GATGAGTCCTGAGTAACAA- 3'
MseI + CAT	5' -GATGAGTCCTGAGTAACAT- 3'
MseI + CAG	5' -GATGAGTCCTGAGTAACAG- 3'

novae-zealandiae were excluded from this analysis due to technical difficulties with the DNA extraction from the leaf material. Dilutions of the genomic DNA extract of 1:10 in ultrapure water were used in PCR reactions. The contiguous ITS1, 5.8S, and ITS2 regions of nuclear ribosomal DNA were PCR-amplified using the primers ITSLEU (Baum et al. 1998) and ITS4 (White et al. 1990) in final reaction volumes of 25 μ l. Positive amplifications were purified using the MO BIO UltraClean PCR Clean-up DNA Purification Kit (MO BIO Laboratories, Inc., Solana Beach, CA). Internal primers ITS2 and ITS3 (White et al. 1990) were used in addition to ITSLEU and ITS4 in cycle-sequencing reactions in order to extend fragments and clarify ambiguities. Fragments were sequenced with the BigDye 3.1 kit (Applied Biosystems, Foster City, CA) following the manufacturer's protocols, and visualized using the ABI PRISM 3100 Genetic Analyzer (Applied Biosystems). Sequences were manually aligned using Sequencher 3.1.1 (GeneCodes Corp., Ann Arbor, MI) and MacClade 4.04 (Maddison and Maddison 2001).

AFLP Methods

AFLP fingerprinting was conducted following a modified protocol based on the methods described by Vos et al. (1995). DNA extracts prepared for ITS analysis also were used for this study undiluted. Approximate DNA concentrations for all samples were estimated to contain a range of concentrations from 10 ng/ μ l to 50 ng/ μ l using an ethidium dot test. DNA template of each sample was digested using the infrequent endonuclease cutter *EcoRI* and the frequent endonuclease cutter *MseI*. Immediately following digestion, the entire digestion reaction was combined with an equal volume of ligation mix.

The resulting fragmented DNA template containing "sticky ends" was diluted five-fold and subsequently amplified by PCR using a pre-selective primer mix. This step effectively reduces the number of possible fragments by approximately 1/16th (Meudt and Clarke 2007). The

pre-selective reaction condition consisted of 30 cycles of 94° for 30 sec, 56° for 1 min, and 72° for 1 min.

Three combinations of selective primer sets were used to produce a final AFLP fingerprint for each sample (Table 2). Each set of selective primers consisted of a primer region matching the known adapter sequence, as well as three selective nucleotides on the 3' end of the *MseI* primer and three selective nucleotides plus a fluorescent label on the 3' end of the *EcoRI* primer. Template for the pre-selective PCR was diluted 6-fold and then combined with a master mix containing one set of selective PCR primers. A step-down PCR was used to amplify the selective fragments in a program consisting of 13 cycles of 94° for 30 sec, 65° for 30 sec (-0.7° per cycle), and 72° for 1 min, followed by 24 cycles of 94° for 30 sec, 56° for 30 sec, and 72° for 10 sec.

The final selective PCR product fragments containing a fluorescently labeled *EcoRI* end and unlabeled *MseI* end were analyzed undiluted using an ABI 3100 genetic analyzer (Applied Biosystems). Initial fragments were sized first using the analysis software GeneScan (Applied Biosystems) and using the program by GeneMarker® (SoftGenetics, State College, PA). After a comparison of fragment calling using both programs, all samples were analyzed using GeneMarker®.

Fragments were recorded for each sample in a data matrix based on a binary system (1 for presence, 0 for absence); a data matrix was developed for each primer combination and then all data was collated into a single data matrix. To test reproducibility of results, twenty percent of all samples selected at random for each primer pair were re-analyzed, starting with the initial DNA extracts. Fragment peaks that were determined to be consistently low (below 300 peak intensity) or unpredictable were dropped from the matrix table.

Data Analysis

Phylogenetic analyses of ITS sequences were conducted using Phylip version 3.68 (Felsenstein 2004). All characters were weighted equally,

character state transformations were treated as unordered, and gaps were treated as missing data. Most-parsimonious trees were obtained in Phylip using the "branch-and-bound" method of exact search implemented by the analysis unit DNA-PENNY. Bootstrap re-sampling (1000 replicates) was used to assess nodal support (Felsenstein 1985). Most parsimonious trees were generated from a search of 100,000 trees and a final tree was derived using a strict consensus tree method (Felsenstein 2004). Additional tree searches were conducted in greater volumes, up to 1,000,000. However, larger searches produced the same final tree, thus a smaller tree search was selected to reduce run-time during bootstrapping. Several combinations of *Lilaeopsis* species outgroups were explored before selecting *L. novae-zelandiae* as the outgroup. This selection was based on indications of a potential sister group relationship between *L. novae-zelandiae* and *L. occidentalis*, which was supported by ITS phylogenetic analysis of this genus within the Apiaceae tribe described in Downie et al. (2008). Genetic distances to determine branch lengths were calculated in Phylip using the Jukes-Cantor method implemented in DNADIST and a Fitch-Margoliash (FITCH) search.

AFLP phylogenetic analysis was performed using the program Phylip version 3.68 (Felsenstein 2004). A genetic distance matrix was created using the techniques described by Nei and Lei (1979) as implemented by RestDist in Phylip (Felsenstein 2004). The output matrix was then input into NEIGHBOR using the UPGMA method of cluster analysis (Felsenstein 2004). Using this approach, an output tree was constructed by successive clustering using an average-linkage method of clustering. The output file was then plotted as both a rooted and unrooted tree. A search for the most parsimonious trees was implemented first using the branch-and-bound algorithm of DOLPENNY (100,000 trees searched) in Phylip following bootstrap analysis using 100 replicates. A 50% majority-rule consensus tree was then generated to condense the results into a final tree, which is presented here. Previous studies of *Lilaeopsis* using AFLP analysis have not previously been reported. As such, outgroup selection for AFLP parsimony analysis was determined following variable, preliminary analysis replicates. *Lilaeopsis schaffneriana* was selected as this species is the closest geographically to both *L. masonii* and *L. occidentalis*. Further, *L. schaffneriana* also demonstrated sufficient genetic differences to be used as an appropriate outgroup.

To further visualize potential multi-dimensional correlation of AFLP data based on genetic similarities, an additional genetic distance matrix was derived using Manhattan distance (StatistiXL; www.statistixl.com). These

data were then analyzed using a principal coordinates analysis (PCA) using the Microsoft Excel® add-in program GenAlEx 6.2 (Peakall and Smouse 2006). To determine whether a measurable degree of genetic dissimilarity among *L. occidentalis* (WA and CA samples) and *L. masonii* (CA samples) could be attributed to geographic distance, an additional test of molecular variance based on geographic origin as measured by Global Position System (GPS) also was tested. A two-way analysis of variance was assessed for collections of *L. occidentalis* and *L. masonii* using an analysis of molecular variance (AMOVA) with GenAlEx 6.2 (Peakall and Smouse 2006). Significance was assessed using 99 permutations.

RESULTS

DNA sequence analysis of the ITS regions ITS1, 5.8S, and ITS2 of nuclear ribosomal DNA, based on a most parsimonious search of 64,631 trees using a branch-and-bound method, revealed no differences between California samples of *L. occidentalis* and *L. masonii* samples, including a GenBank accession for *L. occidentalis* (100 of 100 trees) (Fig. 2). Within the *L. occidentalis*/*L. masonii* clade, samples collected from Washington clustered separately. Distance values between Washington and California samples were low for single collections from Lawrence Lake and Mason's Lake (0.1 and 0.3%, respectively). However, a second sample from Lawrence Lake exhibited higher distance values (1.5%), which may be due to missing data. Distance values for California samples of *L. masonii* and *L. occidentalis* were 0% across all samples. Comparatively, distance values between the additional species used for this study ranged from 1.2–8%. Distance based analysis of ITS sequences found an identical tree structure as the strict consensus tree inferred from most parsimonious results implemented by DNAPENNY. Bootstrap estimates from 1000 replicate analyses yielded 100% nodal support for all branches. Branch placement and relationship of *Lilaeopsis* species used in this study are consistent with results of a previous ITS phylogenetic analyses by Downie et al. (2008), though that study excluded *L. masonii*.

The three AFLP primer combinations generated 274 unique fragments among 29 samples, with only 21 fragments shared or monomorphic between the five species used in this study. Although a small sample size was used, specifically for *L. brasiliensis*, *L. schaffneriana*, and *L. mauritiana*, the large number of shared fragments is potentially indicative of low genetic diversity within this genus, which is consistent with species exhibiting high morphologic plasticity (Linhart and Grant 1996). The number of total diagnostic bands from the three markers combined data set

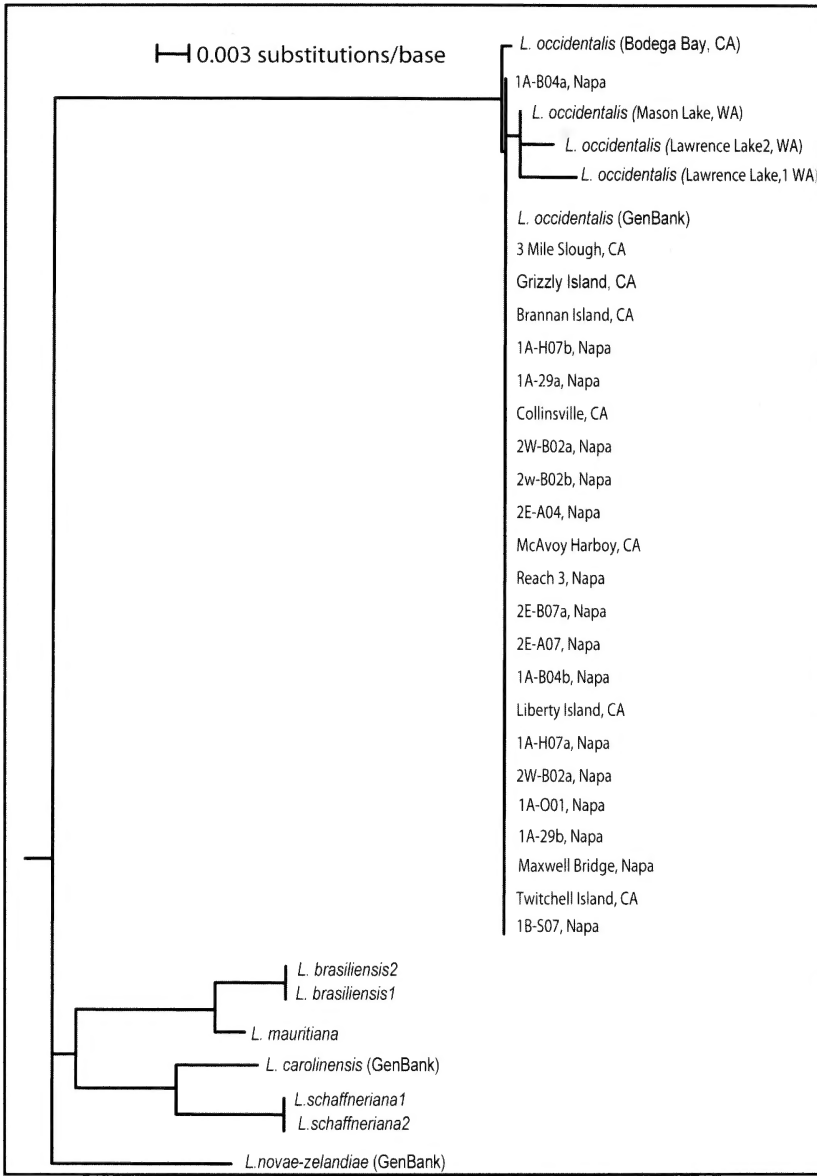


FIG. 2. Strict consensus tree derived from ITS sequence data using the branch and bound method implemented by DOLPENNY. Branch values are Bootstraps. Upper left tree illustrates distance values, branch lengths are proportional to the number of nucleotide substitutions per base.

varied between species, ranging from a low of 98 bands for one sample of *L. schaffneriana*, to a high of 135 bands for the Mason Lake, WA sample of *L. occidentalis*, with a mean number of AFLP bands equaling 123 (SD = 9.5) (Table 3).

Within species genetic distance values (Manhattan distance calculated from the AFLP matrix) ranged from a low of 1.4 for *L. masonii* (Napa River site #1A-H07, large and small forms), to a high of 6.6 for *L. masonii* (Napa site 1A-B04 and Twitchell Island collections). Between species values ranged from a low of 4.1 for *L. occidentalis* (Mason Lake, WA) and *L.*

masonii (Napa River #2W-B02), to high of 11.9 for *L. schaffneriana* and *L. occidentalis* (Lake Lawrence, WA collection).

Principal coordinate analysis (PCA) illustrated an overlapping association between samples of *L. occidentalis* and *L. masonii* (Fig. 3), but a clear differentiation between the *L. occidentalis*/*L. masonii* cluster and all other *Liliaeopsis* species examined in this study, i.e., *L. schaffneriana*, *L. mauritiana*, and *L. brasiliensis*. The small separation observed between the *L. occidentalis* and *L. masonii* data may be attributed to geographic distance. Results of AMOVA analysis derived

TABLE 3. AFLP FRAGMENT NUMBERS FOR EACH SPECIES.

Species	Mean or Total No. of Fragments			
	CAA	CAG	CAT	Total
<i>L. masonii</i>	53.5	46.1	21.9	125.1
<i>L. occidentalis</i>	52.7	50	22.9	128.8
<i>L. schaffneriana</i> subsp. <i>recurva</i>	47.5	34.5	16	99.5
<i>L. brasiliensis</i>	52	39	21	114
<i>L. mauritiana</i>	43	38	16	99
All Fragments				123

from grouping samples based on geographic location indicated that approximately 73% of genetic variation was distributed between groups and thus 23% among groups, supporting the conclusion that most observed genetic variation is due to geographic distance ($P = 0.01$).

The UPGMA cluster phenograms provides additional support for the results of the PCA analysis, illustrating a combined grouping of *L. occidentalis* (CA and WA) and *L. masonii* samples (Fig. 4). Within the *L. occidentalis* and *L. masonii* clade, samples collected from Washington clustered separately from samples collected within California, corroborative of results of AMOVA indicating that variation within this clade is due in large part to geographic distance. Samples of *L. brasiliensis* and *L. mauritiana* cluster separately but are sister to the *L. occidentalis/L. masonii* clade; *L. schaffneriana* samples also cluster separately but are sister to all other specimens/species used for this study. The most parsimonious tree from the maximum parsimony analysis supports a single *L. occidentalis/L. masonii* clade; however, additional reso-

lution within this taxon is less certain of the specific placement of *Lilaeopsis* samples, based on geographic location (Fig. 5).

DISCUSSION

Taxonomic implications. Within the last two decades, the use of genetic techniques to distinguish discrete evolutionary units has become common place in systematic biology. Use of genetic data in the protection of endangered species when morphological (or other character) information is either unreliable or impossible is just one reason why this approach to species identification and delimitation is so important (Avice 2003). Thus, sole reliance on morphological, geographic, reproductive behavior or some combination of non-genetic characters to delimit taxa is no longer defensible when diagnostic genetic information is available and can be readily assessed. In the case of *Lilaeopsis masonii* and *L. occidentalis*, neither ITS sequence nor AFLP fragment length data support the recognition of the *L. masonii* as a distinct evolutionary entity.

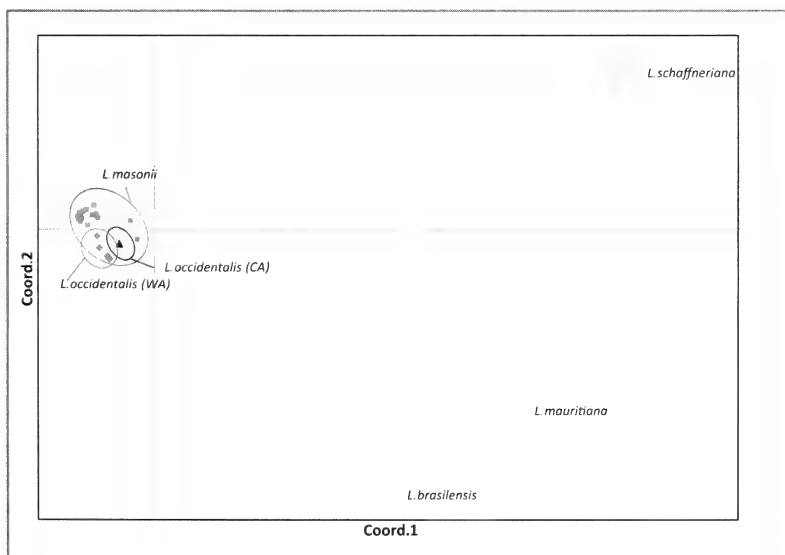


FIG. 3. Principal coordinates analysis (PCA) of AFLP fragment data matrix. Codes for Napa collections, e.g., 1A-H07, indicate different collection locations and dates along the Napa River specific to the Napa River Flood Protection Project.

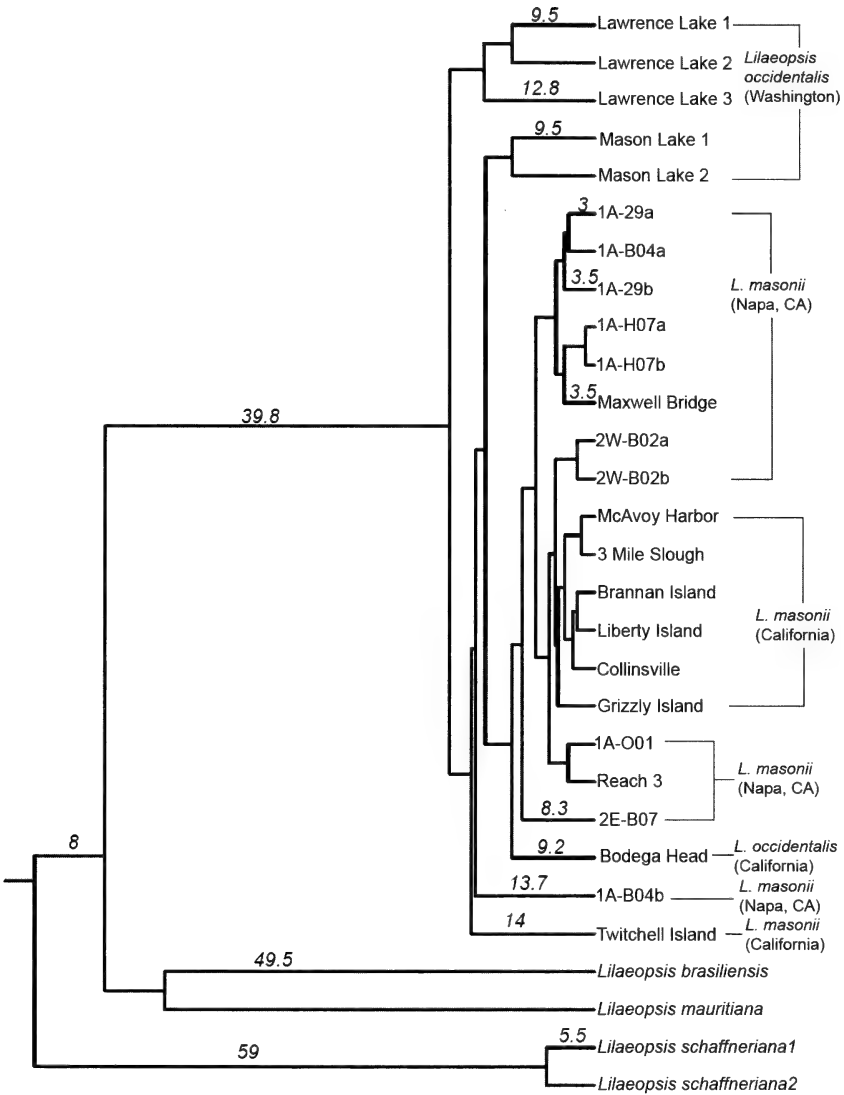


FIG. 4. UPGMA Cluster Phenogram (rooted and unrooted trees) from AFLP data matrix of five species of *Lilaeopsis*. Numbers are distance values. Codes for Napa collections, e.g., 1A-H07, indicate different collection locations and dates along the Napa River specific to the Napa River Flood Protection Project.

The morphological and geographic information to support two distinct taxa is weak, ambiguous, and unreliable at best.

Fallon's (2007) arguments regarding the importance of using genetic information to resolve taxonomic issues for species protection is borne out in our study. While her review focused solely on vertebrates, and on only those species, infraspecific or population segments proposed for listing, not those already listed, our results add further emphasis for use of molecular techniques in conservation efforts. We concur that multiple genetic markers are essential for a thorough assessment of taxonomic or population unit (or at any appropriate level) when considering of formal protection. We further suggest that

use of best available science such as existing or generating new genetic information is equally valid for the periodic reviews of listed species required of both the federal and state agencies. Further and relevant to *L. masonii*, use of genetic data is likely to be essential during a de-listing review process.

Based upon several lines of evidence, including decades of fieldwork throughout the range of *L. masonii*, observations from the most recent monograph (Affolter 1985), and our molecular genetic analyses, we urge that this rare taxon no longer be recognized as a separate taxonomic entity. Rather, *L. masonii* should be subsumed within the larger, much more widespread, common, and equally variable species, *L. occidentalis*.

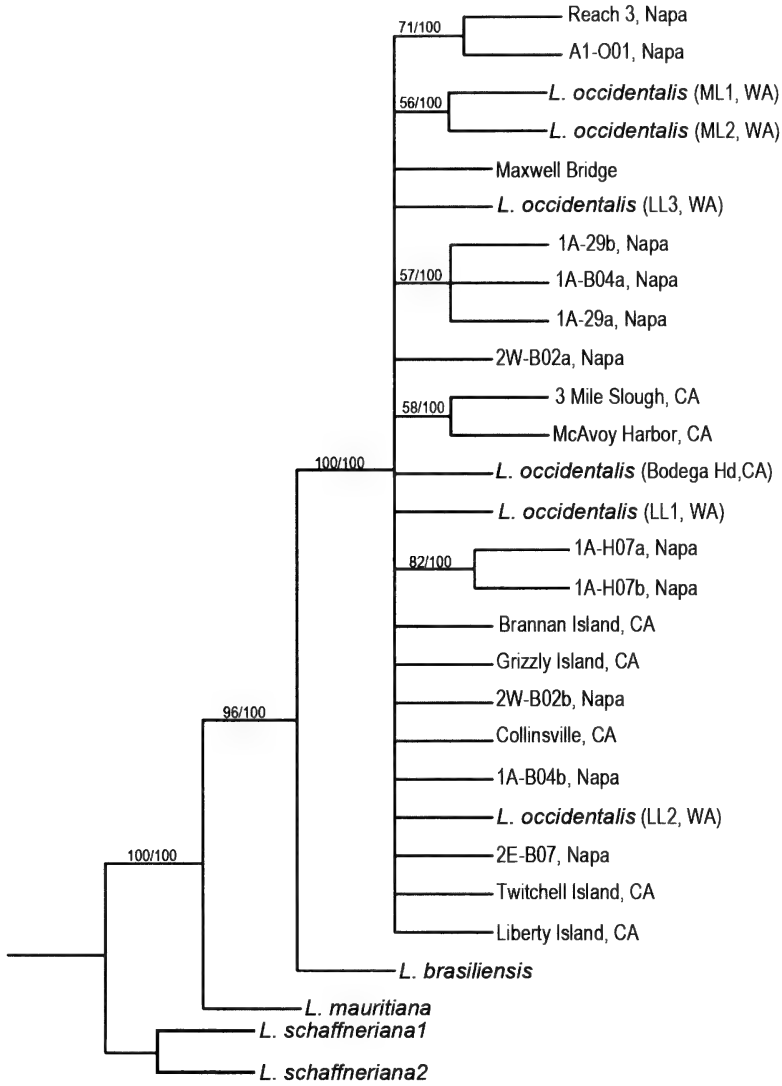


FIG. 5. Most parsimonious tree from AFLP data matrix of five species of *Lilaeopsis*. Codes for Napa collections, e.g., 1A-H07, indicate different collection locations and dates along the Napa River specific to the Napa River Flood Protection Project.

Significant morphological, but limited genetic, variation exists both within and among populations of *Lilaeopsis* throughout the Pacific Coast of North America, from the Queen Charlotte Islands in British Columbia to the inland islands of the Sacramento-San Joaquin Delta in the Great Valley of California. Importantly, this variation does not follow any consistent environmental gradient for either taxon. As such, one intrinsically variable species, not two, of west coast *Lilaeopsis* should be recognized in relevant floras, including those for North America.

Important additional circumstantial support comes from the very wide geographic ranges, some amphitropical, of the great majority of other species of *Lilaeopsis*, including *L. chinensis* Kuntze, *L. carolinensis*, *L. schaffneriana*, *L.*

macloviana A. W. Hill, and *L. novae-zelandiae*, among others. A large geographic range is not surprising for all these species, given their vigorous vegetative reproduction by easily fragmented rhizomes and their restriction to aquatic habitats, many with bi- or multi-directional flow vectors (e.g., Napa River, Sacramento River, Pacific Ocean).

Field observations suggest a possible explanation for the inter- and intra-populational variation in individual ramet size for both western North American *Lilaeopsis*. Periods of rapid spring growth occur during the spring tides and snowmelt from the Sierra Nevada, when temperatures warm sufficiently to encourage an increase in photosynthetic activity. This increased vegetative growth occurs when floodwaters from the

Sacramento, San Joaquin and Napa Rivers are at their height of volume and rate of flow. Thus, the comparatively high kinetic energy of flowing water during the spring run-off, coupled with this species' preference for river banks and shores characterized by high light and open exposure, combine to restrict vegetative growth to a comparatively shorter plant less vulnerable to being dislodged from its habitat. Relatively taller *Lilaeopsis* ramets are invariably found comparatively further from the shoreline in shadier and relatively lower energy microhabitats than comparatively shorter stature ramets. Aquaria enthusiasts who work with various species of *Lilaeopsis* have dubbed the short stature coupled with dense growth phenomenon the "lawn effect" (<http://www.freshwateraquariumplants.com>).

Conversely, observations of *Lilaeopsis* species submerged in (low energy) water reveal individual leaves grow comparatively longer. Affolter's (1985) greenhouse experiments and observations that demonstrated that for least eight of the 13 species *Lilaeopsis* studied (including *L. occidentalis*), material grown in submerged pots had larger and wider leaves, more septae, and wider rhizome diameter. In his monograph of the thirteen species known in 1985, increased periods of inundation result in a suite of morphological changes, including an increase in leaf length and increases in both peduncle and pedicel lengths (Affolter 1985). Lastly, the rejection of leaf length as a key diagnostic character distinguishing two otherwise very similar taxa has precedent in Affolter's lumping of all Andean, Fuegian, and Patagonian material into a single species, *L. macloviana*, synonymizing thirteen previously described taxa.

Regulatory implications. Neither CESA nor the federal ESA, as amended, protects any vascular plant distinct population segment as does the ESA for specific vertebrate populations. While an argument can be made that this is a form of taxon chauvinism, plant species are not protected below the infraspecific level. Such a comparison is important, because some vertebrate species that were listed relatively soon after the ESA was passed have since been determined not genetically distinct from common widespread relatives, but they continue to be formally protected because of the DPS provisions. For example, the San Francisco garter snake (*Thamnophis sirtalis tetrataenia*), a highly restricted taxon in central coastal California, was determined, through an examination of the clade's mtDNA (Janzen et al. 2002), to be a member of a California clade of the widespread common garter snake. These authors concluded that morphologically based subspecies designations of *T. sirtalis* in western North America were invalid because they did not reflect reciprocal monophyly of mtDNA sequences.

Extrapolating Janzen et al.'s (2002) logic to our genetic work with *Lilaeopsis*, the parallel conclusion that the specific designation of *L. masonii* is invalid is compelling. Because neither the CESA nor the ESA include DPS provisions for plant species, *L. masonii* no longer warrants protection as a state "rare" species and the allocation of limited recovery resources. Given the widespread nature of *Lilaeopsis occidentalis* + *L. masonii*, and the large number of projects (both existing and proposed) requiring mitigation and monitoring of the rare *L. masonii*, a timely review of our findings is essential. Conservation dollars are few, and they should be applied to truly rare, threatened, and real discrete species.

Finally, Pavlik (2003) recently examined the role of state- and federally-listed species protecting the ecosystems in which they are found. Of relevance is the notion that some protected species provide a "regulatory umbrella" for other species that are unlisted, but are rare, in decline, or otherwise of conservation concern. *Lilaeopsis masonii* has long served to restrict, prevent, or slow the conversion, degradation or destruction of wetlands throughout the Sacramento-San Joaquin Delta, Suisun Marsh, and San Francisco Bay ecosystems, thereby protecting associated but unlisted species of conservation concern. While a suite of other protected wetland plant taxa exist in these ecosystems (e.g., *Cirsium hydrophilum* Jeps. var. *hydrophilum* [Suisun thistle], *Cordylanthus mollis* A. Gray ssp. *mollis* [soft bird's beak], etc.), there are many more that are rare, in decline, and not listed (e.g., *Cicuta maculata* Lam. var. *bolanderi* (S. Watson) G. A. Mulligan [Bolander's water hemlock], *Plantago elongate* Pursh [slender plantain], *Lycopus asper* Greene) (see Baye et al. 2000). Thus we acknowledge that a delisting of Mason's *lilaeopsis* may further expedite wetland habitat loss in central California. Nonetheless, conservation in the twenty-first century demands the use of best available science, despite the unintended consequences that may occur. Ultimately, government agencies charged with the protection of our biodiversity must redouble their efforts to embrace new scientific results that affect listed species, commit to diligent review of listed and candidate species, and disseminate accurate and up-to-date information. Similarly, conservationists should redouble their efforts to provide the best available science for decision-making. The time to embrace current molecular genetic techniques in routine conservation decision-making has come.

ACKNOWLEDGMENTS

The authors would like to thank the Napa County Flood Control and Water Conservation District, particularly R. Thomasser, for funding this work; L. Garrison for assistance in the field and laboratory;

A. Fullerton for collection of two *Lilaeopsis* from Washington state, and J. Johnson for collection of *L. schaffneriana* subsp. *recurva* from Scotia Canyon in Arizona. We also wish to thank S. L. Krauss and F. Cipriano for guidance in the ITS and AFLP analyses, and the Conservation Genetics Laboratory, San Francisco State University for access to its facility. Lastly, we would like to thank J. Affolter, S. R. Downie, and B. J. Grewell for reading the manuscript and for their helpful comments. Four anonymous reviewers also provided comments that improved this manuscript.

LITERATURE CITED

- AFFOLTER, J. M. 1985. A monograph of the genus *Lilaeopsis* (Umbelliferae). Systematic Botany Monographs 6:1–140.
- AVISE, J. C. 2003. A role for molecular genetics in the recognition and conservation of endangered species. Trends in Ecology and Evolution 3:279–281.
- BAUM, D. A., R. L. SMALL, AND J. F. WENDE. 1998. Biogeography and floral evolution of baobabs (*Adansonia*, Bombacaceae) as inferred from multiple data sets. Taxon 27:317–329.
- BAYE, P. R., P. M. FABER, AND B. GREWELL. 2000. Tidal marsh plants of the San Francisco Estuary. Pp. 9–33 in P. R. Olofson (ed.), Goals project. Baylands ecosystems species and community profiles: life histories and environmental requirements of key plants, fish and wildlife. San Francisco Regional Water Quality Control Board, Oakland, CA.
- CALIFORNIA NATIVE PLANT SOCIETY (CNPS). 2008. Inventory of rare and endangered plants (online edition, v7-08d). California Native Plant Society, Sacramento, CA. Website <http://www.cnps.org/inventory> [accessed 23 Dec. 2008].
- CALIFORNIA NATURAL DIVERSITY DATABASE (CNDDDB) RAREFIND. 2009. *Lilaeopsis masonii* report from Mary Ann Showers. Received March 18, 2009. California Department of Fish and Game, Sacramento, CA.
- DOWNIE, S. R., D. S. KATZ-DOWNIE, AND M. F. WATSON. 2000. A phylogeny of the flowering plant family Apiaceae based on chloroplast DNA *RPL16* and *RPOC1* intron sequences: towards a supra-generic classification of subfamily Apioideae. American Journal of Botany 87:273–292.
- , F.-J. SUN, AND C.-S. LEE. 2008. Phylogeny and biogeography of Apiaceae tribe Oenanthe inferred from nuclear rDNA ITS and cpDNA *psbI-5'trnK*^(U+U) sequences, with emphasis on the North American endemics clade. Botany 86:1039–1064.
- FALLON, S. M. 2007. Genetic data and the listing of species under the U.S. Endangered Species Act. Conservation Biology 21:1186–1195.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using bootstrap. Evolution 39:783–791.
- . 2004. PHYLIP (Phylogeny Inference Package) version 3.6. Distributed by the author. Department of Genome Sciences, University of Washington, Seattle, WA.
- FIEDLER, P. L. AND R. K. ZEBELL. 1993. Final report. Restoration and recovery of Mason's *Lilaeopsis*: Phase 1. Report to the Shell Oil Spill Litigation Settlement Trustee Committee and the California Department of Fish and Game, Endangered Plant Program, Sacramento, CA. Website <http://nrm.dfg.ca.gov/FileHandler.ashx?DocumentVersionID=3708> [accessed 27 July 2011].
- GOLDEN, M. L. 1992. The distribution and ecology of *Lilaeopsis masonii*, a California native rare plant. M.A. thesis, San Francisco State University, San Francisco, CA.
- AND P. L. FIEDLER. 1991. Final report. Characterization of the habitat for *Lilaeopsis masonii* (Umbelliferae): A California state-listed rare plant species. California Department of Fish and Game, Sacramento, CA. Website: <http://nrm.dfg.ca.gov/documents/ContextDocs.aspx?cat=Section6PlantReports> [accessed 16 September 2011].
- HARDWAY, T. M., K. SPALIK, M. K. WATSON, D. S. KATZ-DOWNIE, AND S. R. DOWNIE. 2004. Circumscription of Apiaceae tribe Oenantheae. South African Journal of Botany 70:393–406.
- HICKMAN, J. (ed.) 1993. The Jepson manual. Higher plants of California. University of California Press, Berkeley, CA.
- HILL, A. W. 1927. The genus *Lilaeopsis*: a study in geographical distribution. Journal of the Linnaean Society 47:525–551.
- HOLLAND, B., A. C. CLARKE, AND H. M. MEUDT. 2008. Optimizing automated AFLP scoring parameters to improve phylogenetic resolution. Systematic Biology 57:347–366.
- JANZEN, F. J., J. G. KRENZ, T. S. HASELKORN, E. D. BRODIE, JR., AND E. D. BRODIE, III. 2002. Molecular phylogeography of common garter snakes (*Thamnophis sirtalis*) in western North America: implications for regional historical forces. Molecular Ecology 11:1739–1751.
- LINHART, Y. B. AND M. C. GRANT. 1996. Evolutionary significance of local genetic differentiation in plants. Annual Review of Ecology and Systematics 17:237–277.
- MADDISON, W. P. AND D. R. MADDISON. 2001. MacClade: analysis of phylogeny and character evolution. Version 4.02. Sinauer Associates, Sunderland, MA.
- MASON, H. L. 1957. A flora of the marshes of California. University of California Press, Berkeley, CA.
- MATHIAS, M. E. AND L. CONSTANCE. 1977. Two new local Umbelliferae (Apiaceae) from California. Madroño 24:78–83.
- MEUDT, H. M. AND A. C. CLARKE. 2007. Almost forgotten or latest practice? AFLP applications, analyses and advances. Trends in Plant Science 12:106–117.
- NEI, M. AND W.-H. LEI. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. Proceedings of the National Academy of Sciences, USA 76:5269–5273.
- PAVLIK, B. M. 2003. Plants that protect ecosystems: a survey from California. Biodiversity and Conservation 12:717–729.
- PEAKALL, R. AND P. E. SMOUSE. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.
- PETERSEN, G., O. SEBERG, AND S. LARSEN. 2002. The phylogenetic and taxonomic position of *Lilaeopsis* (Apiaceae), with notes on the applicability of ITS sequence data for phylogenetic reconstruction. Australian Systematic Botany 15:181–191.

- TIBOR, D. (ed.) 2001, CNPS inventory of rare and endangered vascular plants of California. 6th ed. California Native Plant Society, Sacramento, CA.
- VOS, P., R. HOBERS, M. BLEEKER, M. REIJANS, T VAN DE LEE, M. HORNES, A. FRITJERS, J. POT, J. PELEMAN, M. KUIPER, AND M. ZABEAU. 1995. AFLP: a new technique for DNA fingerprinting. *Nucleic Acids Research* 23:4407–4414.
- WHITE, T., J. T. BRUNS, S. LEE, AND J. TAYLOR. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 *in* M. Innis, D. Gelfand, J. Sininsky, and T. White, (eds.), PCR protocols. A guide to methods and applications. Academic Press, San Diego, CA.
- WSP ENVIRONMENTAL STRATEGIES (WSP). 2007, Year 7 (2007) Rare plants of the lower Napa River/Napa Creek Flood Protection Project. Final Monitoring Report prepared for the Napa County Flood Control and Water Conservation District, Napa, CA.
- ZEBELL, R. K. AND P. L. FIEDLER. 1996. Final Report. Restoration and recovery of Mason's lilaeopsis. Phase II. Report to the Shell Oil Litigation Settlement Trustee Committee and the Endangered Plant Program, Natural Heritage Division, California Department of Fish and Game, Sacramento, CA. Website <http://nrm.dfg.ca.gov/FileHandler.ashx?DocumentVersionID=3709> [accessed 28 July 2011].

A COMPARISON OF THE EFFECTS OF Na_2SO_4 AND NaCl ON THE GROWTH OF *HELIANTHUS PARADOXUS* AND *HELIANTHUS ANNUUS* (ASTERACEAE)

M. O. MENDEZ¹ AND O. W. VAN AUKEN

Department of Biology, University of Texas at San Antonio, San Antonio, TX 78249
monica.mendez@tamui.edu

ABSTRACT

Helianthus paradoxus Heiser (Asteraceae, puzzle sunflower), is a federally threatened hybrid species found in salt marshes of west Texas and New Mexico. *Helianthus annuus* L. (Asteraceae, common sunflower) is one of the parent species and is found throughout North America, but it is not present in the inland salt marshes where *H. paradoxus* is found. *Helianthus paradoxus* has previously been described as a halophyte, but its tolerance to Na_2SO_4 , one of the major salts found in its habitat, has not been investigated. However, salinity has been identified as a major abiotic factor influencing the limited distribution of *H. paradoxus* populations. In this greenhouse study, the effects of elevated concentrations of Na_2SO_4 and NaCl , at equal ionic strengths (0.00, 0.09, 0.17, 0.34, and 0.51), on the survival and dry mass of both *H. paradoxus* and *H. annuus* were examined. In the three-way factorial experiment, the effects on dry mass observed were dependent on the species, the type of salt and the ionic strength of the salt. *Helianthus paradoxus* produced more dry mass than *H. annuus* in both salt treatments; however, NaCl was more inhibitory of dry mass production for both species with plants unable to survive the highest salt treatments. While dry mass of *H. annuus* decreased with increasing ionic strengths of both salts, dry mass of *H. paradoxus* increased by 38 to 72% in low to moderate ionic strengths of Na_2SO_4 relative to the nonsaline treatment. Both species were less tolerant of NaCl than Na_2SO_4 with *H. paradoxus* seeming to have moderate and high tolerance to elevated Cl^- and SO_4^{2-} ionic strength, respectively, while *H. annuus* had low to moderate tolerance. Greater dry mass production in Na_2SO_4 , along with tolerance to both salts, suggests that low to moderate sulfate soil salinity will enhance the dry mass production of *H. paradoxus*.

Key Words: Halophyte, *helianthus annuus*, *helianthus paradoxus*, ionic strength, NaCl , Na_2SO_4 , salt tolerance, sunflower.

