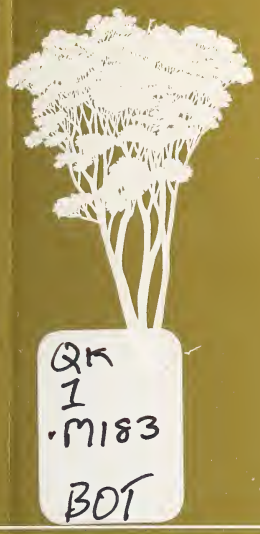

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CENTENNIAL YEAR 1913–2013

POINT OF VIEW

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POINT-OF-VIEW

The California Phenology Project: Tracking Plant Responses to Climate Change

The passing of the seasons is one of the most familiar phenomena on Earth. In California, the appearance of spring wildflowers, farm-fresh produce, and migratory birds and butterflies are welcomed signs of the seasons. Other seasonal hallmarks, however, pose threats to human health and livelihoods, including allergens, crop and vineyard pests, and the high fuel loads that promote wildfires. For better or worse, our health, economies, and resource management practices are intimately connected with seasonal cycles of plants and animals.

The field of science dedicated to studying seasonal biological activities and their responses to environmental variation is phenology. For plants, phenological events and phases (phenophases) comprise every transition in their life cycles, including bud-break, leaf expansion, leaf senescence, flowering, pollen dispersal, the ripening of fruits, and seed dispersal. Long-term observational studies have revealed that for many species the timing and intensity of these phases is sensitive to temperature, precipitation, and/or snowmelt dynamics. This timing inevitably determines an individual's or population's exposure to herbivores, pollinators, seed predators, and fruit dispersers, whose own timing is also sensitive to local environmental conditions. As a result, the timing of seasonal phases—as well as their overlap among interacting species and their responses to climate change—can have strong fitness consequences for individuals, populations, species, and communities, ultimately affecting the diversity and abundance of resources provided by co-occurring plant species. These links between phenology, climate, and climate change are so well known that changes in the phenology of plant and animal species and communities have been identified as a "fingerprint" and key "indicators" of climate change (Parmesan and Yohe 2003; IPCC 2007; EPA 2010).

Recognizing the potential for phenology to provide a rigorous and integrative framework for engaging a wide variety of stakeholders in environmental issues, a consortium of scientists, resource managers, educators, and policy makers have established a continental-scale research, monitoring, and education program focused on phenology. The USA National Phenology Network (USA-NPN), launched in 2007 and operating with major support from the U.S. Geological Survey (USGS), is a collaboration among government agencies, the academic community, non-governmental organizations, and the general public. The USA-NPN harnesses the power of volunteers, researchers, and the internet to collect, to share, and to distribute standardized phenological data through its online observation program, *Nature's Notebook*. These publicly-available data provide baseline information to which future data can be compared, and are currently used to support a variety of contemporary research, education, and management activities.

Leveraging the groundswell of support for the USA-NPN's national framework, the California Phenology Project (CPP) was initiated in 2010 as the first coordinated effort to assess the effects of climate change on California's landscapes (www.usanpn.org/cpp). With funding from the National Park Service Climate Change Response Program (through the Californian Cooperative Ecosystem Studies Unit), the CPP was designed with input from dozens of academic and government scientists and through a collaboration among the National Park Service, the USA-NPN and USGS, and the University of California, Santa Barbara. The primary goals of the CPP are to: 1) recruit, train, and engage scientists, educators, the public, and policy makers in the collection and interpretation of phenological data; 2) detect how phenology is linked to changing climatic conditions over space and time; and 3) collect and analyze data that support stewardship of wildland and managed ecosystems.

The CPP initially formed to develop and test phenological monitoring protocols in California's National Parks in order to inform resource management decisions and to promote climate change interpretation for visitors. A core group of National Park Service resource managers initiated phenological monitoring and education activities in seven pilot parks (www.usanpn.org/cpp/NationalParks; Golden Gate National Recreation Area–Alison Forrestel, Will Elder, and Sue Fritzke; John Muir National Historic Site–Fernando Villalba; Joshua Tree National Park–Josh Hoines; Lassen Volcanic National Park–Janet Coles; Redwood National and State Parks–Stassia Samuels; Santa Monica Mountains National Recreation Area–Christy Brigham; Sequoia and Kings Canyon National Parks–Sylvia Haultain). These efforts provided implementation models and online resources to facilitate monitoring, which are being adapted by additional parks and partners. As a result, the CPP has established a solid foundation of monitoring sites and partnerships throughout the state to support long-term, regionally-coordinated monitoring efforts. The CPP

network has evolved to include the University of California Natural Reserve System (with funding from the UC Office of the President), UC Extension, informal education organizations (e.g., NatureBridge), alternative high school programs (e.g., New Leaf Collaborative), and conservation organizations (e.g., PRBO Conservation Science). The CPP also has offered informational and training sessions at a variety of institutions such as the Desert Institute, botanical gardens, and universities, as well as for members of conservation societies such as the Audubon Society and California Native Plant Society. The CPP is actively seeking organizational and institutional collaborators to lead new and ongoing monitoring efforts. To date, the CPP has:

- developed a scientific framework and research questions to inform long-term and geographically widespread monitoring efforts (www.usanpn.org/cpp/resources);
- led an intensive species selection process, one result of which was the compilation of floras for the University of California Natural Reserve System (Haggerty and Mazer 2011) and California National Parks;
- developed and refined monitoring protocols and resources for 30 widespread, ecologically important plant species in California and coordinated their monitoring across the state;
- conducted >40 half-day to three-day workshops to recruit and train >650 observers, some of whom have delivered subsequent workshops for the staff, volunteers, students, and visitors with whom they engage;
- produced a suite of "phenological literacy" resources with support from USA-NPN and USGS for K–12, college, and public audiences including standards-aligned lesson plans, data analysis activities, guides for phenology gardens and herbarium-based phenology projects, seminar modules, and annotated lectures (www.usanpn.org/cpp/education); and
- contributed >150,000 observation records to the National Phenology Database that is curated by the USA-NPN.

All CPP training, education, outreach, and monitoring resources are available to the public on the CPP website. In addition, documentation of CPP decision-making processes (e.g., scientific framework and species selection) is available on its website so that other regional efforts or national-scale organizations (e.g., National Park Service and National Wildlife Refuge System) can adapt the CPP approach and initiate new networks in coordination with the USA-NPN.

In an effort to increase the value of contemporary phenological data, the CPP also aims to discover and analyze existing historical datasets from which phenological information can be extracted, including unpublished monitoring records; seed collection records; historical photographs repeated at the same location(s) over time; naturalist's journals; and wildflower lists with date and location information. Readers are encouraged to contact the authors with information regarding historical datasets that are available for analysis and digital archiving.

The CPP welcomes new partnerships and opportunities in science, education, and their many applications including resource management and conservation. The interdisciplinary nature of phenological research allows scientists, educators, and students to detect the seasonal rhythms of their local environments using a wide variety of approaches that may be motivated by scientific, cultural, economic, or simply aesthetic interests. With a current network of sites distributed among California's National Parks and UC Natural Reserves, the CPP has developed a foundation upon which graduate students, outdoor educators, classroom instructors, university faculty, and researchers across the biological and physical sciences are invited to build projects and programs. Although the CPP is presently focused on California's flora, the USA-NPN's national framework also includes animal monitoring protocols for terrestrial, coastal, and marine systems, providing potential for the expansion of the CPP scientific framework.

Given that phenological monitoring is easy to conduct and straightforward to teach, the prospective contributions of both professional and citizen scientists to large-scale efforts to track phenological changes are heartening and realistic. The CPP offers an integrative scientific and educational framework for observing and measuring the pace and the timing of the seasons, the onset and duration of which are shifting with the changing climate. Readers are encouraged to explore the California Phenology Project website (www.usanpn.org/cpp) and to contact the authors with queries about getting involved.

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EFFECT OF TRAMPLING ON *AMBROSIA CHAMISSONIS* AND *CAKILE MARITIMA* COVER ON CALIFORNIA BEACHES

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Abstract

California beach plants are capable of dealing with harsh conditions, but little is known about how this community responds to human-induced impacts. The objective of this paper is to determine if beaches experiencing higher degrees of impacts from trampling have more cover of two common plant species thought to grow particularly well under difficult conditions, *Ambrosia chamissonis* (Less.) Greene and *Cakile maritima* Scop. Seventeen sites were sampled between 2007 and 2009 with one meter wide belt transects and the sites were divided into three groups; high (people walk anywhere on the beach), medium (foot traffic is restricted to trails), and low impact levels (little to no access). Cover of all species present were recorded. Cover of *A. chamissonis* is statistically higher on beaches with a high level of impact than low and medium levels. *Cakile maritima* cover is statistically higher on beaches with medium levels than those with low or high levels of impact. However, the total cover of all species is not significantly different between any level of impact.

Key Words: *Ambrosia chamissonis*, *cakile maritima*, cover, fencing, foot-traffic, management, trails, vegetation.

Ambrosia chamissonis (Less.) Greene (Asteraceae; beach-bur) is a California native perennial plant found throughout the state in coastal areas (Hickman 1996) from the high waterline through the dunes, but populations most often peak in the middle section of the beach between the high water line and foredunes (Barbour et al. 1976). *Ambrosia chamissonis* is a maritime-endemic species, endemic to the west coast of North America and restricted to maritime habitats (Breckon and Barbour 1974). It produces 5–10 mm cylindrical burs with ten to twenty or more sharp spines (Hickman 1996; Fig. 1).

Cakile maritima Scop. (Brassicaceae) (Fig. 2) is a European native naturalized in California, introduced in 1935 near San Francisco (Barbour and Rodman 1970). It is an annual found on beaches and dunes along the Pacific coast of North America (Hickman 1996) but has been observed by Boyd and Barbour (1993) to survive two or three reproductive seasons. *Cakile maritima* is found frequently on the leading edge of the vegetation on the beach, but is found throughout the beach with the highest cover of this species in the middle section (Barbour et al. 1976).

Both species are able to tolerate the challenging conditions typical of a beach environment. *Ambrosia chamissonis* is one of the most successful coastal plants at dealing with environmental challenges (Couch 1914). It thrives in the harshest locations on the coast–those with the highest rates of evaporation, unstable soil, high wind velocity, extreme soil temperatures, and intense light (Purer 1936). Capable of rapid growth, it stabilizes flat surfaces and can withstand partial burial (Purer 1936). A long central taproot and adaptations to fluctuations in xylem-sap tension help it survive water stress (DeJong 1979). Barbour and DeJong (1977) found that *A. chamissonis* was less tolerant than expected of high intensity salt spray and salt water inundation, but Fink and Zedler (1990) found *A. chamissonis* to be tolerant of sea spray, sea water over-wash, and sand burial. The distribution of *A. chamissonis* is not influenced by the presence of the invasive European beach grass, *Ammophila arenaria* Link (Poaceae; Boyd 1992).

Cakile maritima has a high tolerance for salt spray and inundation with salt water (Barbour and DeJong 1977). It is able to survive dry periods because of a tolerance for higher xylem-sap tensions and has shallow roots (DeJong 1979). Its cover decreases in areas less than one meter from stands of *A. arenaria* (Boyd 1992).

While many species of plants found on California beaches are adapted to deal with the unique conditions of the natural environment, many seem unable to cope with human-created impacts such as trampling. Schlacher et al. (2007), Schlacher et al. (2008), and Defeo et al. (2009) reviewed the literature related to threats to sandy beaches world-wide. All three indicate that recreation and trampling are a threat to coastal plant communities, but there seems to be very little literature that addresses how recreational activities, such as walking on the beach, affects the plant communities present. No literature on the subject is currently available for California's beaches.

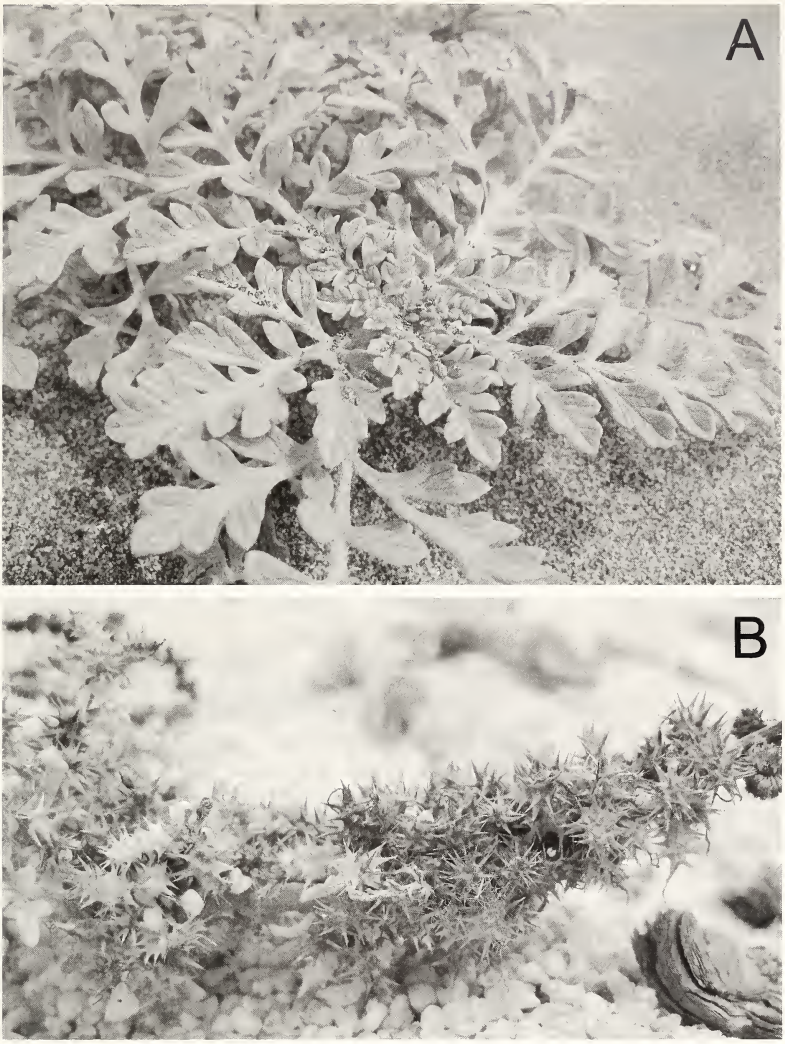

FIG. 1. (A) Foliage of *Ambrosia chamissonis* (B) burs attached to a flower stock in late summer.