Helianthus paradoxus Heiser (Asteraceae, puzzle sunflower) is a federally threatened species with limited distribution in salt marshes in west Texas and New Mexico (Correll and Johnston 1979; Poole and Diamond 1993; McDonald 1999). Hybridization studies (Heiser 1958, 1965; Abbott 1992) and molecular analysis (Rieseberg et al. 1990; Rieseberg 1991; Rieseberg et al. 1991) have determined that *H. paradoxus* is a stabilized hybrid species between *H. annuus* L. (Asteraceae, common sunflower) and *H. petiolaris* Nutt. (plains sunflower). Although *H. paradoxus* shares several morphological and ecophysiological traits with its parental species (Rosenthal et al. 2002), it has diverged and is genetically isolated from its progenitors and considered a separate species. *Helianthus annuus* is common throughout North America and grows in disturbed, heavy clay soils that are moist in the spring and dry out by mid-summer. *Helianthus petiolaris* is found in dry, sandy soils in western North America, while *H. paradoxus* grows in heavy, waterlogged, saline soils (Van Auken and Bush 1998).

Ecological and ecophysiological studies of *H. paradoxus* have determined that this homoploid hybrid species is salt tolerant, unlike its parental species. *Helianthus paradoxus* is restricted to inland salt marshes with salt levels of approximately 10 g kg^{-1} (Poole and Diamond 1993; U.S. Fish and Wildlife Service 2005; Grunstra and Van Auken 2007a, b), while *H. annuus* and *H. petiolaris* can be found in low saline soils ($<0.02 \text{ g kg}^{-1}$ soil sodium, Welch and Rieseberg 2002). *Helianthus paradoxus* is a better competitor than its progenitors in saline soils (Bush and Van Auken 2004). The west Texas and New Mexico salt marshes were key habitats in isolating hybrids (Abbott 1992). The parental species are glycophytes and cannot survive the same habitat as *H. paradoxus*, where other salt tolerant plants are generally present (Poole and Diamond 1993; Lexer et al. 2003; U.S. Fish and Wildlife Service 2005). Additionally, *H. paradoxus* is capable of sequestering higher sodium and sulfur concentrations and produces greater leaf succulence compared to its parental species while maintaining significantly greater fitness when grown in elevated NaCl concentrations (Welch and Rieseberg 2002) or in field-like highly saline soil conditions (Karrenberg et al. 2006).

In the largest known population of *H. paradoxus*, at the Diamond-Y Spring Preserve near

¹Current address: Department of Biology & Chemistry, Texas A&M International University, 5201 University Boulevard, Laredo, TX 78041, USA.

Fort Stockton, Texas, the distribution of *H. paradoxus* is mainly affected by soil salinity and soil moisture gradients when biotic factors are not considered (Bush and Van Auken 1997; Van Auken and Bush 1998; Bush 2006a, b). This large desert spring and associated salt marsh has had 1.44 to 2.70 million *H. paradoxus* plants (Van Auken and Bush 1998), depending on environmental conditions. In addition, there are several rare and federally endangered invertebrates found in the marsh (McDonald 1999). *Helianthus paradoxus* plants consistently establish parallel to the drainage of Leon Creek but their proximity depends on seasonal climatic conditions influencing soil salinity levels and soil water content, both of which decrease dramatically upland from the lowest point in the salt marsh (Van Auken and Bush 1998; Grunstra and Van Auken 2007a, b). When annual rainfall is high, *H. paradoxus* can be found further from the drainage compared to drier years when plants are located closer to the drainage. The population of *H. paradoxus* at the Diamond-Y Spring Preserve seems to be dependent on low to intermediate salinity levels and intermediate moisture levels; however, salinity appears to be the major abiotic factor affecting the local distribution of *H. paradoxus* (Bush 2006a, b).

Previous studies have identified *H. paradoxus* as a salt tolerant species with characteristics of halophytes (Welch and Rieseberg 2002; Bush and Van Auken 2004). However, these studies were done with NaCl, one of the major salt components of the marsh, but not Na₂SO₄ which is also found at high concentrations in soils of its salt marsh habitat (Boghici 1997). In addition, the effects of a limited range of salinity levels have been examined. Chloride is generally more toxic than SO₄²⁻ and even Na⁺ at lower concentrations (Manchanda et al. 1982; Marschner 1995; Franklin and Zwiazek 2004; Munns and Tester 2008); however, SO₄²⁻ salinity can be more growth inhibitive than Cl⁻ for some halophytes (Warne et al. 1990; Egan and Ungar 1998). At the same time, separating specific ion effects is difficult and differential effects of Cl⁻ and SO₄²⁻ salinity on *H. paradoxus* are still unknown; consequently, the influence of these anions on the ecological isolation and distribution of *H. paradoxus* has not yet been elucidated.

Ionic strength rather than salt concentration was used as a treatment variable in the present study. It is used as a normalization procedure and was required because of different numbers of ions present in equal molar solutions of NaCl (2 ions) and Na₂SO₄ (3 ions). Therefore, it was important to compare the two salts at concentrations that allowed osmotic potential of the corresponding treatments to be equal. Concentrations of the two salt treatments were based on equal ionic strengths calculated using procedures in Barrow (1966).

TABLE 1. IONIC STRENGTHS OF EACH TREATMENT AND CORRESPONDING SALT CONCENTRATIONS IN G·KG⁻¹ EXAMINED IN THE STUDY.

Ionic strength	NaCl	Na ₂ SO ₄
	(g kg ⁻¹)	
0.00	0	0
0.09	5	4.1
0.17	10	8.1
0.34	20	16.2
0.51	30	24.3

The objective of this study was to examine the survival, growth and the salt tolerance of *H. paradoxus* in elevated levels of both Na₂SO₄ and NaCl, at equal ionic strengths. Both of these salts are major contributors of the soil salts of the Diamond-Y Spring Preserve. Our experiment also included the more salt tolerant of its parental species, *H. annuus*, a known glycophyte.

MATERIALS AND METHODS

Helianthus paradoxus seeds were collected from the Nature Conservancy's Diamond-Y Spring Preserve near Fort Stockton, Texas (31°00.54'N, 102°55.49'W) and stored dry at 25°C until used. *Helianthus annuus* seeds were purchased from Native American Seed Farm (Junction, Texas 76849) and stored dry at 4°C. Seeds of both species were cold stratified in Ziploc® storage bags lined with paper towels, wet with deionized water, and maintained at 4°C in the dark for 4 weeks (*H. paradoxus*) or 8 weeks (*H. annuus*). To prevent osmotic shock, groups of seeds (approximately 400 seeds for each treatment) were germinated on paper toweling saturated with deionized water (0.00 osmotic strength) in plastic storage bags at 25°C. Germinated seedlings were transferred to equal or increasing levels of the appropriate salt (NaCl and Na₂SO₄ at ionic strengths of 0.00, 0.05, 0.09, 0.13, 0.17, 0.26, 0.34, 0.43, and 0.51) every 2 d until placed in the final salt (NaCl or Na₂SO₄) and ionic strength to be tested (0.00, 0.09, 0.17, 0.34, and 0.51). Seedlings were kept in the appropriate solution for a total of 18 days prior to transplanting to pots in the greenhouse containing the corresponding treatment (Table 1).

For each species, five plants per pot with five replicate pots per treatment (25 plants per species per treatment) were grown for 62 d. Plastic pots (15 cm diameter × 15 cm height) lined with a Ziploc® storage bag (to retain water, salts, and nutrients) were filled with 1.4 kg of air-dried, sieved (5.8 mm mesh screen) soil. The soil was the upper 10 cm of a low nutrient Patrick-series Mollisol (clayey-over-sandy, carbonatic-thermic, typic calciustoll), collected from northern Bexar Co., Texas (Taylor et al. 1966; Van Auken and Bush 1998). The soil was friable, allowing root

TABLE 2. THREE-WAY ANOVA RESULTS FOR THE TOTAL DRY MASS (G) OF TWO SPECIES (*HELIANTHUS PARADOXUS* AND *H. ANNUUS*) GROWN IN TWO SALTS (NaCl AND Na₂SO₄) AND AT FIVE IONIC STRENGTHS (0.00, 0.09, 0.17, 0.34, AND 0.51). All main effects and interactions were significant. ^a Significant interactions are designated (* = P < 0.05; ** = P < 0.01; *** = P < 0.001; **** = P < 0.0001).

Source ^a	df	SS	F	P
Species	1	4.11	35.69	<0.0001
Salt	1	14.75	128.17	<0.0001
Strength	4	5.00	43.44	<0.0001
Species × salt***	1	1.39	12.05	0.0008
Species × strength**	4	0.55	4.78	0.0016
Salt × strength****	4	1.67	14.50	<0.0001
Species × salt × strength*	4	0.40	3.51	0.0108
Error	80	9.21		
Total	99	59.95		

extraction and recovery (Bush and Van Auken 2004). Appropriate amounts of anhydrous salts (Na₂SO₄ or NaCl) and a single nutrient application (0.05 g of P from Na₂HPO₄ · 7H₂O, 0.07 g N from NH₄NO₃, 0.07 g of K from KCl, and 0.03 g of S from MgSO₄ · 7H₂O; Tiedemann and Klemmedson 1986) were added to each pot and thoroughly mixed. Before seedlings were planted, 400 ml of deionized water was added to each pot. Thereafter, soil moisture was maintained at approximately field capacity with distilled water. This study was conducted in a fiberglass greenhouse in which the daytime temperatures ranged from approximately 26° to 38°C and light levels were approximately 36% of full sunlight with a mean photosynthetically active photon flux densities of 562 ± 135 μmol m⁻² s⁻¹ measured with a Li-Cor® LI-188 integrating quantum sensor.

Plant survivorship was assessed at 62 d for each treatment combination (species × salt × ionic strength). Percent survivorship is based on the mean number of erect and green plants out of five plants per replicate pot per treatment.

Shoot and root dry mass were measured at the end of the experiment. For shoot dry mass, plants from each pot were clipped at the soil surface and placed in a pre-weighed paper bag. For the ash-free root dry mass, all of the soil and particulate matter from each pot was carefully washed off the roots. Roots were then wrapped in pre-weighed aluminum foil. All plant material was dried in a forced air oven at 90°C to a constant mass. After drying, roots were ashed in a programmable muffle furnace (Fisher Scientific Isotemp®, Fisher Scientific Research, Pittsburgh, PA) at 625°C for 3 hours to obtain the ash-free root dry mass (Böhm 1979). Total dry mass was also calculated by combining the shoot dry mass and ash-free root dry mass per pot.

All dry mass data was analyzed using SAS statistical software (SAS Institute 1999) with each pot as the unit of replication and P ≤ 0.05 as the criterion for significance. Any plant mortalities because of a treatment effect were taken into account by including a dry mass of zero. To

determine the effects of salt type and ionic strength on the dry mass of each species, a three-way ANOVA including interactions was employed. When significance was detected with the overall ANOVA, two-way and one-way ANOVAs were used followed by Duncan's Multiple Range Test to examine significant differences between all possible combinations of salt type and salt concentration for each species separately. Mean mortality was calculated, but was not analyzed statistically.

RESULTS

All *H. paradoxus* and *H. annuus* plants died in the highest ionic strengths of NaCl examined (0.34 and 0.51). However, both species demonstrated 100% survivorship in the no-salt treatment. For all Na₂SO₄ treatments, 100% of *H. paradoxus* plants survived, while 100% of the *H. annuus* plants survived in each of the Na₂SO₄ treatments except at the 0.51 ionic strength, the highest Na₂SO₄ concentration tested. Plant survivorship for *H. paradoxus* in NaCl treatments was 100% at the 0.09 and 0.17 ionic strengths, while 80% and 40% of *H. annuus* plants survived in these same ionic strengths, respectively.

Three three-way ANOVAs were used to analyze shoot, root, and total dry mass; however, only total dry mass data will be presented. Results were similar for mean shoot and root dry mass (analysis not shown). The three-way ANOVA (Table 2) demonstrated a significant overall species, salt, and ionic strength effect on total dry mass. In addition, the three two-way interactions were significant as was the three-way interaction. To demonstrate more clearly the experimental results, two of the two-way interactions will be presented first. Overall, *H. paradoxus* produced more dry mass than *H. annuus* in both salts (Fig. 1a, species × salt interaction). For both species, more dry mass was produced in the Na₂SO₄ treatment than in the NaCl treatment. In addition, ionic strength was significant with more dry mass in the lower treatments;

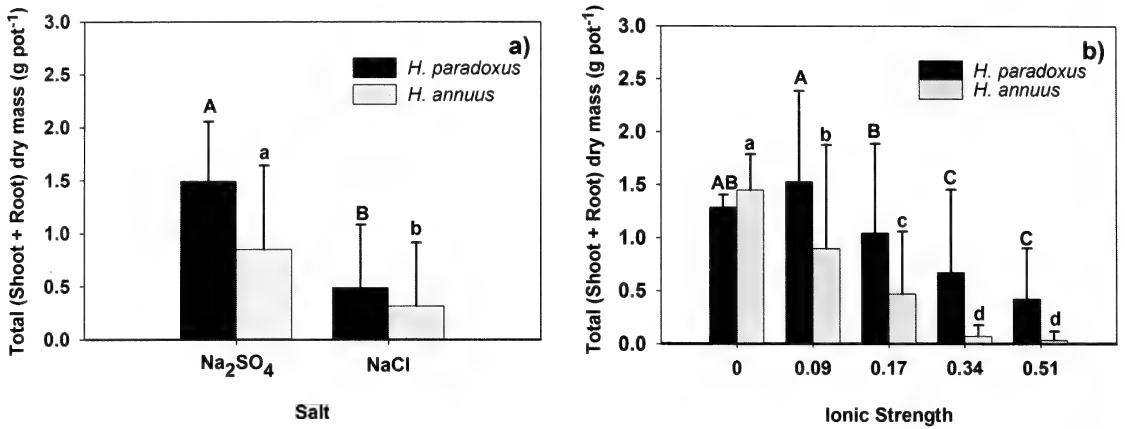


FIG. 1. Two-way interaction plots of total dry mass (bars) as the response variable for (a) salt (NaCl and Na₂SO₄) by species (*Helianthus paradoxus* and *Helianthus annuus*) and (b) ionic strength (0.00–0.51) by species. A three-way ANOVA determined there were significant differences ($P < 0.0001$) between salt treatments and ionic strengths for each species. Different letters indicate significant differences between means (Duncan's Multiple Range Test). Lines above the bars represent + one SD (standard deviation).

however, dry mass of *H. annuus* was significantly lower at an ionic strength of 0.09 (Fig. 1b, species \times ionic strength interaction). The salt \times ionic strength interaction has not been presented because the results can be seen within the three way interaction figure. The significant three-way interaction indicated that dry mass was dependent on species, salt type, and ionic strength (Table 2, Fig. 2a, b). *Helianthus paradoxus* dry mass was higher in Na₂SO₄ compared to NaCl (Fig. 2a), with the greatest dry mass at the mid ionic strengths (Fig. 2a). On the other hand, *H. annuus* dry mass was lower than *H. paradoxus*, but *H. annuus* did produce more dry mass in Na₂SO₄ compared to NaCl (Fig. 2b). In addition, as the ionic strength increased dry mass of *H. annuus* decreased.

In comparison to the Na₂SO₄ treatments, dry mass of both species was significantly reduced in NaCl at elevated ionic strengths (Duncan's Multiple Range Test, $P < 0.0001$, Fig. 2a, b). In the no-salt treatment, growth of *H. annuus* was elevated compared to *H. paradoxus* (not significantly). However, for all levels of salt addition, total dry mass of *H. paradoxus* was greater than *H. annuus*, yet the differences were salt dependent. For both species, mean total dry mass was elevated in Na₂SO₄ at an ionic strength of 0.09 compared to NaCl. Dry mass of *H. paradoxus* was 32% greater than dry mass of *H. annuus* in this treatment. In the 0.17 to 0.51 ionic strengths of Na₂SO₄, mean total dry mass of *H. paradoxus* was 2- to 12-fold greater than *H. annuus*. Both species produced less dry mass in NaCl treatments; however, *H. annuus* dry mass was reduced most by NaCl. Total dry mass of *H. paradoxus* was 7-fold greater than *H. annuus* in the 0.09 NaCl treatment. This difference between species in NaCl increased at the 0.17 and 0.34 ionic

strengths of NaCl where dry mass of *H. paradoxus* was 15-fold greater than *H. annuus*.

DISCUSSION

Salt tolerance is the ability of a species to grow and adjust to the presence of a specific ion (ionic effect) or to adapt to the general effects of low water potentials (osmotic effect) (Ungar 1991). In this study, a potential ionic effect and an osmotic effect were investigated using NaCl and Na₂SO₄ salts at increasing ionic strengths. Both salts are found in *H. paradoxus* habitats at various concentrations (Boghici 1997; Van Auken and Bush 1998; Lexer et al. 2003). To differentiate between the effects of the two salts and the Cl⁻ and SO₄²⁻ anions, equal ionic strengths were used in the separate salt treatments (Barrow 1966). Due to greater salt tolerance of *H. annuus* in NaCl and mixed salt environments compared to *H. petiolaris* (both purported parental species) (Ashraf and Tufail 1995; Welch and Rieseberg 2002; Bush and Van Auken 2004; Karrenberg et al. 2006; DiCaterina et al. 2007), *H. annuus* was used as a comparative species for salt effects on growth of *H. paradoxus*.

As in previous studies, this investigation demonstrated that *H. paradoxus* was more salt tolerant than one of its parental species, *H. annuus*, and even produced slightly more dry mass in low saline soils compared to *H. annuus* (Figs. 1b, 2a, and 2b). *Helianthus paradoxus* produced 70% more dry mass than *H. annuus* over all treatments (data not shown) and consistently produced more dry mass in elevated salinity soils (Fig. 2a, b), especially in the sulfate treatments. Results of this greenhouse study are consistent with observations that *H. paradoxus* has greater fitness in saline conditions than *H.*

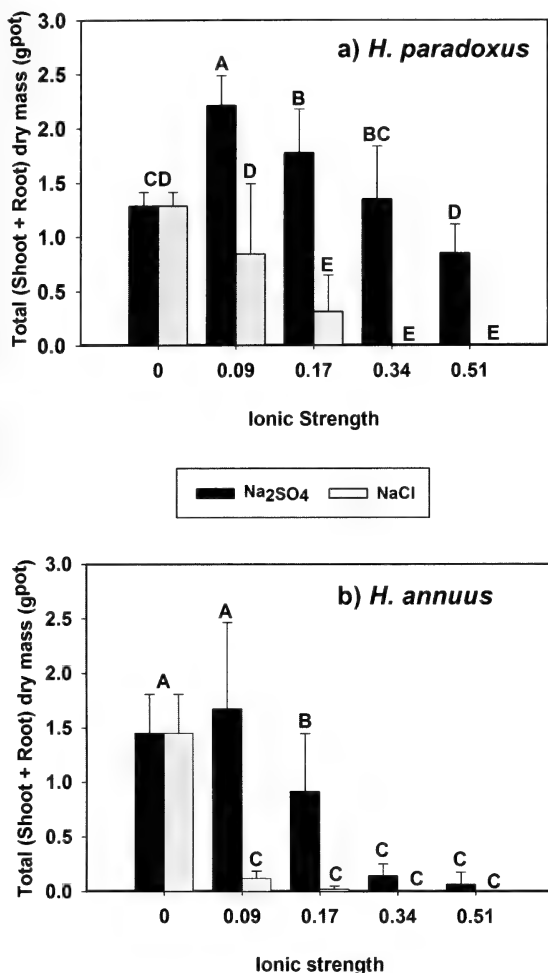


FIG. 2. Three-way interaction plots of total dry mass (bars) as the response variable for (a) *Helianthus paradoxus* and (b) *Helianthus annuus*. Salts were Na₂SO₄ (black bar) and NaCl (gray bar) at ionic strengths of 0.00–0.51. A three-way ANOVA determined there were significant differences ($P < 0.0001$) between salt treatments and ionic strengths for each species. Different letters indicate significant differences between means (Duncan's Multiple Range Test) within a species. Lines above the bars represent + one SD (standard deviation).

annuus (Welch and Rieseberg 2002; Bush and Van Auken 2004; Karrenberg et al. 2006), and that *H. annuus* is not expected to be found in areas with elevated soil salinity where *H. paradoxus* is able to grow and outcompete *H. annuus* and probably other non-halophytic species (Abbot 2003; Van Auken and Bush 2006).

Both *Helianthus* spp. exhibited a specific ionic growth inhibition at elevated levels of Cl⁻, compared to SO₄²⁻, and differences in salt tolerance between species were evident. For both species, NaCl caused plant mortality at ionic strengths of 0.34 and 0.51, yet *H. paradoxus* was

more tolerant than *H. annuus* to low to moderate NaCl concentrations (Fig. 2). Greater dry mass production and survivorship of *H. paradoxus* plants compared to *H. annuus* in NaCl treatments was also observed by Welch and Rieseberg (2002) in corresponding NaCl treatments (100 and 200 mmol L⁻¹ [~ 6 and 12 g kg⁻¹] NaCl). Plant survivorship of *H. annuus* indicated that low Na₂SO₄ levels seem to be less inhibitive than NaCl but significant dry mass reduction was still observed above 0.09 ionic strength treatments. Dry mass of *H. paradoxus*, on the other hand, was enhanced by low to moderate levels of Na₂SO₄ with 38 to 72% greater dry mass, relative to the no-salt treatment. This corresponds to field observations where *H. paradoxus* was most abundant in soil salinities (mainly Na, K, Ca, and Mg chlorides with less SO₄) ranging from 5 to 12 g kg⁻¹ in the Diamond-Y Spring Preserve (Boghici 1997; Van Auken and Bush 1998; Bush 2006b; Grunstra and Van Auken 2007a, b).

Although previous studies did not differentiate between the effects of NaCl and Na₂SO₄ (Welch and Rieseberg 2002; Bush and Van Auken 2004; Karrenberg et al. 2006; Van Auken and Bush 2006), those studies support the salt tolerance of *H. paradoxus* to low concentrations of NaCl. Results consistently demonstrated that biomass of *H. annuus* was statistically reduced by NaCl alone (Welch and Rieseberg 2002) or by low levels of mixed salts (Na⁺, Cl⁻, and SO₄²⁻ included; Bush and Van Auken 2004; Karrenberg et al. 2006), while *H. paradoxus* demonstrated lower productivity in NaCl alone and greater growth and productivity in the presence of SO₄²⁻ as observed in the present study. Greater salt tolerance of *H. paradoxus* to NaCl, as compared to *H. annuus*, has been attributed to significantly greater fitness along with Na⁺ accumulation, leaf succulence, and water use efficiency (Welch and Rieseberg 2002). Because the salts were at equal ionic strengths and Na⁺ seems to serve as an osmoticum for *H. paradoxus* (Welch and Rieseberg 2002), it can be assumed that Cl⁻ is causing reduced productivity in comparison to SO₄²⁻. Molar concentrations of Cl⁻ in the soil water of the Diamond-Y Spring Preserve are approximately 1.5 times that of molar concentrations of SO₄²⁻; therefore, Cl⁻ has the potential of inhibiting growth of *H. paradoxus* in its salt marsh habitat (Boghici 1997). However, these data in conjunction with previous salt studies (Welch and Rieseberg 2002; Bush and Van Auken 2004; Karrenberg et al. 2006) indicate that the presence of soil sulfate may have played an important role in the selection for and adaptation of *H. paradoxus* to the Na-Cl⁻-SO₄²⁻ rich environments. Further, poor tolerance to chloride and sulfate by *H. annuus* has limited its establishment and therefore, fitness in the *H. paradoxus* salt marsh habitat.

It should be noted that in order to maintain equal osmotic potentials between treatments, molar concentrations of Na^+ in NaCl treatments were 3.0 times that of Na_2SO_4 treatments. Nevertheless, the molar equivalents of Na^+ at 0.09 and 0.17 ionic strengths were between that of the 0.34 and 0.51 ionic strengths of Na_2SO_4 where dry mass production of *H. paradoxus* was not inhibited. Since an inert osmotic medium such as polyethylene glycol was not examined, an osmotic effect in combination with an ionic effect cannot be excluded (Katembe et al. 1998; Munns and Tester 2008).

In the limited studies comparing phytotoxicity of both salts, greater toxicity to NaCl compared to Na_2SO_4 has been demonstrated for other salt tolerant glycophytes and halophytes (Manchanda et al. 1982; Curtin et al. 1993; Franklin and Zwiazek 2004; Pagter et al. 2009). Chloride is more toxic to plants than sulfate possibly due to synergistic phytotoxicity effects with Na^+ , differential inhibition of enzyme activity, reduction in plant productivity, and imbalance of nutritional status (Greenway and Munns 1980; Manchanda et al. 1982; Curtin et al. 1993; Wang et al. 1997; Veira Dos Santos and Caldeira 1999; Franklin and Zwiazek 2004). Ion toxicity is dependent on whether the plant possesses adaptations to tolerate the osmotic stress and to exclude and/or compartmentalize the ion. Although not yet documented, it is possible that *H. paradoxus* accumulated Cl^- along with Na^+ and may even be more sensitive to Cl^- compared to SO_4^{2-} due to poor compartmentalization into vacuoles (Greenway and Munns 1980; Flowers et al. 1986; Munns 1993; Rajakaruna et al. 2003). Chloride may be considered more toxic sometimes because of poor salt tolerance response and thus, high accumulation of Cl^- over Na^+ , or in this case SO_4^{2-} . Toxic cytoplasmic Cl^- concentrations have not yet been determined but are assumed to be equal to or slightly lower than Na^+ (Flowers et al. 1986; Greenway and Munns 1980; Munns and Tester 2008).

Sulfate may be required for salt tolerance in *H. paradoxus*. Tissue ion concentrations were not examined in this study, but previous work suggested that (as in other halophytes) SO_4^{2-} , along with Na^+ , may be an important vacuolar osmoticum in plant tissue (Greenway and Munns 1980; Karrenberg et al. 2006; Johnston 2006). Leaf sodium and sulfur concentrations were shown to be inversely related to calcium, magnesium, and potassium concentrations but positively related to biomass and succulence in *H. paradoxus* (Karrenberg et al. 2006). Interestingly, several studies have found a correlation between plants inhabiting waterlogged sulfate rich soils and the presence of vacuole stored flavonoid sulfates which may serve to detoxify excess sulfates alone or in combination with sodium

(Harborne 1975; Tomas-Barberan et al. 1987; Rajakaruna et al. 2003). A possible role of sulphur in the salt tolerance of halophytes also includes the production of methylated sulfonium compounds that accumulate in the cytosol as osmotically compatible organic solutes for compartmentalization of Na^+ and Cl^- in vacuoles. These organic solutes also serve to detoxify sulfides in salt marsh plants (Flowers and Colmer 2008). Flavonoid sulfates or methylated sulfonium compounds have not been measured in tissues of *H. paradoxus*; however, Na_2SO_4 tolerance of this species together with Na^+ and SO_4^{2-} accumulation suggests a possible detoxification mechanism not yet identified.

Ecological isolation of *H. paradoxus* within the inland salt marshes of west Texas and New Mexico may in part depend on the elevated levels of soil salinity found in soils of these habitats (Boghici 1997; McDonald 1999; Van Auken and Bush 1998, 2006; Abbott 2003). Halophytes are limited to saline environments because of an advantageous adaptation to excess salts and a reduction of competitive ability in non-saline environments (Ungar 1991). Distribution of *H. paradoxus* plants appears to be dependent on low to moderate soil salinity levels at the Diamond-Y Spring Preserve where Na^+ , Cl^- and SO_4^{2-} are the prevalent salts from groundwater discharge, while Ca^{2+} , Mg^{2+} , and HCO_3^- are secondary ions (Boghici 1997; Van Auken and Bush 1998; Bush 2006b; Grunstra and Van Auken 2007a, b). In the present study, *H. paradoxus* outperformed *H. annuus* in both soil salt treatments, partially explaining the inability of *H. annuus* to survive the salt marsh habitat of *H. paradoxus* (Lexer et al. 2003; Bush and Van Auken 2004). The presence of salts excluded *H. annuus* from colonizing the salt marsh (Abbott 2003; Lexer et al. 2003), while the salt tolerance of *H. paradoxus* to both NaCl and Na_2SO_4 has allowed this species to establish in the Diamond-Y Spring Preserve and other salt marsh environments in west Texas and New Mexico. Further, tolerance to high concentrations of Na_2SO_4 , as demonstrated by significantly greater productivity relative to non-saline conditions, suggests that *H. paradoxus* may experience a physiological stress response without elevated Na_2SO_4 , which is necessary for optimum growth and perhaps necessary for salt tolerance (Munns and Tester 2008). The establishment of *H. paradoxus* in the Diamond-Y Spring Preserve has been promoted by the selection for transgressive phenotypes promoting salt tolerance (sodium exclusion, calcium uptake, and leaf succulence), as demonstrated by *H. paradoxus*, along with the presence of specific ions (Na^+ , Ca^{2+} , and SO_4^{2-}) in the salt marsh habitat (Abbott 2003; Lexer et al. 2003; Karrenberg et al. 2006). In addition, both parental species are poor competitors in field-like

elevated soil salinity conditions, while *H. paradoxus* is a poor competitor against *H. annuus* in nonsaline conditions (Bush and Van Auken 2004).

The potential for hybridization is still present and environmental conditions isolating hybrid *Helianthus* spp. from parental genotypes appears to have been an important factor in their adaptive evolution of greater fitness in their respective habitats (Lexer et al. 2003; Whitney et al. 2010; Donovan et al. 2010). Populations of *H. annuus* are found in disturbed pockets of isolated deep, nonsaline soil. *Helianthus petiolaris*, the other reported parent species to *H. paradoxus* is also found in some isolated, low saline, sandy soils. However, environmental factors such as the soil conditions required for the isolation and survival of some of the *H. annuus* × *H. petiolaris* hybrids was and continues to be the saline soils surrounding the isolated springs in this area of west Texas and New Mexico (Abbott 2003; Lexer et al. 2003). The unique salt tolerance of *H. paradoxus* compared to its parental species along with establishment in the Na⁺-Cl⁻-SO₄²⁻ dominated salt marshes will continue to promote the ecological isolation of *H. paradoxus*.

ACKNOWLEDGMENTS

Some support for this project was provided by the Nature Conservancy of Texas, the University of Texas at San Antonio, the Texas Department of Parks and Wildlife, the U.S. Fish and Wildlife Service, and Dr. Loyce and Mr. William Collenback. We especially thank Mr. John Karges of the Nature Conservancy of Texas for help and advice during various stages of this project.

LITERATURE CITED

- ABBOTT, R. J. 1992. Plant invasions, interspecific hybridization and the evolution of new plant taxa. *Trends in Ecology and Evolution* 7:401–405.
- . 2003. Sex, sunflowers, and speciation. *Science* 301:1189–1190.
- ASHRAF, M. AND M. TUFAIL. 1995. Variation in salinity tolerance in sunflower *Helianthus annuus* L. *Journal of Agronomy and Crop Science* 174:351–362.
- BARROW, G. M. 1966. The use of constant ionic strength. Pp. 689–691 in *Physical chemistry*. McGraw-Hill Book Company, NY.
- BOGHICI, R. 1997. Hydrogeological investigations at the Diamond Y Springs and surrounding area. M.S. thesis. The University of Texas, Austin, TX.
- BÖHM, W. 1979. Methods of studying root systems. Pp. 1–188 in W. D. Billings, F. Golley, O. L. Lange, and J. S. Olson, (eds.), *Ecological studies*. Springer-Verlag, NY.
- BUSH, J. K. 2006a. Abiotic edaphic factors affecting the growth of a threatened North American sunflower, *Helianthus paradoxus* (Asteraceae). *Plant Ecology* 183:215–225.
- . 2006b. The role of soil moisture, salinity, and oxygen on the growth of *Helianthus paradoxus* (Asteraceae) in an inland salt marsh of west Texas. *Journal of Arid Environments* 64:22–36.
- AND O. W. VAN AUKEN. 1997. The effects of neighbors and grazing on the growth of *Helianthus paradoxus*. *Southwestern Naturalist* 42:416–422.
- AND ———. 2004. Relative competitive ability of *Helianthus paradoxus* and its progenitors, *H. annuus* and *H. petiolaris* (Asteraceae), in varying soil salinities. *International Journal of Plant Science* 165:303–310.
- CORRELL, D. S. AND M. C. JOHNSTON. 1979. *Manual of the vascular plants of Texas*. Texas Research Foundation, Renner, TX.
- CURTIN, D., H. STEPPUHN, AND F. SELLES. 1993. Plant responses to sulfate and chloride salinity: growth and ionic relations. *Soil Science Society of America Journal* 57:1304–1310.
- DICATERINA, R., M. M. GUILIANI, T. ROTUNNO, A. DE CARO, AND Z. FLAGELLA. 2007. Influence of salt stress on seed yield and oil quality of two sunflower hybrids. *Annals of Applied Biology* 151:145–154.
- DONOVAN, L. A., D. R. ROSENTHAL, M. SANCHEZ-VELENOSI, L. H. RIESEBERG, AND F. LUDWIG. 2010. Are hybrid species more fit than ancestral parent species in the current hybrid species habitats? *Journal of Evolutionary Biology* 23:805–816.
- EGAN, T. P. AND I. A. UNGAR. 1998. Effect of different salts of sodium and potassium on the growth of *Atriplex prostrata* (Chenopodiaceae). *Journal of Plant Nutrition* 21:2193–2205.
- FLOWERS, T. J., M. A. HAJIBAGHERI, AND N. J. W. CLIPSON. 1986. Halophytes. *The Quarterly Review of Biology* 61:313–337.
- AND T. D. COLMER. 2008. Salinity tolerance in halophytes. *New Phytologist* 179:945–963.
- FRANKLIN, J. A. AND J. J. ZWIAZEK. 2004. Ion uptake in *Pinus banksiana* treated with sodium chloride and sodium sulphate. *Physiologia Plantarum* 120:482–490.
- GREENWAY, H. AND R. MUNNS. 1980. Mechanisms of salt tolerance in nonhalophytes. *Annual Review of Plant Physiology* 31:149–190.
- GRUNSTRA, M. AND O. W. VAN AUKEN. 2007a. Factors that influence the distribution and cover of *Helianthus paradoxus* in a west Texas salt marsh. *Phytologia* 89:24–42.
- AND ———. 2007b. Using GIS to display complex soil salinity patterns in an inland salt marsh. Pp. 407–431 in D. Sarkar, R. Datta, and R. Hannigan, (eds.), *Developments in environmental science*, volume 5. Elsevier Ltd., Amsterdam, Netherlands.
- HARBORNE, J. B. 1975. Flavonoid sulphates: a new class of sulphur compounds in higher plants. *Phytochemistry* 14:1147–1155.
- HEISER, C. B., Jr. 1958. Three new annual sunflowers (*Helianthus*) from the Southwestern United States. *Rhodora* 60:272–283.
- HEISER, C. B., Jr. 1965. Species crosses in *Helianthus*: III. Delimitation of “Sections”. *Annals of the Missouri Botanical Gardens* 52:364–370.
- JOHNSTON, T. R. 2006. Bio-accumulation of proline and various anions and cations in *Helianthus paradoxus* and *Helianthus annuus* when grown in sodium sulfate. M.S. thesis. The University of Texas at San Antonio, TX.

- KARRENBERG, S., C. EDELST, C. LEXER, AND L. RIESEBERG. 2006. Response to salinity in the homoploid hybrid species *Helianthus paradoxus* and its progenitors *H. annuus* and *H. petiolaris*. *New Phytologist* 170:615–629.
- KATEMBE, W. J., I. A. UNGAR, AND J. P. MITCHELL. 1998. Effect of salinity on germination and seedling growth of two *Atriplex* species (Chenopodiaceae). *Annals of Botany* 82:167–175.
- LEXER, C., M. E. WELCH, O. L. RAYMOND, AND L. H. RIESEBERG. 2003. The origin of ecological divergence in *Helianthus paradoxus* (Asteraceae): selection on transgressive characters in a novel hybrid habitat. *Evolution* 57:1989–2000.
- MANCHANDA, H., S. SHARMA, AND D. BHANDARI. 1982. Response of barley and wheat to phosphorus in the presences of chloride and sulphate salinity. *Plant and Soil* 66:233–241.
- MARSCHNER, H. 1995. Mineral nutrition of higher plants. Academic Press, London, U.K.
- MCDONALD, C. 1999. Endangered and threatened wildlife plants; determination of threatened status for the plant *Helianthus paradoxus* (Pecos sunflower). Federal Register 64:56852–56590.
- MUNNS, R. 1993. Physiological processes limiting plant growth in saline soils; some dogmas and hypothesis. *Plant, Cell and Environment* 16:15–24.
- AND M. TESTER. 2008. Mechanisms of salinity tolerance. *Annual Review of Plant Biology* 59:651–681.
- PAGTER, M., C. BRAGATO, M. MALAGOLI, AND H. BRIX. 2009. Osmotic and ionic effects of NaCl and Na₂SO₄ salinity on *Phragmites australis*. *Aquatic Botany* 90:43–51.
- POOLE, J. M. AND D. D. DIAMOND. 1993. Habitat characterization and subsequent searches for *Helianthus paradoxus* (Puzzle sunflower). Pp. 53–66 in R. C. Sivinski and K. Lightfoot, (eds.), *Southwestern rare and endangered plants*. Miscellaneous Publication No. 2. New Mexico Forestry and Resources Conservation Division. Energy, Minerals and Natural Resources Department, Santa Fe, NM.
- RAJAKARUNA, N., M. Y. SIDDIQI, J. WHITTON, B. A. BOHM, AND A. D. M. GLASS. 2003. Differential responses to Na⁺/K⁺ and Ca²⁺/Mg²⁺ in two edaphic races of the *Lasthenia californica* (Asteraceae) complex: a case for parallel evolution of physiological traits. *New Phytologist* 157:93–103.
- RIESEBERG, L. H. 1991. Homoploid reticulate evolution in *Helianthus* (Asteraceae): evidence from ribosomal genes. *American Journal of Botany* 78:1218–1237.
- , S. M. BECKSTROM-STERBERG, A. LISTON, AND D. M. ARIAS. 1991. Phylogenetic and systematic inferences from chloroplast DNA and isozyme variation in *Helianthus* sect. *Helianthus* (Asteraceae). *Systematics Botany* 16:50–76.
- , R. CARTER, AND S. ZONA. 1990. Molecular test of the hypothesized hybrid origin of two diploid *Helianthus* species (Asteraceae). *Evolution* 44:1498–1511.
- ROSENTHAL, D. M., A. E. SCHWARZBACH, L. A. DONOVAN, O. RAYMOND, AND L. H. RIESEBERG. 2002. Phenotypic differentiation between three ancient hybrid taxa and their parental species. *International Journal of Plant Science* 163: 387–398.
- SAS INSTITUTE. 1999. SAS system for linear models. SAS Institute, Inc., Cary, NC.
- TAYLOR, F. B., R. B. HAILEY, AND D. L. RICHMOND. 1966. Soil survey of Bexar County, Texas. United States Department of Agriculture, Soil Conservation Service, Washington, D.C.
- TIEDEMANN, A. R. AND J. O. KLEMMEDSON. 1986. Long-term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. *Soil Science Society of America Journal* 50:472–475.
- TOMAS-BARBERAN, F. A., J. B. HARBORNE, AND R. SELF. 1987. Twelve 6-oxygenated flavones sulfates from *Lippia nodiflora* and *L. canescens*. *Phytochemistry* 26:2281–2284.
- UNGAR, I. A. 1991. Ecophysiology of vascular halophytes. CRC Press, Boca Raton, FL.
- UNITED STATES (U.S.) FISH AND WILDLIFE SERVICE. 2005. Pecos sunflower recovery plan. U.S. Fish and Wildlife Service, Southwest Region, Albuquerque, NM. Website http://www.fws.gov/southwest/es/Documents/R2ES/Pecos_Sunflower_FINAL_Recovery_Plan.pdf [accessed 04 Jan 2012].
- VAN AUKEN, O. W. AND J. K. BUSH. 1998. Spatial relationships of *Helianthus paradoxus* (Compositae) and associated salt marsh plants. *Southwestern Naturalist* 43:313–320.
- AND ———. 2006. Competition between *Helianthus paradoxus* (Asteraceae) and *Distichlis spicata* (Poaceae). *Phytologia* 88:17–37.
- VEIRA DOS SANTOS, C. L. AND G. CALDEIRA. 1999. Comparative responses of *Helianthus annuus* plants and calli exposed to NaCl: I. Growth rate and osmotic regulation in intact plants and calli. *Journal of Plant Physiology* 155:769–777.
- WANG, L. W., A. M. SHOWALTER, AND I. A. UNGAR. 1997. Effect of salinity on growth, ion content, and cell wall chemistry in *Atriplex prostrata* (Chenopodiaceae). *American Journal of Botany* 84:1247–1255.
- WARNE, P., R. D. GUY, L. ROLLINS, AND D. M. REID. 1990. The effects of sodium sulfate and sodium chloride on growth, morphology, photosynthesis, and water use efficiency of *Chenopodium rubrum*. *Canadian Journal of Botany* 68:999–1006.
- WELCH, M. E. AND L. H. RIESEBERG. 2002. Habitat divergence between a homoploid hybrid sunflower species, *Helianthus paradoxus* (Asteraceae), and its progenitors. *American Journal of Botany* 89: 472–478.
- WHITNEY, K. D., R. A. RANDELL, AND L. H. RIESEBERG. 2010. Adaptive introgression of abiotic tolerance traits in the sunflower *Helianthus annuus*. *New Phytologist* 187:230–239.

THE DIVERSITY AND BIOGEOGRAPHY OF THE ALPINE FLORA OF THE SIERRA NEVADA, CALIFORNIA

PHILIP W. RUNDEL

Department of Ecology and Evolutionary Biology and the Institute of the Environment and Sustainability, University of California, Los Angeles, CA 90095

rundel@biology.ucla.edu

ABSTRACT

The alpine zone of the Sierra Nevada of California, defined as non-forested areas at or above 3500 m, includes 385 species (409 taxa) of native vascular plants. Were the alpine boundary defined as at or above 3300 m, the alpine flora would grow to 536 species (570 taxa). There are 97 species that reach elevations of 4000 m and 27 species that reach to 4200 m. Over half of the alpine species occur in just six families, led by the Asteraceae (55 species, 59 taxa), Poaceae (39 species, 47 taxa), Brassicaceae (34 species), and Cyperaceae (31 species). The largest genus present is *Carex* with 29 species, and 18 more species would be added by lowering the alpine boundary to 3300 m. Next in size are *Draba* (14 species) and *Lupinus* (11 species, 16 taxa). Life forms of the flora are heavily dominated by broad-leaved erect perennials (50%), followed in importance by graminoid perennials (21%) and mats and cushions (11%). Annuals and woody shrubs each account for about 6% of the flora. Only nine species are obligate alpine taxa with a range restricted to elevations of 3500 m or above. An additional 67 species (17% of the flora) occur in both subalpine and alpine habitats but not lower. More than a quarter of the alpine species have elevational ranges that extend as low as foothill habitats defined as occurring below 1200 m. In terms of biogeographic affinities, the broad relationships of the flora include the cordillera of western North America (35%), Intermountain region of the Great Basin (20%), Sierra/Cascade axis (16%), and widespread distributions (14%). There are 36 species in the alpine flora endemic to the Sierra Nevada, and another 31 species that are Californian endemics.

Key Words: Alpine, arctic-alpine flora, cushion plant, Sierra Nevada, treeline.

How large and diverse is the alpine flora of the Sierra Nevada in California and what are its biogeographic relationships? There has been a long history of floristic and ecological studies of the alpine region of the Sierra Nevada addressing this and related issues, but a clear answer to the question has not been achieved. Unlike the majority of alpine regions in the northern hemisphere that share extensive elements of a circumboreal arctic-alpine flora, the Sierra Nevada has developed a unique component to its alpine flora under the influence of mediterranean-climate conditions with relatively dry summers added to other alpine environmental factors of stress. Also significant in the evolution of this alpine flora has been the relative isolation of the range from other high mountain floras of the western United States. Moreover, the Sierra Nevada possesses a complex mosaic of substrate, glacial history, and soil variation superimposed over broad patterns of climatic and topographic heterogeneity.

Interest in the alpine flora dates back to early descriptions by Coville (1893) and Harshberger (1911), who recognized the distinctiveness of the Sierran alpine flora. Hall and Grinnell (1919) gave a very brief description of the alpine zone in the context of a broader description of California life zones, and provided a short list of characteristic species. More significant, however, have

been five studies over the past 80 years that have provided an analysis of the diversity and floristic affinities of the high elevation flora of the Sierra Nevada. The earliest of these was the work of Smiley (1921), whose definition of the boreal region of the Sierra Nevada comprised the Canadian, Hudsonian, and Arctic-Alpine zones as characterized in the Merriam system of life zones (Daubenmire 1938). These life zones roughly correspond to the upper montane, subalpine and alpine zones under current concepts (Fites-Kaufman et al. 2007). Smiley's work was followed by the classic investigation of Sharsmith (1940), and in more recent decades with analyses by Chabot and Billings (1972), Major and Taylor (1977), and Stebbins (1982). Early speculations on the origin of the Sierran alpine flora were contributed by Went (1948, 1953). Beyond these broad floristic surveys, there have been numerous studies of the floristics and vegetation of regional areas of subalpine and alpine vegetation in the Sierra Nevada (Howell 1944, 1951; Klikoff 1965; Pemble 1970; Taylor 1976b; Major and Taylor 1977; Tatum 1979; Benedict and Major 1982; Burke 1982; Ratliff 1982; Benedict 1983; Porter 1983; Constantine-Shull 2000; Sawyer and Keeler-Wolf 2007).

None of the existing literature has provided a satisfactory answer to the fundamental question. How many species are there in the alpine flora of

the Sierra Nevada? The objective of this paper is to present a broad overview of the alpine flora of the Sierra Nevada by providing a detailed and updated analysis of the floristic richness, ecological diversity, and biogeographic relationships of the species present within the alpine zone. The paper takes a conservative approach following Sharsmith (1940) by defining the alpine zone using a lower elevational limit of 3500 m. Climatic treeline typically occurs from 3300–3500 m in the central and southern Sierra Nevada where the great majority of alpine habitat in California is located (Fig. 1). Although the northern Sierra Nevada lacks high elevation areas, it nevertheless has a good representation of alpine species that reach above 3500 m in the central or southern areas of the range. To provide a broader context examining the significance of elevation in the definition of the alpine zone, analyses have been made for all species occurring at or above 3300 m within California.

Beyond an intrinsic interest in the evolution of biodiversity of alpine biota, there are very significant reasons to support Sierran alpine studies that can serve as baseline studies for important early warning systems of potential environmental impacts of climate change. Climate change models for California suggest that there will be significant effects on environmental conditions of subalpine and alpine habitats of the Sierra Nevada (Hayoe et al. 2004; Shafer et al. 2001), and historical data on vertebrate distribution demonstrates that these effects are ongoing today in influencing the distributions of vertebrate species (Moritz et al. 2008; Tingley et al. 2009).

MATERIALS AND METHODS

The Jepson Manual, 2nd Edition (Baldwin et al. 2012) was used to identify California species with an elevational distribution up to or above 3300 m within the state, and which occurred in the Sierra Nevada. This reference is the sole source and reference for binomials used in this article. Species at or above 3500 m in California were considered to comprise the alpine flora. The upper and lower elevational ranges of each of these species were recorded, along with their biogeographic distribution and occurrence within the geographic regions of California (Hickman 1993). These geographic regions included records of species presence in the montane and higher elevations of the northern, central, and southern subregions of the Sierra Nevada, as well as the high Cascade Range, the Klamath/Siskiyou mountains, Transverse and Peninsular ranges of southern California, and ranges east of the Sierra Nevada including the Sweetwater and White-Inyo mountains (Fig. 1). The elevational limits and geographical ranges listed in Baldwin et al.

(2012) are specimen-based records and thus considered reliable. Only native species were included in this analysis, however, alien species recorded as occurring at high elevations in the Sierra Nevada are very few. *Poa pratensis* L. is recorded as reaching 3500 m and *Taraxacum officinale* F. H. Wigg. reaches 3300 m.

Each taxon occurring at elevations of 3300 m or above was categorized into a series of growth forms, based on a modified scheme of Raunkiaer (1934). These categories were broad-leaved herbaceous perennials (tussocks, rosettes, and biennials), graminoid perennials, mats and cushion plants, geophytes, aquatics, annuals, shrubs, woody shrubs (deciduous and evergreen), and trees.

The lower elevational limit of occurrence in California was used to separate alpine species into categories of lowest elevational zone of occurrence on the following basis: 1) foothill habitats of woodland and chaparral— <1199 m; 2) lower montane habitats dominated by mixed conifer and yellow pine forests— 1200–1999 m; 3) upper montane habitats of red fir and lodgepole pine forests— 2000–2699 m; 4) subalpine habitats of open conifer stands near treeline— 2700–3499 m; and 5) alpine habitats— >3500 m. Because elevational boundaries of these major vegetation zones change with latitude, as well as locally with slope exposure, these elevational ranges represent averaged boundaries across the west slope of the central and southern Sierra Nevada.

The biogeographic range of each alpine species was classified into one of six categories. These were: 1) widespread species present in many habitats or regions across North America and/or throughout the world; 2) cordilleran species broadly distributed in mountain regions of the western United States; 3) Sierra/Cascade species with a Pacific Northwest distribution; 4) Intermountain Region species present in the Great Basin; 5) species endemic to the Sierra Nevada; and 6) species endemic to California, broadly defined to include adjacent Great Basin ranges extending into western Nevada (i.e., Sweetwater, Wassuk, and White-Inyo mountains) and southern Oregon. Dividing species into such simple biogeographic categories is inherently arbitrary for some species, and expanded field studies in the future may well change these classifications and alter the list of Sierran endemics based on new records or taxonomic revisions.

RESULTS

The Geography of California Alpine Habitats

The elevational contour interval of 3500 m is highly irregular in the Sierra Nevada, as it defines a relatively continuous area along the crest of the



FIG. 1. Topographic map of California showing the major areas of mountain systems. W/I = White-Inyo Mountains, T = Tehachapi Mountains, SG = San Gabriel Mountains, SB = San Bernardino Mountains, and P = Peninsular Ranges.

central and southern crest of the range extending from northern Tuolumne and Mono counties in the area of Leavitt Peak (3527 m) near Sonoran Pass and south across Yosemite National Park where the highest peak is Mount Lyell (3999 m;

Fig. 2). Further south this belt of alpine habitat continues into Kings Canyon and Sequoia National parks where there are extensive areas of alpine habitat with ten peaks that reach above 4000 m. Mount Whitney at 4421 m is the highest



FIG. 2. Geographic distribution of high elevations of the Sierra Nevada and adjacent ranges. The solid line marks a rough position of the 3000 m contour. Adapted from Hovanitz (1940).

point in the contiguous United States. The southern limit of this extensive and virtually contiguous alpine zone occurs at Cirque Peak (3932 m) in Sequoia National Park at the southern

end of the continuous chain of glaciated peaks in the Sierra Nevada. To the south, the alpine zone reappears on Olancha Peak (3698 m; Fig. 2), the southernmost glaciated summit of the range lying

on the Tulare-Inyo county line (Howell 1951; Tatum 1979). Two major breaks with subalpine elevations but not true alpine provide the only major discontinuity for this primary Sierran alpine region. These are Tioga Pass in Yosemite National Park (3031 m) and Mammoth Pass (Minaret Summit) (2824 m), which is the route for California Highway 203.

The crest of the Sierra Nevada lies at lower elevations to the north of the Tioga Pass area, with only scattered areas of good alpine habitat present. A notable ecological change occurs north of this pass where volcanic substrates replace the granites of the central and southern Sierra Nevada. Fragmented communities of alpine species are present at elevations below 3500 m, particularly along exposed ridgelines and on steep north-facing slopes that were heavily glaciated. However, there are no elevations in the northern Sierra Nevada that reach the 3500 m limit used here to define the alpine zone. Alpine habitats are weakly developed in Alpine Co. (with Sonora Peak reaching 3493 m) and eastern El Dorado Co. (with Freel Peak reaching 3318 m), extending to their northern limit on Mount Rose (3285 m) in the Carson Range east of Lake Tahoe in Nevada (Fig. 2). Nevertheless, there are scattered communities of alpine-like habitat existing at upper elevations in the northern Sierra Nevada, positioned above local edaphically-controlled treelines, and the alpine flora is well represented (Smiley 1915). Despite the floristic relationships of high elevation Sierran species all along the range, Stebbins and Major (1965) linked the Sierra Nevada north of Lake Tahoe with the Cascade Range rather than with the region of the central and southern Sierra Nevada on the basis of the dominance of volcanic substrates.

To the north of the Sierra Nevada, Mount Shasta in the southern Cascade Range reaches an elevation of 4322 m, while Lassen Peak is lower at 3187 m. The highest peaks in the Klamath Mountains of northwestern California and adjacent Oregon are Mount Eddy (2750 m) in Siskiyou Co., Thompson Peak (2744 m) in Trinity Co., and Mount Ashland (2296 m) in Jackson Co., Oregon. These high peaks contain areas with permanent or long-lasting snowfields on north-facing slopes with associated alpine species (Howell 1944; Major and Taylor 1977).

There are several high mountain ranges to the east of the Sierra Nevada at the western margin of the Great Basin. The Sweetwater Mountains, located just 33 km east of the Sierra Nevada, reach 3552 m on Mount Patterson (Hunter and Johnson 1983). The Wassuk Range in west-central Nevada lie 48 km east of the Sweetwater Mountains and 88 km north of the White Mountains, reaching 3427 m on Mount Grant (Bell and Johnson 1980). The White Mountains

have an extensive alpine area and reach to 4344 m on White Mountain Peak, the third highest peak in California (Rundel et al. 2008). To the south, Mount Waucoba forms the high point at 3390 m in the Inyo Mountains. The Panamint Mountains lying east of the White-Inyo Mountains reach a maximum elevation of 3366 m on Telescope Peak. Further south, the Spring Mountains in southwestern Nevada divide the Pahrump Valley and Amargosa River basins from the Las Vegas Valley watershed and define part of the southwestern boundary of the Great Basin. The highest point is Charleston Peak at 3633 m.

High elevations are also present in the Transverse and Peninsular ranges of southern California (Fig. 1) where a subset of Sierran alpine species is present in weakly developed alpine-like communities (Hall 1902; Parish 1917; Horton 1960; Hanes 1976; Major and Taylor 1977; Meyers 1978). Mount San Geronio in the San Bernardino Mountains reaches 3506 m, while other high points are Mount San Jacinto in the San Jacinto Mountains at 3302 m and Mount Baldy in the San Gabriel Mountains at 3068 m. Alpine species are present in both xeric and mesic habitats at high elevation, but alpine communities, defined as extended areas dominated by assemblages of alpine species, are only poorly developed.

The alpine zone of the Sierra Nevada experiences mediterranean-type climate conditions that differ significantly from those that characterize the Rocky Mountains and most of the continental alpine habitats of the world where summer rainfall predominates. The fraction of annual precipitation that falls as winter snow in the Sierra Nevada is about 95% at upper treeline (Stephenson 1998). Deep snow packs and cool temperature at higher elevations mean that snowmelt extends into the spring, but the length and magnitude of the summer drought period experienced by plants is significant. Patterns of rainfall decline gradually from north to south in the Sierra Nevada, and summer drought decreases as elevation increases because of both increased levels of precipitation and cooler temperatures with lower evaporative demand at higher elevations (Stephenson 1998; Urban et al. 2000).

Winter mean monthly low temperatures are moderate in the Sierra Nevada compared to the Rocky Mountains, and soils only rarely freeze to even moderate depth. While, the mean minimum temperature above treeline is below freezing for ten months of the year, with nighttime lows that typically reach only -3 to -6°C , although extremes can reach temperatures of -15°C or lower on the high peaks. Nevertheless, these moderate low temperatures as well as other limiting factors for survival at high elevations sharply reduce the diversity of species able to tolerate such conditions (Körner 2003).

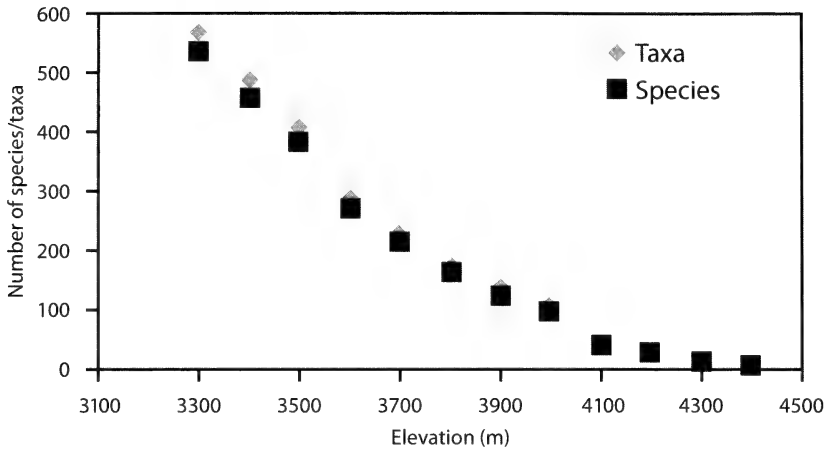


FIG. 3. Elevational distribution of species in the high mountain flora of the Sierra Nevada.

Floristic Richness

The alpine flora of the Sierra Nevada, defined as species reaching 3500 m or more at their upper limit of distribution, comprises 385 vascular plant species. The species total includes 10 ferns and fern relatives (2.6%), five conifers (1.3%), 85 monocots (22.1%), and 285 eudicots (74.0%). With the inclusion of an additional 24 named varieties and subspecies, the total number of alpine taxa is 409.

Of course, the predetermined elevational boundary has a very strong influence on the size of the flora (Fig. 3). If the alpine flora were defined as those species reaching to 3400 m, then 76 additional species would be added for a total of 460 species (488 taxa). Were the limit defined as 3300 m, there would be a flora of 536 species (570 taxa), with the relative proportions of monocots and eudicots virtually unchanged and the addition of five ferns and one conifer.

There are 97 species (101 taxa) with an elevational range that extends as high as 4000 m, an elevation reached by only the highest Sierran peaks (Fig. 3). This number declines to 27 species that reach 4200 m in elevation. These 27 high elevation species do not display dominance by a few families as is the case with the full alpine flora but are rather spread among 15 different families (Appendix 1). Three species have been recorded as reaching to 4400 m. These are *Epilobium anagallidifolium* Lam. (Onagraceae), *Saxifraga hyperborea* R. Br. (Saxifragaceae), and *Erigeron vagus* Payson (Asteraceae). Additional taxa that occur up to or above 4300 m are *Erigeron compositus* Pursh (Asteraceae), *Boechea lemmonii* (S. Watson) W. A. Weber (Brassicaceae), *Cerastium beeringianum* Cham. & Schltld. (Caryophyllaceae), *Calyptridium umbellatum* (Torr.) Greene (Montiaceae), *Festuca brachyphylla* Schult. & Schult. subsp. *breviculmis* Fred., *Poa keckii* Soreng. and *P. lettermannii* Vasey (Po-

aceae), *Phlox pulvinata* (Wherry) Cronquist (Polemoniaceae), *Ranunculus eschscholtzii* Schltld. var. *oxynotus* (A. Gray) Jeps. (Ranunculaceae), and *Potentilla pseudosericea* Rydb. and *Sorbus californica* Greene (Rosaceae).

There are six families that contribute 20 or more taxa to the alpine flora. The largest of these is the Asteraceae with 55 species (59 taxa), followed in size by the Poaceae (39 species, 47 taxa), Brassicaceae (34 species), Cyperaceae (31 species), Rosaceae (21 species, 23 taxa), and Fabaceae (18 species, 27 taxa). These six families together comprise 52% of the alpine flora.

At the generic level, *Carex* stands out prominently with 29 species in the alpine flora, with an additional 18 species present at elevations between 3300 and 3500 m. Next in order of size are *Draba* (Brassicaceae, 14 species), and *Lupinus* (Fabaceae, 11 species, 16 taxa). There are 10 species of *Boechea* (Brassicaceae) and nine species each of *Epilobium* (Onagraceae), *Eriogonum* (Polygonaceae), and *Potentilla* (Rosaceae). There are three genera with eight species—*Penstemon* (Plantaginaceae), *Poa* (Poaceae), and *Salix* (Salicaceae).

Growth Form Distribution

Herbaceous perennial growth forms, broadly defined, comprise the great majority of taxa reaching to or above 3500 m in the Sierra Nevada. This growth form with all of its subgroups includes 343 taxa, or 84% of the 409 taxa that comprise the flora. These herbaceous perennials can be broken down into subgroups of erect herbaceous perennials, perennial graminoids, prostrate mats and cushion plants, biennials, and geophytes. The largest numbers of herbaceous perennials form the category of erect herbaceous perennials, with 186 species (206 taxa; Fig. 4). The most important families for the erect herbaceous perennials are the Asteraceae, Brassi-

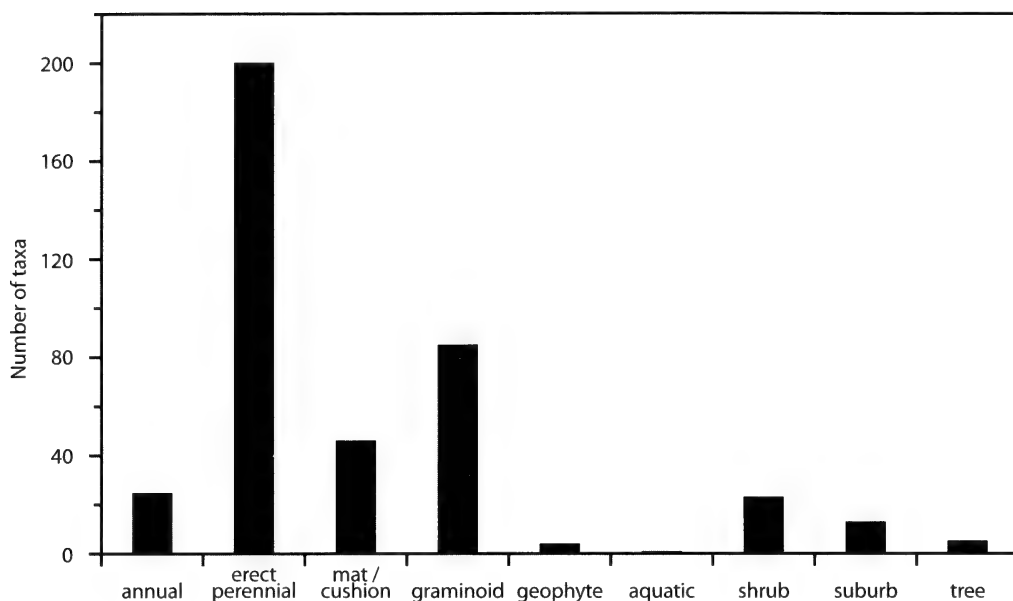


FIG. 4. Growth form distribution of alpine taxa in the alpine flora of the Sierra Nevada.

ceaeae, Fabaceae, Rosaceae, Polygonaceae, and Onagraceae. Among the erect herbaceous perennials are four species that are reported to have the potential to survive as facultative annuals. Although these have not been studied in detail, it is expected that these species have biennial or short-lived perennial life histories in the alpine zone, and they are included here in the totals for erect herbaceous perennials. Three of these are members of the Brassicaceae, each representing a different genus. Among these facultative annuals, only *Androsace septentrionalis* L. (Primulaceae) with an elevation range of 2700–3600 m can be considered as a subalpine and alpine specialist.

There are several additional groups classified broadly as erect herbaceous perennials. The 10 species of ferns and fern relatives included here within the alpine flora represent four families (Pteridaceae, Ophioglossaceae, Woodsiaceae, and Selaginellaceae). Four of these species reach elevation at or above 4000 m—*Botrychium lineare* W. H. Wagner, *B. paradoxum* W. H. Wagner, *Cystopteris fragilis* (L.) Bernh., and *Selaginella watsonii* Underw. Lowering the characterization of the alpine zone lower limit to 3300 m would add five additional fern species (Appendix 2). Also classified as erect perennials are seven species of hemiparasites, all members of the Orobanchaceae, with four species (five taxa) of *Castilleja* and three species of *Pedicularis*. Six more species from this family would be added by lowering the alpine boundary to 3300 m, including five more species of *Castilleja*.

Next in diversity among the herbaceous perennials is the subgroup of graminoids (Cyperaceae, Juncaceae, Juncaginaceae, and Poaceae)

with 83 species (85 taxa, Fig. 4). All of the members of these four families within the alpine flora are perennials, with *Agrostis*, *Bromus*, *Carex*, *Elymus*, *Juncus*, *Luzula*, *Poa*, and *Stipa* forming genera with five or more taxa (Appendix 1). These perennial graminoids include one species of C_4 grass, *Muhlenbergia richardsonis* Rydb. (Sage and Sage 2002). Two other C_4 members of this genus, the perennial *M. montana* Hitchc. and the annual *M. filiformis* Rydb., just miss inclusion, reaching to elevations of 3420 m and 3350 m, respectively. Lowering the alpine boundary to 3300 m would add significantly to the diversity of graminoid perennials, with 43 additional taxa present (Appendix 2).

Prostrate mats and cushion forms of growth are common in some of the herbaceous perennials of the Sierran alpine flora (Fig. 4). These species are low in stature and form a heterogeneous group that shares the characteristic of a prostrate growth form with either a central taproot or multiple points of rooting through layering. Mats and cushions often form an ecologically significant component of plant cover on exposed ridges and fellfield. There are 46 species classified here as mats or cushions, with 19 of these high subalpine and alpine specialists not occurring below 2700 m elevation. The growth form characteristics of mats and cushions may be genetic in some cases but in others is environmentally induced, with mat forms of growth only occurring at higher elevations (personal observations). Alpine mat and cushion species are well represented in the Asteraceae with 13 species (notably taxa of *Antennaria* and *Erigeron*), Polygonaceae (*Eriogonum*) with eight species,

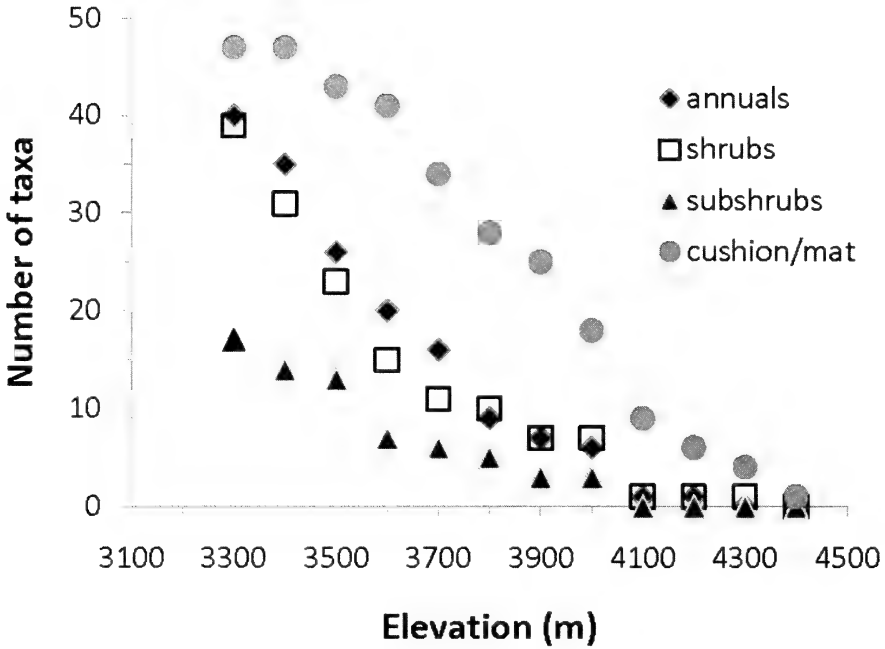


FIG. 5. Elevational distribution of taxa of annuals, shrubs, subshrubs, and mats/cushions in the alpine flora of the Sierra Nevada.

Brassicaceae (*Draba* and *Anelsonia*) with six species, and Fabaceae (*Astragalus*, *Lupinus*, *Oxytropis*, and *Trifolium*) with five species. Also notable in their ecological dominance are mats of Caryophyllaceae (*Cerastium*, *Eremogone*, *Minuartia*) and Polemoniaceae (*Phlox*).

The alpine flora includes just four species of geophytes, which represent the Alliaceae (*Allium obtusum* Lemmon var. *obtusum*), Liliaceae (*Calochortus leichtlinii* Hook. f.), Melanthiaceae (*Veratrum californicum* Durand var. *californicum*), and Themidaceae (*Triteleia dudleyi* Hoover). The highest elevation species among these is *C. leichtlinii*, which reaches up to 4000 m. None of these geophytes can be considered to be high elevation specialists as all reach lower elevational limits of 1200–1500 m in California. There are six species of geophytes that just miss reaching the lower alpine limit, as defined here, but occur at or above 3300 m (Appendix 2). These include *Allium validum* S. Watson (Alliaceae), *Iris missouriensis* Nutt. (Iridaceae), *Lilium kelleyanum* Lemmon (Liliaceae) and three Orchidaceae (*Platanthera dilatata* (Pursh) Lindl. ex L. C. Beck var. *leucostachys* (Lind.) Luer, *P. sparsiflora* Schltr., and *Spiranthes romanzoffiana* Cham.

Only a single species of aquatic plant, *Callitriche palustris* L. (Plantaginaceae), reaches the alpine zone of the Sierra Nevada. This is perhaps not surprising given the relatively small area of oligotrophic lakes that are present above 3500 m. *Potamogeton robbinsii* Oakes (Potamogetonaceae) and *Limosella acaulis* Sessé & Moc.

(Scrophulariaceae) have a range that extends as high as 3300 m, and a number of aquatic species including *Isoetes* (Isoetaceae) reach elevations of 3000 m.

Plants with an annual life history comprise a small but significant component of the alpine flora of the Sierra Nevada, with 24 species (26 taxa) reaching to elevations of 3500 m (Fig. 4). The annual species occurring at the highest elevation is *Gayophytum decipiens* F. H. Lewis & Szweyk. (Onagraceae), which ranges up to 4200 m. Five other species of annuals reach 4000 m in elevation—*Gentianopsis holopetala* (A. Gray) Iltis (Gentianaceae), *Phacelia hastata* Douglas ex Lehm. subsp. *compacta* (Brand) Heckard (Boraginaceae), *Mimulus suksdorfii* A. Gray (Phrymaceae), *Gayophytum racemosum* Torr. & A. Gray (Onagraceae), and *Collinsia torreyi* A. Gray var. *wrightii* (S. Watson) I. M. Johnst. (Plantaginaceae). The number of annual species present increases sharply below the limit set here for inclusion in the alpine flora. Including the above taxa, there are 33 annual species (36 taxa) with a range reaching to or above 3400 m and 38 species (41 taxa) occurring at or above 3300 m (Fig. 5).

Most of the annuals reaching into the alpine zone are species with wide elevational ranges that extend down to lower foothill habitats. Only 13 of the alpine annual species have ranges limited to elevations at or above 1200 m, a distribution that would indicate adaptation to montane and higher elevation habitats. Five annual taxa can be

considered as subalpine and alpine specialists having a lower elevation limit of 2700 m or above and/or a median elevational range above 3000 m. These species, none of which ranges as high as 4000 m or above, are *Comastoma tenellum* (Rottb.) Toyok. (Gentianaceae), *Cryptantha circumscissa* (Hook. & Arn.) I. M. Johnston var. *rosulata* J. T. Howell (Boraginaceae), *Streptanthus gracilis* Eastw. (Brassicaceae), and *Leptosiphon oblanceolatus* (Brand) J. M. Porter & L. A. Johnson and *Gymnosteris parvula* A. Heller (Polemoniaceae). Just missing this criteria, but certainly also a high elevation specialist, is *Phacelia oregones* Brand (Boraginaceae). Four of these six, with *Comastoma tenellum* and *Gymnosteris parvula* as exceptions, are Sierra Nevada endemics.

The most important family in contributing to the annual flora of high elevations is the Boraginaceae, with 11 species (12 taxa) representing five genera. Next in importance are the Polemoniaceae with five species (comprising five genera), and the Onagraceae with four species (five taxa) representing just a single genus. There are four genera that contribute three or more species to the annual flora. These are *Gayophytum* (Onagraceae, four species, five taxa), *Phacelia* (Boraginaceae, four species), *Cryptantha* (Boraginaceae, three species, four taxa), and *Mimulus* (Phrymaceae, three species).

Subshrubs, defined as semi-woody species that maintain living perennial tissue in winter above the ground surface, include 13 species occurring at elevations of 3500 m or above (Fig. 4). The Asteraceae contribute more than 60% of the alpine flora of subshrubs, with eight species. Four species of *Ericameria* (Asteraceae) and three species each of *Penstemon* (Plantaginaceae), and one *Monardella* (Lamiaceae) form subshrubs that reach alpine elevations. Five species are considered to be subalpine and alpine specialists based on a lower elevational limit of 2700 m or a mean elevational range above 3000 m. Four of these are members of the Asteraceae—*Sphaeromeria cana* (D. C. Eaton) A. Heller, *Ericameria parryi* (A. Gray) G. L. Nesom & G. I. Baird var. *monocephala* (A. Nelson & P. B. Kenn.) G. L. Nesom & G. I. Baird, *E. bloomeri* (A. Gray) J. F. Macbr., and *Chrysothamnus viscidiflorus* (Hook.) Nutt. var. *viscidiflorus*. The two latter species have very broad elevational occurrence from 800–4000 m.

There are 23 species of woody shrubs that extend into the alpine zone of the Sierra Nevada (Fig. 4). Just four families account for the majority of the high elevation shrubs. The largest of these is the Salicaceae (eight species of *Salix*), followed by the Ericaceae (five species, each in a different genus), Grossulariaceae (three species of *Ribes*), and Rosaceae (three species, each in a different genus). The highest elevation reached is

reported for *Sorbus californica* at 4300 m. However, this elevation record appears to not be supported by specimen records in the Consortium of California Herbaria (ucjeps.berkeley.edu/consortium), and therefore needs confirmation. There are six additional shrub species that reach elevations of 4000 m—*Salix orestera* C. K. Schneid., *S. planifolia* Pursh, *S. petrophila* Rydb., *Gaultheria humifusa* (Graham) Rydb., *Holodiscus discolor* (Pursh) Maxim. var. *microphyllus* (Rydb) Jeps., and *Ribes montigenum* McClatchie. Only three shrub species can be considered as subalpine and alpine specialists based on a lower elevational limit at or above 2700 m or median range of occurrence above 3000 m. These are *Salix planifolia*, *S. brachycarpa* Nutt. var. *brachycarpa*, and *S. nivalis* Hook. Three more shrub species just miss this definition of high elevation specialist. *Arctostaphylos uva-ursi* (L.) Spreng. has an elevational range of 2400–3300 m, while *Jamesia americana* Torr. & A. Gray (Hydrangeaceae) and *Ribes cereum* Douglas var. *inebrians* (Lindl.) C. L. Hitchc. are alpine species that extend down to lower elevations of 2070 m and 2100 m, respectively. Including the above species, there are a total of 39 shrub species that occur at elevations of 3300 m or above in the Sierra Nevada. This group includes two more species of *Salix*, one additional *Ribes*, five Ericaceae, three Rosaceae, two species of Caprifoliaceae, and a scattered diversity of species from other families (Appendix 2).

Five species of coniferous trees in the Pinaceae have scattered populations that extend well above typical treeline elevation on favorable sites. The treeline pines, *Pinus albicaulis* Engelm., *P. flexilis* E. James and *P. balfouriana* Grev. & Balf., all have local populations that reach as high as 3700 m in elevation in the Sierra Nevada, while *P. contorta* Loudon subsp. *murrayana* (Grev. & Balf.) Critchf. and *Tsuga mertensiana* (Bong.) Carrière reach 3500 m. Just missing the elevation of the alpine zone are scattered trees of *Pinus monticola* Douglas ex D. Don that reach up to 3400 m.

Elevational Amplitude

Separating alpine taxa into categories of elevational ranges over which they occur provides some insight into their ecological amplitude and thus a crude measure of potential niche breadth. There are nine obligate alpine taxa in the Sierra Nevada restricted in occurrence to elevations at or above 3500 m. These are *Boecheira depauperata* (A. Nelson & P. B. Kenn.) Windham & Al-Shehbaz (Brassicaceae), *Botrychium paradoxum* and *B. tunux* Stensvold & Farrar (Ophioglossaceae), *Carex incurviformis* Mack. (Cyperaceae), *Draba sierra* Sharsm. (Brassicaceae), *Eriogonum wrightii* Torr. ex Benth. var. *olanchense*

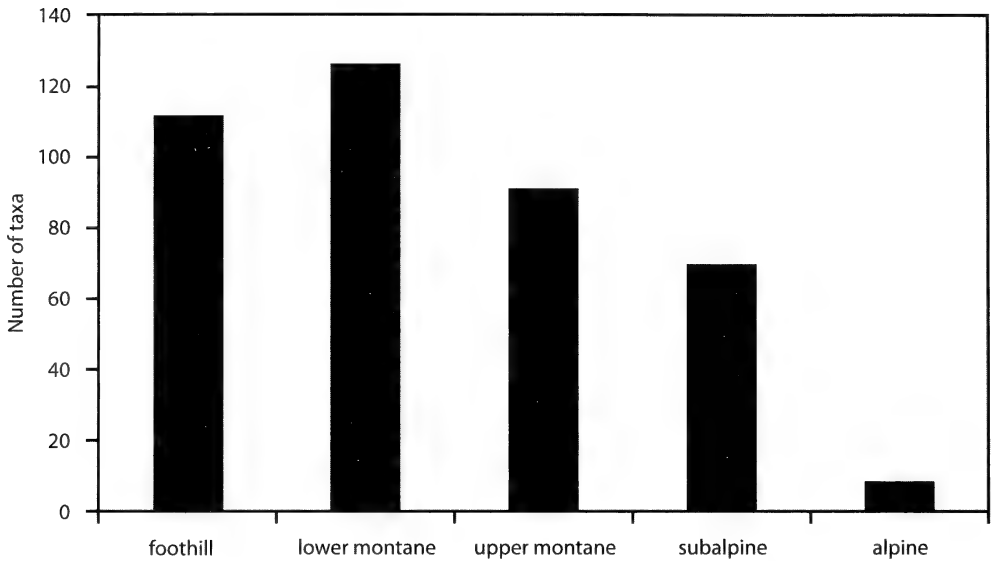


FIG. 6. Lower elevational zone of occurrence for taxa in the alpine flora of the Sierra Nevada. The elevational limits of these zones are 0–1190 m for the foothill zone, 1200–1990 m for the lower montane zone, 2000–2699 m for the upper montane zone, 2700–3490 m for the subalpine zone, and 3500 m and above for the alpine zone.

(J. T. Howell) Reveal (Polygonaceae), *Minuartia stricta* (Sw.) Hiern (Caryophyllaceae), *Phlox dispersa* Sharsm. (Polemoniaceae), and *Poa letermanii* (Poaceae).

There are an additional 67 alpine species (70 taxa, 17.2% of all taxa) with ranges restricted to the elevations of subalpine and alpine habitats at or above 2700 m (Fig. 6). Examining the floristic composition of all 76 species (79 taxa) with a range restricted to subalpine and alpine elevations, just four families comprise more than half of these. These are the Asteraceae (11 species), Brassicaceae (nine species), Rosaceae (eight species, nine taxa), and Poaceae (eight species). Three additional species would be added to the obligate subalpine and alpine flora if the elevational limit were reduced to 3300 m. These are *Astragalus ravenii* Barneby (Fabaceae), *Carex tiogana* D. W. Taylor & J. D. Mastrog. (Cyperaceae), and *Chaenactis douglasii* (Hook.) Hook. & Arn. var. *alpina* A. Gray (Asteraceae).

Looking at the level of all alpine taxa, 22.4% have a lower elevational limit in the upper montane zone (2000–2699 m) and a further 31.0% have a lower limit in the lower montane zone (1200–1999 m). Finally 27.5% of the alpine taxa have a broad elevational amplitude of occurrence extending upward from the foothill zone below 1200 m up into the alpine (Fig. 6).