Ambrosia chamissonis and *C. maritima* are the only two species of beach plants whose range extends the length of the California coast. Both are known to be capable of dealing with many stresses typical of the beach environment, but how they respond to human foot-traffic is not well understood. Different management strategies, such as fencing or marked trails, applied to beaches available for human recreation may affect the amount and type of plant cover present at a particular location, but no research exists on the topic.

Over the course of three years of data collection, my observations suggest that beaches with less protection from human foot-traffic have more cover of *A. chamissonis* and *C. maritima*, less cover of other species, and have overall less plant cover of all species than those with more protection. The objective of this study is to determine whether beaches with a higher degree of human impact have more *A. chamissonis* and *C. maritima* cover and less cover of other species.

METHODS

Study Area

Data were collected in the summer of 2007 at Leo Carrillo State Park, Point Mugu State Park, Point Mugu Naval Air Weapons Station, McGrath State Beach, San Buenaventura State Beach, and Ormond Beach. The following summer, 2008, data were collected at Pacifica State Beach, Pescadero State Beach, MacKerricher State Park, and Redwoods National Park. In 2009, data were collected at Carmel River State Beach, Zmudowski State Beach, Salinas River State Beach, Coal Oil Point Reserve, Pismo State Beach, Montaña de Oro State Park, and Morro Strand State Beach, for a total of 17 sites (Fig. 3). For all

FIG. 2. Foliage of *Cakile maritima*.

three field seasons, data were collected between June and September, when the width of California beaches are most stable (Leatherman 2003).

Sites were carefully selected along the California coastline to maintain physical environmental conditions that are as consistent as possible among different sites. Selected beaches were mainly comprised of sand, not rock or gravel above high water line, and have dry sand at high tide. Beaches were not narrow or backed by houses. Beaches with high cover of *Ammophila arenaria* were avoided because they were narrow, with high dunes close to the high water line. Site selection was also dependent on permission for access from the managing agency.

Data Collection

Measurements were made at each of 17 beaches along four to 20 belt transects (divided into 1-meter square quadrats) parallel to each other and perpendicular to a straight line roughly corresponding to the high water line (Barbour and Robichaux 1976). The number of transects at each beach depended on the length of the vegetated section of the beach. In the 2007 data collection, transects were spaced ten meters apart following the methods of Barbour and Robichaux (1976). In 2008 and 2009, the transects were spaced five meters apart to increase the density of data for better results interpolating cover between points for a related study. The transects began at the high water line (indicated by a change in the sand color and often presence of wrack; Leatherman 2003) and stopped inland at the end of the beach vegetation (indicated either by the top of the foredune, the beginning of inland vegetation, or a human-built area such as a parking lot or road). The percent cover for each species present in every square meter (delineated with a one square meter quadrat frame) along the length of the transect was visually estimated to the nearest 5% for the area that fell within the quadrat frame (Barbour et al. 1976).

Each beach was assigned to one of three treatments (high, medium, or low impact) based on the level of disturbance of the site and the way visitors are managed (Fig. 4). The distribution of foot traffic is visible on a sandy beach in the form of footprints left behind. Beaches assigned to the low impact group were mainly undisturbed, having little or no evidence of human disturbance (footprints, trash, etc.). These sites were either very well protected, with measures like fencing or complete closure, or were sampled at a location on the beach where few visitors are able to access, such as an area far from visitor access points. Beaches assigned to the medium impact group had evidence of at least moderate amounts of foot traffic, but the disturbance was limited mainly to specific areas like trails. Within this group, some beaches had more concentrated traffic than others, but all beaches within this group had some form of trail. Unprotected beaches were assigned to the high impact group and were those with evidence of high amounts of unrestricted foot traffic; visitors walk on most areas of the beach.

Data Analysis

Carmel River State Beach, South Beach at Leo Carrillo State Park, and Mugu Beach at Point

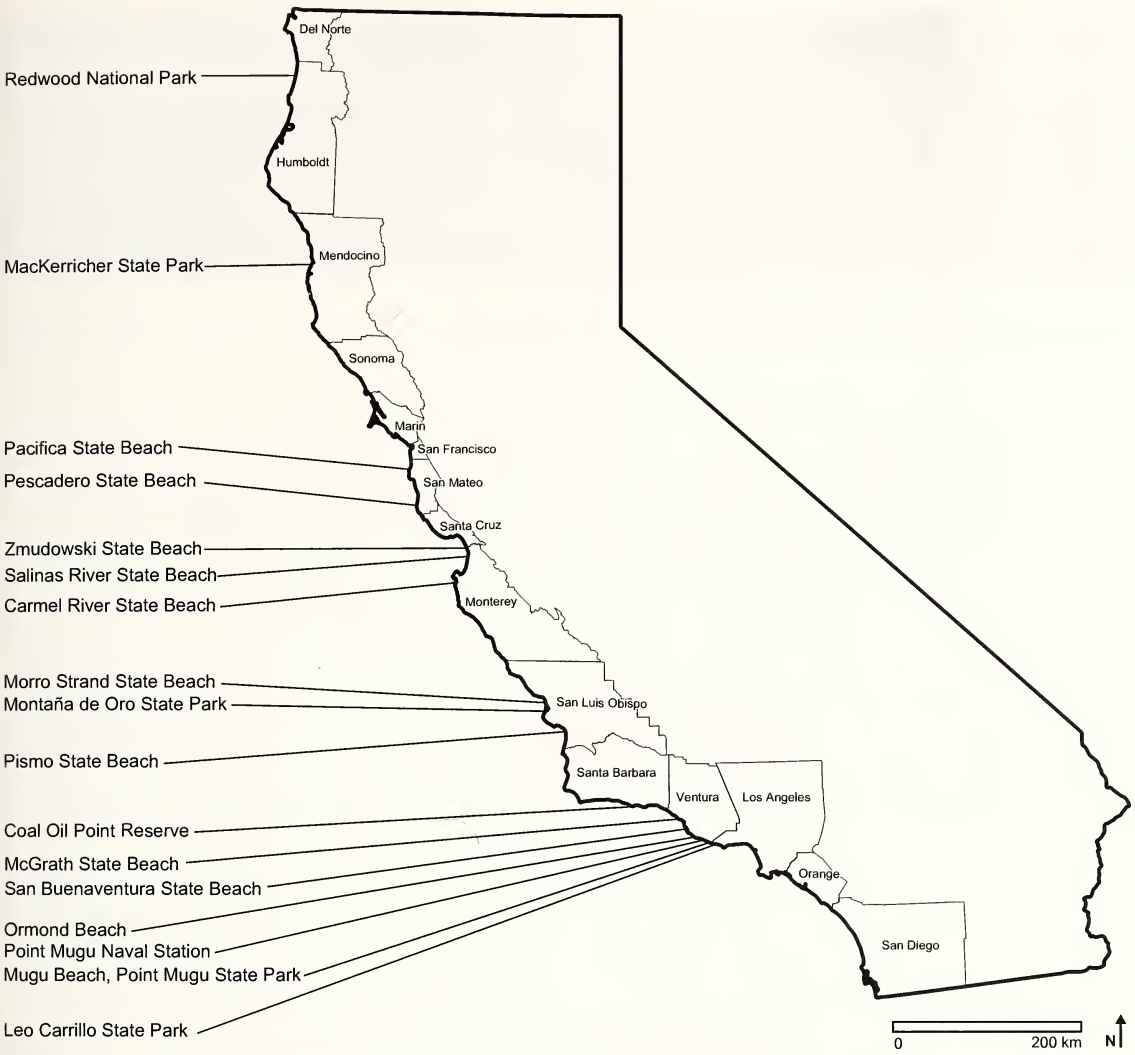

FIG. 3. Locations of sites sampled between 2007 and 2009.

Mugu State Park were assigned to the high impact level group. Ten Mile Dunes at MacKerricher State Park, Morro Strand State Beach, Pacifica State Beach, Pismo State Beach, the beach at Kuchel Visitor Center at Redwood National Park, Salinas River State Beach, Sandspit Beach at Montaña de Oro State Park, San Buenaventura State Beach, and Zmudowski State Park were assigned to the medium impact level group. Sands Beach at Coal Oil Point Reserve, McGrath State Beach, Point Mugu Naval Air Weapons Station, Ormond Beach, and Pescadero State Beach were assigned to the low impact level group.

To test the null hypothesis that higher levels of impact do not lead to dominance of *Ambrosia chamissonis* or *Cakile maritima*, five tests were performed. For each beach, the area was calculated as the area of each species' (either *A. chamissonis* or *C. maritima*) cover (m^2) normalized by the total area sampled (m^2) (i.e., absolute cover percentage expressed as a decimal number). The mean for each group of beaches (e.g., high versus medium versus low impact) was compared using a single factor analysis of variance test. Relative cover for each species was tested as the area of each species' cover (m^2) normalized by the area of all plant cover (m^2) using analysis of variance. Because lower cover of one species might be attributed to lower over-all cover, normalized total plant cover, calculated as the area of all species cover (m^2) divided by the total area sampled (m^2), was analyzed using analysis of variance. Where a significant difference was detected with the analysis of variance tests, a Tukey test was used to determine which groups were significantly different.

FIG. 4. Examples of (A) a low impact level beach, Point Mugu Naval Air Weapons Station, (B) a medium impact level beach, San Buenaventura State Beach, and (C) a high impact level beach, South Beach at Leo Carrillo State Beach.

RESULTS AND DISCUSSION

Ambrosia chamissonis and *Cakile maritima* were present at all the beaches sampled, but were not necessarily present in the sampled areas. Other species typically found on the sampled sites included *Atriplex leucophylla* (Moq.) D. Dietr. (Chenopodiaceae), *Abronia maritima* S. Watson (Nyctaginaceae), *Calystegia soldanella* (L.) R. Br. (Convolvulaceae), *Lathyrus littoralis* Douglas (Fabaceae), *Camissonia cheiranthifolia* (Sprengel) Raim. (Onagraceae), *Abronia latifolia* Eschsch. (Nyctaginaceae), *Leymus mollis* Trin. (Poaceae), *Artemisia pycnocephala* DC (Asteraceae), *Ammophila arenaria* Link (Poaceae), *Carpobrotus* spp. (Aizoaceae), *Abronia umbellata* Lam. (Nyctaginaceae), and *Glehnia littoralis* A. Gray (Apiaceae). Species present that are less typical of beach plant communities present at the sampled sites included *Pennisetum setaceum* Chiov. (Poaceae), *Coreopsis gigantea* (Kellogg) H. M. Hall (Asteraceae), *Chamaesyce albomarginata* Torrey & A. Gray (Euphorbiaceae), *Aster subulatus* Michx. (Asteraceae), *Heliotropium curassavicum* L. (Boraginaceae), *Ehrharta calycina* Sm. (Poaceae), *Cuscuta californica* Hook. & Arn (Cuscutaceae), *Croton californicus* Mull. Arg. (Euphorbiaceae), *Eriogonum parvifolium* Sm. (Polygonaceae), *Yucca whipplei* Torr. (Liliaceae), *Lotus scoparius* (Nutt.) Ottley (Fabaceae), *Distichlis spicata* (L.) Greene (Poaceae), *Tetragonia tetragonioides* (Pall.) Kuntze (Aizoaceae), *Malacothrix saxatilis* (Nutt.) Torr. & A. Gray (Asteraceae), and *Opuntia littoralis* (Engelm.) Cockerell (Cactaceae).

The relative percentage of the total plant cover comprised of *A. chamissonis* was significantly different between the low and ligh impact groups ($P = 0.0016$) and the medium and high impact groups ($P < 0.001$), but not the medium and low impact groups ($P = 0.33$; Fig. 5A). Similarly, the percentage of the total sampled area comprised of *A. chamissonis* was also significantly different between the low and high impact groups ($P < 0.001$) and the medium and high impact groups ($P < 0.001$), but not the medium and low lmpact groups ($P = 0.26$; Fig. 5B). The relative percentage of the total plant cover comprised of *C. maritima* was significantly different between the medium and low impact groups ($P = 0.025$) and the medium and high impact groups ($P = 0.032$), but not the low and high impact groups ($P = 0.945$; Fig. 5C). There was no significant difference ($P = 0.149$) between the groups for the percentage of the sampled area comprised of *C. maritima*, however, the data follows a similar pattern to that of the relative cover for this species (Fig. 5D). The percentage of plant cover of all species of the total area sampled was not significantly different between any of the groups ($P = 0.5$; Fig. 5E).

The results of the analysis of variance tests suggest that unprotected beaches have more cover of *A. chamissonis* than beaches that are at least moderately well protected from foot traffic and beaches with a medium level of impact have more cover of *C. maritima*. Yet, highly impacted beaches may have just as much plant cover as less impacted beaches, but the species composition is different. How the species composition and cover changes has not yet been analyzed. Comparing how species (other than the two discussed here) change at this broad scale is difficult because other species have a more limited distribution and do not occur on many beaches. *Ambrosia chamissonis* and *C. maritima* are the only species with a geographic range allowing them to grow on all the beaches in the study area. To compare how other species change with varying levels of impacts, species would need to be grouped for comparison at a broader geographic scale, for example, into successional roles (which have yet to be determined) or growth forms.