Plotting the elevational amplitude of all of the alpine taxa shows a peak at about 2300 m, with relatively fewer species exhibiting very broad or very narrow elevational amplitudes (Fig. 7). Nevertheless, there are many taxa with surprising broad ranges of elevational occurrence. There are 77 species that have an elevational amplitude of

3000 m or more, and six species that have 4000 m or more of amplitude in California. These latter species, each in a different family, are *Callitriche palustris* (Plantaginaceae), *Calyptridium umbellatum* (Montiaceae), *Cystopteris fragilis* (Woodsiaceae), *Draba cana* Rydb. (Brassicaceae), *Epilobium ciliatum* Raf. subsp. *ciliatum* (Onagraceae), and *Erysimum capitatum* (Hook.) Greene var. *capitatum* (Brassicaceae). Were the elevational definition of the alpine zone lowered to 3300 m, a large number of species with broad elevational amplitudes would be added to the flora. There are 42 species in this group of added taxa that have 3000 m or more of elevational amplitude in their range of occurrence.

Biogeography and Endemism

Within the Sierra Nevada itself, the distributions of the high elevation flora are relatively well spread between the northern, central and southern subregions of the Sierra Nevada. Assessing species reaching an elevational boundary of 3300 m, 70% of the 567 taxa occur in all three subregions. The northern subregion has 76% of the alpine flora present, while the central and southern Sierra Nevada have 90% and 88% of the alpine flora present, respectively. A number of alpine species have their southern limit of distribution in the central Sierra Nevada. These include *Carex whitneyi* Olney (Cyperaceae), *Podistera nevadensis* (A. Gray) S. Watson (Apiaceae), *Claytonia megarhiza* (A. Gray) S. Watson (Montiaceae), *Thalictrum alpinum* L. (Ranunculaceae), *Galium grayanum* Ehrend. var. *grayanum* (Rubiaceae), and *Salix nivalis* (Salicaceae).

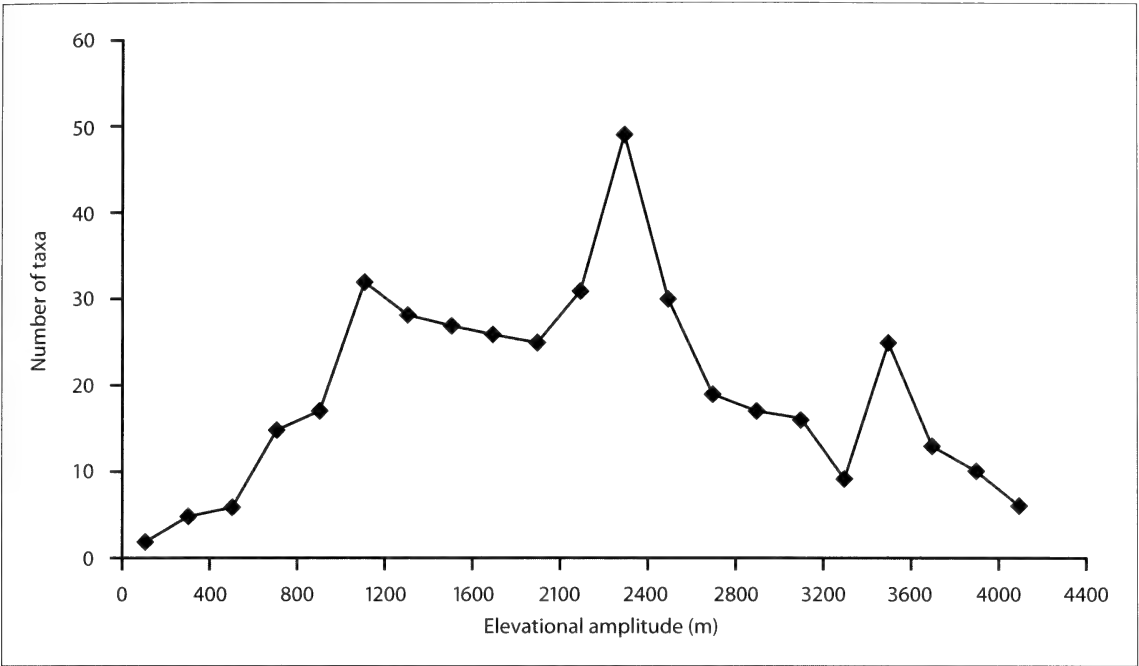


FIG. 7. Elevational amplitude of alpine taxa in the Sierra Nevada. These values are based on the range expressed from upper and lower limits of elevational distribution in California as presented in Baldwin et al. (2012).

The broader biogeographic relationships of the alpine flora at or above 3500 m indicate its diverse origins (Fig. 8). Widespread species distributed across North America and beyond as boreal or arctic-alpine taxa comprise 13.6% of the flora (Table 1). The largest group of taxa (34.3%) shows patterns of distribution as cordilleran species widespread in mountain regions of the western United States. Next in importance

are taxa with a range in the Intermountain Region of the Great Basin, comprising 20.5% of taxa. A group consisting of 15.8% of the taxa has ranges extending along the Sierra Nevada axis to the Cascade Range and often on to the Pacific Northwest.

The alpine flora of the Sierra Nevada includes 36 endemic taxa restricted in their distribution to the Sierra Nevada (Table 2). These endemic taxa

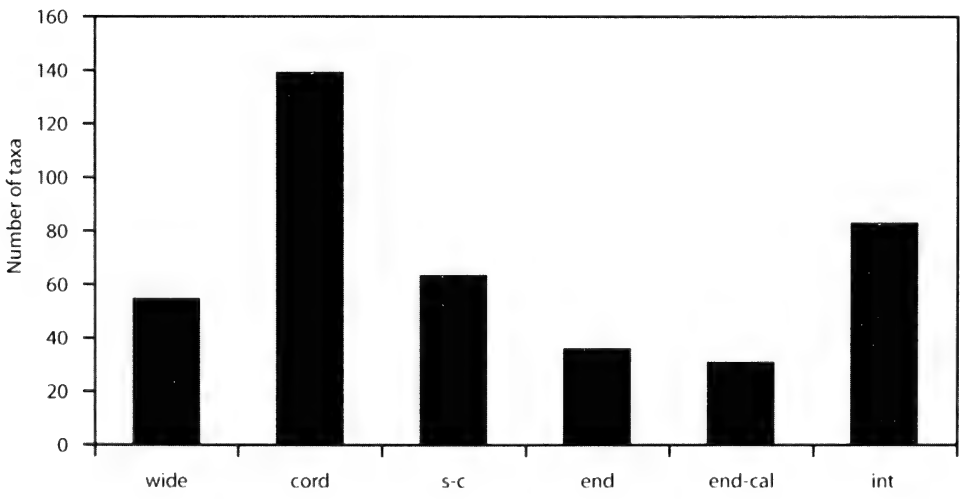


FIG. 8. Biogeographic relationships of the alpine flora of the Sierra Nevada. WIDE = widespread taxa present in many habitats or regions across North America and/or throughout the world; CORD = cordilleran taxa widespread in mountain regions of the western United States; S-C = Sierra/Cascade taxa with a Pacific Northwest distribution; END = taxa endemic to the Sierra Nevada; and END-CAL = taxa endemic to California, as broadly defined; INT = intermountain taxa present in the Great Basin. See text for discussion.

TABLE 1. EXAMPLES OF THE BROADER BIOGEOGRAPHIC RELATIONSHIPS OF THE ALPINE FLORA OF THE SIERRA NEVADA.

Biogeographic range category	Exemplar taxa
Widespread taxa distributed across North America and beyond as circumboreal or arctic-alpine taxa	<i>Anemone drummondii</i> (Ranunculaceae), <i>Carex capitata</i> (Cyperaceae), <i>Crepis nana</i> (Asteraceae), <i>Cystopteris fragilis</i> (Woodsiaceae), <i>Deschampsia cespitosa</i> (Poaceae), <i>Oxyria digyna</i> (Polygonaceae), <i>Phleum alpinum</i> (Poaceae), <i>Rhodiola integrifolium</i> (Crassulaceae), <i>Salix nivalis</i> and <i>S. petrophila</i> (Salicaceae), <i>Sibbaldia procumbens</i> (Rosaceae), <i>Trisetum spicatum</i> (Poaceae)
Cordilleran taxa widespread in mountain regions of the western United States	<i>Antennaria media</i> (Asteraceae), <i>Carex phaeocephala</i> (Cyperaceae), <i>Erigeron vagus</i> (Asteraceae), <i>Gentiana calycosa</i> (Gentianaceae), <i>Lewisia pygmaea</i> (Montiaceae), <i>Phlox condensata</i> (Polemoniaceae), <i>Poa glauca</i> subsp. <i>rupicola</i> (Poaceae), <i>Ribes cereum</i> (Grossulariaceae), <i>Stipa pinetorum</i> (Poaceae)
Intermountain Region taxa distributed across the Great Basin	<i>Cryptantha nubigena</i> (Boraginaceae), <i>Cymopterus cinerarius</i> (Apiaceae), <i>Eriogonum incanum</i> (Polygonaceae), <i>Ivesia shockleyi</i> (Rosaceae), <i>Jamesia americana</i> (Hydrangeaceae), <i>Podistera nevadensis</i> (Apiaceae), <i>Selaginella watsonii</i> (Selaginellaceae), <i>Trifolium monanthum</i> subsp. <i>monanthum</i> (Fabaceae)
Taxa extending from the Pacific Northwest and Cascade Range	<i>Anelsonia eurycarpa</i> (Brassicaceae), <i>Astragalus whitneyi</i> (Fabaceae), <i>Boechera howellii</i> (Brassicaceae), <i>Carex breweri</i> (Cyperaceae), <i>Eriogonum lobbii</i> (Polygonaceae), <i>Gentiana newberryi</i> (Gentianaceae), <i>Potentilla breweri</i> and <i>P. flabellifolia</i> (Rosaceae), <i>Ranunculus alismifolius</i> var. <i>alismellus</i> (Ranunculaceae), <i>Senecio fremontii</i> var. <i>occidentalis</i> (Asteraceae), <i>Silene sargentii</i> (Caryophyllaceae)

are heavily weighted toward subalpine and alpine specialists, with 29 of these restricted in distribution to elevations of 2700 m or above, or with median elevational range above 3000 m. Two generic lineages are prominent among these endemics, with five taxa each of *Draba* and *Eriogonum*. Five of the alpine endemics are annual species—*Orochaenactis thysanocarpha* (A. Gray) Coville (Asteraceae), *Cryptantha circumscissa* var. *rosulata* (Boraginaceae), *Streptanthus gracilis* (Brassicaceae), and *Leptosiphon oblanceolatus* (Polemoniaceae).

The southern Sierra Nevada is the most significant subregion for endemics, with 15 of the 36 endemic taxa (42%) are restricted in distribution to the area from the Kings River drainage south that includes Kings Canyon and Sequoia National parks (Table 2). These are *Draba cruciata* Payson, *D. longisquamosa* O. E. Schulz, *D. sharsmithii* Rollins & R. A. Price, *Eriogonum polypodum* Small, *E. spergulinum* A. Gray var. *pretense* (S. Stokes) J. T. Howell, *E. wrightii* var. *olanchense*, *Galium hypotrichium* A. Gray subsp. *subalpinum* (Hilend & J. T. Howell) Ehrend., *Leptosiphon oblanceolatus*, *Monardella beneolens* Shevock, Ertter & Jockerst, *Oreonana clementis* (M. E. Jones) Jeps., *Orthochaenactis thysanocarpha*, *Phlox dispersa*, *Pinus balfouriana* var. *austina* R. J. Mastrog. & J. D. Mastrog., *Streptanthus gracilis*, and *Trifolium kingie* S. Waston subsp. *dedeckerae* (J. M. Gillett) D. Heller.

Another 13 taxa are restricted to the central and southern Sierra Nevada. Five of the endemics are present across the northern, central and southern subregions of the Sierra Nevada, and three endemic taxa are restricted in occurrence to the central Sierra Nevada. These are *Draba*

sierrae, *Eriogonum ovalifolium* Nutt. var. *caelestinum* Reveal, and *Lupinus gracilentus* Greene (Table 2). Although the absence of peaks above 3500 m in the Sierra Nevada north of Yosemite National Park explains the lack of endemics restricted to this subregion, the scattered lower elevation alpine communities of the northern Sierra Nevada retain moderately high richness of species.

In addition to the members of the alpine flora that are endemic to the Sierra Nevada, there are an additional 31 alpine taxa that are Californian endemics, allowing for a broad interpretation of the floristic region to include the westernmost ranges of the Great Basin lying close to the Sierra Nevada and the southern Cascade Range in Oregon. Many of the Californian endemics have ranges that extend to the Sweetwater and/or White Inyo mountains, while others extend into the high Transverse and Peninsular Ranges of southern California and a small number extend into the southern Cascade Range. The pattern of dominant endemism centered in the southern Sierra Nevada is not seen among these taxa. Twelve of these occur throughout the Sierra Nevada and an additional 12 are restricted to the central and southern areas of the range, while only four species are limited to the southern Sierra Nevada.

If the lower limit of the alpine zone were dropped to 3300 m, 11 additional Sierra Nevada endemics would be added (Table 2). Four of these are restricted to the southern Sierra Nevada (*Astragalus ravenii*, *Boechera pygmaea* (Rollins) Al-Shehbaz, *Castilleja praeterita* Heckard & Bacig., and *Phacelia orogenes*), with three each present in the central and southern Sierra Nevada and in all three regions. One species is restricted

to the central Sierra Nevada. Five additional Californian endemics would be added if the lower alpine limit was dropped to 3300 m (Table 2).

DISCUSSION

Defining the Alpine Zone of California

Critically defining what species should be included in an alpine flora is an imperfect task given the lack of a simple operational definition, as discussed below. The high elevation areas of the Sierra Nevada broadly classified as subalpine and alpine, or upper Hudsonian and Arctic-Alpine in the Merriam life zone classification (Daubenmire 1938), would roughly include those areas lying above about 3000 m elevation (Fig. 2). Such subalpine and alpine habitats cover extensive areas of the central and southern Sierra Nevada, but only scattered areas of the northern Sierra Nevada lying north of Sonora Pass. The higher elevation area of this northern Sierran region, however, supports mosaics of subalpine forest, shrublands, and low alpine-like vegetation (Smiley 1915, 1921).

A simple definition of alpine habitat is that area occurring above treeline, with the caveat that most alpine species are not obligate in inhabiting habitats above treeline and typically occur to varying degrees at lower elevations (Packer 1974). While this approach sounds logical, timberline itself can be highly variable even in a local area depending on slope exposure, erosional history, parent material, disturbance history, and local microclimate (Billings 2000).

Sharsmith (1940) recognized the alpine flora as a distinct subdivision of the overall Californian flora, characterized by its geographic range, growth forms, species composition, and constancy with which the alpine association of species is maintained. Although he described the alpine zone as reaching its lower limit at an average elevation of 3500 m, the limit used in this paper, nowhere in his dissertation is there a clear statement of criteria for his inclusion of species. He stated,

While certain species are absolute indicators of the alpine flora, it is the particular association of species which gives it its characteristic. Although many species occur elsewhere, this special assemblage is not met until the alpine area is reached. Everywhere the flora presents the impression of unity, an impression reinforced by increased field experience.

The combined subalpine and alpine flora of the Sierra Nevada as defined by Smiley (1921) included 633 species, with 41 listed as indicators of the Arctic-Alpine zone. He considered 158 species to be Sierra Nevada endemics and another 20 species to be restricted in distribution to the Sierra Nevada and the southern California mountains. Sharsmith (1940) included 189 species

in his alpine flora of the Sierra Nevada, with 31 of these considered to be endemic. This flora was composed of 183 herbaceous perennials and six annual species, but did not include any woody species. A similar estimate was made by Stebbins (1982) who stated that there were 207 species in the Sierra Nevada alpine flora. Finally, a much higher estimate came from Major and Bamberg (1967) who used the species descriptions in Munz (1959) to estimate a Sierran alpine flora of about 600 species, a number similar to that reported here for taxa reaching 3300 m or above.

Growth Forms

The relative dominance of a herbaceous perennial growth forms present in the alpine flora of the Sierra Nevada is typical of other alpine floras worldwide and does not change dramatically in a gradient from the Rocky Mountains west across the Great Basin (Billings 1978, 2000; Rundel et al. 2008). Herbaceous perennials have the characteristic of maintaining large proportions of total biomass belowground where they play an important role in carbohydrate storage over the winter months (Mooney and Billings 1960; Billings 1974). The herbaceous perennials include species with a variety of ecological forms and life history strategies of carbon allocation to belowground and aboveground vegetative, and reproductive tissues (Rundel et al. 2005), and many of these are relatively long-lived plants surviving for decades (Billings 1974; Pollak 1991).

As in other alpine regions, perennial graminoids in alpine habitats of the Sierra Nevada commonly dominate plant communities of wet meadows that dry earlier than fellfield communities. In contrast, fellfield habitats exhibit a mixed dominance of broad-leaved erect perennials, perennial graminoids, and mats and cushions (Rundel et al. 2005). Mat and cushion growth forms of herbaceous perennials are widespread in the high elevation Sierra Nevada, where the 46 taxa listed here represent 12% of the alpine flora. These are most prominent ecologically on wind-swept rocky slopes or other exposed areas that remain snow-free during the winter.

Because of limiting stress factors of short and severe growing conditions, annual plants are generally rare in the typical circumboreal arctic-alpine floras of the Northern Hemisphere, comprising no more than 1–2% of the flora (Billings 2000). Although not abundant, annuals, nevertheless, are more common in alpine flora of the Sierra Nevada and White Mountains where they comprise about 6–8% of the floras (Jackson and Bliss 1982; Jackson 1985; Rundel et al. 2008). The species richness of alpine annual taxa, however, drops rapidly at elevations above 3300 in the Sierra Nevada (Fig. 5). Went (1948, 1953)

TABLE 2. ENDEMIC TAXA OF THE ALPINE FLORA OF THE SIERRA NEVADA, CALIFORNIA WITH THEIR UPPER RANGE OF OCCURRENCE AND GROWTH FORMS. For range: n = northern Sierra Nevada, c = central Sierra Nevada, and s = southern Sierra Nevada. For growth forms: A = annual, G = geophyte, P = erect herbaceous perennial, P-G = perennial graminoid, P-MAT = mat or cushion, SS = subshrub, T = tree. Species names follow Baldwin et al. (2012).

Endemic group	Family	Range	Growth form
Sierra Nevada endemics >3500 m			
<i>Aquilegia pubescens</i>	Ranunculaceae	n,c,s	P
<i>Calamagrostis muiriana</i>	Poaceae	c,s	P-G
<i>Carex congdonii</i>	Cyperaceae	c,s	P-G
<i>Cryptantha circumscissa</i> var. <i>rosulata</i>	Boraginaceae	n,c,s	A
<i>Dodecatheon subalpinum</i>	Primulaceae	c,s	P
<i>Draba cruciata</i>	Brassicaceae	s	P
<i>Draba lemmonii</i>	Brassicaceae	n,c,s	P
<i>Draba longisquamosa</i>	Brassicaceae	s	P
<i>Draba sharsmithii</i>	Brassicaceae	s	P
<i>Draba sierrae</i>	Brassicaceae	c	P-MAT
<i>Eriogonum nudum</i> var. <i>scapigerum</i>	Polygonaceae	c,s	P
<i>Eriogonum ovalifolium</i> var. <i>caelestinum</i>	Polygonaceae	c	P-MAT
<i>Eriogonum polypodium</i>	Polygonaceae	s	P-MAT
<i>Eriogonum spergulinum</i> var. <i>pratense</i>	Polygonaceae	s	P
<i>Eriogonum wrightii</i> var. <i>olanchense</i>	Polygonaceae	s	P-MAT
<i>Galium hypotrichium</i> subsp. <i>subalpinum</i>	Rubiaceae	s	P
<i>Hazardia whitneyi</i> var. <i>whitneyi</i>	Asteraceae	n,c,s	SS
<i>Ivesia muirii</i>	Rosaceae	c,s	P
<i>Ivesia pygmaea</i>	Rosaceae	c,s	P
<i>Leptosiphon oblanceolatus</i>	Polemoniaceae	s	A
<i>Lewisia disepala</i>	Montiaceae	c,s	P
<i>Lupinus covillei</i>	Fabaceae	c,s	P
<i>Lupinus gracilentus</i>	Fabaceae	c	P
<i>Luzula orestera</i>	Juncaceae	n,c,s	P-G
<i>Monardella beneolens</i>	Lamiaceae	s	SS
<i>Oreonana clementis</i>	Apiaceae	s	P
<i>Oreostemma peirsonii</i>	Asteraceae	c,s	P
<i>Orochaenactis thysanocarpha</i>	Asteraceae	s	A
<i>Phlox dispersa</i>	Polemoniaceae	s	P-MAT
<i>Pinus balfouriana</i> var. <i>austrina</i>	Pinaceae	s	T
<i>Poa stebbinsii</i>	Poaceae	c,s	P-G
<i>Polemonium eximium</i>	Polemoniaceae	c,s	P
<i>Stipa kingii</i>	Poaceae	c,s	P-G
<i>Streptanthus gracilis</i>	Brassicaceae	s	A
<i>Trichophorum clementis</i>	Cyperaceae	c,s	P-G
<i>Trifolium kingii</i> subsp. <i>dedeckeriae</i>	Fabaceae	s	P
Sierra Nevada endemics 3300–3499 m			
<i>Astragalus ravenii</i>	Fabaceae	s	P
<i>Boechera pygmaea</i>	Brassicaceae	s	P
<i>Castilleja praeterita</i>	Orobanchaceae	s	P
<i>Erigeron elmeri</i>	Asteraceae	c,s	P
<i>Hulsea vestita</i> subsp. <i>vestita</i>	Asteraceae	c,s	P
<i>Ipomopsis aggregata</i> subsp. <i>bridgesii</i>	Polemoniaceae	c,s	P
<i>Lilium kelleyanum</i>	Liliaceae	c,s	G
<i>Lomatium torreyi</i>	Apiaceae	n,c,s	P
<i>Phacelia eisenii</i>	Boraginaceae	c,s	A
<i>Phacelia orogenes</i>	Boraginaceae	s	A
<i>Trifolium monanthum</i> subsp. <i>tenerum</i>	Fabaceae	n,c,s	P
Californian endemics >3500			
<i>Astragalus kentrophyta</i> var. <i>danaus</i>	Fabaceae	c,s	P-MAT
<i>Carex mariposana</i>	Cyperaceae	n,c,s	P-G
<i>Castilleja nana</i>	Orobanchaceae	n,c,s	P
<i>Chaenactis alpigena</i>	Asteraceae	n,c,s	P-MAT
<i>Delphinium polycladon</i>	Ranunculaceae	n,c,s	P
<i>Draba breweri</i>	Brassicaceae	n,c,s	P
<i>Draba subumbellata</i>	Brassicaceae	s	P-MAT
<i>Eriogonum gracilipes</i>	Polygonaceae	c,s	P-MAT
<i>Eriogonum umbellatum</i> var. <i>covillei</i>	Polygonaceae	c,s	P-MAT

TABLE 2. CONTINUED.

Endemic group	Family	Range	Growth form
<i>Galium hypotrichium</i> subsp. <i>hypotrichium</i>	Rubiaceae	c,s	P
<i>Hulsea vestita</i> subsp. <i>pygmaea</i>	Asteraceae	c,s	P
<i>Ivesia lycopodioides</i> subsp. <i>lycopodioides</i>	Rosaceae	n,c	P
<i>Ivesia lycopodioides</i> subsp. <i>scandularis</i>	Rosaceae	c,s	P
<i>Ivesia santolinoides</i>	Rosaceae	n,c,s	P
<i>Lewisia glandulosa</i>	Montiaceae	c,s	P
<i>Lupinus breweri</i> var. <i>breweri</i>	Fabaceae	n,c,s	P-MAT
<i>Lupinus breweri</i> var. <i>bryoides</i>	Fabaceae	s	P-MAT
<i>Lupinus latifolius</i> var. <i>parishii</i>	Fabaceae	c,s	P
<i>Lupinus lepidus</i> var. <i>ramosus</i>	Fabaceae	c,s	P
<i>Lupinus padre-crowleyi</i>	Fabaceae	s	P-MAT
<i>Lupinus pratensis</i> var. <i>pratensis</i>	Fabaceae	c,s	P
<i>Phyllodoce breweri</i>	Ericaceae	n,c,s	S
<i>Poa keckii</i>	Poaceae	n.c.s	P-G
<i>Potentilla pseudosericea</i>	Rosaceae	c,s	P
<i>Potentilla wheeleri</i>	Rosaceae	s	P
<i>Primula suffrutescens</i>	Primulaceae	n,c,s	P
<i>Ranunculus eschscholtzii</i> var. <i>oxynotus</i>	Ranunculaceae	n,c,s	P
<i>Tonestus peirsonii</i>	Asteraceae	c	P
<i>Triteleia dudleyi</i>	Themidaceae	c,s	G
<i>Viola pinetorum</i> subsp. <i>grisea</i>	Violaceae	n,c,s	P
<i>Viola purpurea</i> subsp. <i>mesophyta</i>	Violaceae	n,c,s	P
Californian endemics 3300–3499 m			
<i>Eriogonum latens</i>	Polygonaceae	c,s	P
<i>Frasera puberulenta</i>	Gentianaceae	c,s	P
<i>Hordeum brachyantherum</i> subsp. <i>californicum</i>	Poaceae	n,c,s	P-G
<i>Penstemon caesius</i>	Plantaginaceae	s	SS
<i>Plagiobothrys torreyi</i> var. <i>diffusus</i>	Boraginaceae	n,c,s	A

suggested that many of the high elevation annuals in the Sierra Nevada were related to desert species.

Severe winter conditions typically limit the occurrence of woody plants above treeline, with prostrate mats and cushions as prominent exceptions. The upright growth form of woody shrubs and krummholtz tree species exposes their tissues to extreme conditions of temperature and wind exposure (Körner 2003). This impact on shrub occurrence can be seen in Fig. 5 where shrub richness in the Sierra Nevada drops sharply with increasing elevation above 3300 m, similar to the pattern for annual species. Much of the alpine flora of woody species comes from species of *Salix* and members of the Ericaceae, groups which favor moist habitats with some level of protection.

Biogeography and Endemism

The alpine flora of mountain ranges on the western margin of the Great Basin of California and western Nevada exhibit very strong relationships to that of the Sierra Nevada (Rundel et al. 2008). The Sweetwater Mountains supports a flora of 173 species in 16 km² of alpine habitat, with 94% of this flora common to the Sierra Nevada (Hunter and Johnson 1983). The Wassuk Range has an alpine flora of 70 species in just 2.6 km² of alpine habitat (Bell and Johnson 1980). Again, this flora is has stronger floristic

relationships to the Sierra Nevada than the Rocky Mountains.

As with the Sweetwater Mountains and Wassuk Ranges, the flora of the White Mountains exhibits much stronger floristic relationships to the Sierra Nevada than to the Rocky Mountains. About 90% of the species in the alpine flora of the White Mountains are also found in the Sierra Nevada (Rundel et al. 2008), compared with only 58% that occur in the ranges of the central Rocky Mountains (Scott 1995). These values are significantly higher for both ranges than earlier estimates made on incomplete data (Lloyd and Mitchell 1973).

Mountain ranges in the central Great Basin generally show strong floristic linkages to the Rocky Mountains and weaker links to the Sierra Nevada (Billings 1978). Loope (1969) reported 189 alpine species from the Ruby Mountains in northeastern Nevada, with this flora heavily linked to the Rocky Mountains. The isolated San Francisco Mountains in Arizona with only 5.2 km² of alpine habitat has 80 species, and likewise shows strong floristic relationships to the Rocky Mountains despite its separation of about 200 km (Schaak 1983).

The level of endemism in the alpine Sierra Nevada flora is a relatively small part of the overall endemism for the montane and higher parts of the range. Based on current information, there are 205 taxa endemic to what *The Jepson*

Manual (Hickman 1993) classifies as the northern, central, and southern high Sierra Nevada, i.e., the montane, subalpine and alpine zones above foothill habitats (R. Moe, Univ. of California, Berkeley, personal communication). The 36 Sierran endemics present in the alpine flora would thus comprise 18% of the endemic flora of the higher Sierra Nevada.

The unique California component of the alpine flora of the Sierra Nevada is considerably greater if one considers the endemic component of 31 species in the alpine flora that are not uniquely limited to the Sierra Nevada but are Californian endemics as defined earlier. Combining the endemic taxa with Sierran and Californian limits of distribution, the total of 66 taxa represents 16% of the alpine flora. This is a relatively high figure compared to other alpine ranges in continental North America and Europe, and reflects the environmental stress conditions associated with the summer-dry mediterranean-type climate present in the Sierra Nevada.

Stebbins (1982) analyzed the flora of the high Sierra Nevada, defined similarly to that of Smiley (1921) as the upper montane to alpine zones, and identified 119 endemic species, 13.5% of the total flora. He further noted that another 60% of the flora extended beyond the Sierra Nevada only as far as southern California, western Nevada, and southern Oregon.

Raven and Axelrod (1978) briefly discussed the diversity and evolution of the subalpine and alpine flora of the Sierra Nevada, listing 68 endemics for this region. Their table of endemics, however, is outdated by more recent information on distribution patterns and species concepts. Shevock (1996) gave a figure of 405 endemic taxa of vascular plants for the entire Sierra Nevada. The 36 alpine endemics reported here would comprise 9% of this total. Of the three geographical subregions (northern, central, and southern) of the entire range, the southern Sierra Nevada is the richest in endemics, rare species, and total floristic composition (Shevock 1996), a finding similar to that reported here.

The Evolution of the Sierran Alpine Flora

A detailed assessment of the biogeographic and evolutionary origin of the alpine flora of the Sierra Nevada is beyond the scope of this review. Broad interpretations of biogeographic relationships within alpine lineages have been discussed by previous authors (e.g., Smiley 1921; Sharsmith 1940; Chabot and Billings 1972; Taylor 1977; Major and Taylor 1977; Raven and Axelrod 1978; Stebbins 1982) but recent phylogenetic studies have made many of these earlier interpretations subject to re-evaluation.

Evidence for a north to south route of colonization of high mountain areas of the Sierra

Nevada comes from a pattern of decreasing presence of Rocky Mountain floristic elements and an increasing number of endemics alpine species as one moves from the northern to southern crest of the range (Chabot and Billings 1972; Raven and Axelrod 1978). The southern limit of a number of alpine species on Mount Lassen suggests the possibility that some of these and other Cascade Range species may well have been present in the Sierra Nevada in the late Pliocene or early Pleistocene. Although the species composition of lower and middle elevation conifer forests of Lassen National Park are strongly related to that of the Sierra Nevada, the summits of the highest peaks in Lassen support an alpine flora that exhibits stronger floristic links to Mount Shasta and the Cascade Range to the north (Gillett et al. 1995). Alpine species with disjunct patterns of distribution from Mount Lassen to the Cascade Range volcanoes include *Cardamine bellidifolia* L. (Brassicaceae), *Carex illota* L. H. Bailey (Cyperaceae), *Collomia larsenii* (A. Gray) Payson (Polemoniaceae), *Draba aureola* S. Watson (Brassicaceae), *Erigeron elegantulus* Greene and *E. nivalis* Nutt. (Asteraceae), *Hulsea nana* A. Gray (Asteraceae), *Polemonium pulcherrimum* Hook. var. *pilosum* (Greenm.) Brand (Polemoniaceae), and *Silene suksdorfii* B. L. Rob. (Caryophyllaceae). The Klamath Mountains also mark the southern distribution limit of a number of boreal species that do not occur in the high elevations of the Sierra Nevada (Howell 1944).

Alpine and subalpine species characteristic of wet meadows and other moist sites typically have broad geographic ranges but become increasing habitat specific moving to the south in the Sierra Nevada as precipitation decreases (Kimball et al. 2004; Moore et al. 2007). The relative isolation of the Sierra Nevada from northern ranges and the summer-dry have clearly acted as a filter to exclude some widespread circumpolar arctic-alpine species such as *Dryas integrifolia* Vahl (Rosaceae) and *Silene acaulis* L. (Caryophyllaceae) which do not occur anywhere in California. Species growing in xeric rocky habitats show higher levels of endemism and smaller range size due to isolation and divergence from ancestral populations distributed in wetter habitats to the north.

More controversial, however, is the origin of disjunct Rocky Mountain species present in the central and southern Sierra Nevada, often growing in azonal soil conditions. There is both geological and paleobotanical evidence to suggest that the mean elevation of the Great Basin was as much as 1500 m higher in the Miocene and that the current Basin and Range topography is the result of subsidence rather than uplift (Wernicke et al. 1988; Wolfe et al. 1997). The presence of higher elevations in the Great Basin during the

Pleistocene could possibly have provided stepping stones to allow the dispersal of alpine organisms from the east (Major and Bamberg 1967; Taylor 1976a). Molecular evidence indicates that at least one lineage of butterflies entered the Sierra Nevada by this route (Nice and Shapiro 2001). However, other authors feel that the majority of these disjunct plant species reached the Sierra Nevada by the same dominant route from the Western Cordillera via the Cascade Range and south (Chabot and Billings 1972).

Modes of speciation in the development of the endemic alpine flora of the Sierra Nevada are clearly complex. Polyploidy and associated apomixis are widely recognized as major factors in plant evolution, and these factors have had a relatively recent impact on speciation in producing stable self-propagating lineages (Soltis et al. 2009). In the alpine region of the Sierra Nevada, as in other alpine regions, diploid lineages of polyploid complexes often occupy unglaciated areas and resist introgression due hypothetically to a significantly higher seed set. However, asexual apomictic populations are more widespread than their sexual relatives in glaciated areas. Sexual and asexual polyploids may become distinct stabilized species through hybrid origin.

Reproductive isolation and stability of tetraploids within their respective distribution as well as the value of uniparental reproduction provide the advantages of apomixis. Many important genera in the alpine flora of the Sierra Nevada are notable for the presence of apomixis, with *Boechnera* (Schranz et al. 2005; Dobes et al. 2007), *Draba* (Jordon-Thaden and Koch 2008), and *Antennaria* (Bayer and Stebbins 1987) as examples. Additional speciose genera in the Sierra Nevada known to have complex apomictic populations include *Arnica* and *Crepis* (Asteraceae; Noyes 2007), *Poa* and *Calamagrostis* (Poaceae), and *Potentilla* (Rosaceae) (Asker and Jerling 1992).

Other modes of alpine speciation have also been described for the Sierra Nevada. Some speciation, for example, has hypothetically come from lowland arid-adapted taxa colonizing the glaciated terrain of the range at the end of the Pleistocene (Went 1948, 1953). Speciation has also been shown to be the result of population disjunction and reproductive isolation (Chase and Raven 1975).

Although the Transverse and Peninsular ranges are well separated from the higher elevations of the Sierra Nevada, more than one third of the Sierran alpine flora has a range of distribution that extends to these southern California ranges. While some of these species occur at lower elevations, others are typically subalpine and alpine species that must have crossed the Mojave Desert during the cold conditions of the Pleisto-

cene. This latter group includes *Androsace septentrionalis* (Primulaceae), *Hulsea vestita* A. Gray subsp. *pygmaea* (A. Gray) Wilken (Asteraceae), *Oxyria digyna* (L.) Hill (Polygonaceae), and *Podistera nevadensis* (Apiaceae).

There are lessons to be learned from recent studies of the patterns of diversification in the European alpine flora. These strongly demonstrate that speciation have been promoted by diverse ecological, evolutionary, and life history traits related to population structure, phylogenetic relationships, breeding system, dispersal syndromes, ecophysiological ranges of habitat requirements, and competitive abilities (Comes and Kadereit 1998; Taberlet et al. 1998; Hewitt 2000; Gugerli and Holderegger 2001; Vargas 2003). The complex and dynamic climatic and geological history of the Sierra Nevada operating on such traits suggests that there have been a range of different colonization and extinction histories that are species specific. Much more work on the comparative phylogeography of alpine plants in the Sierra Nevada will be necessary before we understand all of the factors responsible for present distributions and predominant modes of speciation in the alpine flora of the range.

Research Needs

There is little doubt that the stability of the ecotone between alpine and treeline ecosystems in the Sierra Nevada and other high mountain regions has been and continues to be a function of complex interactions, with multiple drivers operating across diverse scales of time and space. This ecotone has been highly dynamic in the past and given the importance of temperature in controlling the elevation of treeline and higher alpine ecosystems, this ecotone and associated species are likely to be particularly sensitive to climate change in the future (Lloyd and Graumlich 1997; Graumlich et al. 2005; Grabherr et al. 2010). Beyond treeline studies, the expansion of woody shrub species into alpine habitats has been shown to also be a sensitive indicator of potential climate change, with significant feedbacks on microclimate and soil ecosystems (Hallinger et al. 2010), as well as species facilitation (Callaway et al. 2002). The potential sensitivity of alpine ecosystems to climate change has been the stimulus for establishing the worldwide research program Global Observation Research Initiative in Alpine Environments (GLORIA, <http://www.gloria.ac.at>) with the aim of providing long-term observations on the state and dynamics of alpine biota.

ACKNOWLEDGMENTS

I thank Bruce Baldwin and Richard Moe for their help in accessing the Jepson Manual database. Peggy

Moore and Sylvia Haultain kindly shared species lists for Yosemite and Sequoia/Kings Canyon National Parks, respectively. This work is a contribution from the UCLA La Kretz Center for California Conservation Science.