The differences in survival between these two plants might be due to differences in their physical characteristics – for example, *A. chamissonis* is woody with a deep tap root while *C. maritima* is succulent with spreading shallow roots. *Ambrosia chamissonis* is likely not outcompeting other species in the areas of high foot traffic, but rather is one of the only species to do well in an environment characterized by flat and constantly shifting substrate. Couch (1914)

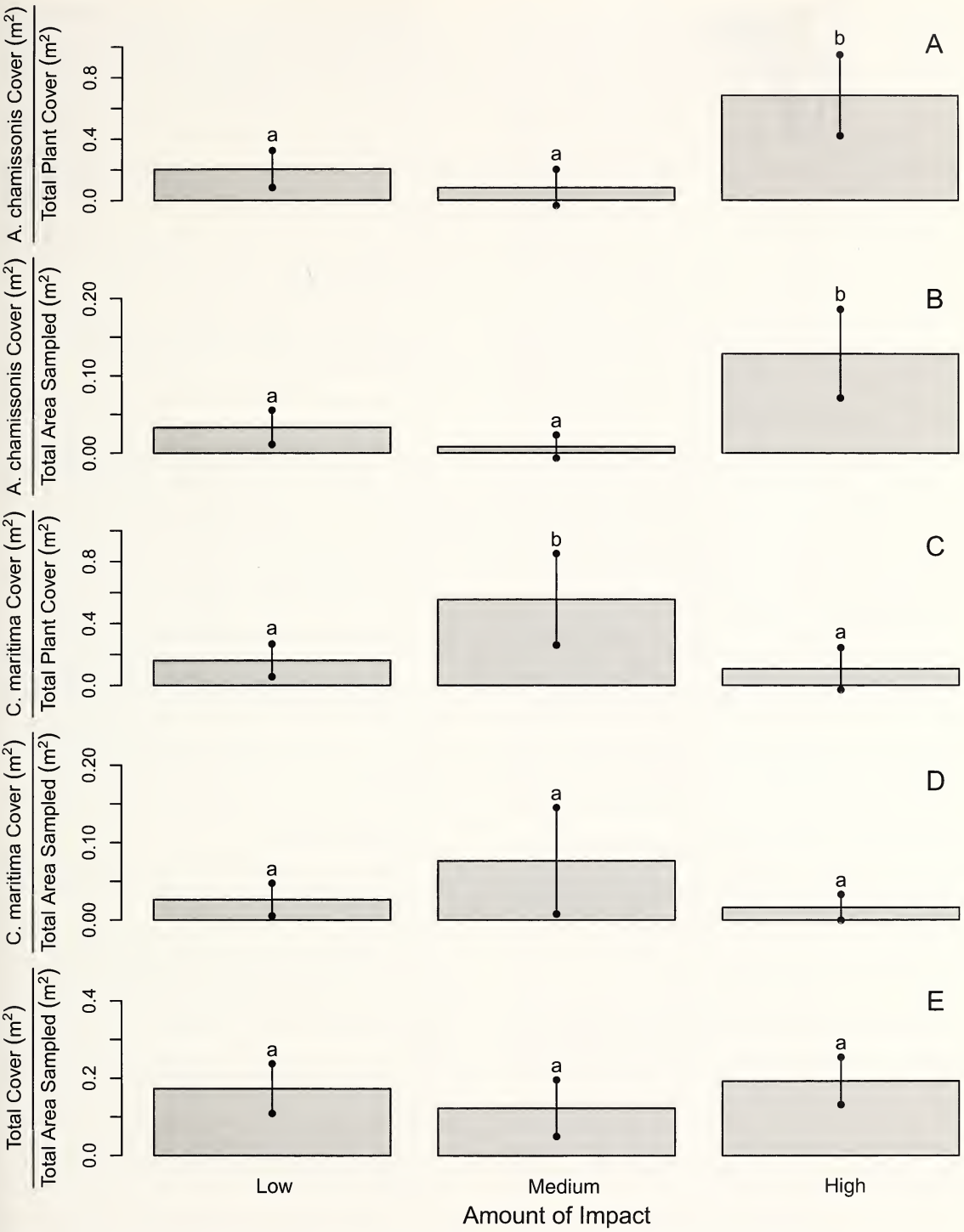

FIG. 5. Measures of species cover for low, medium, and highly impacted beaches: (A) Mean percent cover of the total plant cover comprised of *A. chamissonis;* (B) mean percentage of the total sampled area comprised of *A. chamissonis*; (C) mean percent cover of the total plant cover comprised of *C. maritima;* (D) mean percentage of the total sampled area comprised of *C. maritima*; (E) mean cover of all species as a percent of the total area sampled. Within each graph, different lowercase letters indicate values that are statistically different.

hypothesized that plants struggle more against the environment on the windward slope of the foredunes (the beach) than with each other. *Ambrosia chamissonis* seems to be occupying an environmental niche that other species have difficulty accessing. It is thought to help stabilize existing slopes and to colonize flat areas without accumulating significant mounds (Couch 1914; Ramaley 1918; Purer 1936) and has been found to thrive under some of the harshest conditions on the beach (Purer 1936; Fink and Zedler 1990).

The elevated presence of *C. maritima* on beaches with a medium impact level is also likely due to the creation of favorable conditions. Because *C. maritima* has succulent leaves and stems and has shallow roots, it probably does not survive trampling well. Trampling would easily damage the stems, leaves, and roots. On beaches with a low level of impact, there may be less available space for this plant to grow. It tends to occur on the leading edge of the vegetation on a beach closest to the high water line (Barbour 1990), so it may prefer to live in disturbed areas, which may be minimal on well-protected beaches. Beaches with medium levels of disturbance may provide more potential area for *C. maritima* to establish itself yet provide enough protection from trampling.

The results presented here have important implications for beach managers. While unprotected beaches may have a similar amount of cover compared to better protected beaches, the species composition appears to be different. Because *A. chamissonis* stabilizes flat areas (Couch 1914; Ramaley 1918; Purer 1936), a shift in species composition to increased area of this species could mean less sand-holding capacity. Intermediate levels of disturbance seem to support more *C. maritima* which collects small mounds of sand around it as it grows (personal observation) and is a species that could potentially play a role in dune-building and sand holding to prevent coastal erosion.

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HABITAT, SEED DORMANCY, AND ALLOZYME VARIATION OF THE RARE ENDEMIC *PHACELIA COOKEI* (BORAGINACEAE)

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Abstract

We conducted habitat, germination, and population genetic studies to inform management priorities for *Phacelia cookei* Constance & Heckard (Boraginaceae), a diminutive annual herb known from only four populations near Mt. Shasta in Siskiyou Co., California. Habitat surveys characterized soil, vegetation, and ground cover of extant populations and attempted to identify potentially suitable, but uncolonized, habitat. We were unable to distinguish any sites based on tests of soil characteristics. *Nama densum* Lemmon occurred at all sites where *P. cookei* was present. We identified several areas near existing populations that appeared to be suitable, but uncolonized, habitat. We tested the effects of various factorial combinations of after-ripening, scarification, stratification, and variable germination temperatures on breaking seed dormancy. Seed viability by tetrazolium tests ranged between 89% and 93%, but the highest germination from any treatment combination was 14% after adjusting for seed viability. We resolved 19 putative allozyme loci, two of which were polymorphic. Apparent genetic diversity was low both within and among the three sampled populations compared to similar endemic species, and populations were genetically similar. Management plans could consider attempting to expand existing populations by sowing seeds from existing populations into similar habitat.

Key Words: Conservation, endemism, genetic diversity, habitat, *Phacelia cookei*, rarity, seed dormancy.

Rare plants are an important component of biologically diverse ecosystems. Rare species can be widespread but infrequent throughout their distribution or have a very narrow geographical range with varying abundance; the latter are considered endemic species (Rabinowitz 1981). Narrow endemism often appears to be the result of adaptation to environments that are geographically restricted (Mason 1946). Endemic species with few individuals and/or populations are often especially susceptible to extinction due to their low numbers as well as their habitat specificity. Biodiversity hotspots, such as the California Floristic Province, where nearly 27% of the plant species are endemic, hold particularly high levels of endemism and have been targeted for focused conservation efforts (Myers et al. 2000).

Interactions between plants in a community, biotic factors, and abiotic stress can be important in determining community structure and species survival. Knowledge of these interactions is particularly important for understanding the distribution and protection of endemic plant species (Callaway and Walker 1997; Pugnaire and Luque 2001; Reynolds et al. 2003). A coarse-scale environmental component that can limit plant distribution is soil; edaphic endemism, for example, has been documented in several rare species (Kruckeberg 1954; Fiedler 1985; Cowling et al. 1994). Conservation programs, moreover, have used disturbance methods such as fire or soil disturbance to manage rare species (Preston and Whitehouse 1986; Hobbs and Huenneke 1992; Pendergrass et al. 1999). Intermediate levels of disturbance are thought to maintain the highest species diversity (Connell 1978), and diverse plant communities are more likely to support rare species (Myers et al. 2000). The response of rare species to disturbance should be carefully evaluated to avoid establishment of non-native species, which can out-compete or displace rare species, particularly in disturbed areas (Hobbs and Huenneke 1992; McIntyre and Lavorel 1994; Wilcove et al. 1998; Huston 2004).

Identifying appropriate germination cues can help to determine the feasibility of reintroduction of seeds from rare plants into uncolonized habitats in the field (Cochrane et al. 2002). Germination cues thus identified could also be used to predict germination time in the field based on local weather patterns. Germination rates tend to be

lower in small populations (Menges 1991; Keller and Waller 2002; Kochánková and Mandák 2009). For example, population size and germination rate were correlated in the recently fragmented prairie species *Silene regia* Sims (Menges 1991). Populations of this species with more than 150 individuals had consistent germination rates greater than 85%. Populations with fewer than 150 individuals had variable germination rates within and between populations, possibly due to recent fragmentation and/or inbreeding depression. Small endemic populations may have difficulty increasing population size or simply persisting due to decreased germination rates; so understanding their germination requirements could inform management and prevent extinction.

Understanding the genetic structure of a population can also inform management decisions to enhance genetic variability and survival (Ellstrand and Elam 1993; Alsos et al. 2002; Dolan et al. 2004). Population genetic studies can determine the degree to which populations are genetically distinct and can have important implications for managing narrow species. For example, the introduction of seed without careful consideration of population genetic structure and fitness can result in harmful changes to populations (Millar and Libby 1989). Experimental introduction of plants from multiple seed stocks could increase the success of re-establishment via heterosis and increased genetic diversity (Barrett and Kohn 1991); however, such practices risk disrupting locally adapted gene combinations (Antonovics 1976; Simberloff 1988; Barrett and Kohn 1991). Re-establishing populations from mixed seed sources will decrease population differentiation, but successfully re-established populations with long-term survival will likely differentiate again over time (Barrett and Kohn 1991). Introducing seeds from ecologically similar, but genetically diverse populations to maintain environmental adaptations and increase genetic diversity within the populations is recommended (Godt et al. 1996). Conservation plans that are approached experimentally increase our knowledge of population biology and can inform specific goals of future conservation plans (Barrett and Kohn 1991).

We studied *Phacelia cookei* Constance & Heckard (Boraginaceae), a rare annual limited to a 5 km^2 area near Mt. Shasta in Siskiyou County, California. The purpose of this study was to determine the habitat preferences, germination requirements, and population genetic structure to improve species management plans.

Methods

Species Description

Phacelia cookei is an annual herb, 2–15 cm tall, which occurs in areas of high disturbance in and along dirt roads where there is low surface organic matter and low competition from other plants (Horner-Till 1982). Flowers are 1–1.5 mm wide and can produce seeds in a growth chamber free of pollinators (Patterson unpublished), indicating that *P. cookei* is likely capable of self-fertilization. The species completes its life cycle between late May and early August. Populations occur on 0–35% slopes, and at elevations of 1330–1650 m in Siskiyou Co., California. The community associations in which it has been found include the *Chrysothamnus nauseosus* association, *Pinus ponderosa* association, and *Arctostaphylos patula*/*Ceanothus velutinus* association (Sawyer and Keeler-Wolf 1995; Barbour et al. 2007). Species nomenclature herein follows Baldwin et al. (2012).

A previous study examined the habitat characteristics and seed dispersal of *P. cookei* (Horner-Till 1982). The only populations found were in highly disturbed areas, primarily annually graded road banks, unused road beds, fuel breaks, or other frequently disturbed sites, despite intensive surveys of the area. Approximately 50% of seeds produced were found to fall beneath the parent plant, with the remainder held within the plant and dispersing with senesced plant tissue by wind. Mark-recapture studies revealed that whole plants and plant fragments can function as wind-tumbled diaspores, with some fragments moving as much as 22 m within a day. A series of pilot seed-germination experiments was also conducted, in which light duration, light intensity, temperature, scarification, and stratification were manipulated to identify germination cues. Treatment combinations were not applied consistently, however, and all treatments had germination <11%, with most treatments ranging from 0–2.5% (Horner-Till 1982).

Since the Horner-Till (1982) study, the number of known populations of *P. cookei* (40 reported) has decreased. These populations were not mapped, but a few (including the experimental populations used in this study) were documented in herbaria and likely include populations that Horner-Till studied. During surveys conducted on May 25 and 26, 2008, 10 populations were located (Edwards and Schierenbeck unpublished), including several that were not previously documented in herbaria. Habitat descriptions in Horner-Till (1982) indicate the occurrence of periodic fires, and firebreaks in the area contained populations of *P. cookei*.

Four spatially distinct populations were identified for this study, all of which were within a short distance and ranged in elevation from 1107 m–1408 m. Populations 1 and 4 were separated by approximately 2.4 km, and populations 6 and 7, which were closely adjacent, were approximately 5.3 km from population 1 (Table 1).

TABLE 1. SITE LOCATIONS AND SITE CATEGORIZATION FOR A SURVEY OF *PHACELIA COOKEI* HABITAT IN SISKIYOU CO., CALIFORNIA, USA, AUGUST 2009. *Indicates *Phacelia cookei* was present at the survey site.