LITERATURE CITED

- ASKER, S. E. AND L. JERLING. 1992. Apomixis in plants. CRC Press, Boca Raton, FL.
- BALDWIN, B. G., D. H. GOLDMAN, D. J. KEIL, R. PATTERSON, AND T. J. ROSATI. 2012. The Jepson manual: vascular plants of California. 2nd ed. University of California Press, Berkeley, CA.
- BAYER, R. J. AND G. L. STEBBINS. 1987. Chromosome numbers, patterns of distribution, and apomixis in *Antennaria* (Asteraceae: Inuleae). *Systematic Botany* 12:305–319.
- BELL, K. L. AND R. E. JOHNSON. 1980. Alpine flora of the Wassuk Range, Mineral County, Nevada. *Madroño* 27:25–35.
- BENEDICT, N. B. 1983. Plant associations of subalpine meadows, Sequoia National Park, California, USA. *Arctic and Alpine Research* 15:383–396.
- AND J. MAJOR. 1982. A physiographic classification of subalpine meadows of the Sierra Nevada, California. *Madroño* 29:1–12.
- BILLINGS, W. D. 1974. Adaptations and origins of alpine plants. *Arctic and Alpine Research* 6:129–142.
- . 1978. Alpine phytogeography across the Great Basin. *Great Basin Naturalist Memoirs* 2:105–117.
- . 2000. Alpine vegetation. Pp. 536–572 in M. G. Barbour and W. D. Billings (eds.), *North American terrestrial vegetation*, 2nd ed. Cambridge University Press, Cambridge, UK.
- BURKE, M. T. 1982. The vegetation of the Rae Lakes Basin, southern Sierra Nevada. *Madroño* 29:164–179.
- CALLAWAY, R. M., R. W. BROOKER, P. CHOLER, Z. KIKVIDZE, C. J. LORTIE, R. MICHALET, L. PAOLINI, F. I. PUIGNAIRE, B. NEWINGHAM, E. T. ASCHEHOUG, C. ARMAS, V. D. KIKODZE, AND B. J. COOK. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417:844–848.
- CHABOT, B. F. AND W. D. BILLINGS. 1972. Origins and ecology of the Sierran alpine flora and vegetation. *Ecological Monographs* 42:163–199.
- CHASE, V. C. AND P. H. RAVEN. 1975. Evolutionary and ecological relationships between *Aquilegia formosa* and *A. pubescens* (Ranunculaceae), two perennial plants. *Evolution* 29:474–486.
- COMES, P. H. AND J. W. KADEREIT. 1998. The effect of Quaternary climatic changes on plant distribution and evolution. *Trends in Plant Science* 3:432–438.
- CONSTANTINE-SHULL, H. M. 2000. Floristic affinities of the San Joaquin Roadless Area, Inyo National Forest, Mono County, California. M.S. Thesis, Humboldt State University, Arcata, CA.
- COVILLE, F. V. 1893. Botany of the Death Valley expedition. Contributions from the U.S. National Herbarium 4:1–363.
- DAUBENMIRE, R. F. 1938. Merriam's life zones of North America. *Quarterly Review of Biology* 13:327–332.
- DOBES, C., T. F. SHARBEL, AND M. KOCH. 2007. Towards understanding the dynamics of hybridization and apomixis in the evolution of the genus *Boechea* (Brassicaceae). *Systematics and Biodiversity* 5:321–331.
- FITES-KAUFMAN, J. A., P. W. RUNDEL, N. STEPHENSON, AND D. A. WEIXELMAN. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. Pp. 456–501 in M. Barbour, A. Schoenherr, and T. Keeler-Wolf (eds.), *Terrestrial vegetation of California*, 2nd ed. University of California Press, Berkeley, CA.
- GILLETT, G. W., J. T. HOWELL, AND H. LESCHKE. 1995. A flora of Lassen Volcanic National Park, California. California Native Plant Society, Sacramento, CA.
- GRABHERR, G., M. GOTTFRIED, AND H. PAULI. 2010. Climate change impacts in alpine environments. *Geography Compass* 4:1133–1153.
- GRAUMLICH, L., L. WAGGONER, AND A. BUNN. 2005. Detecting global change at alpine treeline: coupling paleoecology with contemporary studies. *Advances in Global Change Research* 23:501–508.
- GUGERLI, F. AND R. HOLDEREGGER. 2001. Nunatak survival, *tabula rasa* and the influence of the Pleistocene ice-ages on plant evolution in mountain areas. *Trends in Plant Science* 6:397–398.
- HALL, H. M. 1902. A botanical survey of San Jacinto Mountain. University of California Publications in Botany 1:1–140.
- AND J. GRINNELL. 1919. Life-zone indicators in California. *Proceedings of the California Academy of Sciences* 9:37–67.
- HALLINGER, M., M. MANTHEY, AND M. WILMKING. 2010. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist* 186:890–899.
- HANES, T. L. 1976. Vegetation types of the San Gabriel Mountains. Pp. 65–76 in J. Latting (ed.), *Plant communities of southern California*. Symposium Proceedings Special Publication Number 2. California Native Plant Society, Sacramento, CA.
- HARSHBERGER, J. W. 1911. *Phytogeographic survey of North America*. Stechert and Co., New York, NY.
- HAYHOE, K., D. CAYAN, C. B. FIELD, AND 16 OTHERS. 2004. Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Science* 101:12422–12427.
- HEWITT, G. M. 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405:907–913.
- HICKMAN, J. (ed). 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley, CA.
- HORTON, J. S. 1960. *Vegetation types of the San Bernardino Mountains*. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Technical Paper 44, Berkeley, CA.
- HOVANITZ, W. 1940. Ecological color variation in a butterfly and the problem of “protective coloration”. *Ecology* 21:371–380.
- HOWELL, J. T. 1944. Certain plants of the Marble Mountains in California with remarks on the boreal flora of the Klamath area. *Wasmann Collector* 6:13–19.
- . 1951. The arctic-alpine flora of three peaks in the Sierra Nevada. *Leaflets of Western Botany* 6:141–56.
- HUNTER, K. L. AND R. E. JOHNSON. 1983. Alpine flora of the Sweetwater Mountains, Mono County, Nevada. *Madroño* 30:89–105.

- JACKSON, J. L. 1985. Floristic analysis of the distribution of ephemeral plants in treeline areas of the western USA. *Arctic and Alpine Research* 17:251–260.
- AND L. C. BLISS. 1982. Distribution of ephemeral herbaceous plants near treeline in the Sierra Nevada, California, USA. *Arctic and Alpine Research* 14:33–44.
- JORDON-THADEN, I. AND M. KOCH. 2008. Species richness and polyploid patterns in the genus *Draba* (Brassicaceae): a first global perspective. *Plant Ecology & Diversity* 1:255–263.
- KIMBALL, S., P. WILSON, AND J. CROWTHER. 2004. Local ecology and geographic ranges of plants in the Bishop Creek watershed, Sierra Nevada, California. *Journal of Biogeography* 31:1637–1657.
- KLIKOFF, L. G. 1965. Microenvironmental influence on vegetational pattern near timberline in the central Sierra Nevada. *Ecological Monographs* 35:187–211.
- KÖRNER, C. 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems*. Springer Verlag, Berlin, Germany.
- LOYD, A. H. AND L. J. GRAUMLICH. 1997. Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology* 78:1199–1210.
- LOYD, R. M. AND R. S. MITCHELL. 1973. *A flora of the White Mountains of California*. University of California Press, Berkeley, CA.
- LOOPE, L. L. 1969. Subalpine and alpine vegetation of northeastern Nevada. Ph.D. Dissertation. Duke University, Durham, NC.
- MAJOR, J. AND S. A. BAMBERG. 1967. Some cordilleran plants disjunct in the Sierra Nevada of California and their bearing on Pleistocene ecological conditions. Pp. 171–188 in H. E. Wright and W. H. Osburn (eds.), *Arctic and alpine environments*. Indiana University Press, Bloomington, IN.
- AND D. W. TAYLOR. 1977. *Alpine*. Pp. 601–675 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. Wiley, New York, NY.
- MEYERS, P. A. 1978. A phytogeographic survey of the subalpine and alpine regions of southern California. Ph.D. Dissertation. University of California, Santa Barbara, CA.
- MOONEY, H. A. AND W. D. BILLINGS. 1960. The annual carbohydrate cycle of alpine plants as related to growth. *American Journal of Botany* 47:594–598.
- MORITZ, C., J. L. PATTON, C. J. CONROY, J. L. PARRA, G. C. WHITE, AND S. R. BEISSINGER. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261–264.
- MOORE, P. E., A. E. L. COLWELL, AND D. GROSSEN-BACHER. 2007. Rare plant surveys in unusual habitats of Yosemite National Park, California. U.S. Geological Survey, Sacramento, CA. Website <http://www.werc.usgs.gov/ProductDetails.aspx?ID=3632> [accessed 04 January 2012].
- MUNZ, P. A. 1959. *A California flora*. University of California Press, Berkeley, CA.
- NICE, C. C. AND A. M. SHAPIRO. 2001. Patterns of morphological, biochemical, and molecular evolution in the *Oeneis chryxus* complex (Lepidoptera: Satyridae): a test of historical biogeographical hypotheses. *Molecular Phylogenetics and Evolution* 20:11–123.
- NOYES, R. D. 2007. Apomixis in the Asteraceae: diamonds in the rough. *Functional Plant Science and Biotechnology* 1:208–222.
- PACKER, J. G. 1974. Differentiation and dispersal in alpine floras. *Arctic and Alpine Research* 6:117–128.
- PARISH, S. G. 1917. An enumeration of the pteridophytes and spermatophytes of the San Bernardino Mountains, California. *Plant World* 20:163–178, 208–223, 245–259.
- PEMBLE, R. H. 1970. Alpine vegetation in the Sierra Nevada of California as lithosequences and in relation to local site factors. Ph.D. Thesis. University of California, Davis, CA.
- POLLACK, O. 1991. Morphology and dynamics in alpine populations of *Ivesia lycopodioides* subsp. *scandularis* from the White Mountains of California. Pp. 97–116 in C. A. Hall, V. Doyle Jones, and B. Widawski (eds.), *Natural history of eastern California and high-altitude research*. White Mountains Research Station Symposium Vol. 3. White Mountain Research Station, University of California, Los Angeles, CA.
- PORTER, B. R. 1983. *A flora of the Desolation Wilderness, El Dorado County, California*. M.S. Thesis, Humboldt State University, Arcata, CA.
- RATLIFF, R. D. 1982. *A meadow site classification for the Sierra Nevada, California*. General Technical Report PSW-60. USDA Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.
- RAUNKIAER, C. 1934. *The life forms of plants and statistical plant geography*. Clarendon Press, Oxford, UK.
- RAVEN, P. H. AND D. I. AXELROD. 1978. Origin and relationships of the California flora. *University of California Publications in Botany* 72:1–134.
- RUNDEL, P. W., A. C. GIBSON, AND M. R. SHARIFI. 2005. Plant functional groups in alpine fellfield habitats of the White Mountains, California. *Arctic, Antarctic and Alpine Research* 37:358–365.
- , ———, AND ———. 2008. The alpine flora of the White Mountain, California. *Madroño* 55:204–217.
- SAGE, R. F. AND T. L. SAGE. 2002. Microsite characteristics of *Muhlenbergia richardsonis* (Trin.) Rydb., an alpine C₄ grass from the White Mountains, California. *Oecologia* 132:501–508.
- SAWYER, J. O. AND T. KEELER-WOLF. 2007. Alpine vegetation. Pp. 539–573 in M. Barbour, A. Schoenherr, and T. Keeler-Wolf (eds.), *Terrestrial vegetation of California*, 2nd ed. University of California Press, Berkeley, CA.
- SCHAAK, C. G. 1983. The alpine vascular flora of Arizona. *Madroño* 30:79–88.
- SCHRANZ, M. E., C. DOBEŠ, M. A. KOCH, AND T. MITCHELL-OLDS. 2005. Sexual reproduction, hybridization, apomixis and polyploidization in the genus *Boechea* (Brassicaceae). *American Journal of Botany* 92:1797–1810.
- SCOTT, R. W. 1995. *The alpine flora of the Rocky Mountains: Vol. 1. The Middle Rockies*. University of Utah Press, Salt Lake City, UT.
- SHAFER, S. L., P. J. BARTLEIN, AND R. S. THOMPSON. 2001. Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. *Ecosystems* 4:200–215.
- SHARSMITH, C. 1940. *A contribution to the history of the alpine flora of the Sierra Nevada*. Ph.D.

- Dissertation, University of California, Berkeley, CA.
- SHEVOCK, J. R. 1996. Status of rare and endemic plants. Pp. 691–707 in *Sierra Nevada ecosystem project: final report to Congress. Vol. II: assessments and scientific basis for management options*. Wildland Resources Center Report No. 37. Centers for Water and Wildland Resources, University of California, Davis, CA. Website <http://ceres.ca.gov/snep/pubs/v2.html> [accessed 04 January 2012].
- SMILEY, F. J. 1915. The alpine and subalpine vegetation of the Lake Tahoe region. *Botanical Gazette* 59:265–286.
- . 1921. A report upon the boreal flora of the Sierra Nevada of California. University of California Publications in Botany 9:1–423.
- SOLTIS, D. E., V. A. ALBERT, J. LEEBENS-MACK, C. D. BELL, A. H. PATERSON, C. ZHENG, D. SANKOFF, C. W. DEPAMPHILIS, P. KERR WALL, AND P. S. SOLTIS. 2009. Polyploidy and angiosperm diversification. *American Journal of Botany* 96:336–348.
- STEBBINS, G. L. 1982. Floristic affinities of the high Sierra Nevada. *Madroño* 29:189–99.
- AND J. MAJOR. 1965. Endemism and speciation in the California flora. *Ecological Monographs* 35:1–35.
- STEPHENSON, N. L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography* 25:855–870.
- TABERLET, P., L. FUMAGALLI, A. G. WUST-SAUCY, AND J.-F. COSSONS. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology* 7:453–464.
- TATUM, J. W. 1979. The vegetation and flora of Olancha Peak, southern Sierra Nevada, California. M.S. Thesis. University of California, Santa Barbara, CA.
- TAYLOR, D. W. 1976a. Disjunction of Great Basin plants in the northern Sierra Nevada. *Madroño* 29:301–310.
- . 1976b. Ecology of the timberline vegetation at Carson pass, Alpine County, California. Ph.D. Dissertation. University of California, Davis, CA.
- . 1977. Floristic relationships along the Cascade-Sierran axis. *American Midland Naturalist* 97:333–349.
- TINGLEY, M. W., W. B. MONAHANC, S. R. BEISSINGERA, AND C. MORITZ. 2009. Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Science (USA)* 106:19637–19643.
- URBAN, D. L., C. MILLER, P. N. HALPIN, AND N. L. STEPHENSON. 2000. Forest gradient response in Sierran landscapes: the physical template. *Landscape Ecology* 15:603–620.
- VARGAS, P. 2003. Molecular evidence for multiple diversification patterns of alpine plants in Mediterranean Europe. *Taxon* 52:463–476.
- WENT, F. W. 1948. Some parallels between desert and alpine floras in California. *Madroño* 9:241–249.
- . 1953. Annual plants at high altitudes in the Sierra Nevada, California. *Madroño* 12:109–114.
- WERNICKE, B., G. J. AXEN, AND J. K. SNOW. 1988. Basin and Range extensional tectonics at the latitude of Las Vegas, Nevada. *Geological Society of America Bulletin* 100:1738–1757.
- WOLFE, J. A., H. E. SCHORN, C. E. FOREST, AND P. MOLNAR. 1997. Paleobotanical evidence for high altitudes in Nevada during the Miocene. *Science* 276:1672–1675.

APPENDIX 1. Annotated checklist of the alpine flora of the Sierra Nevada, including all taxa reaching an elevation of 3500 m. Lower and upper elevations limits are those for all of California and taken from Baldwin et al. (2012). Growth form abbreviations are: P = erect broad-leaved perennial; G = geophytes; P-G = graminoid perennial; P-MAT = mat or cushion; A = annual; Q = aquatic perennial; SS = subshrub; S = woody shrub; and T = tree. Biogeographic relationships are abbreviated as follows: WIDE = widespread taxa present in many habitats or regions across North America and/or throughout the world; CORD = cordilleran taxa widespread in mountain regions of the western North America; S-C = Sierra/Cascade taxa with a Pacific Northwest distribution; INT = intermountain taxa present in the Great Basin; END = taxa endemic to the Sierra Nevada; and END-CAL = taxa endemic to California, as broadly defined in the text. Species names follow Baldwin et al. (2012).

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
PTERIDOPHYTA					
Ophioglossaceae	<i>Botrychium crenulatum</i>	1500	3600	P	CORD
Ophioglossaceae	<i>Botrychium lineare</i>	2500	4000	P	CORD
Ophioglossaceae	<i>Botrychium paradoxum</i>	4000	4200	P	CORD
Ophioglossaceae	<i>Botrychium simplex</i> var. <i>compositum</i>	1500	3800	P	WIDE
Ophioglossaceae	<i>Botrychium tunux</i>	3600	3600	P	WIDE
Pteridaceae	<i>Pellaea breweri</i>	1500	3700	P	INT
Selaginellaceae	<i>Selaginella watsonii</i>	1350	4100	P	INT
Woodsiaceae	<i>Athyrium distentifolium</i> var. <i>americanum</i>	1700	3700	P	WIDE
Woodsiaceae	<i>Cystopteris fragilis</i>	50	4100	P	CORD
Woodsiaceae	<i>Woodsia scopulina</i>	1300	3500	P	WIDE
CONIFERAE					
Pinaceae	<i>Pinus albicaulis</i>	2135	3700	T	CORD
Pinaceae	<i>Pinus balfouriana</i> var. <i>austrina</i>	2700	3700	T	END
Pinaceae	<i>Pinus contorta</i> subsp. <i>murrayana</i>	1525	3500	T	S-C
Pinaceae	<i>Pinus flexilis</i>	2600	3700	T	CORD
Pinaceae	<i>Tsuga mertensiana</i>	1200	3500	T	S-C
MONOCOTYLEDONAE					
Alliaceae	<i>Allium obtusum</i> var. <i>obtusum</i>	1500	3500	G	INT
Cyperaceae	<i>Carex albonigra</i>	3000	4200	P-G	CORD
Cyperaceae	<i>Carex breweri</i>	2000	3900	P-G	S-C
Cyperaceae	<i>Carex capitata</i>	1200	3900	P-G	WIDE
Cyperaceae	<i>Carex congdonii</i>	2600	3900	P-G	END
Cyperaceae	<i>Carex deflexa</i> var. <i>boottii</i>	0	3800	P-G	CORD
Cyperaceae	<i>Carex douglasii</i>	300	3800	P-G	CORD
Cyperaceae	<i>Carex filifolia</i> var. <i>erostrata</i>	1500	3700	P-G	CORD
Cyperaceae	<i>Carex haydeniana</i>	2400	4200	P-G	CORD
Cyperaceae	<i>Carex helleri</i>	2400	4100	P-G	S-C
Cyperaceae	<i>Carex heteroneura</i>	1300	4000	P-G	INT
Cyperaceae	<i>Carex hoodii</i>	650	3600	P-G	CORD
Cyperaceae	<i>Carex incurviformis</i>	3700	4000	P-G	CORD
Cyperaceae	<i>Carex jonesii</i>	900	3500	P-G	CORD
Cyperaceae	<i>Carex lenticularis</i> var. <i>lipocarpa</i>	0	3600	P-G	CORD
Cyperaceae	<i>Carex leporinella</i>	1900	4000	P-G	CORD
Cyperaceae	<i>Carex mariposana</i>	750	3600	P-G	END-CAL
Cyperaceae	<i>Carex multicostata</i>	1900	3500	P-G	CORD
Cyperaceae	<i>Carex nigricans</i>	1900	3700	P-G	CORD
Cyperaceae	<i>Carex phaeocephala</i>	2500	4000	P-G	CORD
Cyperaceae	<i>Carex praeceptorium</i>	2200	3500	P-G	CORD
Cyperaceae	<i>Carex proposita</i>	3000	4100	P-G	S-C
Cyperaceae	<i>Carex rossii</i>	0	3800	P-G	CORD
Cyperaceae	<i>Carex scirpoidea</i> var. <i>pseudoscirpoidea</i>	2800	3700	P-G	CORD
Cyperaceae	<i>Carex specifica</i>	1200	3500	P-G	INT
Cyperaceae	<i>Carex spectabilis</i>	1800	3700	P-G	CORD
Cyperaceae	<i>Carex stramineiformis</i>	1700	4100	P-G	S-C
Cyperaceae	<i>Carex subfusca</i>	700	3800	P-G	INT
Cyperaceae	<i>Carex subnigricans</i>	2600	3800	P-G	CORD
Cyperaceae	<i>Carex tahoensis</i>	3200	3700	P-G	CORD

APPENDIX I. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Cyperaceae	<i>Carex vernacula</i>	1800	4000	P-G	CORD
Cyperaceae	<i>Eleocharis quinqueflora</i>	40	3600	P-G	WIDE
Cyperaceae	<i>Trichophorum clementis</i>	2400	3600	P-G	END
Juncaceae	<i>Juncus bryoides</i>	600	3600	P-G	CORD
Juncaceae	<i>Juncus drummondii</i>	200	3500	P-G	CORD
Juncaceae	<i>Juncus mertensianus</i>	1200	3500	P-G	CORD
Juncaceae	<i>Juncus mexicanus</i>	0	3800	P-G	WIDE
Juncaceae	<i>Juncus orthophyllus</i>	1200	3500	P-G	CORD
Juncaceae	<i>Juncus parryi</i>	2000	3800	P-G	CORD
Juncaceae	<i>Luzula divaricata</i>	2100	3700	P-G	S-C
Juncaceae	<i>Luzula orestera</i>	2700	3600	P-G	END
Juncaceae	<i>Luzula spicata</i>	2900	3700	P-G	WIDE
Juncaceae	<i>Luzula subcongesta</i>	2000	3500	P-G	S-C
Juncaginaceae	<i>Triglochin palustris</i>	2400	3500	P-G	WIDE
Liliaceae	<i>Calochortus leichtlinii</i>	1300	4000	G	S-C
Melanthiaceae	<i>Veratrum californicum</i> var. <i>californicum</i>	0	3500	G	CORD
Poaceae	<i>Agrostis idahoensis</i>	0	3500	P-G	CORD
Poaceae	<i>Agrostis pallens</i>	200	3500	P-G	CORD
Poaceae	<i>Agrostis scabra</i>	100	3500	P-G	WIDE
Poaceae	<i>Agrostis thurberiana</i>	1300	3500	P-G	CORD
Poaceae	<i>Agrostis variabilis</i>	1600	4000	P-G	CORD
Poaceae	<i>Alopecurus aequalis</i> var. <i>aequalis</i>	50	3500	P-G	WIDE
Poaceae	<i>Bromus carinatus</i> var. <i>carinatus</i>	0	3500	P-G	S-C
Poaceae	<i>Bromus carinatus</i> var. <i>marginatus</i>	0	3500	P-G	S-C
Poaceae	<i>Bromus orcuttianus</i>	560	3500	P-G	S-C
Poaceae	<i>Bromus porteri</i>	550	3500	P-G	CORD
Poaceae	<i>Bromus richardsonii</i>	1200	3600	P-G	CORD
Poaceae	<i>Calamagrostis muiriana</i>	2480	3900	P-G	END
Poaceae	<i>Calamagrostis purpurascens</i>	1300	4000	P-G	WIDE
Poaceae	<i>Deschampsia cespitosa</i> subsp. <i>cespitosa</i>	0	3820	P-G	WIDE
Poaceae	<i>Elymus elymoides</i> subsp. <i>californicus</i>	275	4200	P-G	CORD
Poaceae	<i>Elymus multisetus</i>	0	3800	P-G	CORD
Poaceae	<i>Elymus scribneri</i>	2900	4200	P-G	CORD
Poaceae	<i>Elymus sierrae</i>	1800	3530	P-G	INT
Poaceae	<i>Festuca brachyphylla</i> subsp. <i>breviculmis</i>	2800	4300	P-G	WIDE
Poaceae	<i>Festuca minutiflora</i>	2850	4050	P-G	CORD
Poaceae	<i>Hordeum jubatum</i> var. <i>jubatum</i>	20	3500	P-G	WIDE
Poaceae	<i>Koeleria macrantha</i>	0	3840	P-G	WIDE
Poaceae	<i>Muhlenbergia richardsonis</i>	1220	3670	P-G	CORD
Poaceae	<i>Phleum alpinum</i>	0	3700	P-G	WIDE
Poaceae	<i>Poa abbreviata</i> subsp. <i>pattersonii</i>	3300	3660	P-G	CORD
Poaceae	<i>Poa cusickii</i> subsp. <i>epilis</i>	2400	3600	P-G	CORD
Poaceae	<i>Poa cusickii</i> subsp. <i>purpurascens</i>	2100	3500	P-G	S-C
Poaceae	<i>Poa glauca</i> subsp. <i>rupicola</i>	3300	4100	P-G	CORD
Poaceae	<i>Poa keckii</i>	3300	4340	P-G	END-CAL
Poaceae	<i>Poa lettermanii</i>	3500	4300	P-G	CORD
Poaceae	<i>Poa secunda</i> subsp. <i>secunda</i>	0	3900	P-G	CORD
Poaceae	<i>Poa stebbinsii</i>	2700	3700	P-G	END
Poaceae	<i>Poa wheeleri</i>	1300	3800	P-G	CORD
Poaceae	<i>Stipa hymenoides</i>	60	3500	P-G	CORD
Poaceae	<i>Stipa kingii</i>	2000	3650	P-G	END
Poaceae	<i>Stipa nelsonii</i> subsp. <i>dorei</i>	450	3500	P-G	CORD
Poaceae	<i>Stipa occidentalis</i> subsp. <i>pubescens</i>	1200	3500	P-G	CORD

APPENDIX I. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Poaceae	<i>Stipa pinetorum</i>	2000	3900	P-G	INT
Poaceae	<i>Stipa webberi</i>	1450	3500	P-G	INT
Poaceae	<i>Torreyochloa erecta</i>	2000	3500	P-G	INT
Poaceae	<i>Torreyochloa pallida</i> var. <i>pauciflora</i>	0	3500	P-G	CORD
Poaceae	<i>Trisetum spicatum</i>	1370	3900	P-G	WIDE
Themidaceae	<i>Triteleia dudleyi</i>	1200	3500	G	END-CAL
EUDICOTS					
Adoxaceae	<i>Sambucus racemosa</i> var. <i>melanocarpa</i>	1800	3600	S	CORD
Apiaceae	<i>Cymopterus cinerarius</i>	2100	3500	P	INT
Apiaceae	<i>Oreonana clementis</i>	1500	4000	P	END
Apiaceae	<i>Podistera nevadensis</i>	3000	4000	P	INT
Apiaceae	<i>Sphenosciadium capitellatum</i>	0	3500	P	CORD
Asteraceae	<i>Achillea millefolium</i>	0	3650	P	WIDE
Asteraceae	<i>Ageratina occidentalis</i>	0	3700	P	CORD
Asteraceae	<i>Agoseris aurantiaca</i> var. <i>aurantiaca</i>	1500	3500	P	CORD
Asteraceae	<i>Agoseris monticola</i>	2500	3800	P	S-C
Asteraceae	<i>Antennaria media</i>	1800	3900	P-MAT	CORD
Asteraceae	<i>Antennaria pulchella</i>	2800	3700	P-MAT	INT
Asteraceae	<i>Antennaria rosea</i> subsp. <i>confinis</i>	1200	3700	P	WIDE
Asteraceae	<i>Antennaria rosea</i> subsp. <i>rosea</i>	1200	3700	P-MAT	CORD
Asteraceae	<i>Antennaria umbrinella</i>	1800	3900	P-MAT	WIDE
Asteraceae	<i>Arnica chamissonis</i>	1800	3500	P	WIDE
Asteraceae	<i>Arnica lanceolata</i> subsp. <i>prima</i>	2200	3500	P	CORD
Asteraceae	<i>Arnica longifolia</i>	1300	3500	P	CORD
Asteraceae	<i>Arnica mollis</i>	2500	3500	P	CORD
Asteraceae	<i>Arnica ovata</i>	1800	3600	P	CORD
Asteraceae	<i>Artemisia arbuscula</i> subsp. <i>arbuscula</i>	1500	3800	S	CORD
Asteraceae	<i>Artemisia ludoviciana</i> subsp. <i>incompta</i>	0	3500	P	INT
Asteraceae	<i>Artemisia norvegica</i> subsp. <i>saxatilis</i>	2300	3800	P	WIDE
Asteraceae	<i>Artemisia spiciformis</i>	2100	3700	P	CORD
Asteraceae	<i>Chaenactis alpigena</i>	220	3900	P-MAT	END-CAL
Asteraceae	<i>Chaenactis douglasii</i> var. <i>douglasii</i>	400	3500	P	CORD
Asteraceae	<i>Chrysothamnus viscidiflorus</i> var. <i>viscidiflorus</i>	900	4000	SS	INT
Asteraceae	<i>Cirsium arizonicum</i> var. <i>arizonicum</i>	2300	3500	P	INT
Asteraceae	<i>Cirsium occidentale</i> var. <i>venustum</i>	0	3600	P	INT
Asteraceae	<i>Cirsium scariosum</i> var. <i>americanum</i>	1600	3500	P	CORD
Asteraceae	<i>Crepis nana</i>	2000	4000	P-MAT	CORD
Asteraceae	<i>Ericameria bloomeri</i>	900	4000	SS	INT
Asteraceae	<i>Ericameria discoidea</i>	2300	3800	SS	INT
Asteraceae	<i>Ericameria nauseosa</i> var. <i>speciosa</i>	50	3500	S	INT
Asteraceae	<i>Ericameria parryi</i> var. <i>monocephala</i>	2800	3700	SS	INT
Asteraceae	<i>Ericameria suffruticosa</i>	2100	3800	SS	INT
Asteraceae	<i>Erigeron algidus</i>	2600	3700	P	INT
Asteraceae	<i>Erigeron compositus</i>	2000	4300	P-MAT	WIDE
Asteraceae	<i>Erigeron lonchophyllus</i>	1800	3550	P-A	WIDE
Asteraceae	<i>Erigeron pygmaeus</i>	2900	4100	P-MAT	S-C
Asteraceae	<i>Erigeron vagus</i>	3300	4400	P-MAT	INT

APPENDIX I. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Asteraceae	<i>Eriophyllum lanatum</i> var. <i>integrifolium</i>	1400	3500	P	CORD
Asteraceae	<i>Hazardia whitneyi</i> var. <i>whitneyi</i>	1200	3500	SS	END
Asteraceae	<i>Hieracium nudicaule</i>	1800	3500	P	S-C
Asteraceae	<i>Hieracium triste</i>	1650	3550	P	CORD
Asteraceae	<i>Hulsea algida</i>	3000	4000	P	INT
Asteraceae	<i>Hulsea vestita</i> subsp. <i>pygmaea</i>	3200	3900	P	END-CAL
Asteraceae	<i>Hymenoxys hoopesii</i>	1500	3650	P	CORD
Asteraceae	<i>Oreostemma alpigenum</i> var. <i>andersonii</i>	1200	3500	P	S-C
Asteraceae	<i>Oreostemma peirsonii</i>	3000	3800	P	END
Asteraceae	<i>Orochaenactis thysanocarpha</i>	1600	3800	A	END
Asteraceae	<i>Packera cana</i>	1200	3500	P	S-C
Asteraceae	<i>Packera wernerifolia</i>	3000	3650	P	S-C
Asteraceae	<i>Pyrrcoma apargioides</i>	2200	3800	P	S-C
Asteraceae	<i>Raillardella argentea</i>	1800	3900	P	S-C
Asteraceae	<i>Raillardella scaposa</i>	2000	3500	P	S-C
Asteraceae	<i>Senecio fremontii</i> var. <i>occidentalis</i>	2800	4000	P-MAT	S-C
Asteraceae	<i>Senecio integerrimus</i> var. <i>major</i>	100	3600	P	CORD
Asteraceae	<i>Senecio pattersonensis</i>	3000	3700	P	INT
Asteraceae	<i>Senecio scorzonella</i>	1600	3500	P	S-C
Asteraceae	<i>Senecio spartioides</i>	1000	3500	SS	CORD
Asteraceae	<i>Solidago multiradiata</i>	1250	3950	P	CORD
Asteraceae	<i>Sphaeromeria cana</i>	1800	4000	SS	CORD
Asteraceae	<i>Stenotis acaulis</i>	1800	3600	P-MAT	INT
Asteraceae	<i>Tonestus peirsonii</i>	2900	3700	P	END-CAL
Boraginaceae	<i>Cryptantha circumscissa</i> var. <i>circumscissa</i>	150	3650	A	CORD
Boraginaceae	<i>Cryptantha circumscissa</i> var. <i>rosulata</i>	2950	3650	A	END
Boraginaceae	<i>Cryptantha glomeriflora</i>	1800	3750	A	S-C
Boraginaceae	<i>Cryptantha humilis</i>	1700	3600	P	INT
Boraginaceae	<i>Cryptantha nubigena</i>	2400	3900	P	INT
Boraginaceae	<i>Hackelia micrantha</i>	1200	3500	P	CORD
Boraginaceae	<i>Hackelia sharsmithii</i>	3150	3700	P	INT
Boraginaceae	<i>Nama densum</i>	880	3560	A	INT
Boraginaceae	<i>Phacelia hastata</i> subsp. <i>compacta</i>	1500	4000	A	S-C
Boraginaceae	<i>Phacelia mutabilis</i>	900	3500	P	S-C
Boraginaceae	<i>Phacelia ramosissima</i>	0	3800	P	CORD
Brassicaceae	<i>Anelsonia eurycarpa</i>	1600	4100	P-MAT	S-C
Brassicaceae	<i>Boechea depauperata</i>	3650	3900	P	INT
Brassicaceae	<i>Boechea howellii</i>	1500	3800	P	S-C
Brassicaceae	<i>Boechea inyoensis</i>	1200	3500	P	INT
Brassicaceae	<i>Boechea covillei</i>	2200	3500	P	S-C
Brassicaceae	<i>Boechea inyoensis</i>	1200	3500	P	INT
Brassicaceae	<i>Boechea lemmonii</i>	2000	4350	P	INT
Brassicaceae	<i>Boechea lyallii</i>	2000	3900	P	CORD
Brassicaceae	<i>Boechea paupercula</i>	2500	3700	P	CORD
Brassicaceae	<i>Boechea repanda</i>	1400	3600	P	INT
Brassicaceae	<i>Boechea tiehmii</i>	3000	3600	P	INT
Brassicaceae	<i>Cardamine cordifolia</i>	600	3600	P	CORD
Brassicaceae	<i>Descurainia incana</i>	100	3500	P	CORD
Brassicaceae	<i>Draba albertina</i>	900	3700	P-A	CORD
Brassicaceae	<i>Draba breweri</i>	3100	4100	P	END-CAL
Brassicaceae	<i>Draba cana</i>	0	4100	P	CORD
Brassicaceae	<i>Draba cruciata</i>	2500	3963	P	END
Brassicaceae	<i>Draba densifolia</i>	1900	3650	P-MAT	INT
Brassicaceae	<i>Draba lemmonii</i>	3050	4000	P	END

APPENDIX I. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Brassicaceae	<i>Draba lonchocarpa</i>	2800	4000	P	WIDE
Brassicaceae	<i>Draba longisquamosa</i>	3000	3900	P	END
Brassicaceae	<i>Draba novolympica</i>	1500	3700	P-MAT	CORD
Brassicaceae	<i>Draba oligosperma</i>	2000	3900	P-MAT	CORD
Brassicaceae	<i>Draba praealta</i>	2500	4100	P	WIDE
Brassicaceae	<i>Draba sharsmithii</i>	3300	3800	P	END
Brassicaceae	<i>Draba sierrae</i>	3500	4114	P-MAT	END
Brassicaceae	<i>Draba subumbellata</i>	3300	4100	P-MAT	END-CAL
Brassicaceae	<i>Erysimum capitatum</i> var. <i>capitatum</i>	0	4000	P	WIDE
Brassicaceae	<i>Erysimum perenne</i>	2000	4000	P	S-C
Brassicaceae	<i>Lepidium densiflorum</i>	0	3500	P-A	WIDE
Brassicaceae	<i>Rorippa curvipes</i>	100	3500	P-A	CORD
Brassicaceae	<i>Rorippa curvisiliqua</i>	0	3500	A	CORD
Brassicaceae	<i>Streptanthus gracilis</i>	2600	3600	A	END
Brassicaceae	<i>Streptanthus tortuosus</i>	200	4100	P	S-C
Caryophyllaceae	<i>Cerastium beeringianum</i>	2900	4300	P-MAT	WIDE
Caryophyllaceae	<i>Ereomogone kingii</i> var. <i>glabrescens</i>	2100	4050	P-MAT	S-C
Caryophyllaceae	<i>Minuartia nuttallii</i> var. <i>gracilis</i>	2600	3800	P-MAT	S-C
Caryophyllaceae	<i>Minuartia obtusiloba</i>	3150	3700	P-MAT	CORD
Caryophyllaceae	<i>Minuartia rubella</i>	2400	3800	P	CORD
Caryophyllaceae	<i>Minuartia stricta</i>	3500	3900	P	CORD
Caryophyllaceae	<i>Sagina saginoides</i>	1000	3800	P	WIDE
Caryophyllaceae	<i>Silene bernardina</i>	1350	3600	P	CORD
Caryophyllaceae	<i>Silene sargentii</i>	2400	3800	P	S-C
Caryophyllaceae	<i>Stellaria calycantha</i>	1700	3800	P	WIDE
Chenopodiaceae	<i>Chenopodium atrovirens</i>	300	3500	A	CORD
Chenopodiaceae	<i>Monolepis nuttalliana</i>	0	3700	A	CORD
Crassulaceae	<i>Rhodiola integrifolia</i>	1800	4000	P	WIDE
Crassulaceae	<i>Sedum obtusatum</i> subsp. <i>obtusatum</i>	1200	3700	P	S-C
Ericaceae	<i>Cassiope mertensiana</i>	1800	3505	S	CORD
Ericaceae	<i>Gaultheria humifusa</i>	1350	4000	S	CORD
Ericaceae	<i>Kalmia polifolia</i> subsp. <i>microphylla</i>	1000	3500	S	CORD
Ericaceae	<i>Phyllodoce breweri</i>	1200	3500	S	END-CAL
Ericaceae	<i>Pterospora andromedea</i>	60	3700	P	WIDE
Ericaceae	<i>Rhododendron columbianum</i>	0	3630	S	CORD
Fabaceae	<i>Astragalus kentrophyta</i> var. <i>danaus</i>	2900	4000	P-MAT	END-CAL
Fabaceae	<i>Astragalus kentrophyta</i> var. <i>tegetarius</i>	2700	3600	P	CORD
Fabaceae	<i>Astragalus lentiginosus</i> var. <i>ineptus</i>	1250	3700	P	INT
Fabaceae	<i>Astragalus platytropus</i>	2350	3500	P	INT
Fabaceae	<i>Astragalus purshii</i> var. <i>lectulus</i>	1500	3650	P	INT
Fabaceae	<i>Astragalus whitneyi</i> var. <i>whitneyi</i>	1550	3500	P	S-C
Fabaceae	<i>Lupinus adsurgens</i>	1000	3500	P	S-C
Fabaceae	<i>Lupinus angustiflorus</i>	1000	3500	P	INT
Fabaceae	<i>Lupinus argenteus</i> var. <i>meionanthus</i>	1500	3500	P	INT
Fabaceae	<i>Lupinus argenteus</i> var. <i>montigenus</i>	2500	3500	P	INT
Fabaceae	<i>Lupinus breweri</i> var. <i>breweri</i>	1000	4000	P-MAT	END-CAL
Fabaceae	<i>Lupinus breweri</i> var. <i>bryoides</i>	2500	4000	P-MAT	END-CAL
Fabaceae	<i>Lupinus breweri</i> var. <i>grandiflorus</i>	2000	3500	P-MAT	INT
Fabaceae	<i>Lupinus covillei</i>	2500	3500	P	END
Fabaceae	<i>Lupinus gracilentus</i>	2500	3500	P	END

APPENDIX 1. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Fabaceae	<i>Lupinus latifolius</i> var. <i>columbianus</i>	1000	3500	P	S-C
Fabaceae	<i>Lupinus latifolius</i> var. <i>parishii</i>	0	3500	P	END-CAL
Fabaceae	<i>Lupinus lepidus</i> var. <i>lobbii</i>	2000	3500	P	S-C
Fabaceae	<i>Lupinus lepidus</i> var. <i>ramosus</i>	3000	4000	P	END-CAL
Fabaceae	<i>Lupinus obtusilobus</i>	2500	3500	P	S-C
Fabaceae	<i>Lupinus padre-crowleyi</i>	2500	4000	P-MAT	END-CAL
Fabaceae	<i>Lupinus pratensis</i> var. <i>pratensis</i>	1000	3500	P	END-CAL
Fabaceae	<i>Oxytropis borealis</i> var. <i>australis</i>	3300	3900	P	INT
Fabaceae	<i>Oxytropis borealis</i> var. <i>viscida</i>	3300	3900	P	CORD
Fabaceae	<i>Oxytropis parryi</i>	3100	3800	P-MAT	INT
Fabaceae	<i>Trifolium kingii</i> subsp. <i>dedeckerae</i>	2100	3500	P	END
Fabaceae	<i>Trifolium monanthum</i> subsp. <i>monanthum</i>	1700	3900	P-MAT	INT
Gentianaceae	<i>Comastoma tenellum</i>	3200	3900	A	WIDE
Gentianaceae	<i>Gentiana calycosa</i>	1300	3900	P	CORD
Gentianaceae	<i>Gentiana newberryi</i> var. <i>tiogana</i>	1500	4000	P	S-C
Gentianaceae	<i>Gentianella amarella</i> subsp. <i>acuta</i>	1500	3500	A	WIDE
Gentianaceae	<i>Gentianopsis holopetala</i>	1800	4000	A	S-C
Grossulariaceae	<i>Ribes cereum</i> var. <i>inebrians</i>	2100	3850	S	INT
Grossulariaceae	<i>Ribes montigenum</i>	800	4000	S	CORD
Grossulariaceae	<i>Ribes velutinum</i>	700	3500	S	CORD
Hydrangeaceae	<i>Jamesia americana</i>	2070	3700	S	INT
Lamiaceae	<i>Monardella beneolens</i>	2500	3600	SS	END
Lamiaceae	<i>Monardella linoides</i> subsp. <i>sierrae</i>	1000	3500	SS	INT
Lamiaceae	<i>Monardella odoratissima</i> subsp. <i>glauca</i>	1000	3500	SS	INT
Linaceae	<i>Linum lewisii</i>	400	3657	P	INT
Montiaceae	<i>Calyptidium monospermum</i>	300	3970	P	INT
Montiaceae	<i>Calyptidium roseum</i>	1500	3800	A	CORD
Montiaceae	<i>Calyptidium umbellatum</i>	240	4300	P	CORD
Montiaceae	<i>Claytonia nevadensis</i>	2200	3500	P	S-C
Montiaceae	<i>Lewisia disepala</i>	1300	3500	P	END
Montiaceae	<i>Lewisia glandulosa</i>	3000	4000	P	END-CAL
Montiaceae	<i>Lewisia nevadensis</i>	609	3596	P	S-C
Montiaceae	<i>Lewisia pygmaea</i>	1700	4020	P	CORD
Montiaceae	<i>Lewisia triphylla</i>	1300	3500	P	CORD
Montiaceae	<i>Montia chamissoi</i>	1100	3700	P	S-C
Onagraceae	<i>Epilobium anagallidifolium</i>	1500	4500	P	WIDE
Onagraceae	<i>Epilobium ciliatum</i> subsp. <i>ciliatum</i>	0	4000	P	CORD
Onagraceae	<i>Epilobium ciliatum</i> subsp. <i>glandulosum</i>	0	3500	P	WIDE
Onagraceae	<i>Epilobium clavatum</i>	1200	4200	P	CORD
Onagraceae	<i>Epilobium glaberrimum</i> subsp. <i>fastigiatum</i>	1200	3800	P	CORD
Onagraceae	<i>Epilobium hallianum</i>	100	3700	P	CORD
Onagraceae	<i>Epilobium hornemannii</i> subsp. <i>hornemannii</i>	1200	3900	P	WIDE
Onagraceae	<i>Epilobium obcordatum</i>	1700	4000	P	S-C
Onagraceae	<i>Epilobium oregonense</i>	1200	3500	P	CORD
Onagraceae	<i>Epilobium saximontanum</i>	1400	3500	P	CORD
Onagraceae	<i>Gayophytum decipiens</i>	1800	4200	A	INT
Onagraceae	<i>Gayophytum diffusum</i> subsp. <i>diffusum</i>	800	3700	A	S-C

APPENDIX I. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Onagraceae	<i>Gayophytum diffusum</i> subsp. <i>parviflorum</i>	800	3700	A	INT
Onagraceae	<i>Gayophytum racemosum</i>	1000	4000	A	CORD
Onagraceae	<i>Gayophytum ramosissimum</i>	500	3500	A	INT
Orobanchaceae	<i>Castilleja applegatei</i> subsp. <i>pallida</i>	1900	3600	P	INT
Orobanchaceae	<i>Castilleja applegatei</i> subsp. <i>pinetorum</i>	300	3600	P	INT
Orobanchaceae	<i>Castilleja lemmonii</i>	1550	3700	P	S-C
Orobanchaceae	<i>Castilleja miniata</i> subsp. <i>miniata</i>	1500	3500	P	INT
Orobanchaceae	<i>Castilleja nana</i>	2400	4200	P	END-CAL
Orobanchaceae	<i>Pedicularis atollens</i>	1200	4000	P	S-C
Orobanchaceae	<i>Pedicularis groenlandica</i>	1000	3600	P	S-C
Orobanchaceae	<i>Pedicularis semibarbata</i>	1500	3500	P	S-C
Parnassiaceae	<i>Parnassia palustris</i>	0	3600	P	WIDE
Phrymaceae	<i>Mimulus suksdorfii</i>	1100	4000	A	INT
Plantaginaceae	<i>Callitriche palustris</i>	0	4000	Q	WIDE
Plantaginaceae	<i>Collinsia parviflora</i>	800	3500	A	WIDE
Plantaginaceae	<i>Collinsia torreyi</i> var. <i>wrightii</i>	800	4000	A	INT
Plantaginaceae	<i>Penstemon davidsonii</i>	2000	3750	P-MAT	INT
Plantaginaceae	<i>Penstemon heterodoxus</i> var. <i>heterodoxus</i>	2700	3900	P-MAT	S-C
Plantaginaceae	<i>Penstemon newberryi</i> var. <i>newberryi</i>	1000	3700	P-MAT	INT
Plantaginaceae	<i>Penstemon procerus</i> var. <i>formosus</i>	2100	3600	P-MAT	INT
Plantaginaceae	<i>Penstemon roezlii</i>	300	3500	SS	INT
Plantaginaceae	<i>Penstemon rostriflorus</i>	500	3500	SS	INT
Plantaginaceae	<i>Penstemon rydbergii</i> var. <i>oreocharis</i>	1000	3600	P	INT
Plantaginaceae	<i>Penstemon speciosus</i>	850	3800	P	INT
Plantaginaceae	<i>Veronica wormskjoldii</i>	1500	3500	P	WIDE
Polemoniaceae	<i>Collomia linearis</i>	600	3650	A	WIDE
Polemoniaceae	<i>Gymnosteris parvula</i>	2400	3700	A	CORD
Polemoniaceae	<i>Ipomopsis congesta</i> subsp. <i>montana</i>	1500	3700	P	S-C
Polemoniaceae	<i>Leptosiphon oblanceolatus</i>	2800	3700	A	END
Polemoniaceae	<i>Linanthus pungens</i>	1700	4000	P	CORD
Polemoniaceae	<i>Phlox condensata</i>	2000	4000	P-MAT	CORD
Polemoniaceae	<i>Phlox diffusa</i>	1100	3600	P-MAT	CORD
Polemoniaceae	<i>Phlox dispersa</i>	3600	4200	P-MAT	END
Polemoniaceae	<i>Phlox pulvinata</i>	3300	4300	P-MAT	CORD
Polemoniaceae	<i>Polemonium eximium</i>	3000	4200	P	END
Polemoniaceae	<i>Polemonium pulcherrimum</i> var. <i>pulcherrimum</i>	2400	3700	P	S-C
Polygonaceae	<i>Eriogonum gracilipes</i>	2900	3900	P-MAT	END-CAL
Polygonaceae	<i>Eriogonum incanum</i>	2100	4000	P-MAT	INT
Polygonaceae	<i>Eriogonum lobbii</i>	1600	3800	P-MAT	S-C
Polygonaceae	<i>Eriogonum nudum</i> var. <i>scapigerum</i>	2800	3800	P	END
Polygonaceae	<i>Eriogonum ovalifolium</i> var. <i>caelestinum</i>	3000	3600	P-MAT	END
Polygonaceae	<i>Eriogonum ovalifolium</i> var. <i>nivale</i>	1700	4200	P-MAT	INT
Polygonaceae	<i>Eriogonum polypodium</i>	2800	3500	P-MAT	END
Polygonaceae	<i>Eriogonum rosense</i> var. <i>rosense</i>	2300	4000	P-MAT	INT
Polygonaceae	<i>Eriogonum spergulinum</i> var. <i>pratense</i>	1300	3500	P	END
Polygonaceae	<i>Eriogonum umbellatum</i> var. <i>covillei</i>	3000	3600	P-MAT	END-CAL
Polygonaceae	<i>Eriogonum wrightii</i> var. <i>olanchense</i>	3500	3600	P-MAT	END

APPENDIX 1. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Polygonaceae	<i>Oxyria digyna</i>	1800	4000	P	WIDE
Polygonaceae	<i>Rumex californicus</i>	0	3500	P	CORD
Polygonaceae	<i>Rumex paucifolius</i>	1500	4000	P	S-C
Polygonaceae	<i>Rumex salicifolius</i>	0	3500	P	INT
Polygonaceae	<i>Rumex utahensis</i>	1000	3500	P	CORD
Primulaceae	<i>Androsace septentrionalis</i>	2700	3600	P-A	WIDE
Primulaceae	<i>Dodecatheon redolens</i>	2400	3600	P	INT
Primulaceae	<i>Dodecatheon subalpinum</i>	2100	4000	P	END
Primulaceae	<i>Primula suffrutescens</i>	2000	4200	P	END-CAL
Pteridaceae	<i>Pellaea breweri</i>	1500	3700	P	INT
Ranunculaceae	<i>Aconitum columbianum</i> subsp. <i>columbianum</i>	300	3500	P	CORD
Ranunculaceae	<i>Aquilegia pubescens</i>	2600	3650	P	END
Ranunculaceae	<i>Delphinium polycladon</i>	2200	3600	P	END-CAL
Ranunculaceae	<i>Ranunculus alismifolius</i> var. <i>alismellus</i>	1400	3600	P	S-C
Ranunculaceae	<i>Ranunculus eschscholtzii</i> var. <i>eschscholtzii</i>	2200	3600	P	S-C
Ranunculaceae	<i>Ranunculus eschscholtzii</i> var. <i>oxynotus</i>	2700	4300	P	END-CAL
Ranunculaceae	<i>Ranunculus glaberrimus</i>	1200	3600	P	CORD
Ranunculaceae	<i>Thalictrum alpinum</i>	2900	3700	P	WIDE
Ranunculaceae	<i>Thalictrum sparsiflorum</i>	1400	3500	P	CORD
Rosaceae	<i>Dasiphora fruticosa</i>	2000	3600	S	WIDE
Rosaceae	<i>Drymocaulis lactea</i> var. <i>lactea</i>	1800	3700	P	INT
Rosaceae	<i>Drymocaulis pseudorupestris</i> var. <i>crumiana</i>	3200	3900	P	CORD
Rosaceae	<i>Drymocaulis pseudorupestris</i> var. <i>saxicola</i>	2300	3500	P	CORD
Rosaceae	<i>Holodiscus discolor</i> var. <i>microphyllus</i>	1159	4000	S	CORD
Rosaceae	<i>Ivesia gordonii</i> var. <i>ursinorum</i>	1800	3500	P	INT
Rosaceae	<i>Ivesia lycopodioides</i> subsp. <i>lycopodioides</i>	3000	4000	P	END-CAL
Rosaceae	<i>Ivesia lycopodioides</i> subsp. <i>scandularis</i>	3000	4115	P	END-CAL
Rosaceae	<i>Ivesia muirii</i>	2900	4000	P	END
Rosaceae	<i>Ivesia pygmaea</i>	2700	4000	P	END
Rosaceae	<i>Ivesia santolinoides</i>	1500	3600	P	END-CAL
Rosaceae	<i>Ivesia shockleyi</i>	2700	4000	P-MAT	INT
Rosaceae	<i>Potentilla breweri</i>	1500	3700	P	S-C
Rosaceae	<i>Potentilla flabellifolia</i>	1700	3700	P	S-C
Rosaceae	<i>Potentilla bruceae</i>	1200	3700	P	INT
Rosaceae	<i>Potentilla glaucophylla</i> var. <i>glaucopylla</i>	2600	3500	P	WIDE
Rosaceae	<i>Potentilla gracilis</i> var. <i>fastigiata</i>	800	3500	P	INT
Rosaceae	<i>Potentilla jepsonii</i>	2700	3800	P	INT
Rosaceae	<i>Potentilla pensylvanica</i>	2700	3800	P	WIDE
Rosaceae	<i>Potentilla pseudosericea</i>	3200	4300	P	END-CAL
Rosaceae	<i>Potentilla wheeleri</i>	1800	3500	P	END-CAL
Rosaceae	<i>Sibbaldia procumbens</i>	1820	3700	P	WIDE
Rosaceae	<i>Sorbus californica</i>	1200	4300	S	INT
Rubiaceae	<i>Galium bifolium</i>	1500	3700	A	CORD
Rubiaceae	<i>Galium grayanum</i> var. <i>grayanum</i>	1830	3500	P	S-C
Rubiaceae	<i>Galium hypotrichium</i> subsp. <i>hypotrichium</i>	3000	4200	P	END-CAL
Rubiaceae	<i>Galium hypotrichium</i> subsp. <i>subalpinum</i>	2650	3880	P	END
Salicaceae	<i>Salix brachycarpa</i> var. <i>brachycarpa</i>	3200	3500	S	CORD

APPENDIX 1. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Salicaceae	<i>Salix eastwoodiae</i>	1600	3800	S	CORD
Salicaceae	<i>Salix geyeriana</i>	1450	3600	S	CORD
Salicaceae	<i>Salix lemmonii</i>	1400	3500	S	CORD
Salicaceae	<i>Salix nivalis</i>	3100	3500	S	CORD
Salicaceae	<i>Salix orestera</i>	1100	4000	S	S-C
Salicaceae	<i>Salix petrophila</i>	1670	4000	S	CORD
Salicaceae	<i>Salix planifolia</i>	2500	4000	S	WIDE
Saxifragaceae	<i>Heuchera rubescens</i>	1000	4000	P	CORD
Saxifragaceae	<i>Lithophragma glabrum</i>	0	3750	P	CORD
Saxifragaceae	<i>Micranthes aprica</i>	1600	3600	P	CORD
Saxifragaceae	<i>Micranthes bryophora</i>	1600	3500	P	CORD
Saxifragaceae	<i>Micranthes nidifica</i>	1000	3500	P	CORD
Saxifragaceae	<i>Micranthes tolmiei</i>	1980	3596	P	CORD
Saxifragaceae	<i>Pectiantia breweri</i>	1500	3500	P	S-C
Saxifragaceae	<i>Saxifraga hyperborea</i>	3000	4500	P	WIDE
Valerianaceae	<i>Valeriana californica</i>	1500	3700	P	INT
Violaceae	<i>Viola adunca</i>	0	3570	P	WIDE
Violaceae	<i>Viola bakeri</i>	900	3800	P	INT
Violaceae	<i>Viola macloskeyi</i>	609	3600	P	WIDE
Violaceae	<i>Viola pinetorum</i> subsp. <i>grisea</i>	1981	3700	P	END-CAL
Violaceae	<i>Viola purpurea</i> subsp. <i>mesophyta</i>	1400	3598	P	END-CAL

APPENDIX 2. Annotated checklist of the flora of the Sierra Nevada with an upper elevational limit of 3300–3499 m. Abbreviations as in Appendix 1. Species names follow Baldwin et al. (2012).

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
PTERIDOPHYTA					
Aspleniaceae	<i>Asplenium septentrionale</i>	2500	3350	P	WIDE
Ophioglossaceae	<i>Botrychium lunaria</i>	2300	3400	P	WIDE
Pteridaceae	<i>Adiantum aleuticum</i>	0	3400	P	WIDE
Pteridaceae	<i>Aspidotis densa</i>	100	3400	P	CORD
Pteridaceae	<i>Cryptogramma acrostichoides</i>	1400	3400	P	INT
CONIFERAE					
Pinaceae	<i>Pinus monticola</i>	150	3400	T	S-C
MONOCOTS					
Alliaceae	<i>Allium validum</i>	1200	3400	G	CORD
Cyperaceae	<i>Carex abrupta</i>	1200	3450	P-G	S-C
Cyperaceae	<i>Carex aurea</i>	1100	3300	P-G	WIDE
Cyperaceae	<i>Carex buxbaumii</i>	0	3300	P-G	WIDE
Cyperaceae	<i>Carex davyi</i>	1400	3300	P-G	S-C
Cyperaceae	<i>Carex disperma</i>	1100	3400	P-G	WIDE
Cyperaceae	<i>Carex fissuricola</i>	1500	3300	P-G	CORD
Cyperaceae	<i>Carex fracta</i>	250	3300	P-G	S-C
Cyperaceae	<i>Carex illota</i>	2100	3400	P-G	CORD
Cyperaceae	<i>Carex integra</i>	800	3400	P-G	S-C
Cyperaceae	<i>Carex microptera</i>	1500	3400	P-G	CORD
Cyperaceae	<i>Carex pellita</i>	60	3300	P-G	WIDE
Cyperaceae	<i>Carex petasata</i>	600	3400	P-G	CORD
Cyperaceae	<i>Carex preslii</i>	1800	3400	P-G	CORD
Cyperaceae	<i>Carex simulata</i>	0	3300	P-G	CORD
Cyperaceae	<i>Carex tiogana</i>	3100	3350	P-G	S-C
Cyperaceae	<i>Carex utriculata</i>	0	3400	P-G	WIDE
Cyperaceae	<i>Carex vesicaria</i>	0	3300	P-G	WIDE
Cyperaceae	<i>Carex whitneyi</i>	1200	3400	P-G	S-C

APPENDIX 2. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Cyperaceae	<i>Eleocharis acicularis</i> var. <i>acicularis</i>	0	3300	P-G	WIDE
Cyperaceae	<i>Eleocharis acicularis</i> var. <i>gracilescens</i>	0	3300	P-G	WIDE
Cyperaceae	<i>Eleocharis suksdorfiana</i>	0	3400	P-G	CORD
Cyperaceae	<i>Eriophorum criniger</i>	2000	3350	P-G	S-C
Iridaceae	<i>Iris missouriensis</i>	900	3400	G	CORD
Juncaceae	<i>Juncus hemiendytus</i> var. <i>abjectus</i>	1400	3400	P-G	INT
Juncaceae	<i>Juncus nevadensis</i> subsp. <i>nevadensis</i>	1200	3300	P-G	CORD
Juncaceae	<i>Luzula parviflora</i> var. <i>parviflora</i>	1000	3300	P-G	WIDE
Liliaceae	<i>Lilium kelleyanum</i>	2200	3300	G	END
Orchidaceae	<i>Platanthera dilatata</i> var. <i>leucostachys</i>	0	3400	G	CORD
Orchidaceae	<i>Platanthera sparsiflora</i>	100	3400	G	CORD
Orchidaceae	<i>Spiranthes romanoffiana</i>	0	3300	P	WIDE
Poaceae	<i>Agrostis humilis</i>	1500	3350	P-G	CORD
Poaceae	<i>Bromus suksdorfii</i>	1250	3300	P-G	S-C
Poaceae	<i>Calamagrostis canadensis</i> var. <i>canadensis</i>	1500	3400	P-G	WIDE
Poaceae	<i>Calamagrostis canadensis</i> var. <i>langsdorfii</i>	1500	3400	P-G	WIDE
Poaceae	<i>Calamagrostis stricta</i> subsp. <i>inexpansa</i>	0	3400	P-G	WIDE
Poaceae	<i>Calamagrostis stricta</i> subsp. <i>stricta</i>	1500	3350	P-G	WIDE
Poaceae	<i>Danthonia intermedia</i> var. <i>intermedia</i>	1460	3450	P-G	WIDE
Poaceae	<i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i>	0	3400	P-G	WIDE
Poaceae	<i>Hordeum brachyantherum</i> subsp. <i>brachyantherum</i>	0	3400	P-G	CORD
Poaceae	<i>Hordeum brachyantherum</i> subsp. <i>californicum</i>	0	3400	P-G	END-CAL
Poaceae	<i>Melica bulbosa</i>	0	3400	P-G	CORD
Poaceae	<i>Melica stricta</i>	1200	3350	P-G	INT
Poaceae	<i>Muhlenbergia filiformis</i>	150	3350	A	CORD
Poaceae	<i>Muhlenbergia montana</i>	1640	3420	P-G	WIDE
Poaceae	<i>Stipa nevadensis</i>	1000	3450	P-G	CORD
Poaceae	<i>Stipa occidentalis</i> subsp. <i>californica</i>	150	3450	P-G	CORD
Poaceae	<i>Stipa occidentalis</i> subsp. <i>occidentalis</i>	1200	3450	P-G	CORD
Poaceae	<i>Trisetum wolfii</i>	1740	3300	P-G	CORD
EUDICOTS					
Apiaceae	<i>Angelica lineariloba</i>	1700	3300	P	END-CAL
Apiaceae	<i>Ligusticum grayi</i>	1000	3300	P	CORD
Apiaceae	<i>Lomatium torreyi</i>	1100	3300	P	END
Apiaceae	<i>Perideridia parishii</i> subsp. <i>latifolia</i>	2000	3400	P	S-C
Asteraceae	<i>Agoseris parviflora</i>	1400	3400	P	CORD
Asteraceae	<i>Artemisia cana</i> subsp. <i>bolanderi</i>	1200	3300	S	S-C
Asteraceae	<i>Artemisia dracunculus</i>	0	3400	P	INT
Asteraceae	<i>Chaenactis douglasii</i> var. <i>alpina</i>	3000	3400	P-MAT	CORD
Asteraceae	<i>Crepis acuminata</i>	1000	3300	P	CORD
Asteraceae	<i>Crepis intermedia</i>	800	3300	P	CORD
Asteraceae	<i>Ericameria parryi</i> var. <i>aspera</i>	1900	3300	SS	INT
Asteraceae	<i>Erigeron barbellulatus</i>	2100	3300	P	END-CAL
Asteraceae	<i>Erigeron clokeyi</i> var. <i>pinzliae</i>	2200	3400	P	INT
Asteraceae	<i>Erigeron coulteri</i>	1900	3400	P	CORD
Asteraceae	<i>Erigeron elmeri</i>	1300	3300	P	END
Asteraceae	<i>Erigeron glacialis</i> var. <i>glacialis</i>	1300	3400	P	CORD
Asteraceae	<i>Erigeron tener</i>	2300	3400	P-MAT	CORD
Asteraceae	<i>Helenium bigelovii</i>	0	3400	P	S-C
Asteraceae	<i>Hieracium albiflorum</i>	0	3300	P	WIDE
Asteraceae	<i>Hieracium horridum</i>	1350	3300	P	S-C
Asteraceae	<i>Hulsea vestita</i> subsp. <i>vestita</i>	2400	3350	P	END
Asteraceae	<i>Microseris nutans</i>	1000	3400	P	CORD
Asteraceae	<i>Nothocalais alpestris</i>	1300	3400	P	S-C
Asteraceae	<i>Packera pauciflora</i>	1800	3300	P	WIDE
Asteraceae	<i>Senecio triangularis</i>	100	3300	P	CORD
Asteraceae	<i>Tetradymia canescens</i>	1000	3400	S	CORD
Asteraceae	<i>Tonestus eximius</i>	1800	3300	P	CORD
Asteraceae	<i>Wyethia mollis</i>	900	3400	P	S-C

APPENDIX 2. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Boraginaceae	<i>Cryptantha watsonii</i>	1250	3300	A	CORD
Boraginaceae	<i>Cryptantha confertiflora</i>	1050	3350	P	INT
Boraginaceae	<i>Lappula redowskii</i>	1300	3300	A	WIDE
Boraginaceae	<i>Mertensia ciliata</i>	1310	3380	P	S-C
Boraginaceae	<i>Phacelia bicolor</i>	700	3400	A	INT
Boraginaceae	<i>Phacelia eisenii</i>	1300	3400	A	END
Boraginaceae	<i>Phacelia orogenes</i>	2060	3400	A	END
Boraginaceae	<i>Plagiobothrys hispidulus</i>	1200	3400	A	CORD
Boraginaceae	<i>Plagiobothrys torreyi</i> var. <i>diffusus</i>	1200	3400	A	END-CAL
Brassicaceae	<i>Barbarea orthoceras</i>	0	3400	B/P	WIDE
Brassicaceae	<i>Boechea calderi</i>	2050	3350	P	CORD
Brassicaceae	<i>Boechea davidsonii</i>	1200	3400	P	S-C
Brassicaceae	<i>Boechea pygmaea</i>	2600	3400	P	END
Brassicaceae	<i>Boechea stricta</i>	1800	3400	P	CORD
Brassicaceae	<i>Cardamine oligosperma</i>	50	3300	A/B	CORD
Brassicaceae	<i>Descurainia californica</i>	1700	3400	A/B	CORD
Brassicaceae	<i>Draba asterophora</i>	2600	3300	P	INT
Brassicaceae	<i>Physaria occidentalis</i>	600	3350	P	INT
Caprifoliaceae	<i>Lonicera conjugialis</i>	140	3300	S	S-C
Caprifoliaceae	<i>Symphicarpos rotundifolius</i> var. <i>parishii</i>	1100	3300	S	INT
Caryophyllaceae	<i>Ereomogone congesta</i> var. <i>subfrutescens</i>	1200	3300	P	INT
Ericaceae	<i>Arctostaphylos patula</i>	750	3350	S	CORD
Ericaceae	<i>Arctostaphylos uva-ursi</i>	2400	3300	S	WIDE
Ericaceae	<i>Vaccinium caespitosum</i>	0	3400	S	WIDE
Ericaceae	<i>Vaccinium uliginosum</i> subsp. <i>occidentale</i>	0	3400	S	WIDE
Fabaceae	<i>Astragalus bolanderi</i>	1400	3300	P	INT
Fabaceae	<i>Astragalus ravenii</i>	3400	3450	P	END
Fabaceae	<i>Trifolium monanthum</i> subsp. <i>tenerum</i>	1600	3300	P	END
Fagaceae	<i>Chrysolepis sempervirens</i>	700	3300	S	S-C
Gentianaceae	<i>Frasera puberulenta</i>	1700	3400	P	END-CAL
Gentianaceae	<i>Gentianopsis simplex</i>	1200	3400	P	INT
Grossulariaceae	<i>Ribes inerme</i> var. <i>inerme</i>	1200	3300	S	CORD
Lamiaceae	<i>Monardella breweri</i> subsp. <i>lanceolata</i>	0	3400	A	INT
Montiaceae	<i>Claytonia megarhiza</i>	2600	3300	P	CORD
Montiaceae	<i>Lewisia leana</i>	1300	3350	P	S-C
Onagraceae	<i>Chamerion angustifolium</i> subsp. <i>circumvagum</i>	0	3300	P	WIDE
Orobanchaceae	<i>Castilleja arachnoidea</i>	1300	3300	P	INT
Orobanchaceae	<i>Castilleja linariifolia</i>	1000	3350	P	INT
Orobanchaceae	<i>Castilleja peirsonii</i>	1500	3400	P	S-C
Orobanchaceae	<i>Castilleja pilosa</i>	1200	3400	P	INT
Orobanchaceae	<i>Castilleja praeterita</i>	2200	3400	P	END
Orobanchaceae	<i>Orobanche fasciculata</i>	0	3300	P	WIDE
Papaveraceae	<i>Dicentra uniflora</i>	1000	3300	P	CORD
Phrymaceae	<i>Mimulus breweri</i>	1200	3400	A	CORD
Phrymaceae	<i>Mimulus nanus</i> var. <i>mephiticus</i>	1520	3445	A	S-C
Phrymaceae	<i>Mimulus tilingii</i>	1400	3400	P	CORD
Plantaginaceae	<i>Penstemon caesius</i>	1800	3400	SS	END-CAL
Plantaginaceae	<i>Veronica americana</i>	0	3300	P	WIDE
Polemoniaceae	<i>Ipomopsis aggregata</i> subsp. <i>bridgesii</i>	1800	3300	P	END
Polemoniaceae	<i>Microsteris gracilis</i>	0	3300	A	WIDE
Polemoniaceae	<i>Navarretia breweri</i>	1000	3300	A	CORD
Polemoniaceae	<i>Polemonium occidentale</i> subsp. <i>occidentale</i>	900	3300	P	WIDE
Polygonaceae	<i>Eriogonum latens</i>	2600	3400	P	END-CAL
Polygonaceae	<i>Eriogonum microthecum</i> var. <i>alpinum</i>	2500	3300	SS	END-CAL
Polygonaceae	<i>Eriogonum microthecum</i> var. <i>ambiguum</i>	1100	3300	SS	INT
Polygonaceae	<i>Eriogonum saxatile</i>	800	3400	P-MAT	INT
Polygonaceae	<i>Eriogonum spergulinum</i> var. <i>reddingianum</i>	1300	3400	A	INT
Polygonaceae	<i>Eriogonum wrightii</i> var. <i>subscaposum</i>	200	3400	P-MAT	INT

APPENDIX 2. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Polygonaceae	<i>Polygonum polygaloides</i> subsp. <i>kelloggii</i>	1500	3300	P	CORD
Polygonaceae	<i>Polygonum shastense</i>	2100	3400	P	S-C
Potamogetonaceae	<i>Potamogeton robbinsii</i>	1600	3300	Q	WIDE
Primulaceae	<i>Dodecatheon alpinum</i>	1700	3400	P	CORD
Ranunculaceae	<i>Anemone drummondii</i>	1200	3350	P	S-C
Ranunculaceae	<i>Aquilegia formosa</i>	0	3300	P	S-C
Ranunculaceae	<i>Caltha leptosepala</i> var. <i>biflora</i>	900	3300	P	CORD
Ranunculaceae	<i>Delphinium nuttallianum</i>	300	3300	P	CORD
Rhamnaceae	<i>Ceanothus cordulatus</i>	365	3365	S	INT
Rosaceae	<i>Amelanchier utahensis</i>	200	3400	S	INT
Rosaceae	<i>Fragaria virginiana</i>	1200	3300	P	WIDE
Rosaceae	<i>Geum macrophyllum</i> var. <i>perincisum</i>	1000	3300	P	WIDE
Rosaceae	<i>Horkelia fusca</i> subsp. <i>parviflora</i>	1400	3300	P	CORD
Rosaceae	<i>Ivesia gordonii</i> var. <i>alpicola</i>	2100	3300	P	INT
Rosaceae	<i>Ivesia saxosa</i>	900	3300	P	INT
Rosaceae	<i>Rosa woodsii</i> subsp. <i>gratissima</i>	800	3400	S	INT
Rosaceae	<i>Spiraea splendens</i>	548	3400	S	S-C
Salicaceae	<i>Salix jepsonii</i>	1000	3400	S	S-C
Salicaceae	<i>Salix scouleriana</i>	1	3400	S	CORD
Scrophulariaceae	<i>Limosella acaulis</i>	0	3300	A-Q	WIDE

A NEW SPECIES OF *ASTRAGALUS* (FABACEAE) FROM THE WASATCH MOUNTAINS OF UTAH

BETH LOWE CORBIN

Owyhee Field Office, Bureau of Land Management, 20 First Ave. W, Marsing, ID 83639
ecorbin@blm.gov

ABSTRACT

Astragalus kelseyae B.L. Corbin, sp. nov. is described as a new species from the central Wasatch Mountains, where it is known from only one small occurrence in Weber County, Utah. It grows in shale talus within the Gambel oak and bigtooth maple shrubland.

Key Words: *Astragalus*, Fabaceae, rare plant, Utah, Wasatch Mountains.

A new species of *Astragalus* is described from a single population in the foothills of the Wasatch Mountains in Weber County, Utah. This distinctive milkvetch's fruit shape and texture resemble some forms of *A. lentiginosus* Douglas ex Hooker, but plants differ in having a branching, subterranean caudex, a smaller fruit beak, and generally larger (and fewer) flowers and fruit. Its humistrate growth form and fruit shape resemble *A. amblytropis* Barneby, but it has firmer fruits and larger flowers. Its large pods are similar to *A. megacarpus* (Nutt.) A. Gray, and flowers and leaflets are similar to *A. beckwithii* Torr. & A. Gray, but it differs from both species by having bilocular fruit, shorter leaves, and larger flowers. It differs significantly from each of those species by having dolabriform (malpighian) hairs.

TAXONOMIC TREATMENT

Astragalus kelseyae B.L. Corbin, sp. nov. (Fig. 1)
— Type: USA, Utah, Weber Co., talus slope above Ogden, T6N, R1W, Sec 26, SLM, 41°14'N, 111°55'W, 1625 m (5340 ft) elevation, 28 May 2010, *Beth Lowe Corbin 1292* (holotype: UT; isotypes: NY, CIC, UVSC, to be distributed).

Planta similis *A. lentiginosus* Douglas ex Hooker var. *negundo* S.L. Welsh & N.D. Atwood et *A. amblytropis* Barneby in legumina biloculares et e var. *negundo* in caudices subteranneis elongate et e ambo in legumina cartilagineis nec chartaceis et pubescentiis dolabriformis differt.

Perennial herb from branched, subterranean, woody caudex branches. Above-ground stems 10–20 cm long, prostrate (Fig. 2). Leaves humistrate, 3.0–5.2 cm long, 1.5–3.0 cm wide, with (5) 7–11 (13) leaflets, the terminal jointed. Leaflets widely elliptical, 8–15 mm long, 6–12 mm wide, tips rounded to obtuse, more or less alternate on the rachis. Leaves and stems silvery green with appressed dolabriform hairs about 0.5–0.8 mm long. Stipules free, triangular, 4–5 mm long. Inflorescence 2–7 flowered, congested, not much

elongating in fruit. Peduncle 13–25 mm; flowering axis 5–10 mm. Calyx 13–16 mm long, 3.5–4.5 mm wide, with narrow teeth 3–4 mm long; calyx pinkish, with light and dark hairs. Petals white, with keel tip slightly purple. Banner 22–26 mm long, 9–11 mm wide, bent midway at about a 120° angle. Wings 19–21 mm long, narrow, slightly cupped. Keel 18–19 mm long. Fruit firm, cartilaginous, fleshy, inflated, bilocular, humistrate, sessile, with narrow and shallow dorsal and ventral grooves, not curved, sometimes red mottled. Fresh pod 35–53 mm long, 18–30 mm thick, 10–17 mm tall (dorsiventrally compressed), with a small beak 3–6 mm long, and short, dolabriform hairs. Dehiscence through the beak, after separation.

Paratypes (topotypes): 19 May 2009 *Beth Lowe Corbin 1235* (BRY), 4 September 2011 *Beth Lowe Corbin 1523* (UTC — to be distributed).

DISTRIBUTION AND HABITAT

Astragalus kelseyae grows on the lower, west/southwest-facing slope of the central Wasatch Mountains, on talus openings within *Quercus gambelii* Nutt. (Gambel oak) and *Acer grandidentatum* Nutt. (bigtooth maple) shrublands. The talus consists of fine-textured Ophir shale on about 50–60% slope, at about 1625 m elevation. This habitat is just above the old shoreline of the Pleistocene Lake Bonneville. Precipitation is about 51–64 cm (20–25 inches) per year. The site is within the Uinta-Wasatch-Cache National Forest. *Astragalus kelseyae* is known only from the type locality, where about 150–200 plants were seen in a localized area of about 0.1 ha. It was first found in 2009, and revisited in 2010 and 2011. A popular hiking trail bisects the occurrence, and additional undesig-nated trails occur within the habitat.

The geology of the Wasatch Mountains is a complicated mix of sedimentary, metamorphic (such as quartzite), and igneous deposits (Yonkee and Lowe 2004). Ophir shale is a Paleozoic era

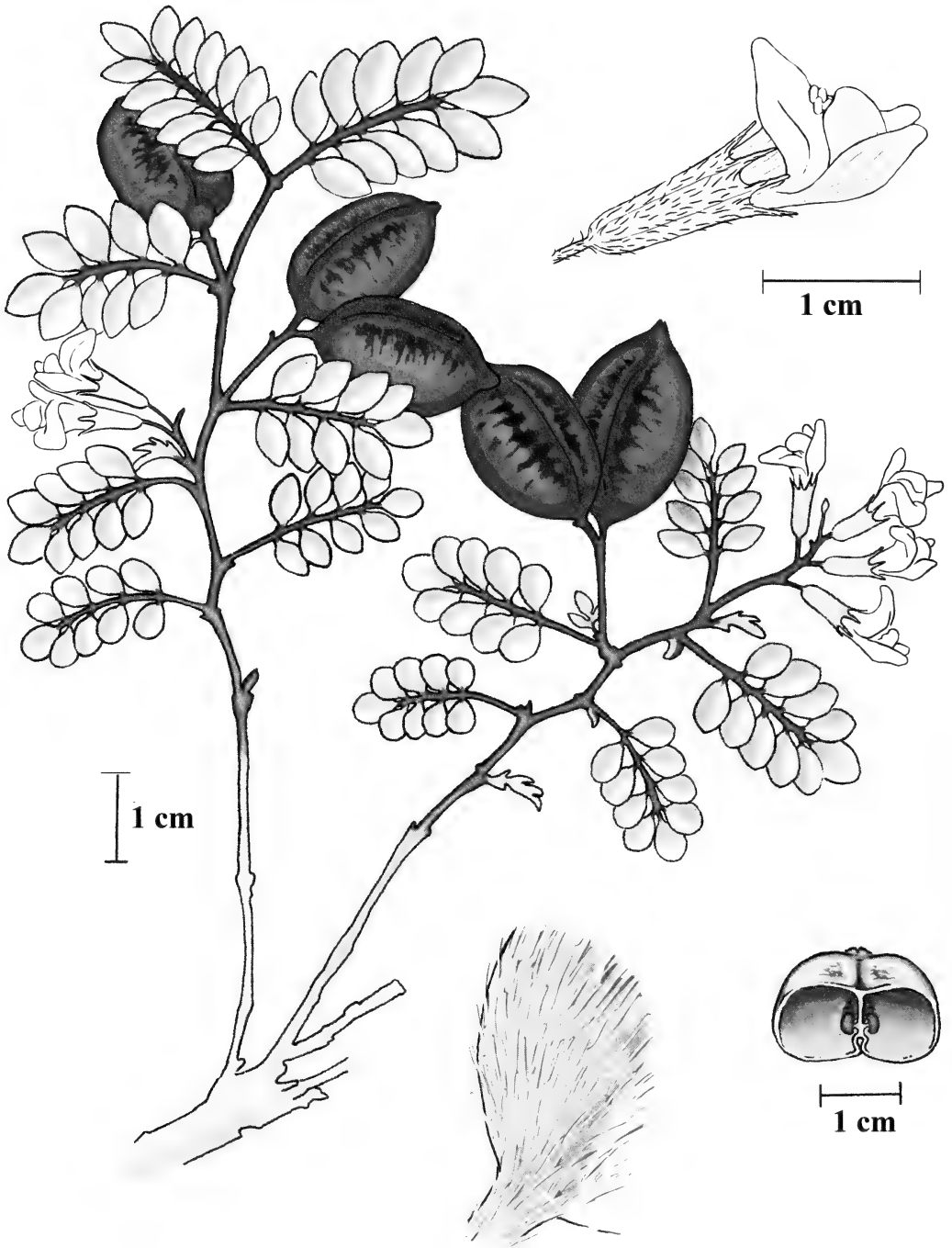


FIG. 1. *Astragalus kelseyae* habit, flower detail, pod cross section, and leaf hair detail.

sedimentary deposit. Bands of Ophir shale and other similar talus types occur in scattered locations across the Wasatch Front, and additional occurrences of *Astragalus kelseyae* may be found in the future.

The talus microsite is very open, with low cover by associates, including *Scutellaria angustifolia*

Pursh subsp. *micrantha* Olmstead, *Asclepias asperula* (Decne.) Woodson, *Apocynum androsaemifolium* L., *Epilobium canum* (Greene) P.H. Raven subsp. *garrettii* (A. Nelson) P.H. Raven, *Hedysarum boreale* Nutt., *Erysimum capitatum* (Douglas) Greene, *Eriogonum umbellatum* Torr., *Pseudoroegneria spicata* (Pursh) Á. Löve, *Ame-*



FIG. 2. *Astragalus kelseyae* in its shale talus habitat.

lanchier utahensis Koehne, and *Phacelia hastata* Douglas ex Lehm. Although no weeds occur directly with the *Astragalus*, several weedy species occur in the vicinity, including *Isatis tinctoria* L., *Linaria dalmatica* (L.) Mill., *Euphorbia myrsinites* L., and *Bromus tectorum* L., and pose a threat to this species.

RELATIONSHIPS

Astragalus kelseyae appears to have similarities to *A. lentiginosus*, *A. amblytropis*, *A. megacarpus*, and *A. beckwithii*, but differs significantly from each (S. Welsh, Brigham Young Univ., personal communication). Its pod resembles *A. lentiginosus* var. *negundo* with a large, bilocular fruit, but differs in having a less prominent beak, generally wider fruit, fewer flowers, a branched, subterranean caudex, and dolabriform hairs. It is similar to *A. amblytropis* in having a subterranean caudex, humistrate stems, leaves, and fruit, and somewhat similar fruit shape, but differs in having firmer pods, larger flowers, free stipules, and dolabriform hairs. It superficially appears similar to *A. megacarpus* or *A. oophorus* S. Watson with its large pods, and *A. beckwithii* with its white flowers, but differs from these species in the section *Megacarpis* by both its

bilocular fruit and dolabriform hairs. Thus, *A. kelseyae* differs from each of these species by the presence of dolabriform hairs, and other characteristics as shown in Table 1. The new species' resemblance to *A. lentiginosus* is likely due to independent parallel evolution, rather than a close relationship; the evolution of a fruit septum (and dolabriform hairs) does not necessarily imply shared ancestry with other species with these characters (J. Alexander, Utah Valley Univ., personal communication). Dolabriform hairs have apparently arisen independently in several sections within genus, but none of the other species with dolabriform hairs have large, bilocular pods, relatively few, large flowers, and prostrate stems. The combination of characteristics present in *A. kelseyae* appears unique.