Site	Location (UTME, UTMN)	Site category
01*	0566220, 4600778	historical occurrence
02	0566895, 4599400	historical occurrence
03	0566956, 4599347	historical occurrence
04*	0567069, 4598387	historical occurrence
05	0567639, 4597927	potential habitat
06*	0562769, 4598057	historical occurrence
07*	0562978, 4597937	historical occurrence
08	0563037, 4597904	potential habitat
09	0561107, 4599508	potential habitat
10	0560233, 4599200	volcanic rock pit
11	0559970, 4598891	volcanic rock pit
12	0562392, 4597949	potential habitat
13	0562466, 4597915	potential habitat
14	0562629, 4598024	potential habitat
15	0562743, 4589015	potential habitat

Habitat Survey

Habitat was surveyed for associated vegetation; percent cover of bare ground, litter, and vegetation; and soil characteristics. Fifteen sites were surveyed on August 17 and 18, 2009, following the California Native Plant Society (CNPS) Vegetation Rapid Assessment Protocol (CNPS Vegetation Committee 2007), for associated species, elevation, and habitat and vegetation descriptions. At each site, the 10–20 most common or abundant species were recorded within each stand; stands were defined by their structural and compositional integrity (see CNPS Vegetation Committee 2007 for more information). In addition to rapid assessment surveys, percent cover of bare ground, litter, and vegetation was measured within three to five 0.5 m^2 quadrats haphazardly placed in areas considered to be suitable habitat for *P. cookei*. A 0.5 m^2 quadrat was used because habitat areas were typically small or along narrow road margins. Vegetation cover was recorded as the percent cover of individual species within 0.5 m^2. Habitat data (percent bare ground, litter, and vegetation) were significantly heteroscedastic among site categories (see below), even after transformation, thus data were compared among site categories using a non-parametric Kruskal-Wallis test.

Surveyed sites included: (a) locations in which *P. cookei* currently or historically occurred ("historical locations") based on herbarium collection records and recent surveys (conducted by Edwards and Schierenbeck, unpublished); (b) areas of potentially suitable habitat ("potential habitat"); and (c) pits with rock of volcanic origin that had been mined for road construction ("volcanic rock pits"). All sites were within an area of approximately 5 km^2 (Table 1). Potential habitat locations were chosen based on apparent similarity to historical sites. Potential habitat was considered similar to historical sites if it was within the geographical range of *P. cookei* and had two or more of the following characteristics: a high level of disturbance as evidenced by tire tracks, a low percent canopy cover, low amounts of competing vegetation and/or litter, and/or a sandy substrate. Volcanic rock pits were surveyed because extant *P. cookei* populations are closely associated with dirt road margins that are maintained with a layer of volcanic rock. Seed could have been distributed in the volcanic roadbed material or it could be otherwise critical to habitat soil properties. The volcanic rock pits are located near the *P. cookei* sites and produce rocks very similar to that found in the roadbed.

A soil sample was collected from the approximate center of each survey site for analysis to determine whether soil texture and nutrient content limit colonization into new habitat. Soil was air-dried and passed through a 2 mm sieve to remove gravels. Cations were extracted using pH 7.0 ammonium acetate (Thomas 1982), with quantification of Ca, Mg, Na, and K by atomic adsorption/emission spectroscopy and data converted to meq/100 g. Extractable cations are a robust measurement of potentially available forms (Thomas 1982). The soil cation exchange capacity (CEC) was gauged by the sum of extractable cations. Immiscible displacement (ID) was used as a proxy for cations and anions in the soil-solution (Mubarak and Olsen 1976) with cations Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+} quantified by atomic adsorption/emission spectroscopy and anions Cl^{-} and SO_4^{-2}, and ortho-P by ion chromatography. Cations and anions in the soil solution are readily available for plant root uptake. Given the pH of these soils, we employed the Bray method to gauge phosphorus availability with quantification by vanomolybdate chemistry, a colorimetric reagent, using flow injection to use small samples (Bray and Kurtz 1945). The ratio of Bray extractable to ID phosphorus was calculated to more accurately measure the amount of phosphorus in the soil.

Nitrogen availability was quantified by KCl-extraction (Bundy and Meisinger 1994), with quantification of ammonium and nitrate using the Lachat autoanalyzer. The mole percent of ammonium in KCl extracts was determined as it often is related by plant succession and disturbance history (R. Blank, USDA Agriculture Research Service, Reno, NV, personal communication). Soil pH was measured twice: in a 0.01 $CaCl_2$ matrix and in a NaF matrix. The reaction of F- with poorly ordered hydrous oxides causes an increase in pH relative to that measure in aqueous matrix and can be a good proxy for levels of volcanic ash in the sample (R. Blank,

personal communication). To assess soil texture, coarse weight, fine weight, total weight, and percent coarse fragments were measured. Percentage water at saturation was measured to determine the water holding capacity of the soil. Soil tests were conducted at USDA Agriculture Research Service in Reno, Nevada.

Soil test data did not conform to assumptions of parametric tests, thus we compared soil across site categories using non-parametric Kruskal-Wallis tests.

Seed Germination

To clarify and possibly improve upon the methods reported by Horner-Till (1982), we conducted two experiments to identify cues to break seed dormancy, information that could then be used to estimate germination windows in the field and determine the feasibility of *ex situ* propagation.

Collection and seed separation. Twenty-five dried plants were collected on August 9, 2008 from populations 1 and 4, and an additional 25 from populations 6 and 7 combined, as the two sites were in close proximity and sparsely populated. Seeds were separated from dried plant material and stored in coin envelopes labeled by parent plant at room temperature for three months.

Seed viability. Four samples of 50 seeds from each population were tested for viability using 1% 2,3,5-triphenyl tetrazolium (Lakon 1949). Seeds were pierced and soaked in a 1% tetrazolium solution overnight in the dark. Seeds were considered viable if embryos stained dark pink. Germination rates from dormancy experiments were divided by mean viability within each population to correct for proportion viable.

Germination experiment 1. Seeds from three different populations were subjected to 14 different treatment combinations in a factorial design including acid scarification (5, 10, or 15 min), cold-moist stratification (present or absent), and temperature during germination (cycling 5°C in the dark for 12 hours followed by 25°C or 30°C in the light; Table 2). One seed from each maternal plant was used for each treatment combination (approximately 20 per population). Seeds were soaked in concentrated sulfuric acid for 5, 10, or 15 minutes and then rinsed for two minutes in deionized water. Treated seeds were allowed to dry overnight. Seeds assigned to receive cold-moist stratification were placed in beakers with moist perlite on October 31, 2008, and stored at 4°C for five weeks. Seeds that did not receive cold-moist stratification were treated on December 12, 2008.

Following scarification or stratification, seeds from within a population and treatment combination were placed on moist filter paper in 9-cm diameter Petri dishes. Each treatment combination, therefore, included three Petri dishes, one from each population, each of which contained a single seed from each maternal family collected. Petri dishes were incubated for four weeks at one of two fluctuating temperature regimes. In one group, seeds were held for 12 hours each day at 5°C and then temperature was increased to 25°C for the reminder of each 24-hour period. The second group was held 12 hours each day at 5°C and then the temperature was increased to 30°C for the remainder of the 24-hour period.

TABLE 2. TREATMENTS APPLIED TO *PHACELIA COOKEI* SEEDS IN TESTS TO BREAK DORMANCY ("GERMINATION EXPERIMENT 1"—SEE METHODS). Treatments included sulfuric acid scarification, cold-moist stratification, and temperature fluctuations, in which 24-hr cycles consisted of 12 hr at the low temperature and 12 hr at the high temperature indicated.

Acid scarification	Cold moist stratification	Temperature
5 min	5 wk	5°C/25°C
10 min	5 wk	5°C/25°C
15 min	5 wk	5°C/25°C
0 min	none	5°C/25°C
5 min	none	5°C/25°C
10 min	none	5°C/25°C
15 min	none	5°C/25°C
5 min	5 wk	5°C/30°C
10 min	5 wk	5°C/30°C
15 min	5 wk	5°C/30°C
0 min	none	5°C/30°C
5 min	none	5°C/30°C
10 min	none	5°C/30°C
15 min	none	5°C/30°C

Germination experiment 2. Germination success was relatively low in the first experiment, so we also conducted a second germination experiment with an expanded range of treatments in an attempt to identify germination cues. During the second experiment, we tested the effects of two after-ripening treatments in conjunction with cold-moist stratification on germination. Twelve different treatment combinations were applied to the seeds (Table 3). Treatments were chosen using the Horner-Till thesis (1982) and a germination decision tree (Meyer 2006). Seeds were placed on 12 separate 50-mm diameter Petri dishes per individual plant. Population 1 had 16 individuals, population 4 had 14 individuals, and Populations 6 and 7 had 25 individuals each included in this experiment, for a total of 660 plates. The number of seeds in each dish varied between 1–10 seeds depending on the number available per plant. All seeds from a single plant assigned to receive the 40°C treatment were combined into a single sealed vial to prevent loss of seed moisture, after which they were separated into Petri plates for cold stratification.

TABLE 3. TREATMENTS APPLIED TO *PHACELIA COOKEI* SEEDS IN TESTS TO BREAK DORMANCY ("GERMINATION EXPERIMENT 2"—SEE METHODS). Treatments included after-ripening, cold stratification, and temperature fluctuations, in which each 24-hr cycle consisted of 12 hr at the low temperature alternating with 12 hr at the high temperature indicated.

After-ripening (2 weeks)		Cold stratification	
Temp.	Moisture	at 2°C	Temperature
----	----	8 wk	2°C/10°C
----	----	8 wk	5°C/25°C
----	----	12 wk	2°C/10°C
----	----	12 wk	5°C/25°C
15°C	wet	8 wk	2°C/10°C
15°C	wet	8 wk	5°C/25°C
15°C	wet	12 wk	2°C/10°C
15°C	wet	12 wk	5°C/25°C
40°C	dry	8 wk	2°C/10°C
40°C	dry	8 wk	5°C/25°C
40°C	dry	12 wk	2°C/10°C
40°C	dry	12 wk	5°C/25°C

For both experiments, the criterion for germination was the protrusion of the radicle, which was visible to the naked eye. The percentage germination within each Petri dish was compared among populations and treatments using Kruskal-Wallis tests, as data did not conform to assumptions for parametric tests.

Isozyme Variation

A survey of allozyme variation was conducted to characterize population genetic variation within and among populations.

Sample collection and extraction. Leaves from 50 living plants were collected from each of populations 1 and 4, and 24 samples were collected from populations 6 and 7 (sites 6 and 7 were combined into one population due to the low number of individuals in each population and the close physical proximity of the two populations) on June 8, 2009 and stored in a plastic bag on ice or refrigerated up to 48 hours until extraction. All tissue samples were crushed in a chilled ceramic spot plate using a glass pestle with an extraction buffer modified from Broyles and Wyatt (1990). The extract was filtered through Miracloth, adsorbed onto 3 × 10 mm wicks cut from Whatmann 3MM chromatography paper, and stored at −70°C until electrophoresis was performed. Wicks were loaded onto 12.5% hydrolyzed potato starch gels and subjected to horizontal electrophoresis following Soltis and Soltis (1989).

Gel systems. The following isozymes and buffer combinations were used to estimate genetic variability within and between populations. A tris-citrate buffer (pH8.0) (Meizel and Markert 1967) was used to resolve isocitrate dehydrogenase (IDH:EC:1.1.1.41), 6-phosphoguconate (PGD:EC:1.1.1.44), glyceraldehyde-6-phosphate dehydrogenase (G6PDH:EC:1.1.1.49), glutamate dehydrogenase (GDH:EC:1.4.1.2), and glyceraldehyde-3-phosphate dehydrogenase (G-3PDH: EC:1.2.1.9). A histidine-citrate buffer (pH 7.0) (Fildes and Harris 1966) was used to resolve phosphoglucomutase (PGM:EC:5.4.2.2), menadione reductase (MNR:EC:1.6.99), malic enzyme (ME:EC:1.1.1.40), phosphglucoisomerase (PGI: EC:5.3.1.9), and triose-phosphate isomerase (TPI: EC:5.3.1.1). A tris-borate-EDTA buffer (pH 8.6) (Markert and Faulhaber 1965) was used to resolve diaphorase (DIA:EC:1.6.2.2), UTP-glucose 1-phosphate uridylyltranferase (UGPP: EC:2.7.7.9), aldolase (ALD:EC:4.1.2.13), glutimate oxaloacetate transaminase (GOT:EC:2.6.1. 1), and shikimate dehydrogenase (SHK:EC:1.1.1. 25). All enzyme assays followed Wendel and Weeden (1989) except UGPP, which followed Manchenko (1994). Stains were incubated at 37°C in the dark until bands appeared.

Analysis. POPGENE (Yeh and Boyle 1997) was used to calculate allele frequencies, F-statistics, geneflow, heterozygosity, and the effective number of alleles. F-statistics were calculated following Weir (1990) to determine deviations from Hardy-Weinberg equilibrium. Total gene diversity (H_t) and mean diversity within populations (H_s) were calculated following Nei (1973, 1978). The effective number of alleles was calculated following Hartl and Clark (1989).

RESULTS

Habitat Survey

Percentage bare-ground cover did not differ among types of habitat (mean [SD] historical occurrence = 74.59 [34.33], potential habitat = 77.86 [31.79], and volcanic rock pits = 85.83 [22.45]; $H = 2.89$, $P = 0.2$). Percentage cover by litter also did not differ among sites (mean [SD] historical occurrence = 20.18 [34.24], potential habitat = 17.38 [23.58], and volcanic rock pits = 2.50 [4.18]; $H = 3.71$, $P = 0.2$). Percentage vegetation cover, however, was significantly higher in the historical occurrence and volcanic rock pit sites than in the potential habitat (mean [SD] historical occurrence = 14.64 [28.37], volcanic rock pits = 11.67 [19.15], potential habitat = 4.05 [11.53]; $H = 8.28$, $P = 0.016$).