Astragalus lentiginosus, with its plethora of varieties, is widespread, including Weber Co., Utah; var. *negundo* is known from Box Elder Co. (which is adjacent to the north side of Weber Co.) and Millard and Tooele counties (southwest of Weber Co.), Utah, so its range somewhat overlaps that of *A. kelseyae* (Welsh 2007). *Astragalus amblytropis* is limited to the vicinity of Challis, in Custer and Lemhi counties, Idaho, some 290 miles north of *A. kelseyae* (Welsh 2007). *Astragalus megacarpus* is known from Wyoming

TABLE 1. MORPHOLOGICAL COMPARISON OF *ASTRAGALUS KELSEYAE* AND SIMILAR SPECIES. Measurements (except *A. kelseyae*) come from Barneby 1989, Welsh et al. 2008, and Welsh 2007.

Character	<i>A. kelseyae</i>	<i>A. lentiginosus</i> var. <i>negundo</i>	<i>A. amblytropis</i>	<i>A. megacarpus</i>	<i>A. beckwithii</i>	<i>A. oophorus</i>
Pubescence	dolabriform	basifixed diffuse; 19–32 cm; caudex superficial	basifixed humistrate; 10–40 cm; caudex subterranean	basifixed subcaulescent; <5 cm; caudex superficial	basifixed decumbent to erect; (2) 7–35 (90) cm; caudex superficial	basifixed decumbent to ascending; 10–25 (30) cm; caudex superficial
Stem	cm; caudex subterranean					
Fruit	large, 3.5–5.3 cm long; inflated; firm; bilocular; rounded at base; beak short	smaller, 2.3–3.4 cm long; moderately inflated; stiffly papery; bilocular; rounded at base; beak longer	smaller, 2–3.5 cm long; inflated; papery; bilocular; rounded at base; beak short	large, (3.5) 4–7 (7.5) cm long; inflated; papery; unilocular; rounded at base; beak short	smaller, (1.5) 1.9–3.2 (3.7) cm long; narrower; firm; unilocular; pointed at base; beak longer	large, (2) 3–5.5 cm long; inflated; papery; unilocular; rounded at base; beak short
Flowers	white; banner 22–26 mm; calyx 13–16 mm	whitish (to purple); banner 14–21 mm; calyx 8–12.5 mm	yellowish; banner 6.4–8.3 mm; calyx (2.8) 4–5 mm	pink-purple (to white); banner 16–22 mm; calyx 8.5–14 (16) mm	ochroleucous, whitish, to pink-purple; banner 16.5–21 mm; calyx 7–13.5 mm	white to reddish purple; banner 11–23 mm; calyx 6–12 mm
Inflorescence	2–7 flowered	5–11 flowered	(4) 6–10 (13) flowered	3–5 (8) flowered	(3) 4–10 (14) flowered	(3) 4–10 (14) flowered
Leaves	3–5.2 cm long; (5) 7–11 (13) leaflets; humistrate	(2.5) 4–11 cm long; (7) 13–19 leaflets; spreading	1–3 (4.5) cm long; 9–13 leaflets; humistrate	(2) 5–17 cm long; (7) 9–15 leaflets; stiffly erect	(2) 4–15 cm long; (7) 11–27 leaflets; spreading	(3) 5–15 (21) cm long; 7–25 leaflets; spreading

(at least 50 miles east of this occurrence), central Utah (about 120 miles south), Nevada, and Colorado, while *A. beckwithii* occurs in Weber Co. and generally to the west in Utah, and in Idaho, Nevada, Oregon, Washington, and British Columbia (Albee et al. 1988; Welsh et al. 2008; Shultz et al. 2010; USDA 2010). *Astragalus oophorus* occurs mostly in the southern Great Basin, east into western Colorado, but is also recorded from northwest Utah (Box Elder and Tooele counties) (Welsh et al. 2008; USDA 2010). Thus, the location of *A. kelseyae* is at the east edge of the ranges of *A. lentiginosus* var. *negundo* and *A. beckwithii*, close to the northern edge of the ranges of *A. megacarpus* and *A. oophorus*, and disjunct from *A. amblytropis*.

Astragalus kelseyae is named in honor of Ann Kelsey, plant collection manager for the University of Utah, with whom I've spent many pleasant field days in the mountains and deserts of Utah.

This plant is of conservation concern because only one occurrence with few individuals is known, and because potential threats exist from trails and invasive weeds.

KEY TO SIMILAR SPECIES
(adapted from Barneby 1989 and Welsh 2007)

1. Hairs dolabriform; pods fully bilocular . . . *A. kelseyae*
- 1'. Hairs basifixed; pods unilocular or bilocular
 2. Pods unilocular
 3. Pod 1.5–3.7 cm long, valves leathery. *A. beckwithii*
 - 3'. Pod (2) 3–6 (7.5) cm long, valves papery
 4. Plants subcaulescent, stems 1–5 cm long. *A. megacarpus*
 - 4'. Plants caulescent, stems mostly 5–20 cm long *A. oophorus*
 - 2'. Pods bilocular
 5. Stipules connate; caudex deeply subterranean *A. amblytropis*
 - 5'. Stipules free; caudex superficial (near soil surface) *A. lentiginosus*

ACKNOWLEDGMENTS

I thank Stanley Welsh (Brigham Young University, BRY) for detailed information, the Latin diagnosis, and access to the herbarium. I also thank Stephen Clark (Weber State University, WSCO), Don Mansfield (College of Idaho, CIC), Michael Piep (Utah State University, UTC) and Ann Kelsey (University of Utah, UT) for access to collections. Jason Alexander (Utah Valley University) provided helpful comments and insights. Dan Scott produced the illustration, which was funded by the Intermountain Region of the U.S. Forest Service, thanks to Teresa Prendusi, who also reviewed a draft of this article, as did Don Mansfield. This paper was also improved by reviews from Stanley Welsh and Leila Shultz; however, any mistakes are all mine.

LITERATURE CITED

ALBEE, B. J., L. M. SHULTZ, AND S. GOODRICH. 1988. Atlas of the vascular plants of Utah. Utah Museum of

- Natural History, University of Utah, Salt Lake City, UT.
- BARNEBY, R. C. 1989. Fabaceae. Pp. 12–267 in A. Cronquist, A. H. Holmgren, N. H. Holmgren, J. L. Reveal, and P. K. Holmgren (eds.), Intermountain flora, Vol. 3, pt. B: Fabales. The New York Botanical Garden, Bronx, NY.
- SHULTZ, L. M., R. D. RAMSEY, W. LINDQUIST, AND C. GARRARD. 2010. Digital atlas of the vascular plants of Utah. Utah State University, Logan, UT. Website <http://earth.gis.usu.edu/plants/> [accessed 01 September 2011].
- USDA, NRCS. 2010. The PLANTS Database. National Plant Data Center, Baton Rouge, LA. Website <http://plants.usd.gov> [accessed 01 Oct 2010].
- WELSH, S. L. 2007. North American species of *Astragalus* Linnaeus (Leguminosae): a taxonomic revision. Brigham Young University, Provo, UT.
- , N. D. ATWOOD, S. GOODRICH, AND L. C. HIGGINS. 2008. A Utah flora, fourth edition, revised. Brigham Young University, Provo, UT.
- YONKEE, A. AND M. LOWE. 2004. Geologic map of the Ogden 7.5-minute quadrangle, Weber and Davis Counties, Utah. Utah Geological Survey, Salt Lake City, UT.

**GRIMMIA VAGINULATA, (BRYOPSIDA, GRIMMIACEAE) A NEW SPECIES
FROM THE CENTRAL COAST OF CALIFORNIA**

KENNETH KELLMAN

California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118

kkellman@sbcglobal.net

ABSTRACT

A new California endemic species, *Grimmia vaginulata*, is described and illustrated. It is characterized by its very small size, julaceous habit, immersed capsule on a straight, centrally inserted seta, very large annulus, keeled unistratose leaves, autoicous sexuality, and a large cylindrical ochrea atop the vaginula that sheathes the seta to the base of the capsule. The differentiation and ecology of the new species is discussed.

Key Words: California, endemic moss, *Grimmia vaginulata*, Grimmiaceae, new species, ochrea, vaginula.

In the summer of 2008, prior to the annual meeting of the American Bryological and Lichenological Society, Dale Vitt asked to see *Orthotrichum kellmanii* D. H. Norris, Shevock & Goffinet in the field. During that short trip Dale noticed tiny little plants growing on the same sandstone boulders that supported the *Orthotrichum*. These plants were so scattered and insignificant that they appeared to be immature stems of a small *Grimmia*, and not worth collecting. That impression proved incorrect. Upon microscopic examination, it was immediately obvious that these plants represented a remarkable plant that was unlike any other *Grimmia* in North America.

Chief among the distinguishing characteristics was a transparent extension of the vaginula that extended to the base of the capsule. This extension, known as an ochrea, is not present in any North American *Grimmia*, and it is not mentioned in any North and Central American *Grimmia* literature (Flowers 1973; Crum and Anderson 1981; Crum 1994; Hastings and Greven 2007; Muñoz 1999; Muñoz and Allen 2002). To the casual student of the genus, this novel character suggested the possibility of a new genus. That hypothesis was supported by the scattered growth habit. A wider examination of *Grimmia* was undertaken resulting in the expansion of the North American parameters of the genus.

TAXONOMY

Grimmia vaginulata Kellman, sp. nov. (Figs. 1A, 1C, 2, 3, 4, 5)—Type: USA, California, Santa Cruz Co., Big Basin Redwoods State Park, on dry vertical walls of calcareous sandstone boulders eroded from the sandstone bedrock in open chaparral, above the Basin Trail and below China Grade Road ca. 1.5 mi. beyond

the northern intersection with SR 236, elev. 685 m, 37°12'40"N, 122°12'42"W, 13 Aug 2008. *Kellman, Vitt, & Shevock 5869* (holotype: CAS).

Species *Grimmia capillata* De Notaris affinis, sed differt ab statura brevior, foliis statu madido vel sicco persistenter julaceis, ochrea cylindracea longiore usque ad prope basem capsulae extendenti differt.

Plants up to 2 mm tall, scattered to very loosely tufted (Fig. 5), simple, or with a short, tightly appressed branch; green when young, tan or white in age; julaceous wet or dry. Lower and perigonal leaves short ovate, 1:1, muticous, increasing in length upwards. Upper stem and perichaetial leaves (Fig. 2B) obovate or elliptical, soft when moist, weakly keeled concave, unistratose throughout, with at least some portion of the leaf margin hyaline, most common at the base and often extending to midleaf or slightly beyond; 1–1.65 mm long × 0.4–0.75 mm wide (without the awn); the keel is even less pronounced in transverse section, appearing more convex, even tubular, especially on non-sporophytic plants (Fig. 4); apex acute or occasionally slightly acuminate. Basal juxtacostal cells short rectangular with thin to moderately thick, straight; relatively uniform across the base, but outer basal cells often somewhat narrower in 1 to 3 marginal rows. Distal and medial cells decreasing in length gradually from the base to the apex, 1–1.5(2.5):1, 12–16(26) μm long × 7–13 μm wide; rectangular, triangular, or irregularly polygonal, thick-walled, often with some portion of the lumen rounded creating small trigones, not or weakly sinuose; in transverse section plane to slightly bulging. Margins weakly recurved on one or both sides; unistratose. Costa narrow, to 40 μm wide at the base, broadening toward the apex; excurrent in a hyaline, weakly toothed awn shorter than the lamina, decurrent at most 1–2 cells down the margin, and those often projecting

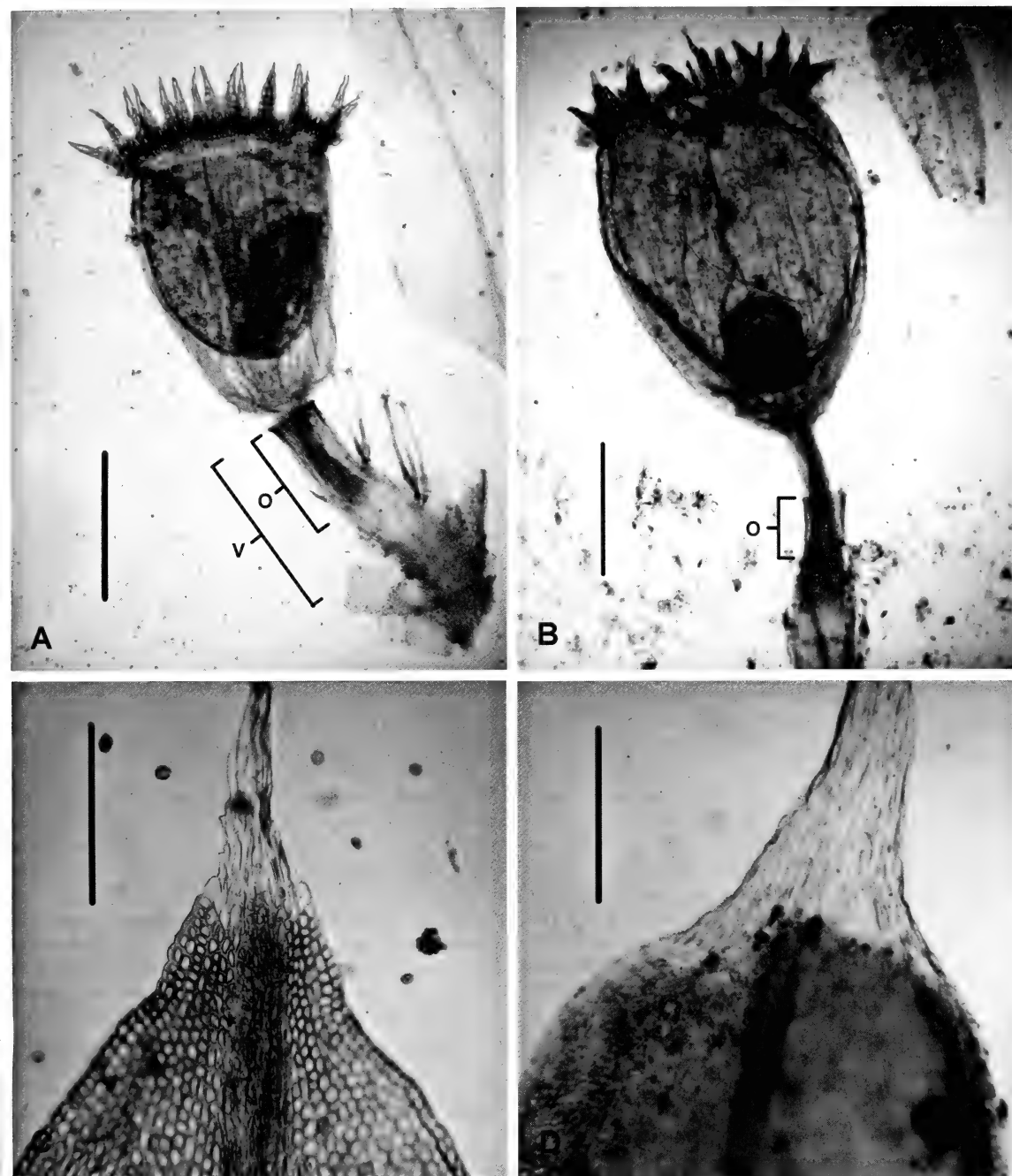


FIG. 1. A. *Grimmia vaginulata* with leaves stripped exposing the sporophyte. (O) ochrea (V) entire vaginula. Scale bar = 500 μ m (from the type); B. *G. capillata* with leaves stripped exposing the sporophyte. (O) ochrea. Scale bar = 500 μ m (Handel-Mazetti 1778, FH: syntype of *G. mesopotamica*); C. Detail of typical upper leaf apex of *G. vaginulata* Scale bar = 80 μ m; D. Detail of typical upper leaf apex of *G. capillata* Scale bar = 175 μ m.

as short, blunt teeth; costa in transverse section at midleaf with two homogenous rows of cells, 2 cells wide adaxially. Gonioautoicous or cladautoicous. Calyptra irregularly crenate at the base, conical or campanulate, hyaline at the extreme apex and at the base, naked and smooth, just covering the operculum. Vaginula (Fig. 1A),

measured with ochrea, 0.5–0.6 mm long, epidermal cells irregular, about 2–3:1, with very thin, straight walls; distally with a cylindrical ochrea surrounding but not connate to the seta and flaring just below the base of the capsule, 340–430 μ m long. Seta straight, attached to the center of the capsule, 0.5 mm long. Capsule immersed

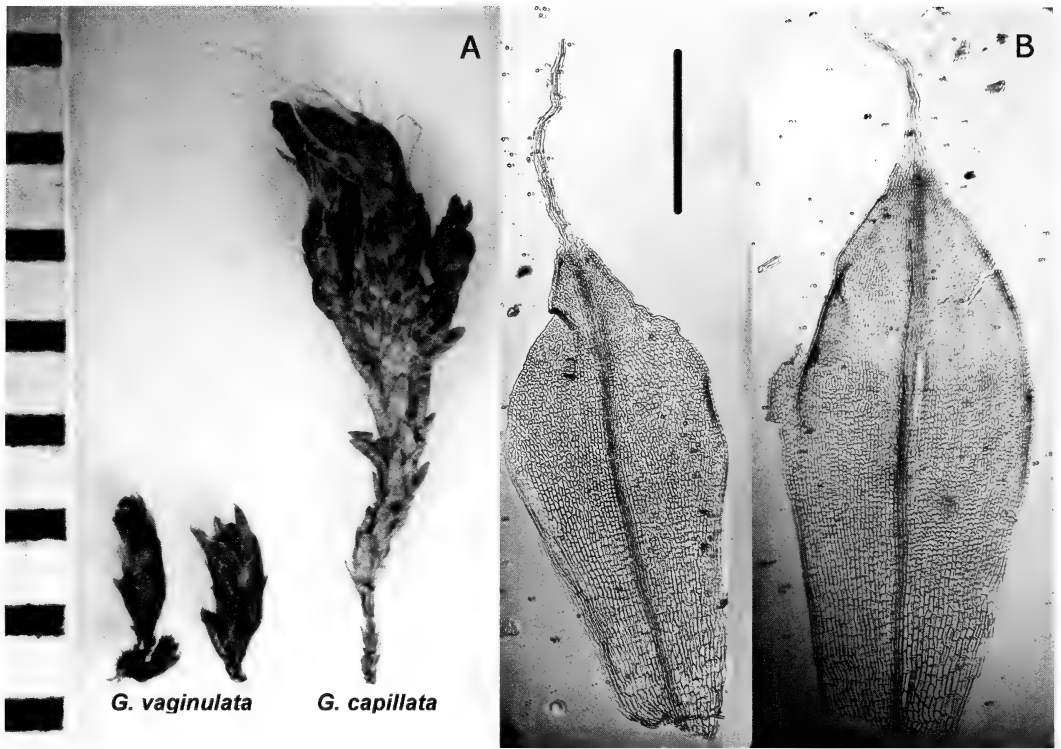


FIG. 2. A. Sporophytic plants of *Grimmia vaginulata* and *G. capillata* showing size difference. Marks are 1 mm apart; B. *G. vaginulata*, two upper and perichaetial leaves. Scale bar = 500 μm .

with only the operculum exposed, irregularly wrinkled when dry, slightly wrinkled when wet, obloid, 0.9 mm long \times 0.6 mm wide, abruptly contracted to the seta. Annulus (Fig. 3) of 3 rows of differentiated, transparent, thick-walled enlarged and elongated cells; remaining on the urn after dehiscence, but gradually falling off in sections. Operculum mammilose to low conical, crenulate to erose at the base. Exothecial cells irregularly rectangular to hexagonal, thin-walled, almost transparent when mature, easily revealing the stalked theca within. Stomata present. Peristome (Fig. 3) of 16 orange-red cribrate-dissected teeth, irregularly divided nearly to the base into 3–4 strongly spiculate filaments, ca. 185 μm long. Spores smooth, 10–13 μm in diameter.

The specific epithet refers to the persistent cylindrical ochrea atop the vaginula, which extends nearly to the base of the capsule.

IDENTIFICATION AND TAXONOMIC RELATIONSHIPS

Grimmia vaginulata can be distinguished from all other North American *Grimmia* by the following combination of characters: very small plants that are julaceous wet or dry, upper leaves with hyaline margins, dissected peristome, and a conspicuous and persistent ochrea sheathing the entire seta to just below the base of the capsule.

Grimmia vaginulata resembles *G. anodon* Bruch & Schimp. and *G. plagiopodia* Hedw. in leaf shape. However, *G. vaginulata* remains julaceous wet or dry, and is a much smaller and narrower plant. The straight, centrally inserted seta of *G. vaginulata* contrasts with the sigmoid, eccentrically inserted seta that characterizes both *G. anodon* and *G. plagiopodia*. The extremely dissected peristome resembles *G. orbicularis* Bruch and *G. moxleyi* R.S. Williams. *Grimmia orbicularis* shares the unistratose margins, and the autoicous sexuality with *G. vaginulata*, but the awns of *G. orbicularis* are evenly distributed along the stem. *Grimmia moxleyi* has awns restricted to the upper leaves like *G. vaginulata*, but the leaf margins are bistratose. Furthermore, both *G. orbicularis* and *G. moxleyi* have exerted capsules on arcuate setae. Again, both are much larger than *G. vaginulata*.

Both gametophytically, and sporophytically, *G. vaginulata* appears most closely related to *G. capillata* De Not., a species scattered around the Mediterranean Sea (Grevén 2003). They share the keeled, entirely unistratose lamina with the margins at least somewhat recurved on one or two sides, a costa that broadens in the distal half of the leaf, perichaetial leaves with proximal hyaline areas, and autoicous sexuality. Sporophytically, the two taxa are very close. Lastly, both prefer calcareous substrates. Again, *G. vaginulata*

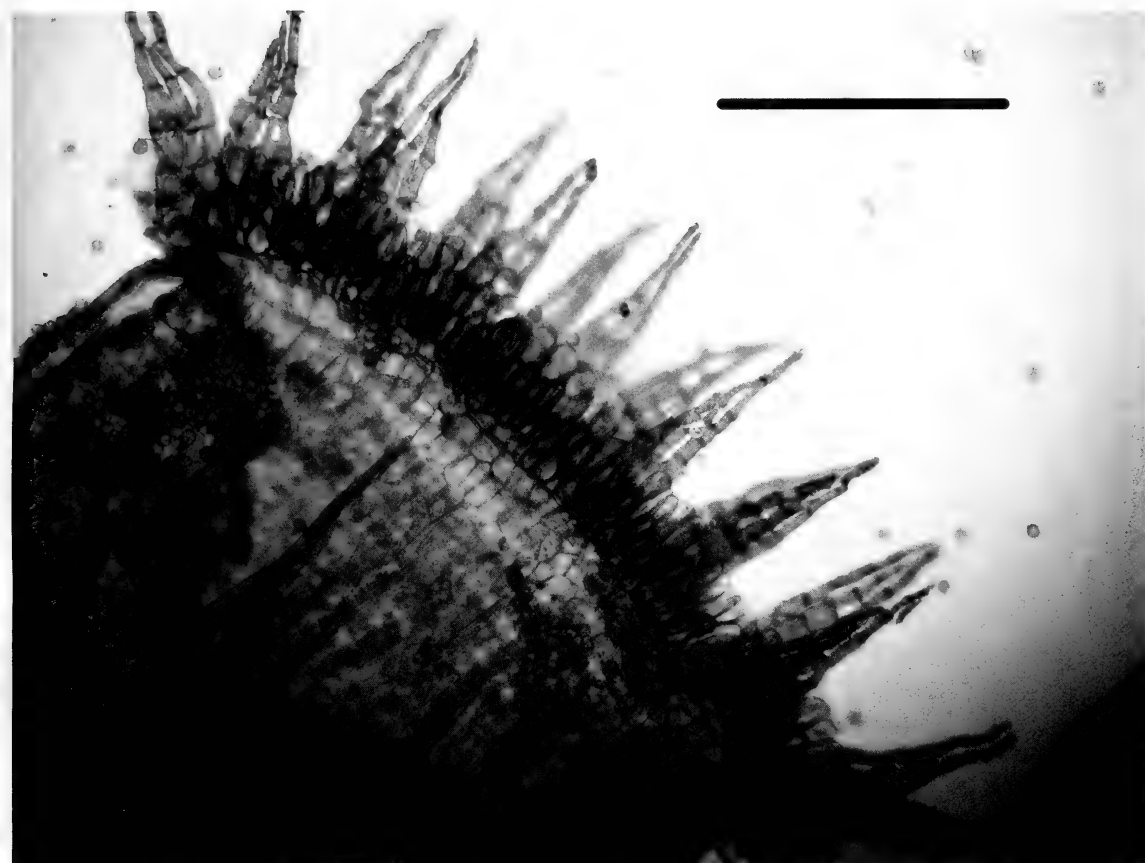


FIG. 3. Detail of annulus and peristome of *Grimmia vaginulata*. Scale bar = 120 μ m.

is a much smaller plant that stays tightly julaceous wet or dry. My examination of 16 specimens of *G. capillata* and *G. mesopotamica* Schiffn. (a synonym of *G. capillata* fide Muñoz and Pando 2000; Greven 2003) from FU, MUB, and NY show plant size in *G. capillata* averages around 7 mm, dwarfing *G. vaginulata*. (Fig. 2A) The dry leaves of *G. capillata* are erect to erect-patent and are usually strongly keeled. Thus the costae project from the rest of the leaves giving the dry plants a more tumid and textured appearance. When moist, the leaves of *G. capillata* are at least erect-patent, and are relatively easy to dissect from the stem. The tiny and tightly appressed leaves of *G. vaginulata* are very difficult to strip for examination without tearing. Leaf size is another point of separation, with the upper stem leaves of *G. capillata* measuring 2–3 mm long (Cortini Pedrotti 2001; Ignatova and Muñoz 2004), while the much smaller *G. vaginulata* has leaves with a maximum length of 1.65 mm. In *G. capillata*, the more or less rounded apex (Fig. 1D) is the most commonly hyaline portion of the leaf, while in *G. vaginulata*, the margins are hyaline, and the apex is acute. There is some small portion at the base of the awn that is hyaline, but at most it is one to two cells down the margin (Fig. 1C).

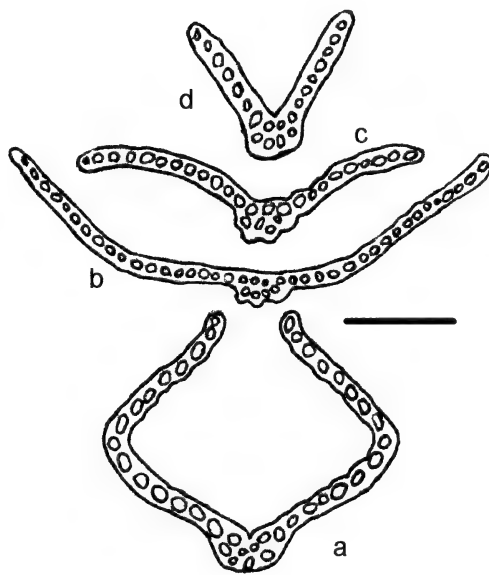


FIG. 4. Drawings of leaf cross sections, *Grimmia vaginulata*; a) leaf from sterile plant taken at midleaf; b, c, d) upper leaf from sporophytic plant. Scale bar = 100 μ m.

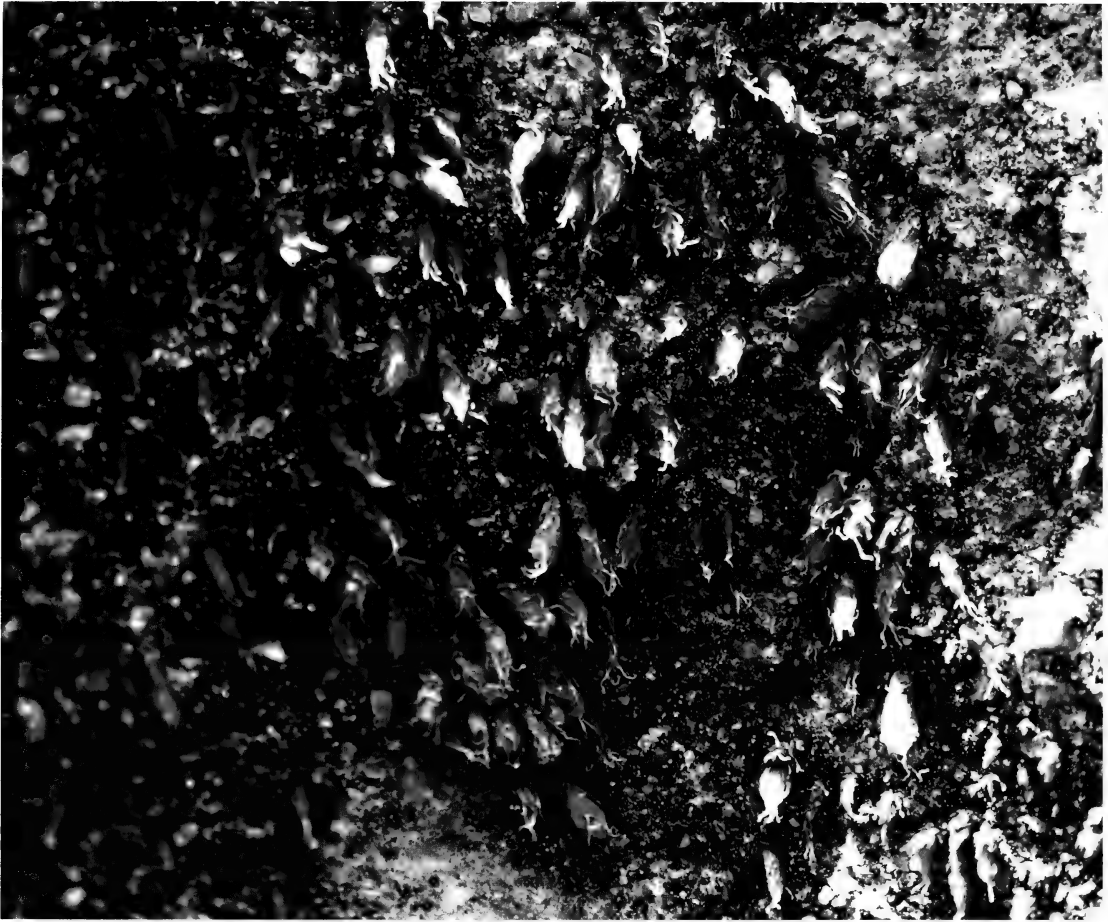


FIG. 5. *Grimmia vaginulata*. Photograph of growth habit on sandstone.

Although evidence is admittedly sparse, with the only known population being the type, the growth habit of *G. vaginulata* adds another basis for separation. In *G. vaginulata*, the plants are at best loosely associated (Fig. 5), not forming a continuous turf or clump. In *G. capillata*, the plants form dense green mats of sterile plants interspersed with a few fertile plants (Cortini Pedrotti 2001; Greven 2003; Heyn and Herrnstadt 2004; Ignatova and Muñoz 2004). The base of the capsule in *G. capillata* is less abruptly contracted to the seta than is seen in *G. vaginulata*. Lastly, in *G. capillata* the ochrea, while pronounced, extends only half way up the seta, not to the base of the capsule as in *G. vaginulata*. (Figs. 1A, B)

Grimmia pseudoanodon Deguchi, described in 1987 from Peru (Deguchi 1987), is another small autoicous plant (ca 5 mm tall) with immersed sporophytes with a centrally attached, straight seta, and like *G. vaginulata*, the base of its capsule is abruptly contracted. Examination of an isotype from NY, showed several important differences from *G. vaginulata*. First, *G. pseudoanodon* grows in cushions, contrasting the scattered habit of *G.*

vaginulata. *G. pseudoanodon* has no peristome, its cauline leaves are not reduced down the stem, being linear to lanceolate and bearing awns to the base of the plant. They are patent to spreading when moist, and are easy to separate from the stem. Similar to *G. capillata*, the apex of the leaf is hyaline for 15–20 cells, and the awn is often decurrent down the margins of the leaf. Most leaves of *G. pseudoanodon* show bistratose margins. The vaginula of *G. pseudoanodon* is extended, demonstrated by the aborted archegonia scattered throughout its length, however, the ochrea is at most represented by a few hyaline flaps at the apex of the vaginula, far from the tube sheathing the seta of *G. vaginulata*. Interestingly, slight pressure expels the seta from the end of the vaginula, leaving a conical stub at the base of the seta.

GENERIC TAXONOMY

It is clear that this new plant belongs in the Grimmiaceae. The only other familial possibility is Ptychomitriaceae, and that is ruled out by the

unlobed calyptra. Within Grimmiaceae, other genera can easily be dismissed as well. The large annulus, and the operculum falling independent of the columnella deny placement in *Schistidium*. Although the cribrose peristome resembles those of both *Coscinodon* and *Jaffuelobryum*, and the autoicous sexuality, unistratose lamina and large annulus further support placement in *Jaffuelobryum*, both genera require a pleated and somewhat sheathing calyptra (Churchill 1987; Hastings 2007; Spence 2007). The calyptra of *G. vaginulata* is so short that it does not even split or tear during capsule development, sitting instead just atop the operculum. *Racomitrium* (*sensu lato*) is ruled out by the lack of sinuosity in the cell walls of the lamina or the vaginula (Deguchi 1978).

Not only can we suggest placement in *Grimmia* by elimination, but the dramatic characters displayed by *G. vaginulata* fit well within the limits of variation of plants already in that genus. Deguchi (1978) describes the "Affinis type" annulus as "well differentiated, composed of (2) 3-4 rows of cells, which are thick walled, but transparent, and becoming increasingly larger from the lower to the upper rows. ... Upper rows of cells of the annulus are also removed when the lid falls, but their lower rows usually remain attached to the orifice of the urn, disjoining little by little in the course of time." This is a perfect description of the annulus in *G. vaginulata*. He attributes this "Affinis type" annulus to "*G. affinis*, *G. anomala*, *G. apiculata*, *G. brachydityon*, *G. curvata*, *G. olympica*, and *G. pilifera*." Muñoz (1999) assigns this annulus type to "*G. involucrata*, *G. longirostris*, *G. poecilostoma*, and *G. trichophylla*" in the introductory section, and 14 other taxa in the species descriptions.

The ochrea is a structure that is poorly understood and has received little taxonomic discussion. Deguchi (1978) makes it clear that the ochrea is only a section of the vaginula, but Magill (1990) defines ochrea as "vaginula, or upper part of vaginula". The haploid vaginula includes cells originating from both the archegonium and the upper part of the stem (Deguchi 1978). Deguchi's proof of this contention is the "occurrence of aborted archegonia at the basal part of the vaginule" (Fig. 1A).

Maier (2002) discusses the vaginula and the ochrea and describes *Grimmia donniana* Sm. ex Spruce with "ochrea broad", with most other species with ochrea "short" or "small". Some species such as *G. orbicularis* (a close relative of the aforementioned *G. moxleyi*) she describes with "vaginula 0.8 mm, with ochrea." Unfortunately, she does not provide illustrations to inform that aspect of her excellent descriptions, nor does she describe how she measures the vaginula. Delgadillo (Universidad Nacional Autónoma de México, personal communication)

wrote "I believe the ochrea is a fairly common feature of the neotropical species of *Grimmia*. It can be demonstrated in *G. americana*, *G. donniana* and *G. elongata*. It is particularly evident in *G. anodon*." But more convincing examples can be found in the persistent ochreae of *G. capillata* and *G. involucrata* Cardot.

Being clear then that this new plant properly belongs in *Grimmia*, it is necessary to at least explore its relationships within the genus. The history of the genus *Grimmia*, *s.l.*, is a tortured and complex story of confused concepts, alternating periods of splitting and lumping, and regional authors describing numerous plants that have been later synonymized in worldwide treatments (Muñoz and Pando 2000; Greven 2003). Deguchi (1978) and Ochyra et al. (2003) both provide a good summary of this nomenclaturally difficult subject. Although Hernández-Maqueda et al. (2008) casts some doubt on *Coscinodon*, most modern authorities agree on the separation of *Jaffuelobryum*, *Schistidium*, and *Coscinodon* from *Grimmia*, but there is disagreement whether *Grimmia* itself requires further subdivision. Ochyra et al. (2003) proposed to split *Grimmia* into five genera, with each genus corresponding in concept with the subgenera reluctantly suggested by Hastings and Greven (2007). Both systems are rooted in the work of Hagen (1909) and are summarized in Table 1.

Grimmia vaginulata can be ruled out of *Gasterogrimmia* based on the straight, centrally attached seta. *Litoneuron* requires 2-stratose, concave leaves with the costa not prominently projecting abaxially; *Grimmia vaginulata* meets none of these criteria. An expanded *Guembelia* that included unistratose leaves would fit all characters of *G. vaginulata*, but if one were to accept the Ochyra et al. (2003) concept of *Dryptodon*, which includes plants with short straight setae and plicate or wrinkled capsules, then *G. vaginulata* would belong there. In fact, Ochyra et al. (2003) places *G. capillata* in *Dryptodon*.

The difficulty is compounded, however, by statements by various authors suggesting that pairs of plants within *Grimmia s.l.* are closely related, but subsequent authors treat each member of the pair in separate subgenera or genera. For example, *G. capillata* is often paired with *G. crinita* Brid. (Greven 2003; Ignatova and Muñoz 2004) and in fact De Notaris (1836, 1838), who first described *G. capillata* in 1836, reduced it to a variety of *G. crinita* in 1838, and Maier (2010) reduced *G. capillata* into synonymy with *G. crinita*. In this pair, *G. crinita* is universally placed in *Gasterogrimmia* (*Grimmia sensu* Ochyra et al. 2003) but as stated above *G. capillata* is placed in *Dryptodon*. These cross subgeneric or generic affinities, as well as the taxa that defy placement within any system, illustrate the

TABLE 1. COMPARISON OF TAXONOMIC TREATMENTS OF *GRIMMIA*.

Hastings and Greven (2007)	Ochyra et al. (2003)	Description
<i>Gasterogrimmia</i>	<i>Grimmia</i>	Capsules immersed, smooth, seta sigmoid and eccentrically attached to the capsule, leaves 1- or 2-stratose that are concave or concave-keeled.
<i>Guembelia</i>	<i>Orthogrimmia</i>	Capsules immersed to exerted, smooth, seta straight and centrally attached to the capsule, leaves mostly 2-stratose and keeled.
<i>Litoneuron</i>	<i>Guembelia</i>	Capsules exerted or emergent, smooth, seta straight and centrally attached to the capsule, leaves 2-stratose that are concave with the costa not prominent dorsally.
<i>Rhabdogrimmia</i>	<i>Dryptodon</i>	Capsules emergent to exerted, ribbed, seta arcuate and centrally attached to the capsule, leaves mostly 1-stratose (2-stratose at the margins) and keeled.

complexity of *Grimmia s.l.* It is likely that this will only be sorted out by a massive study combining worldwide genetic and morphological data.

The very dramatic and persistent ochrea in *G. vaginulata* opens the question of the importance of the ochrea in *Grimmia* taxonomy. Only Maier (2002) and Deguchi (1978) discuss this character. Deguchi briefly mentions the ochrea in his introduction, and then does not use it in his species descriptions. It is ignored in Crum (1994), Muñoz (1999), Cortini Pedrotti (2001), Greven (2003), Ignatova and Muñoz (2004), and Hastings and Greven (2007). Maier (2002) lists *G. donniana* with ochrea "broad", and *G. elatior* with ochrea "distinct". Many other species were described with ochrea "small" or the character was ignored altogether. A quick examination of five specimens in CAS annotated by R. Hastings as *G. donniana* displayed three with no ochrea, one very juvenile capsule with an ochrea already disintegrating, and one specimen with a persistent ochrea about as long as broad at the base of a mature sporophyte. Thus, it seems that this character by itself does not seem to be reliable enough to be useful for separating *G. donniana*, one of the few taxa that Maier thought had a distinctive ochrea; it is likely, therefore, that the character is not useful beyond the *G. capillata-vaginulata* group. Nonetheless, further study of such taxa as *G. involuocrata* may show that the ochrea could be an additional character useful for identification.