Nama densum Lemmon was the species most closely associated with *P. cookei* as it was found at all sites that had *P. cookei* present and was not found at any site without *P. cookei* (Table 4), and was thus the species most closely associated with *P. cookei*. Other species commonly associated with *P. cookei* were *Bromus tectorum* L., *Gayophytum heterozygum* F.H. Lewis & Szweyk.,

TABLE 4. PERCENT COVER OF PLANTS PRESENT AT SITES SURVEYED IN A STUDY CHARACTERIZING HABITAT OF *PHACELIA COOKEI*. Site numbers correspond to locations in Table 1. Missing values indicate that the species was not present at that location. Surveys were conducted in Siskiyou County, CA, USA in August 2009.

Taxon	Site number														
	1	4	6	7	2	3	5	8	9	12	13	14	15	10	11
Achillea millefolium									1						
Agrostis idahoensis	1				1	1				2			1		1
Arctostaphylos nevadensis							1								
Artemisia tridentata	5				5			5	3	20	5		1		1
Bromus carinatus												1			
Bromus tectorum	1	1	1		1		1			3	30	1	1		
Castilleja arachnoidea											1				
Ceanothus velutinus							1								
Chaenactis douglasii							1								
Chamaesyce glyptosperma		1													
Chenopodium atrovirens	1		1					1							
Collomia grandiflora					1	1									
Cryptantha intermedia													1		
Delphinium nuttallianum							1								
Dysphania botrys		5													
Elymus elymoides	1				1	1	1								
Epilobium sp.	1				1		1								
Ericameria nauseosa	5	5			1						3		1	1	
Erigeron filifolius	1	1	1		1		1	1							
Eriogonum baileyi			1												
Eriogonum nudum		1													
Eriogonum umbellatum				1											
Eriophyllum lanatum var. *obovatum*															1
Gayophytum heterozygum	1	1		1		1	1							1	
Gilia sinuata					1						1				
Gutierrezia microcephala	1	1	5				1								
Juniperus occidentalis															1
Linanthus pungens	1				1				2						
Mentzelia albicaulis		1	1												
Nama densum	1	1	5	1											
Nicotiana attenuata							1								
Penstemon laetus var. *sagittatus*		1													
Phacelia cookei	2	1	<1	<1											
Phacelia hastata		5					1								
Pinus ponderosa	1					75									
Pterospora andromedea						1									
Purshia tridentata	15				5	5		5							
Ribes cereum						5									

TABLE 4. CONTINUED.

Taxon	Site number													
	1	4	6	7	2	3	5	8	9	12	13	14	15	10	11
Sisymbrium altissimum			1												
Stephanomeria sp.		1													
Stipa occidentalis	1				1	1								1	
Verbascum thapsus														3	
Total vegetative cover	40	26	17	4	20	91	12	12	6	25	40	2	5		4

Erigeron filifolius Nutt., and *Gutierrezia microcephala* (DC.) A. Gray, which were found at three of the four sites that had *P. cookei* present. *Stipa occidentale* S. Watson, *Agrostis idahoensis* Nash, *Artemisia tridentata* Nutt., *Chenopodium atrovirens* Rydb., *Dysphania botrys* (L.) Mosyakin & Clemants, *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & G.I. Baird, *Elymus elymoides* (Raf.) Swezey, *Epilobium* sp., *Linanthus pungens* (Torr.) J.M. Porter & L.A. Johnson, *Penstemon laetus* var. *sagittatus* (D.D. Keck) McMinn, *Phacelia hastata* subsp. *compacta* (Brand) Heckard, *Pinus ponderosa* Douglas ex Lawson & C. Lawson, *Purshia tridentata* (Pursh) DC., and *Sisymbrium altissimum* L. were present at half of the sites that had *P. cookei* present.

Bromus tectorum was documented at nine of the 14 sites, three of which also had *P. cookei*. Most sites, including those with *P. cookei*, had very low percent cover (1%) of *Bromus tectorum,* except site 13 where it reached 30%. Disturbance, as evident from tire tracks and crushed vegetation, was observed at all sites with *P. cookei* except site 4, which was near railroad tracks.

In general, soils at the study sites were sandy in texture, which is characteristic of Delany and Oosen-Avis soil families in the area (USDA/NRCS 2010). The mean coarse weight at the volcanic rock pits, however, was higher than the course weight of potential habitat and historic habitat (Table 5), likely because the volcanic rock pits are sources of a rocky roadbed material whereas the historic and potential habitat areas are relatively sandier. In addition, mean pH was lower at volcanic rock pit sites than at potential habitat and historical occurrence sites (Table 5). Nonetheless, no significant differences were detected among sites surveyed for any of the soil characteristics we measured (Table 5). Historical sites without extant *P. cookei* populations did not differ significantly from those with *P. cookei* present, so they were grouped for analysis. The similarities among sites suggests that soil characteristics do not limit the distribution of *P. cookei*, at least within its known geographical range.

Seed Germination

Viability testing. A high percentage of seeds stained positive for enzyme activity following the tetrazolium test (positive test observed in 89%, 90%, and 93% of seeds respectively, from populations 1, 4, and 6/7).

Germination experiment 1. We found no significant differences in percentage germination among any of the population by treatment combinations ($H = 0.07$, $P = 0.9$), so we combined data across populations for subsequent analyses to increase our power to detect treatment effects. Nonetheless we found no difference

TABLE 5. MEAN (SD) RESPONSES FROM SOIL ANALYSES CONDUCTED DURING A SURVEY OF HABITAT OF *PHACELIA COOKEI*. Sites were categorized as historical occurrence (n = 6), potential habitat (n = 7), or volcanic rock pit sites (n = 2; see Table 1). Soil samples were collected during August 2009 in Siskiyou Co., California. See Methods for explanation of soil analysis. Test statistic was calculated using the non-parametric Kruskal-Wallis test to determine significant differences in ranked means. † $0.1 > P > 0.6$.

Soil analysis	Historical occurrence. Mean (SD)	Potential habitat. Mean (SD)	Volcanic rock pits. Mean (SD)	Test stat. (H)
meq/100 g acetate Ca	2.15 (2.22)	1.09 (0.60)	3.40 (3.71)	0.59
meq/100 g acetate Mg	0.57 (0.72)	0.16 (0.08)	0.98 (0.91)	3.21
meq/100 g acetate K	0.29 (0.23)	0.09 (0.05)	0.34 (0.34)	3.37
meq/100 g acetate Na	4.51 (0.75)	4.62 (0.21)	4.65 (0.59)	0.0
CEC by sum of cations (meq/100 g)	7.53 (2.48)	5.96 (0.64)	9.36 (4.36)	4.34
ug/g Bray P as P	79.48 (57.4)	93.69 (34.03)	17.47 (18.99)	4.03
ug/mL ID Ca	3.13 (1.64)	7.54 (7.48)	3.75 (3.75)	1.14
ug/mL ID Mg	1.63 (1.65)	2.14 (1.62)	2.65 (2.33)	0.71
ug/mL ID K	6.90 (5.40)	5.03 (2.62)	5.85 (6.72)	0.35
ug/mL ID Na	2.42 (1.87)	2.27 (1.22)	2.60 (0.42)	0.7
coarse wt.	22.24 (26.28)	34.37 (27.92)	221.76 (164.07)	5.67†
fine wt.	285.38 (106.46)	393.66 (88.28)	310.8 (64.45)	3.84
total wt.	307.62 (123.90)	428.03 (75.15)	532.52 (228.52)	3.75
% coarse frag	6.47 (6.00)	8.52 (7.45)	38.58 (14.26)	5.16†
ppm KCl NH4	0.61 (0.23)	1.10 (1.19)	1.07 (1.00)	0.68
ug/g KCL (mmol/kg)	1.81 (0.68)	3.25 (3.56)	3.19 (3.00)	0.49
KCl NH4 (mmol/kg)	0.10 (0.04)	0.18 (0.2)	0.18 (0.17)	0.49
ppm KCl NO3	2.24 (1.93)	4.33 (3.63)	3.7 (3.86)	1.54
ug/g KCl NO3	6.58 (5.66)	12.70 (10.63)	11.08 (11.61)	0.54
KCl NO3 (mmol/kg)	0.11 (0.09)	0.20 (0.17)	0.18 (0.19)	1.53
total KCl N (mmol/kg)	0.21 (0.12)	0.39 (0.3)	0.36 (0.35)	0.99
mole %KCl as NH4	57.75 (24.64)	50.36 (27.04)	52.39 (5.26)	1.54
ug/ml ID Cl	1.97 (1.12)	1.28 (0.79)	1.49 (1.07)	1.87
ug/mL ID SO4	2.34 (1.39)	2.53 (2.32)	4.25 (3.90)	0.75
ug/ml ID P as P	0.29 (0.4)	0.46 (0.41)	0.26 (0.18)	2.06
CaCl pH	5.79 (0.2)	5.50 (0.45)	6.26 (0.43)	4.23
NaF pH	9.07 (0.47)	8.52 (0.62)	8.51 (0.41)	3.56
pH diff	3.28 (0.5)	3.02 (0.32)	2.26 (0.02)	5.63†
% water at saturation	28.85 (6.97)	25.84 (2.7)	26.41 (6.25)	0.22
ug/g ID P as P	0.10 (0.15)	0.12 (0.11)	0.07 (0.06)	0.91
ratio Bray to ID P	2085.07 (1518.57)	2267.67 (3725.59)	199.06 (81.95)	3.73

in percentage germination between the two germination temperature cycles (5/25°C vs. 5/30°C) ($H = 0.20$, $P = 0.66$; Table 6) or among scarification times in acid ($H = 2.39$, $P = 0.50$; Table 6) (we note, however, that the 15-min treatment severely damaged the seeds). We did not find percentage germination in the acid-only versus the acid-and-cold-stratification treatments to differ significantly ($H = 0.15$, $P = 0.70$; Table 6). Likewise, we found no significant differences among treatments when comparing all ten treatment combinations ($H = 11.40$, $P = 0.6$).

Germination experiment 2. Percentage germination did not differ among any of the population by treatment combinations ($H = 0.17$ to 2.51, $P = 0.3$ to 0.9; Table 7), so data were combined across populations for subsequent analyses to increase power to detect treatment effects.

TABLE 6. MEAN (SD) PERCENT GERMINATION OF *PHACELIA COOKEI* SEEDS IN TESTS OF DORMANCY CUES ("GERMINATION EXPERIMENT 1"—SEE METHODS). Germination values were corrected for mean population seed viability, as estimated by tetrazolium tests.

Treatment	Percent germination. Mean (SD)	Test statistic (H)
Acid scarification time		2.39
0 min	2.07 (2.31)	
5 min	6.05 (12.02)	
10 min	1.09 (2.03)	
15 min	0.88 (3.03)	
Cold stratification		0.15
none	3.2 (8.47)	
5 wk	1.8 (4.21)	
Germination temperature		0.20
5/25°C	3.34 (9.06)	
5/30°C	1.83 (3.91)	

TABLE 7. MEAN (SD) PERCENT GERMINATION OF *PHACELIA COOKEI* SEEDS IN A TEST OF DORMANCY CUES ("GERMINATION EXPERIMENT 2"—SEE METHODS). Treatments included after-ripening, cold stratification, and germination temperature cycle. * $P < 0.05$.

Treatment	Percent germination. Mean (SD)	Test statistic (H)
After-ripening		1.42
none	3.40 (4.09)	
warm/moist (15°C)	14.40 (14.83)	
hot/dry (40°C)	3.28 (4.97)	
Cold stratification (2°C)		0.03
8 wk	8.40 (12.25)	
12 wk	5.68 (8.24)	
Germination temp.		7.41*
5/25°C	13.35 (11.10)	
2/10°C	0.70 (1.71)	

Percentage germination was not affected by after-ripening treatment ($H = 1.42$, $P = 0.50$; Table 7) or length of cold stratification ($H = 0.03$, $P = 0.87$; Table 7). Percentage germination was higher among seeds that were exposed to a 5/25°C temperature cycle than those in the 2/10°C temperature cycle ($H = 7.41$, $P = 0.01$; Table 7).

No germination was observed under the following conditions: (1) 8 weeks cold stratification/germinated at 2/10; (2) 12 weeks of cold stratification/germinated at 2/10°C; (3) warm after-ripening/8 weeks cold stratification/germinated at 2/10°C; (4) hot after-ripening/8 weeks cold stratification/germinated at 2/10°C; and (5) hot after-ripening/12 weeks cold stratification/germinated at 2/10°C.

Isozyme Variation

Seventeen of the 19 putative allozyme loci resolved were monomorphic (Table 8). Only DIA and MNR were polymorphic. Both DIA and MNR stain for a varied group of flavoproteins with little specificity and in some plants these two markers stain for the same allozyme, or there may be overlap between the stains (Soltis and Soltis 1989). However, banding patterns were dissimilar for *P. cookei*, thus they were treated as distinct loci. All populations had 10.53% polymorphic loci. The mean number of alleles at each population was 1.16. The effective number of alleles for populations 1, 4, and 6/7 was 1.06, 1.13, and 1.14 respectively. The effective number of alleles did not deviate significantly from the mean number of alleles. Allele frequencies did not significantly deviate from Hardy-Weinberg equilibrium (DIA: $\chi^2 = 1.99$, df = 1, $P = 0.2$; MNR: $\chi^2 = 7.24$, df = 3, $P = 0.06$).

TABLE 8. ALLELE FREQUENCIES AT TWO VARIABLE ISOZYME LOCI IN THREE POPULATIONS OF *PHACELIA COOKEI*. Sample size per locus: Pop 1 (50); Pop 4 (50); Pop 6/7 (24). Mean expected heterozygosity (H_s) and mean number of alleles per locus per polymorphic loci (AP) are shown for each population.

Locus	Allele	Populations 1	4	6/7
DIA	a	0.18	0.39	0.44
	b	0.82	0.61	0.56
MNR	a	0.08	0.25	0.23
	b	0.20	0.24	0.27
	c	0.72	0.51	0.5
H_s		0.04(0.12)	0.06(0.18)	0.06(0.18)
AP		2.5	2.5	2.5

TABLE 9. GENETIC DIVERSITY, AS ESTIMATED BY ALLOZYME VARIATION, IN THREE *PHACELIA COOKEI* POPULATIONS. Jackknife estimates of heterozygote deficit within individuals (F_{is}), observed total (H_t) and population-level (H_s) heterozygosities were calculated according to Nei (1973) using GenePop. Estimates for two polymorphic allozyme loci, as well as population mean estimates, are provided.

Locus	F_{is}	H_T	H_s
Population 1			
MNR	−0.265	0.560	0.435
DIA	0.007	0.240	0.295
Pop. means	−0.095	0.042(0.14)	0.038(0.12)
Population 4			
MNR	−0.194	0.740	0.620
DIA	0.117	0.420	0.476
Pop. means	−0.059	0.061(0.19)	0.058(0.17)
Population 6/7			
MNR	−0.335	0.833	0.624
DIA	−0.101	0.542	0.492
Pop. means	0.187	0.072(0.22)	0.057(0.18)
All populations			
MNR	−0.271	0.686	0.564
DIA	0.049	0.371	0.431
means	−0.134	0.056(0.18)	0.052(0.16)

Individual-locus estimates of inbreeding (F_{IS}) were negative for MNR, as well as for the mean for all populations (Table 9). F_{IS} estimates for DIA in population 1 and 4 were positive but negative in population 6/7. In contrast, F_{IS} estimates for MNR were consistently negative. Jackknife estimates of genetic differences among populations (F_{ST}) for MNR and DIA were 0.0292, and 0.0561 respectively, and mean F_{ST} was 0.0409. Due to low allozyme variation observed, these estimates should be considered provisional.

DISCUSSION

We identified a number of areas near existing populations that appeared to be suitable (low vegetation and litter cover and high bare ground), but uncolonized, habitat. We have identified treatment combinations that can break seed

dormancy, albeit at low frequencies (<15%). Thus, managers could consider attempting to expand existing populations into some of these new areas by sowing seeds in to areas with low vegetation and litter cover. Genetic variation appears to be limited in *P. cookei*, which may ultimately limit its prospects for recovery.

Habitat

Associated species and percent cover of bare ground, litter, and vegetation may be useful for locating potential habitat and new populations. Bourg et al. (2005), for example, successfully used classification and regression tree (CART) modeling and geographic information systems (GIS) computer software with habitat characteristics, such as forest type and elevation, to locate eight new occupied habitat patches of the rare forest species *Xerophyllum asphodeloides*. We found *Nama densum* to be most frequently associated with *P. cookei*, suggesting that targeting habitat with *N. densum* may also help protect *P. cookei*.

Soil did not differ among the categories of sites we examined, which suggests that soil characteristics might not be limiting the spread of *P. cookei* within its geographical range. The volcanic rock roadbed material, moreover, was not significantly different than the sand substrate, so a sandy substrate may not be a habitat requirement. The current limited distribution of *P. cookei* may instead reflect the limitations of its gravity and tumbleweed-type seed dispersal (Horner-Till 1982), or perhaps the distribution of the Delaney and Oosen-Avis soil families (USDA/NRCS 2010). Another characteristic that might limit the expansion of *P. cookei* populations is the extent of bare soil or disturbance in areas adjacent to extant populations. Most extant populations had signs of disturbance and all had extensive bare ground and low percent cover of vegetation and litter. We did not measure the amount of bare soil or disturbance in areas other than the surveyed sites, but qualitatively these characteristics appeared to be distinctive in *P. cookei* habitat.

Germination

In a series of experiments, Horner-Till (1982) reported low germination success (all treatment combinations ≤11%). Similarly, germination was low in our experiments (<15%) and not strongly affected by physical (scarification) or physiological (stratification and after-ripening) treatments, suggesting *P. cookei* may have multiple dormancy cues that have yet to be identified or non-cue responsive dormancy (Meyer 2006). Seeds with non-cue responsive dormancy can be challenging to propagate from seed, so in situ, conservation measures are more likely to be successful. The 5/25°C temperature cycle, however, produced significantly higher germination rates than the 2/10°C temperature cycle. These temperatures are similar to the field temperatures reported by Horner-Till (1982) and may provide guidance for expanding the range into uncolonized, but apparently suitable, habitat.

Table 10. The Relationship of Geographical Range to Allozyme Variability in Plants (after Hamrick 1983).

Geographical region	No. of studies	H_t	H_s
Endemic	10	0.275	0.208
Narrow	31	0.261	0.177
Regional	38	0.238	0.154
Widespread	43	0.380	0.293
Phacelia cookei	1	0.056	0.053

Isozyme Variation

Overall, isozyme variation was very low, which suggests *P. cookei* harbors limited population genetic diversity. Hamrick and Godt (1989) found that endemic, short-lived, selfing dicots with gravity-dispersed seed (all characteristics of *P. cookei*) typically have low amounts of genetic diversity. The populations were very similar genetically (low F_{ST}), so there appears to be little concern for disrupting locally adapted genotypes if land managers dispersed seeds among populations or used them to colonize new sites. Population sizes could be expected to vary substantially from year to year, so if seeds are collected for this purpose, we suggest that the number of seeds harvested from each population be proportionate to the population size.

Our estimates of population genetic variation may have been low in part because samples of *P. cookei* tissue were collected during only one field season. Plants with small populations can maintain genetic diversity through a genetically diverse seed bank, so plants growing during one season need not be representative of total genetic diversity, including both living plants and dormant seeds (Del Castillo 1994). However, our sample sizes from populations 1 and 4 (50 individuals each) were adequate to sample at least some rare alleles across the 19 loci resolved, and the populations in that year contained several hundred individuals. Seventeen of those loci appeared to be fixed. Therefore, sampling across multiple years (Ellstrand and Elam 1993; Cabin et al. 1998; McCue and Holtsford 1998) may be unlikely to reveal much additional population variation. Nonetheless, since sampling across years could increase the probability of finding rare alleles, new populations established in suitable habitat should be seeded across

multiple years to maximize the evolutionary potential of each population established.

Hamrick (1983) surveyed the relationship between geographical range and allozyme variability (Table 10). As the geographic range increases, total allelic diversity, mean diversity within populations, and population differentiation increases (Table 10). H_t and H_s for *P. cookei* were significantly lower than what has been reported for endemic plants (Hamrick 1983). Very low diversity at the population level indicates decreased potential for evolutionary change in response to environmental change, which could pose a challenge for population persistence in the future.

The closest known relative to *P. cookei* is *P. keckii* Munz & I.M. Johnst. (Walden 2010). *Phacelia keckii* is an annual endemic to the Santa Ana Mountains that grows on volcanic soils in chaparral and knobcone pine communities (Stephenson and Calcarone 1999). After fire has occurred, *P. keckii* populations have been documented to increase in size (Stephenson and Calcarone 1999). Horner-Till (1982) documented the fire history of the area and speculated about the relationship between fire and *P. cookei*. Investigations into the role of fire and other sources of disturbance in *P. cookei* habitat may provide additional insights into management treatments beneficial to population growth.

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CRYPTANTHA WIGGINSII (BORAGINACEAE): A PRESUMED EXTINCT SPECIES REDISCOVERED

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Abstract

Cryptantha wigginsii I.M. Johnston (Boraginaceae) had previously been known from a single collection made in April 1931, at a locality 18 miles south of Tijuana, Baja California, Mexico. This species is distinctive and unique in the genus in having nutlets with a surface that is smooth and glossy near the base and densely tuberculate at the apex. Because of the absence of subsequent collections, the species was presumed extinct. However, a population of *C. wigginsii* was recently discovered in Carlsbad, San Diego Co., California, constituting a new county, state, and country plant species record. Subsequent field investigations and study of (mis-identified) *Cryptantha* specimens at several California herbaria has turned up additional documented populations of this species in the USA and coastal northwestern Baja California, Mexico. In addition to the three adjacent Carlsbad populations and the type locality in Baja California, populations known to date include: 1) five from Santa Catalina Island, Los Angeles Co.; 2) one from Riverside Co.; and 3) three from northwestern Baja California. *Cryptantha wigginsii* is commonly found in, but apparently not restricted to, clay soil. Although additional populations may be found now that the taxon has been rediscovered, it is rare enough to warrant future listing as a sensitive and rare plant. Appropriate measures should be taken to preserve existing populations, some of which may be in danger of extirpation. The identification of vouchers of this species from existing herbarium collections highlights the need for depositories of plant collections and for their continued study by taxonomists and systematists.

Key Words: Baja California, Boraginaceae, clay, conservation, *Cryptantha*, *Cryptantha wigginsii*.

Cryptantha is a genus of annual and perennial herbs of the family Boraginaceae. The genus as traditionally defined (*Cryptantha s.l.*) consists of approximately 200 species, distributed in western North America and western South America (Hasenstab-Lehman and Simpson 2012; Simpson 2012). These taxa have been grouped together by a feature of their fruits ("nutlets"), which have a characteristic ventral (adaxial) groove running the length of the nutlet, corresponding to the point of attachment to the central gynobase. Species and infraspecies of *Cryptantha* have been distinguished in large part on the size, shape, sculpturing, and ventral groove morphology of these nutlets. In addition, plant duration, leaf position, leaf morphology, vestiture, calyx morphology, and corolla size, shape, and color can be important in diagnosis and taxon identification (Simpson and Hasenstab 2009; Kelley et al. 2012).

Based on a recent molecular phylogenetic study (Hasenstab-Lehman and Simpson 2012), *Cryptantha s.l.* has been split into five genera: *Eremocarya* (one species), *Greeneocharis* (two species), *Johnstonella* (13 species), *Oreocarya* (ca. 62 species), and a reduced *Cryptantha* s.s. (ca. 120 species). These five genera can be distinguished from one another morphologically (see key in Hasenstab-Lehman and Simpson 2012).

Cryptantha wigginsii I.M. Johnston 1939, a species in *Cryptantha s.s.* of Hasenstab-Lehman and Simpson (2012), was originally described from a 1931 collection made in northwestern Baja California, Mexico by Ira L. Wiggins (*Wiggins 5107*, 2 April 1931; see Table 1). Wiggins cited the

FIG. 1. Scan of holotype specimen of *Cryptantha wigginsii, Wiggins 5107* (GH 00096301).

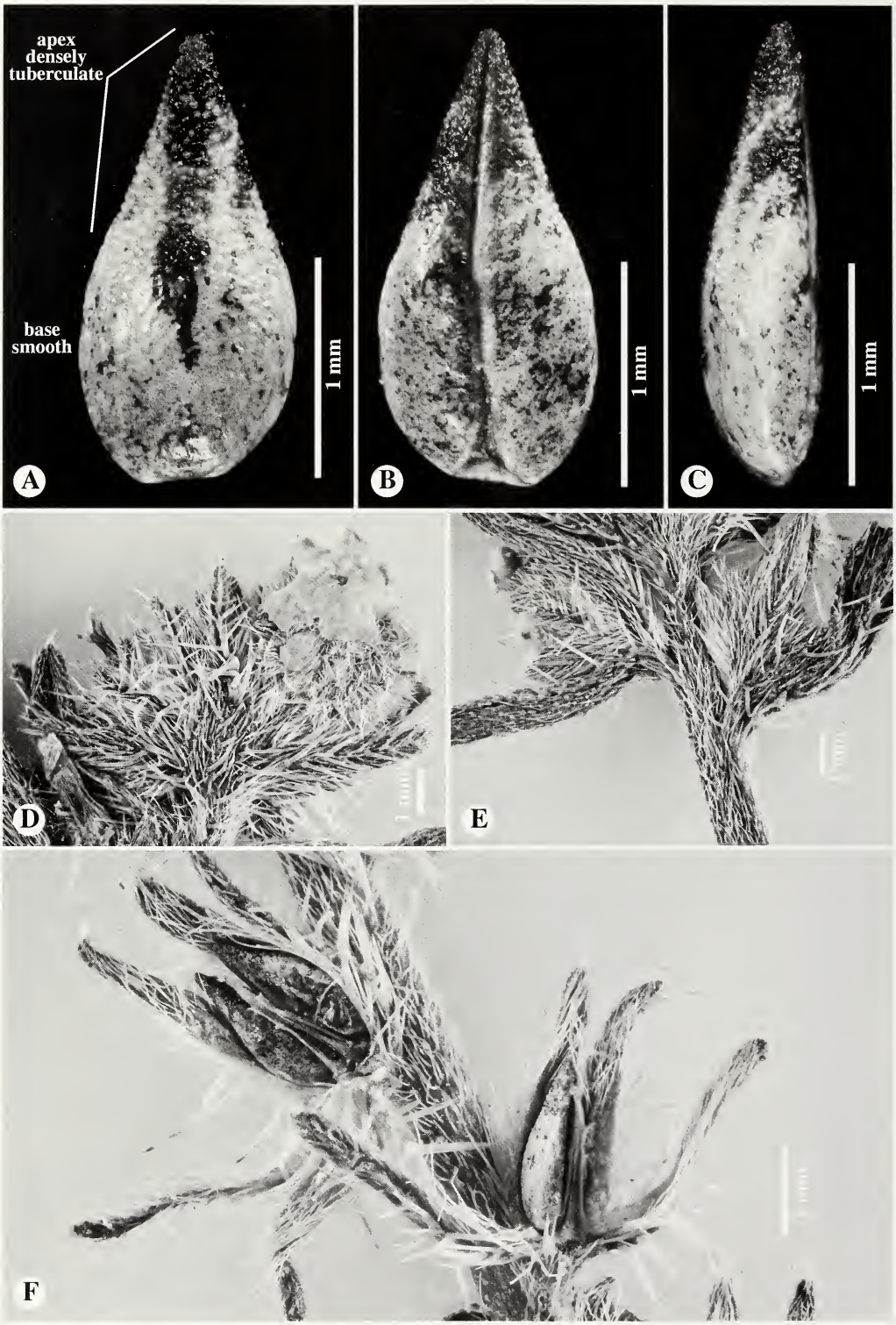

FIG. 2. Images of components of *Cryptantha wigginsii* holotype specimen (GH 00096301). A–C. Nutlets, in dorsal, ventral, and lateral views (left to right). D–E. Inflorescence units, showing open corolla (D) and stem and calyx vestiture (E). F. Fruits, showing calyx and nutlets attached to gynobase.