ECOLOGY AND DISTRIBUTION

Grimmia vaginulata has thus far only been found on vertical or underhanging surfaces on calcareous sandstone boulders that have eroded out of less calcareous sandstone bedrock of the Butano Formation. These rocks are scattered through a variably dense chaparral comprised of

Adenostoma fasciculatum Hook. & Arn., *Arctostaphylos tomentosa* (Pursh.) Lindl., *Ceanothus cuneatus* (Hook.) Nutt., *C. papillosus* Torr. & A. Gray, and *Eriodictyon californicum* Hook. & Arn.. The climate is Mediterranean with moderate but rainy winters, and hot rainless summers (Kellman 2003). The elevation is slightly below 700 meters, placing the site above all but the thickest summer maritime fog. The lack of summer fog keeps these sites very hot and dry until the winter storms arrive.

One of the more peculiar aspects of this very interesting plant is the substrate. With the exception of one recent collection from marble rock (Kellman, Shevock & Lodder 6133 [CAS]) the boulders are also the sole known substrate of *Orthotrichum kellmanii*, another rare coastal California endemic (Norris et al. 2004). The bedrock was deposited in the Upper Eocene, and is part of the Butano Sandstone Formation (Brabb 1989), but the geologic history of the boulders is not known. Presumably, the rocks were formed and eroded into their rounded shape some time prior to the Eocene deposits that formed the bedrock. In Santa Cruz Co., the Butano Formation is exposed along the western slopes of the highest mountains on the eastern side of the county (Brabb 1989), but the boulders are only present in a small patch in Big Basin Redwoods State Park. There is also a small field of the boulders in southern San Mateo Co., also in Butano State Park. Recently, this same formation with exposed boulders has been found in Monterey Co. within the Ventana Wilderness of the Los Padres National Forest. *Orthotrichum kellmanii* was collected here although much of the area remains to be surveyed. The new population greatly expanded its range to the south. Although access to these sandstone outcrops was difficult due to hiking through

dense stands of chaparral, the area subsequently burned in the summer of 2008. This area is now among the highest priority sites to survey for *G. vaginulata*—and to document the extent of *Orthotrichum kellmanii* in this area.

Associated bryophytes growing on and around the boulders include *Amphidium californicum* (Hampe ex Müll. Hal.) Broth., *Antitrichia californica* Sull. in Lesq., *Gemmabryum californicum* (Sull.) Spence, *Didymodon vinealis* (Brid.) R.H. Zander, *Tortula muralis* Hedw., *Grimmia torenii* Hastings, *G. pulvinata* (Hedw.) J. E. Smith, *Gymnostomum calcareum* Nees & Hornsch., *G. viridulum* Brid., *Orthotrichum kellmanii*, and *Cephaloziella divaricata* (Sm.) Warnst.

CONSERVATION

At the type location, *G. vaginulata* has been found on only four out of several hundred boulders, and these fit within a circle of ten meters. It is imperative that no further collections should be made until more populations are found. Additional surveys need to be conducted throughout the highly restricted habitat within the Butano Formation within State Park Lands and a federally designated wilderness area. Even if additional occurrences are discovered, *Grimmia vaginulata* will almost certainly remain a very narrowly restricted endemic that could be adversely impacted by stochastic events.

Even though the chaparral is a fire adapted ecosystem (Schoenherr 1992), the extreme rarity of *G. vaginulata* leaves open the possibility of fire killing the entire known population. In March of 2009, the author visited the Bonny Doon Ecological Preserve in Santa Cruz Co. Nine months before, in June of 2008, a very hot fire raced through the preserve, where sandstone rocks are scattered through a chaparral very similar to that found at the type location of *G. vaginulata*. Even in places where the brush was minimal, virtually all bryophytes were killed on the rocks, especially those bryophytes growing on the walls and underhanging surfaces of the rocks. A few mosses and liverworts survived on the tops of a few rocks. Apparently the heat of the fire was trapped under the rocks and then bathed the vertical surfaces, killing all plant life. It is conceivable that thick cushions, or gemmiform plants with densely imbricate leaves could insulate at least some part of a dry moss plant from the heat, but the loose colonies and cylindrical plant form of *G. vaginulata* offers no such protection.

To date, *G. vaginulata* is known only from the type and in general, taxonomic novelties should not be based on a single specimen, particularly in variable genera such as *Grimmia*. However, this plant's combination of characters, unique to *Grimmia* in North America, along with the conservation implications of its rarity, demand a

full description. Of course, it is always possible that further collections from new locations could alter the concept of *G. vaginulata*. Of all the characters discussed above, the most likely features to change would be the size and the growth form. It is possible that other populations of *G. vaginulata* could be composed of larger plants. Arguing against that possibility is the fact that both sterile and fruiting plants exhibit the same size and growth form in the type population. It seems more likely that *G. vaginulata* could be found growing in turfs or small cushions. However, turf and cushion formation require the survival of the originating stems. There are no subapical innovations in the type population which suggest that this species may be short lived and that individuals die after sexual reproduction.

ACKNOWLEDGMENTS

I am indebted to Jim Shevock and Dan Norris for teaching me how to do the research necessary to write a paper of this type. They may or may not have been aware that they were teaching me these methods, but an interested student learns as much by observation as by lecture and discussion. I honor their example. I would also like to thank Roxanne Hastings for teaching me the basic understanding of *Grimmia*, and for a thorough review of this paper resulting in many positive changes. I thank Henk Greven for his review of this paper, and the suggestion to compare *Grimmia vaginulata* with *G. pseudoanodon*. David Toren deserves credit for pointing out the illustration of *Grimmia mesopotamica* in the Bryophyte Flora of Israel that put me onto the similarities of *G. vaginulata* and *G. capillata*. Thanks also to Eva Maier, and Claudio Delgadillo, for their insights on the vaginula and ochrea. I also appreciate Claudio Delgadillo and Jesus Muñoz for their helpful comments on an earlier version of this paper. Steve Lodder was invaluable in providing the beautiful photographs. I thank Patricia Eckel for providing the Latin description. I would like to thank the curators of MUB, FH, and NY for the loan of specimens of *Grimmia capillata*, *Grimmia mesopotamica*, and *Grimmia pseudoanodon*, and Deb Trock at CAS who arranged for the loans.

LITERATURE CITED

- BRABB, E. E. 1989. Geologic map of Santa Cruz County, California. Miscellaneous Investigation Series. U.S. Geological Survey, Denver, CO.
- CHURCHILL, S. P. 1987. Systematic and biogeography of *Jaffueliobryum* (Grimmiaceae). *Memoirs of the New York Botanical Garden* 45:691–708.
- CORTINI PEDROTTI, C. 2001. *Flora dei muschi d'Italia: Sphagnopsida, Andreaeopsida, Bryopsida* (1 Parte). Antonio Delfino Editore, Rome, Italy.
- CRUM, H. 1994. *Grimmiales*. 386–415. in A. J. Sharp, H. Crum, and P. M. Eckel (eds.), *The moss flora of Mexico*. *Memoirs of the New York Botanical Garden* 69:1–1113.
- AND L. ANDERSON. 1981. *Mosses of Eastern North America*. Columbia University Press, New York, NY.
- DE NOTARIS, G. 1836. *Memorie della Reale Accademia delle Scienze di Torino* 39:248.

- . 1838. Syllabus Muscorum in Italia et in Insulis Circumstantibus Hucusque Cognitorum, Turin, Italy.
- DEGUCHI, H. 1978. A revision of the genera *Grimmia*, *Schistidium* and *Coscinodon* (Musci) of Japan. Journal of Science of the Hiroshima University Series B, Div. 2 (Botany) 16:121–256.
- . 1987. Studies on some Peruvian species of the *Grimmiaceae*. Pp. 19–74 in H. Inoue (ed.), Studies on cryptogams in Southern Peru. Tokai University Press, Tokyo, Japan.
- FLOWERS, S. 1973. Mosses: Utah and the West. Brigham Young University Press, Provo, UT.
- GREVEN, H. C. 2003. Grimmiids of the world. Bachuys, Leyden, The Netherlands.
- HAGEN, I. 1909. Forarbejder til den Norske løvmosflora. IX. Grimmiaceae. Det Kongelige Norske Videnskabs Selskabs Skrifter 1909(5):1–94.
- HASTINGS, R. I. 2007. *Coscinodon*. Pp. 258–262 in Flora of North America Editorial Committee (eds.), Flora of North America North of Mexico, Vol. 27. Oxford University Press, New York, NY.
- , H. C. GREVEN. 2007. *Grimmia*. Pp. 225–258 in Flora of North America Editorial Committee (eds.), Flora of North America North of Mexico, Vol. 27. Oxford University Press, New York, NY.
- HERNÁNDEZ-MAQUEDA, R., D. QUANDT, O. WERNER, AND J. MUÑOZ. 2008. Phylogeny and classification of the *Grimmiaceae*/*Ptychomitriaceae* complex (*Bryophyta*) inferred from cpDNA. Molecular Phylogenetics and Evolution 46:863–877.
- HEYN, C. C. AND I. HERRNSTADT. 2004. The bryophyte flora of Israel and adjacent regions. The Israel Academy of Sciences and Humanities, Jerusalem, Israel.
- IGNATOVA, E. A. AND J. MUÑOZ. 2004. The genus *Grimmia* in Russia. Arctoa 13:101–182.
- KELLMAN, K. M. 2003. A catalog of the mosses of Santa Cruz County, California. Madroño 50:61–82.
- MAGILL, R. E. 1990. Glossarium Polyglottum Bryologiae, a multilingual glossary for bryology. Missouri Botanical Garden, Saint Louis, MO.
- MAIER, E. 2002. The genus *Grimmia* (Musci, Grimmiaceae) in the Himalaya. Candollea 57:143–238.
- . 2010. The genus *Grimmia* Hedw. (Grimmiaceae, Bryophyta) - a morphological-anatomical study. Boissiera 63:1–377.
- MUÑOZ, J. 1999. A revision of *Grimmia* (Musci, Grimmiaceae) in the Americas. 1: Latin America. Annals of the Missouri Botanical Garden 86:118–191.
- AND F. PANDO. 2000. A world synopsis of the genus *Grimmia* (Musci, Grimmiaceae). Missouri Botanical Garden Press, St. Louis, MO.
- AND B. ALLEN. 2002. *Grimmia*. Pp. 221–231 in B. Allen (ed.), Moss flora of Central America, Part 2. *Encalyptaceae–Orthotrichaceae*. Missouri Botanical Garden Press, Saint Louis, MO.
- NORRIS, D. H., J. R. SHEVOCK, AND B. GOFFINET. 2004. *Orthotrichum kellmanii* (Bryopsida, Orthotrichaceae), a remarkable new species from the central coast of California. The Bryologist 107:209–214.
- OCHYRA, R., J. ŻARNOWIEC, AND H. BEDNAREK-OCHYRA. 2003. Census catalog of Polish mosses. Polish Academy of Sciences, Kraków, Poland.
- SCHOENHERR, A. A. 1992. A natural history of California. University of California Press, Berkeley and Los Angeles, CA.
- SPENCE, J. R. 2007. *Jaffueliobryum*. Pp. 262–264 in Flora of North America Editorial Committee (eds.), Flora of North America North of Mexico, Vol. 27. Oxford University Press, New York, NY.

REVIEW

Introduction to California Chaparral. By RONALD D. QUINN AND STERLING C. KEELEY. 2006. University of California Press, Berkeley, CA. 344 pp. ISBN 9780520219731, \$55.00, hardcover; ISBN 9780520245662, \$21.95, paperback.

In *Introduction to California Chaparral*, authors Ronald D. Quinn and Sterling C. Keeley condense the beauty and diversity of California's most prominent habitat into a beginners guide suitable for curling up with on the couch or toting along on a hike. The diminutive tome attempts to familiarize the casual observer not only with that superficial "bluish-green blanket gently covering the hills," but also with the dynamic interplay of organisms and underlying ecological processes beneath that oft go largely unseen. It is a monumental task to be sure. To accomplish this task, the authors guide us through the climatic forces that shape the system; the dominant plant, animal and insect species that inhabit it; and other forces such as fire, flooding and urban encroachment that affect it. In addition to describing the chaparral world that modern day adventurers might observe, Quinn and Keeley take us briefly through the history of the chaparral to provide a backdrop of the forces that created such diversity.

In distilling such broad and complex subject matter, the authors only stumble in perhaps the most complex of chaparral arenas: wildfire. Dedicating roughly 1/6 of the book specifically to fire and regularly referring to it throughout the rest, the authors succeed in divulging most of the issues surrounding fire in chaparral. However, their attempt at presenting those issues together in a cohesive and coherent whole falls short and proves dangerously misleading. Notwithstanding, the authors bring hundreds of years of scientific discovery, field observation and a love of California's defining ecosystem into an accessible and enjoyable guide for the masses.

This attractive collection consists of 302 pages of text, color photos, black and white diagrams, plus a glossary and reference section for those who wish to dig deeper. All this is printed on thick, sturdy pages that will no doubt survive the jostles of the many hikes it is sure to inspire.

Quinn and Keeley, Professors of biological science and botany, respectively, draw on a wide range of sources and personal research in compiling this guide. They use these sources to paint a colorful mural of wood-rat nests, heat-seeking fire beetles, iridescent hummingbirds and an impressive array of plants that have managed to survive eons of yearly drought and occasional wildfire. The descriptions are presented at an

accessible level of detail for its intended audience. Plant and animal common names are provided in conjunction with their scientific equivalents. Throughout the guide, the particular adaptations that help chaparral plants and animals survive this difficult environment, i.e., the very features that make them uniquely chaparralian, are highlighted. Reference especially is often given to a particular species' relationship to fire. The authors provide not only colorful descriptions but interesting facts that keep even the most hardened urbanite engaged.

Unfortunately, colorful language occasionally gives way to literary excess. The authors too often employ personification, especially with respect to plant characteristics, that can undermine the integrity of the data presented.

An example on the innocuous end of the spectrum involves a species of monkey flower, *Mimulus aurantiacus*. The authors describe the unique stigma that assumes a closed position when pollinated or even just touched by an insect or animal. The authors then claim that in so doing the plants "advertise their status" as pollinated or not, presumably giving pollinators the plant kingdom's equivalent of a wedding ring to would-be suitors. Does a closed stigma make it more likely that pollinators will move to another flower, or is there some other evolutionary incentive for the stigma closing? It's a question the authors don't address, nor is the conclusion supported with cited research. In this case, it's an admittedly harmless conclusion.

The authors' phrasing becomes critically dangerous with regard to fire. The first example comes in the punctuating sentence of the introductory paragraphs to the fire section. It reads: "In short, where there is chaparral, there is fire." While this may technically be true, it is misleading. Where there is chaparral there *is* going to be fire. But where there are grasslands there is fire. Where there are conifer forests there is fire. In other words, the presence of fire in chaparral is not due to something inherent in the plant community. Rather, where there is chaparral there is a Mediterranean climate and where there is a Mediterranean climate (or any other dry climate with enough moisture to sustain vegetative growth) and an ignition source there will be fire, regardless of vegetation type.

The phrase implies that chaparral fosters a fire environment rather than the more accurate paradigm that chaparral species exist because they are able to survive infrequent fires. The result of the authors' approach is a subtle perpetuation of the oft repeated and poorly

applied concept that chaparral needs to burn. As the authors themselves state, certain species do produce seeds that require fire cues to germinate. On the other hand, we know chaparral stands existing for more than a century without fire are perfectly healthy systems and if chaparral stands burn too frequently they can be converted to non-native grasslands. Extrapolating this dichotomy is a tightrope that the authors have difficulty walking.

The most prominent example comes in their "Living with the Chaparral" chapter. In it, the authors describe the merits of prescribed fire and clearing fuel breaks, offering them as effective means to reduce mature chaparral and thus reduce the hazards fire presents to humans. Young chaparral, they suggest, burns less intensely and cuts off the fuel supply, extinguishing fires. Later, not as a counterpoint but as a discrete section, they explain that extreme weather conditions drive fires right through fuel breaks and fuel-age mosaics presumably negating the value of such "barriers".

Further on, the intrinsic watershed value of mature chaparral stands is described in detail. The authors explain that "mature chaparral acts as a sponge" retaining rainfall in the soil and aquifers beneath. Without a mature chaparral and root system, water skims off the soil surface creating disastrous debris flows and leaving no water behind for the ecosystem. That the previously advocated prescribed burning and man-made fuel breaks destroy this important "sponge" mechanism is a conclusion never fully reconciled by the authors.

In truth, land management with respect to wildfire, watershed values, and protecting lives and property is very much a balancing act that few, if any, have yet to master. It is perhaps unfair

then to expect the authors to provide solutions to this dilemma. Rather than offer a cohesive recommendation, the authors drop all the issues in our lap and leave us to sort them out. It is a safe approach. Nevertheless, since this work appears to imply that mature chaparral is a threat to humans rather than the other way around, it will likely draw ire from some ecologists and conservationists. And in that sense it is perplexing to find the text demonizing an ecosystem because it can be inconvenient to humans. While perhaps not packaged in the most ideal manner, the authors at least conclude the wildfire section with a plea for humans to take responsibility for their urban planning practices to avoid further losses.

Muddled fire issues aside, this is an "Introduction to California Chaparral" and in that sense it serves its purpose well. Quinn and Keeley's work is a celebration of a unique and teeming habitat. To the reader unfamiliar with that amorphous blanket of shrubs covering the hillsides outside their car windows, *Introduction to California Chaparral* provides a comprehensive glimpse into that complex habitat. Where the authors particularly shine is in capturing the sheer diversity and dynamic drama found within the often impenetrable chaparral canopy. Were the reader to carry this guide out into the field with them they would likely recognize many more twitters, rustles and floral displays than ever before. Ultimately, creating that connection to the natural environment is the greatest gift any environmental author can bestow upon a reader. In *Introduction to California Chaparral* Quinn and Keeley are likely to succeed in doing so many times over.

—CHRISTOPHER BLAYLOCK, California Chaparral Institute, P.O. Box 545, Escondido, CA 92033; chris@blaylock.org.

NOTEWORTHY COLLECTION

CALIFORNIA

PORPHYRA SUBORBICULATA Kjellman 1897:10–13 (BANGIACEAE).—Marin Co., epizoic on barnacles attached to pilings in the upper intertidal at Nick's Cove, Tomales Bay, 38°11'57.42"N, 122°55'16.40"W, thalli sterile and fertile, 12 May 2011, *J. R. Hughey s.n.* (UC 1966687, UC 1966688) and 20 July 2011, *J. R. Hughey s.n.* (UC 1966689).

Previous knowledge. *Porphyra suborbiculata* is naturally distributed throughout Asia (type locality: Goto-etto, Nagasaki Prefecture, Japan (Silva et al. 1996) and reportedly also occurs naturally in the Indian Ocean, Australia, and New Zealand (Broom et al. 2002). However, based on recent molecular evidence some *P. suborbiculata* from Australia and New Zealand, as well as North America (Mexico and the Atlantic coast of North America) represent introduced populations (Broom et al. 2002; Klein et al. 2003; Neefus et al. 2008). The occurrence of this seaweed in areas associated with increased shipping activity suggest that its numerous introductions were the result of hitchhikers on the hulls of seagoing vessels (Broom et al. 2002). In the eastern Pacific, *P. suborbiculata* was first collected in 1985 from Baja California, Mexico (Aguilar-Rosas and Aguilar-Rosas 2003). Although *P. suborbiculata* shows some variation in morphology, it is generally characterized as being a relatively small (0.5–4 cm in diameter), monostromatic alga, with brownish red to pink, or bronze and violet colored blades that are ovate to cordate or reniform in shape (Broom et al. 2002; Aguilar-Rosas and Aguilar-Rosas 2003; Neefus et al. 2008).

Significance. First report of *P. suborbiculata* in California. The gametophytic thalli collected from Tomales Bay are in agreement with descriptions and illustrations of this species. Specimens from California are cordate at the base, and ovate to deeply reniform in shape. The margins are slightly ruffled and appear dentate to the unaided eye. Under microscopic examination thalli show the diagnostic marginal teeth. The blade color is reddish-brown in spring and steel greenish in summer, and fronds are more or less equal in width and height, measuring to 1.8 cm. Spot checks for this alga at Marshall and Marconi failed to yield additional specimens. Identification of this invasive species was confirmed using *rbcL* (GenBank JN413680) and ITS-1 (GenBank JN413679) DNA sequences. The *rbcL* sequence was identical to two sequences from Japan (Kanagawa, Yokosuka, Sajima and Yamaguchi, Shimomoseki, Tsunoshima) and differed from others in the database by 2 or more bp. The ITS-1 sequence was identical to fifteen other sequences deposited in GenBank representing populations from around the world. Since the *rbcL* sequence generated for *P. suborbiculata* from Tomales Bay matches specimens from Japan and the ITS-1 sequence is identical to other invasive populations of this species from Australia, Baja California, New Zealand, and the western Atlantic, it is concluded that the population from California is also

the result of an introductory event. In Tomales Bay, *P. suborbiculata* joins a list of five other non-native algae: *Caulacanthus ustulatus* (Turner) Kützing, *Codium fragile* subsp. *tomentosoides* (van Goor) P. C. Silva, *Gelidium vagum* Okamura, *Lomentaria hakodatensis* Yendo, and *Sargassum muticum* (Yendo) Fensholt (C. K. Kjeldsen, Sonoma State University, unpublished data; Hughey 1995; Hughey et al. 1996). The mariculture of oysters in Tomales Bay began around 1907 (Barrett 1963), and oysters are the likely vector for the introduction of *P. suborbiculata* in the bay.

—JEFFERY R. HUGHEY, Department of Science and Engineering, Hartnell College, Salinas, CA 93901. jhughey@hartnell.edu.

LITERATURE CITED

- AGUILAR-ROSAS, R. AND L. E. AGUILAR-ROSAS. 2003. El género *Porphyra* (Bangiales, Rhodophyta) en la costa Pacífico de México. I. *Porphyra suborbiculata* Kjellman. *Hidrobiológica* 13:51–56.
- BARRETT, E. M. 1963. Fish Bulletin 123. The California oyster industry. Scripps Institution of Oceanography Library, UC San Diego, San Diego, CA. Website <http://escholarship.org/uc/item/1870g57m> [accessed 10 September 2011].
- BROOM, J. E., W. A. NELSON, C. YARISH, W. A. JONES, R. AGUILAR ROSAS, AND L. E. AGUILAR ROSAS. 2002. A reassessment of the taxonomic status of *Porphyra suborbiculata*, *Porphyra carolinensis* and *Porphyra lilliputiana* (Bangiales, Rhodophyta) based on molecular and morphological data. *European Journal of Phycology* 37:227–235.
- HUGHEY, J. R. 1995. A systematic study of *Chondracanthus* Kützing (Rhodophyceae) with a contribution to the marine flora of Tomales Bay, California. M.A. thesis, Sonoma State University, Rohnert Park, CA.
- , C. K. KJELSDEN, P. C. SILVA, R. L. MOE, AND T. C. DECEW. 1996. Noteworthy Collections. *Madroño* 43:432.
- KLEIN, A. S., A. C. MATHIESON, C. D. NEEFUS, D. F. CAIN, H. A. TAYLOR, B. W. TEASDALE, A. L. WEST, E. J. HEHRE, J. BRODIE, C. YARISH, AND A. L. WALLACE. 2003. Identification of northwestern Atlantic *Porphyra* (Bangiaceae, Bangiales) based on sequence variation in nuclear SSU and plastid *rbcL* genes. *Phycologia* 42:109–122.
- NEEFUS, C. D., A. C. MATHIESON, T. L. BRAY, AND C. YARISH. 2008. The distribution, morphology, and ecology of three introduced Asiatic species of *Porphyra* (Bangiales, Rhodophyta) in the northwestern Atlantic. *Journal of Phycology* 44:1399–1414.
- SILVA, P. C., P. W. BASSON, AND R. L. MOE. 1996. Catalogue of the benthic marine algae of the Indian Ocean. University of California Publications in Botany, Berkeley, CA.

NOTEWORTHY COLLECTION

CALIFORNIA

SEQUIOIA DENDRON GIGANTEUM (Lindl.) J. Buchholz (CUPRESSACEAE) (giant sequoia, big tree, or Sierra redwood).—Riverside Co., northwestern San Jacinto Mts., northeast of HW 243 about 18 highway km NW of Idyllwild, in the southern unit of the San Bernardino National Forest, on the northwestern flank of Black Mt. along both sides adjacent to and well back from the Black Mountain Trail, from upper Hall Canyon, through the sloping plateau or saddle near the westerly ridge, and into the final switchback ascent to the summit (elev. 2369 m). Species seen from 2036 to 2236 m elev. in mixed-conifer forest (Lower Montane Coniferous Forest) on sandy granitic soil; associates include: *Abies concolor*, *Pinus coulteri*, *P. ponderosa* var. *pacific*, and *Quercus chrysolepis* dominant at lower elevations; *P. jeffreyi* and *P. lambertiana* dominant at higher elevations; *Calocedrus decurrens*, *P. flexilis*, and *Ribes nevadense* throughout most of area; 1 May 2009.

Collections (vouchers to be deposited at RSA, UC, and UCR). Tree DBH 65 cm, sterile, just left (as ascending) of trail on slope by large trunk lying across trail, N33 49.540, W116 45.977, 2036 m elev., *R. Schmid & M. Schmid 2009-1*; tree with abundant male cones, right (as ascending) of trail on slope covered with *Pteridium aquilinum* and near drainage (Indian Creek) with *Alnus rhombifolia*, N33 49.579, W116 45.891, 2066.5 m elev., *R. Schmid & M. Schmid 2009-2*; mature seed cones with opened cone scales and dislodged seeds, plus mix of sandy granitic soil and sparse duff, along Black Mountain Trail above drainage (Indian Creek) and below sloping plateau or saddle, ca. 2070 m elev., *R. Schmid & M. Schmid 2009-4*; tree DBH 20 cm, with medium-sized female cones, right (as ascending) side of trail in flat open area, N33 49.607, W116 45.854, 2093 m elev., *R. Schmid & M. Schmid 2009-5*; tree ca. 5.5 m high, with many, very large, immature female cones, just left (as ascending) of trail in flat open area, N33 49.713, W116 45.773; 2144 m elev., *R. Schmid & M. Schmid 2009-6*.

In addition to these collections made on 1 May 2009, we did a GPS census in the vicinity of the Black Mountain Trail, starting in upper Hall Canyon. The census revealed both in the canyon and upslope beyond it at least 157 individuals from 2036 to 2236 m elev. (ca. 0.7 km linear distance, ca. 0.1 km²), plus an outlier sapling 450 m distant at 2361 m elev. near the summit of Black Mt. (2369 m). Our set of plots involved four groups at progressively higher elevations: (1) at the head of Indian Creek in the drainage (including vouchers 2009-1 and 2009-2); (2) on the slope coming out of the drainage (including voucher 2009-4); (3) at the sloping plateau or saddle (including vouchers 2009-5 and 2009-6); (4) on the northwest-facing slope closer to the summit. This species alien to southern California is regenerating prolifically on Black Mt., as revealed by multiple age classes, from seedlings and saplings (juveniles) about 20–60 cm tall to trees over 6 m tall, about 40 years old, and reproductively mature.

Previous knowledge. The monotypic California endemic *Sequoiadendron giganteum* is native to the western slope of the Sierra Nevada, where it occurs in

isolated groves in mixed-conifer forest (Lower Montane Coniferous Forest) between 825 and 2700 m elev. The 67 groves are mostly of very restricted extent and/or threatened. They occur in a narrow strip measuring about 395 km long (northwest-southeast) and 19–21 km at the widest points (east-west) and extending over seven counties from southern Placer Co. southeasterly to southern Tulare Co. (Flint 2002; Willard 2000).

This species has been extensively planted in California as an ornamental, as part of afforestation attempts, and as reforestation efforts, especially post-fire revegetation ones. For example, Burns and Sauer (1992) noted that 22,900 seedlings of *S. giganteum* were planted in southern California in the San Gabriel Mts. alone, but neither this species nor 44 other alien conifer species planted there as part of afforestation projects “are invading adjacent natural habitats” (p. 49). However, Rogers (1986: p. 33) wrote: “On the San Bernardino [National Forest] about 5000 to 10,000 seedlings are planted each year, and at least one instance of natural regeneration from some of the early plantings has been observed.” Rogers’s “one instance” may well be the introduction of *S. giganteum* after the Aug. 1974 fire in Hall Canyon (Keeler-Wolf 1990; Cheng 2004) and its subsequent naturalization on Black Mt., which is the subject of the present preliminary report. Our extensive analysis of the print and Internet literature for the floristics and ecology of southern California suggests *S. giganteum* is possibly also naturalized in the San Gabriel Mts. of Los Angeles Co. and southwestern San Bernardino Co., and in the San Bernardino Mts. of San Bernardino Co.

Significance. First report and collections for Riverside Co. and the San Jacinto Mts. (see the database of the Consortium of California Herbaria, <http://ucjeps.berkeley.edu/consortium>). More importantly, first documented record for naturalization of this Sierra-Nevada endemic species in montane southern California. State and regional floras for California should acknowledge in their keys and descriptions such naturalizations. Details of these findings will be published elsewhere (Schmid and Schmid in press).

—RUDOLF SCHMID, Department of Integrative Biology, University of California, Berkeley, CA 94720-3140; MENA SCHMID, Somerville, MA 02144. schmid@berkeley.edu.

LITERATURE CITED

- BURNS, C. AND J. SAUER. 1992. Resistance by natural vegetation in the San Gabriel Mountains of California to invasion by introduced conifers. *Global Ecology and Biogeography Letters* 2:46–51.
- CHENG, S. (tech. ed). 2004. Forest Service Research Natural Areas in California. General Technical Report PSW-GRT-188. USDA Forest Service, Pacific Southwest Research Station, Albany, CA. Website http://www.fs.fed.us/psw/publications/documents/psw_gtr188/ [accessed 20 June 2011].
- FLINT, W. D. 2002. To find the biggest tree, revised ed. Sequoia Natural History Association, Three Rivers, CA.

- KEELER-WOLF T. 1990. Ecological surveys of Forest Service Research Natural Areas in California. General Technical Report PSW(GTR)-125. USDA Forest Service, Pacific Southwest Research Station, Berkeley, CA. Website http://www.fs.fed.us/psw/publications/documents/psw_gtr125/ [accessed 20 June 2011].
- ROGERS, R. R. 1986. Management of giant sequoia in the national forests of the Sierra Nevada, California. Pp. 32–36 in C. P. Weatherspoon, Y. R. Iwamoto, and D. D. Piirto (tech. coordinators). Proceedings of the workshop on management of giant sequoia, May 24–25, 1985, Reedley, California. General Technical Report PSW(GTR)-95. USDA Forest Service, Pacific Southwest Forest and Range Experimental Station, Berkeley, CA. Website http://www.fs.fed.us/psw/publications/documents/psw_gtr095/ [accessed 20 June 2011].
- SCHMID, R. AND M. SCHMID. In Press. Naturalization of *Sequoiadendron giganteum* (Cupressaceae) in montane southern California. *Aliso* 30.
- WILLARD, D. 2000. A guide to the sequoia groves of California. Yosemite Association, Yosemite National Park, CA.

NOTEWORTHY COLLECTION

COLORADO

DRABA WEBERI R.A. Price & Rollins (BRASSICA-CEAE).—Park Co., Middle Fork of the South Platte, near Magnolia Mill, Pike National Forest, in mossy depressions on north side of granite boulder, 10 plants in flower and fruit, at 39.36112°N, 106.09013°W, 3,398 m elev., 20 July 2010, *Bernadette Kuhn 7927a* and *7927b*, along with Gina Glenne, Sheila Lamb, Alicia Langton, Ellen Mayo, Steve Olson, and Jeff Sprovkin (MO). Dr. Ihsan Al-Shehbaz verified the identification.

Previous knowledge. Global distribution is limited to the type locality in the Monte Cristo Creek drainage, below the Upper Blue Lake Reservoir Dam, on the west side of Continental Divide, Summit County, Colorado. As described in the original publication (Price and Rollins 1991) the holotype (Price #464) was collected from “crevices of rocks beside cascades, amid rocks at edge of stream”. The type locality was described by Price as containing “perhaps 100 individuals”, and in 2009, 81 individuals were reported present at the site (Colorado Natural Heritage Program 2011). All individuals documented are on private land owned and operated by Colorado Springs Utility, though the site is surrounded by National Forest System lands (Decker 2006).

Significance. Second documented occurrence. For twenty years botanists have been searching for another occurrence outside the species’ type locality. Our collection, located 2.8 km to the south, expands the known distribution of *D. weberi* to another county (Park), and to the east side of the Continental Divide. In addition, it confirms the long-suspected presence of *D. weberi* on National Forest System land. This finding, along with the recent addition of *D. weberi* to the

USDA Forest Service Sensitive List, may present new opportunities for the management and conservation of this extremely rare Colorado endemic (USDA Forest Service 2011).

—BERNADETTE KUHN, Colorado Natural Heritage Program, 254 General Services Building, 1474 Campus Delivery, Fort Collins, CO 80523-1474. bernadette.kuhn@colostate.edu.

LITERATURE CITED

- COLORADO NATURAL HERITAGE PROGRAM. 2011. Biodiversity Tracking and Conservation System (BIOTICS). Colorado State University, Fort Collins, CO. Website <http://www.cnhp.colostate.edu/exchange/request.asp> [accessed 01 May 2011].
- DECKER, K. 2006. *Draba weberi* Price & Rollins (Weber’s draba): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region, Golden, CO. Website <http://www.fs.fed.us/r2/projects/scp/assessments/drabaweberi.pdf> [accessed 1 May 2011].
- PRICE, R. A. AND R. C. ROLLINS. 1991. New taxa of *Draba* (Brassicaceae) from California, Nevada, and Colorado. *Harvard Papers in Botany* 3:75–77.
- USDA FOREST SERVICE. 2011. Supplement No. 2600-2011-1. Chapter 2670—Threatened, endangered, and sensitive plants and animals. USFS Forest Service Manual, FSM 2600—Wildlife, Fish, and Sensitive Plant Habitat Management. USDA Forest Service, Rocky Mountain Region (Region 2), Denver, CO. Website http://www.fs.fed.us/im/directives/field/r2/fsm/2600/fsm_r2_2670_2011-1.docx [6 January 2012].

NOTEWORTHY COLLECTION

MEXICO

ANEMONE TUBEROSA Rydb. (RANUNCULACEAE).—Baja California, Municipio of Ensenada, Ejido Nativos del Valle heading W to Santo Tomas, 31.42561°N, 116.34858°W (WGS 84), 434 m/1428 ft, 26 March 2010, *Sula Vanderplank, Sean Lahmeyer, Ben Wilder and Karen Zimmerman* 100326-29 (RSA), Less than 100 plants observed growing with *Zigadenus* sp. on N-facing side of a steep limestone outcrop. Most plants in full flower.

Previous knowledge. The general habitat of this species is given by Dutton et al. (1997), in the Flora of North America, as from rocky slopes and stream sides 800–2500 m. It is known from desert regions of the southwestern USA (CA, NM, NV, TX, UT) and NW Mexico (Baja California, Sonora), and has been well documented within the Sonoran and Mojave deserts: Wiggins (1980) reports it from the western edge of the Colorado Desert and the eastern Mojave Desert; Wilken (1993) gives the range in California as eastern Desert Mountains; 900–1900 m; Munz (1974) reports elevations of 3000–5,000 ft (914–1520 m), in Joshua Tree Woodland and Pinyon-Juniper Woodland, western edge of the Colorado Desert, eastern Mojave Desert. The westernmost known collections for this taxon in California are from the southern Cuyamaca Mtns., near the southwestern end of Poser Mtn, March 19 1995, *Jeri Hirshberg* 253 (RSA) 60 km from the Pacific coast; and the Laguna Mountains, below Desert View, 06 April 1939, *A. J. Stover* 245 (SD), 80 km from the Pacific coast (CCH 2011). In Arizona, Kearney and Pebbles (1951) report elevations of 2,500–5000 ft (760–1520 m). In Mexico, the two Baja California collections closest to the Pacific Ocean are both 50 km inland (30–45 km from the Gulf of California to the east) in the central desert, close to the narrowest part of the peninsula: summit of volcanic hill at top of Jaraguay Grade, 24 Feb 1973, *Reid Moran* 20248 (SD), elev. 875 m, (the lowest documented elevation for this species in the state); Sierra San Borja, summit of Cerro la Chona, 19 Mar 1966, *Reid Moran* 12782 (SD), 1450 m (San Diego Natural History Museum 2011). There are a small number of California specimens from ~400 m elev., all from a small area within the Whipple Mountains, on the border with Arizona (CCH).

Significance. First collection of this species west of the peninsular ranges and inside the California Floristic Province. This collection represents a range extension of ca. 70 km west from the peninsular ranges, and is the most coastal collection documented to date, being just 15 km (9 mi) from the Pacific Ocean. The elevation is the lowest recorded in Baja California, and is near the lowest elevation recorded for the species anywhere. Further investigation of the foothills surrounding this site may help determine if this small population is indeed isolated from the core range, perhaps as a result of the unusual habitat provided by the limestone outcrop.

—SULA VANDERPLANK, Department of Botany & Plant Sciences, University of California, Riverside, CA, 92507; SEAN LAHMEYER, The Huntington Library, Art Collections, and Botanical Gardens, 1151 Oxford Road, San Marino, CA 91108. sula.vanderplank@gmail.com.

LITERATURE CITED

- CONSORTIUM CALIFORNIA HERBARIA (CCH). 2011. University of California, Berkeley, CA, Website <http://ucjeps.berkeley.edu/consortium/> [accessed 3 March 2011].
- DUTTON, B. E., C. S. KEENER AND B. A. FORD. 1997. *Anemone*. Pp. 139–158 in Flora of North America Editorial Committee (eds.), Flora of North America North of Mexico, Vol. 3. Oxford University Press, New York, NY.
- KEARNEY, T. H. AND R. H. PEBBLES. 1951. Arizona flora. University of California Press, Berkeley, CA.
- MUNZ, P. A. 1974. A flora of southern California. University of California Press, Berkeley, CA.
- SAN DIEGO NATURAL HISTORY MUSEUM, 2011. The flora of Baja California. San Diego Natural History Museum, San Diego, CA. Website <http://bajaflora.org/> [accessed 3 March 2011].
- WIGGINS, I. 1980. The flora of Baja California. Stanford University Press, Stanford, CA.
- WILKEN, D. H. 1993. *Anemone*. Pp. 912–913 in J. C. Hickman (ed.), The Jepson manual: higher plants of California. University of California Press, Berkeley, CA.

SUBSCRIPTIONS—MEMBERSHIP

The California Botanical Society has several membership types (individuals \$35 per year; family \$40 per year; emeritus \$27 per year; students \$27 per year for a maximum of 7 years). Late fees may be assessed. Beginning in 2011, rates will increase by \$5 for all membership types except life memberships, for which rates will increase by \$100, and student memberships, which will not show a rate increase. Members of the Society receive *MADROÑO* free. Institutional subscriptions to *MADROÑO* are available (\$70). Membership is based on a calendar year only. Life memberships are \$750. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Membership Chair. Requests and rates for back issues, changes of address, and undelivered copies of *MADROÑO* should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

Submit manuscripts to <http://www.edmgr.com/madrono/>. If you are submitting a manuscript for the first time to the *MADROÑO* PeerTrack website, you must first register by clicking "register now" and following the instructions. Manuscripts by authors having outstanding page charges will not be sent for review.

Manuscripts may be submitted in English or Spanish. English-language manuscripts dealing with taxa or topics of Latin America and Spanish-language manuscripts must have a Spanish RESUMEN and an English ABSTRACT.

For all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.), follow the format used in recent issues for the type of item submitted. Detailed information for contributors, including instructions for manuscript preparation, is available at the California Botanical Society website, www.calbotsoc.org; follow the link for *MADROÑO*. Authors are encouraged to include the names, addresses, and e-mail addresses of two to four potential reviewers with their submitted manuscript.

All California Botanical Society members current in the volume year that their contributions are published are allowed five free pages per volume year. Additional pages will be charged at the rate of \$40 per page. Joint authors may apply all or a portion of their respective five-page allotments to a jointly-published article. Partial pages will be charged as full. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing *MADROÑO* on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for color plates and other complex matter (including illustrations, charts, maps, photographs) will be charged at cost. Author's changes after typesetting @ \$4.50 per line will be charged to authors. Page charges are important in maintaining *Madrono* as a viable publication, and timely payment of charges is appreciated.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01661 0313