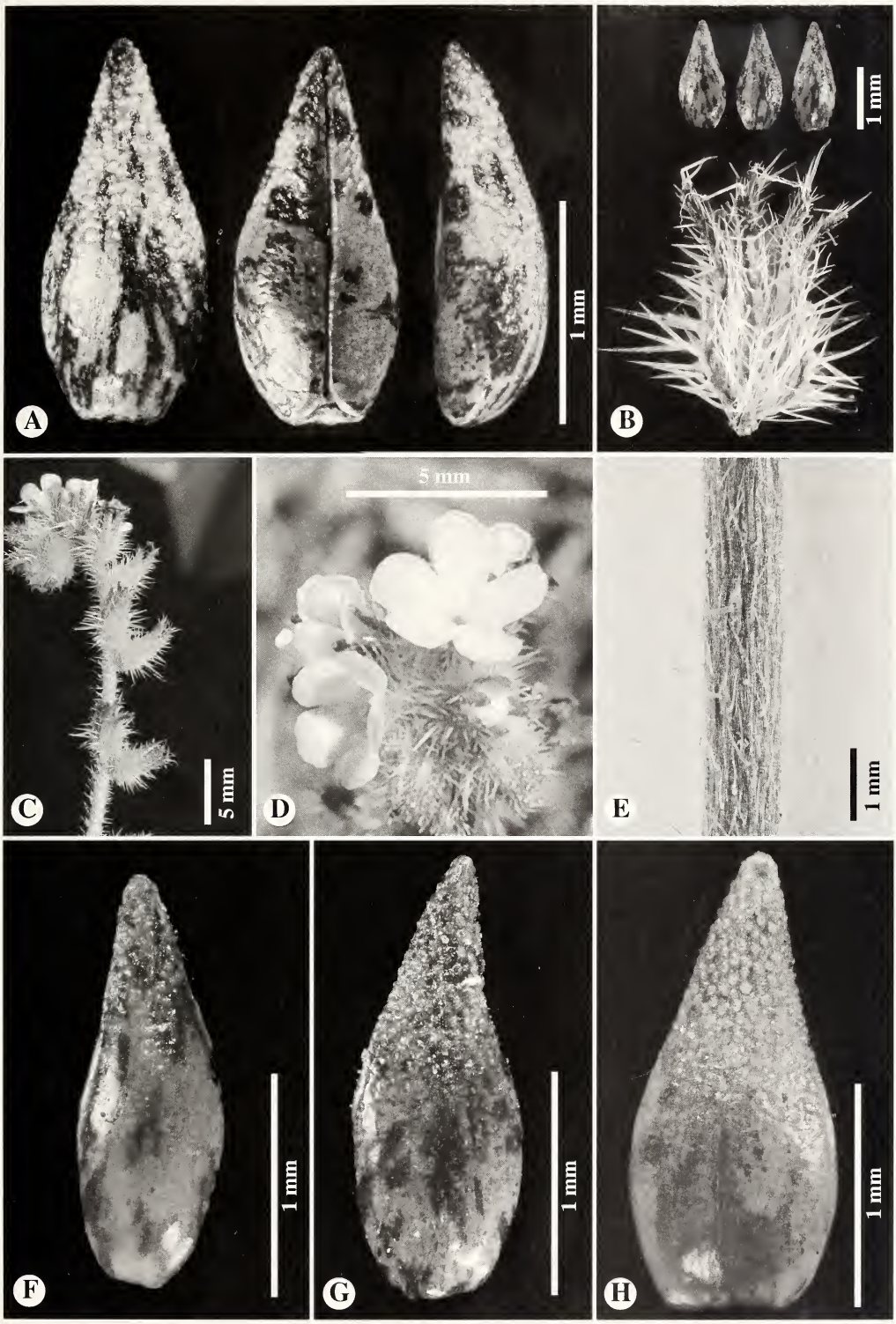

FIG. 3. *Cryptantha wigginsii* from mainland USA. A–G. Carlsbad, San Diego Co. A, B. *McConnell s.n.* (SDSU 19477) voucher. A. Nutlet, in dorsal, ventral, and lateral views (left to right). B. Fruit, with calyx (below) and three nutlets removed (above). C–F. *Simpson 3674* (SDSU 20063) voucher. C. Inflorescence unit, a circinate scorpioid cyme. D. Flowers, with showy, white corollas, the limb up to 5 mm in diameter. E. Close-up of stem below inflorescence unit, showing antrorsely appressed and spreading trichomes. F. Nutlet, dorsal view. G. *Simpson 3675* (SDSU 20019) voucher, nutlet dorsal view. H. Riverside County population. *Boyd 1979* (RSA 407732) voucher, nutlet dorsal view.

TABLE 1. LOCALITY, COLLECTOR, GEO-REFERENCE DATA, ACCESSION NUMBERS, AND COMMUNITY/SUBSTRATE FOR ALL KNOWN POPULATIONS OF *CRYPTANTHA WIGGINSII*, ARRANGED CHRONOLOGICALLY BY COLLECTION DATE. All latitude/longitude data, except that estimated from herbarium label locality information, were obtained from topographic maps or GPS devices (databases various). All specimens, except the type collections, were originally identified as other species of *Cryptantha*. Symbols: [T] = type collection; [H] = holotype; [I] = isotypes; * = latitude/longitude estimated from locality information on herbarium label; ** = *Cryptantha* aff. *wigginsii*.

Population and locality	Collector, collection date	Latitude/longitude (elevation)	Accession no(s).	Community/ substrate
Near Rancho Cuevas, 18 mi S of Tijuana, Baja California, MEXICO	*Wiggins 5107*[T], 2 Apr 1931	32.27/-117.02* (6 m)	GH 00096301[H], RSA 0008263[I], US 00118523[I]	red clay soil, very rocky, gentle slope along ocean
Santa Catalina Island: between Cherry Valley and Howland's Landing, Los Angeles Co., CA, USA	*Fosberg 4934*, 21 May 1931	33.4567/-118.5157* (20 m)	POM 368370	steep slope, facing ocean, upper Sonoran Zone
Santa Catalina Island: Cottonwood Canyon, Los Angeles Co., CA, USA	*Thorne 35850*, 5 Apr 1966	33.3884/-118.4434* (172 m)	SD 69480	rocky, dry, S-facing slope above stream
Santa Catalina Island: N of Marine Science Station at Fisherman's Cove, elev. ca. 150 ft, Los Angeles Co., CA, USA.	*Thorne 42470*, 12 Feb 1973	33.4458/-118.4822* (46 m)	RSA 353854	bare, clayey openings in coastal sage scrub
Punta Mezquite, 1 km S of Medio Camino, Baja California, MEXICO	*Moran 30019*, 13 Mar 1982	32.167/-116.9 (40 m)	SD 110406	common in grassy, cleared area in adobe soil
Southwestern Perris Basin: Hill W of Skunk Hollow, Riverside Co., CA, USA	*Boyd 1979*, 1 May 1986	33.5588/-117.1088* (274 m)	RSA 407732	gabbro substrate; Skunk Hollow vernal pool with silty clay
Ca. 0.1 mi E from Mexican Hwy 1 along dirt road to Ejido Benito Juarez, ca. 1.5 mi S of Colonet, Baja California, MEXICO	*Marsden 20III92B*, 20 Mar 1992	31.0479/-116.2025* (91 m)	SDSU 5460	closed mixed coastal succulent scrub/ open sandy soil
Carlsbad: open space between housing, just W of Hidden Canyon Community Park, ca. 0.5 mi S of Hwy 78, 0.1 mi SW of Vancouver St., San Diego Co., CA, USA	*McConnell s.n.*, 7 May 2010 *McConnell 170*, 1 Jun 2010 *McConnell s.n.*, 11 Mar 2011 *Simpson 3673*, 18 Apr 2012	33.17330/-117.31621 (58 m) 33.173/-117.316 (58 m) 33.17330/-117.31621 (58 m) 33.17329/-117.31615 (71 m)	SD 208177, SDSU 19477 SD 214896 SD 214622, SDSU 19479 SDSU 20062	opening of coastal sage scrub/heavy clay soil
Mesa N of Colonet Mesa, approx. 6 km N of main N-S trending access road at the northern end of Colonet Mesa, and 4 km N of Johnson Ranch. Along a narrow, NW-SE trending dirt road, Baja California, MEXICO	*Guilliams 1796*, 21 Mar 2012	31.14161/-116.28507 (109 m)	SDSU 20081, SD 222116, UC 1999566	plant along upper margin of clayey vernal pool in matrix of maritime succulent scrub
NE Carlsbad, Calavera Hills, Roberston Ranch Preserve, Village X parcel, accessed from dirt road running S-SW from Basin Rd., San Diego Co., CA, USA	*Simpson 3674*, 18 Apr 2012	33.15985/-117.29615 (46 m)	SDSU 20063	opening of coastal sage scrub/ brownish-red, rocky clay soil

Table 1. Continued.

Population and locality	Collector, collection date	Latitude/longitude (elevation)	Accession no(s).	Community/ substrate
Carlsbad open space, ca. 75 m N of College Ave., nearby Crossings golf course, adjacent to undeveloped pad, San Diego Co., CA, USA	*Simpson 3675*, 18 Apr 2012	33.13006/-117.29552 (74 m)	SDSU 20019, SD 222118, UC 1999563	opening of coastal sage scrub/gray-brown, sandy/ gravelly diablo clay
Santa Catalina Island: W-facing road cut, on road between Cherry Cove and Howland's Landing, Los Angeles Co., CA, USA	*Simpson 3682***, 21 Apr 2012	33.45508/-118.51696 (51 m)	SDSU 20031, 20032, UC 1999565	coastal sage scrub/ rocky, tan, silty soil
	*Clohessy s.n.***, 27 May 2012	33.45508/-118.51696 (51 m)	SDSU 20082, SD 222117	
Santa Catalina Island: road cut on N side of St. Catherine Way Rd., ca. 0.25 mi along road S of entrance to Hamilton Cove Villa, Los Angeles Co., CA, USA	*Simpson 3684*, 22 Apr 2012	33.35123/-118.33192 (55 m)	SDSU 20033, UC 1999564	coastal sage scrub/ rocky granite rock, S-facing road cut; gravelly, brown, silty-sand soil

locality as "18 mi. south of Tia Juana, gentle slope along ocean, very rocky, red-clay soil." The holotype specimen resides at the Gray Herbarium (GH 00096301; Fig. 1), with known isotypes at the herbaria of Rancho Santa Ana Botanic Garden (RSA 0008263) and the Smithsonian Institute (US 00118523). In the protologue publication of *Cryptantha wigginsii*, Johnston (1939) noted:

> This is probably a relative of *C. clevelandii* Greene but is readily distinguished from that species and allies by its roughened nutlets. Below the middle the back of the nutlet is smooth lustrous and somewhat mottled. Above the middle the back is roughened by minute wart-like tuberculations or by low sinuous ridges resulting from the confluence of the warts. There are 4 ovules and all frequently mature into nutlets. The abaxial nutlet is always present. The scorpioid cymes are solitary or rarely geminate and are always leafy bracted towards the base.

Johnston described the nutlet number as varying from 1–4, nutlet length as "ca. 2.1 mm long." He described the stem vestiture as sparse, appressed, falcate, and inconspicuous, and corollas with a limb diameter of 3–3.5 mm. (Fig. 2 shows details of the inflorescence, flowers, and nutlets of the *C. wigginsii* holotype.) We note that *C. clevelandii* Greene (with two varieties: var. *clevelandii* and var. *florosa* I.M. Johnston), which appears to be the closest relative to *C. wigginsii*, differs in having nutlets that are smooth and glossy throughout, lacking any tuberculations. From our qualitative observations, *C. wigginsii* appears to resemble *C. clevelandii* var. *c.* in stem pubescence, having both appressed and spreading trichomes, whereas *C. clevelandii* var. *florosa* has predominantly spreading trichomes. On the other hand, *C. wigginsii* resembles *C. clevelandii* var. *florosa* in having a larger corolla limb width, a more inclined calyx, and a greater nutlet number [the last described as "1–4" in *C. wigginsii* (Johnston 1939)], "(1–2)3–4" in *C. clevelandii* var. *florosa,* and "1–2" in *C. clevelandii* var. *clevelandii* (Kelley et al. 2012).

Wiggins (1980), in his *Flora of Baja California*, lists *C. wigginsii* in the key to *Cryptantha* taxa, indicating that the species occurs on "coastal slopes between Tijuana and Ensenada; endemic to B.C." But aside from the original 1931 type collection, there were no known specimens of *Cryptantha wigginsii* (BajaFlora 2011; CCH 2011; Kartesz 2011; SEINet 2011), and this taxon had been presumed extinct. However, specimens collected at a single site in Carlsbad, San Diego Co., California (*McConnell s.n.*, 7 May 2010 (SD, SDSU); *McConnell 170,* 1 Jun 2010 (SD); *McConnell s.n.*, 11 Mar 2011 (SD, SDSU) were subsequently identified as *Cryptantha wigginsii* (Fig. 3A, B; Table 1). These constituted a new county, state, and national record for this taxon. These plants fit the holotype specimen and Johnston's (1939) description. Subsequent field surveys documented two other populations in the Carlsbad region (Fig. 3C–G; Table 1), resembling the first population in all respects. However, the corolla of these and other populations was observed to be up to 5 mm when measured in the field (e.g., Fig. 3D), larger than what Johnston reported. It should be noted that corollas of *Cryptantha* may shrink significantly upon drying, and Johnston's description was based on dried herbarium material.

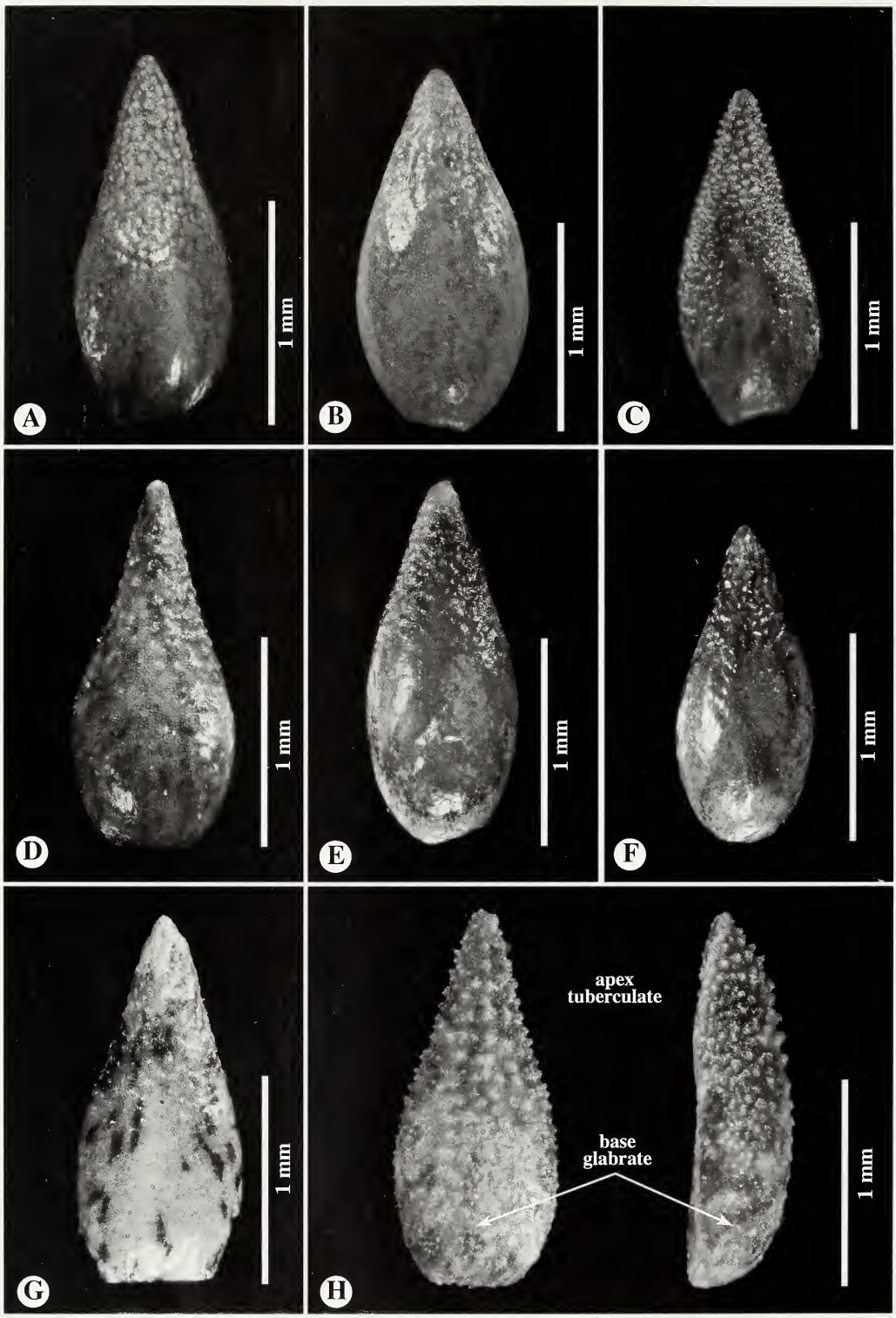

FIG. 4. A–G. *Cryptantha wigginsii.* A–C. Nutlets, dorsal view, from additional populations in Baja California, Mexico. A. *Marsden 20III92B* (SDSU 5460) voucher. B. *Moran 30019* (SD 110406) voucher. C. *Guilliams 1796* (UC 1999566) voucher. D–G. Nutlets, dorsal view, from sites on Santa Catalina Island, Los Angeles Co. D. *Fosberg 4934* (POM 368370) voucher. E. *Thorne 35850* (SD 69480) voucher. F. *Thorne 42470* (RSA 353854) voucher. G. *Simpson 3684* (SDSU 20033) voucher. H. *Cryptantha* aff. *wigginsii, Simpson 3682* (SDSU 20031) voucher, nutlet, dorsal view. Note more numerous, but less dense, tubercles extending to near nutlet base, base becoming glabrate.

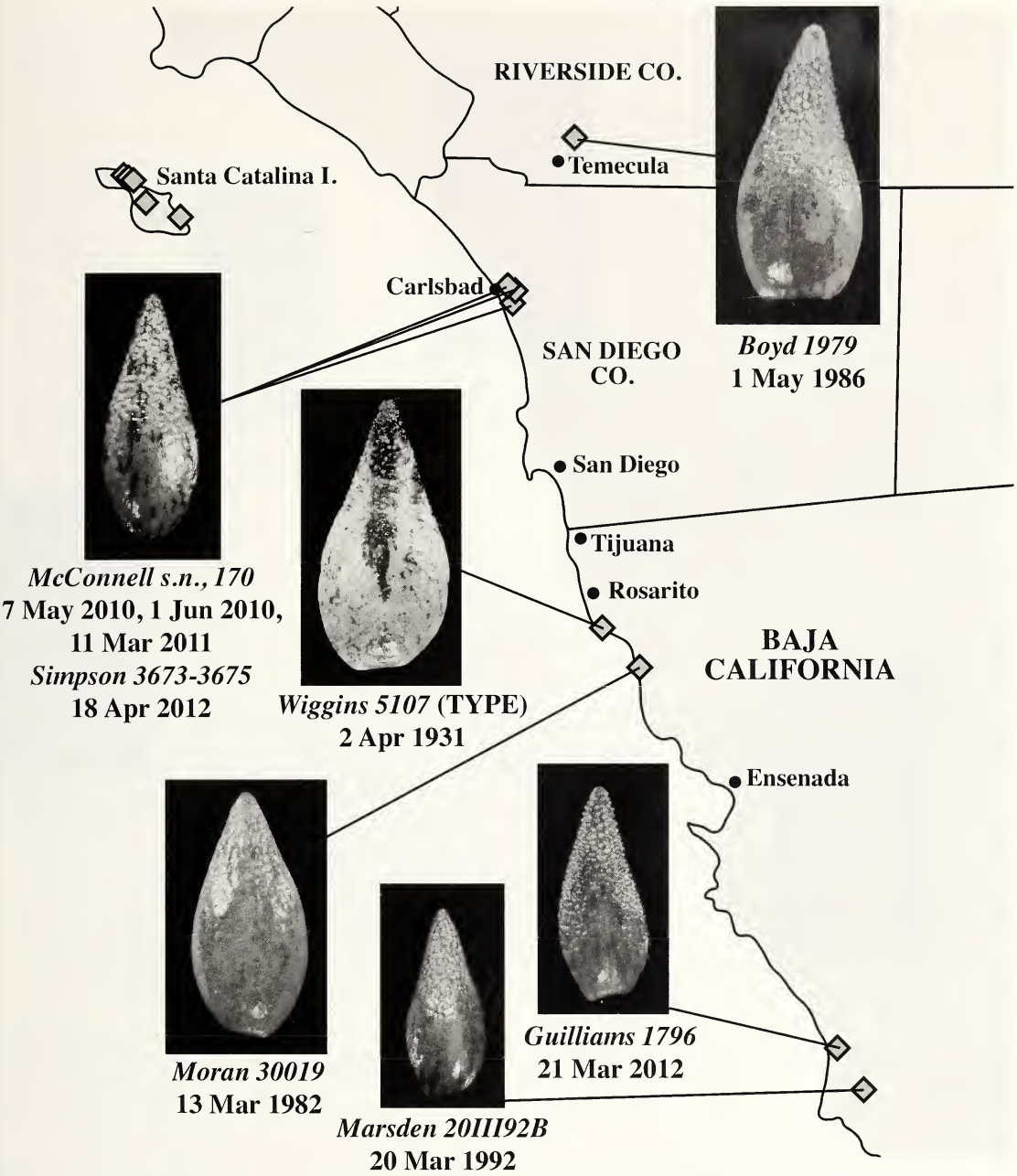

FIG. 5. Distribution map of *Cryptantha wigginsii* on mainland, with nutlet images shown to scale.

A search of specimens at RSA-POM, SD, SDSU, and UC-JEPS revealed six additional populations of this species (Figs. 3H, 4A, B, D–F; Table 1), all of which had previously been identified as other *Cryptantha* species, usually as *C. clevelandii*. In addition, recent field surveys have documented one additional population in northwestern Baja California (Fig. 4C) and two on Santa Catalina Island (Fig. 4G, H; Table 1). These additional collections have expanded the known range of *C. wigginsii* to include a total of four populations (including the type locality) in northwestern Baja California, one in Riverside Co., five on Santa Catalina Island, Los Angeles Co., and the three, adjacent populations in Carlsbad, San Diego Co.

An examination of fruit morphology of these specimens reveals some variation in nutlet size, coloration, and (most importantly) sculpturing of the known populations of *C. wigginsii*. Nutlets of the mainland San Diego Co. (Fig. 3A–G) and Riverside Co. (Fig. 3H) populations and of the two southernmost populations in northwestern

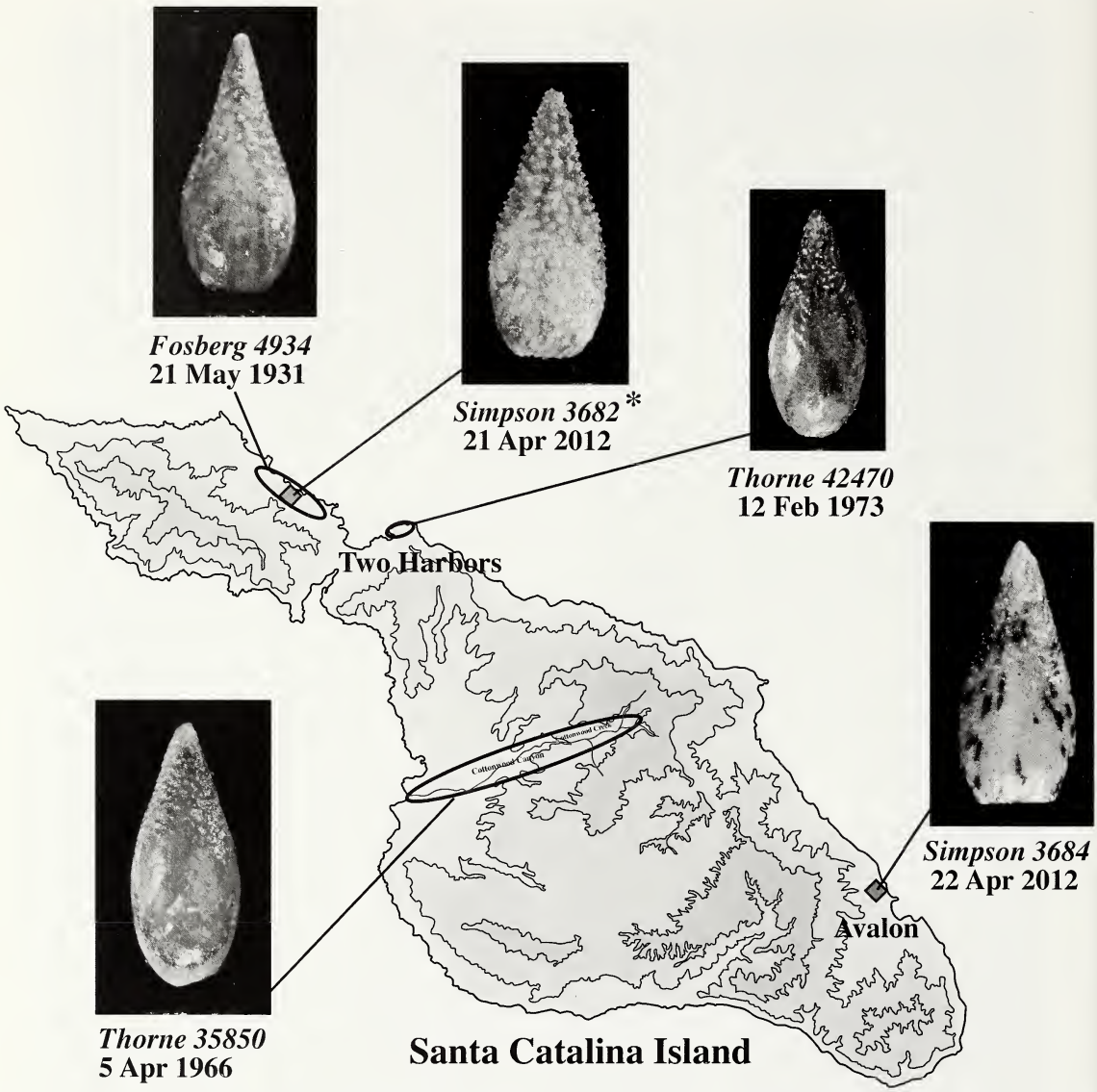

FIG. 6. Distribution map of *Cryptantha wigginsii* and *C.* aff. *wigginsii* (*) on Santa Catalina Island, with nutlet images shown to scale. Isoclines delimit elvations of 0–200 m (light gray), 200–400 m (medium gray), and 400–600 m (dark gray).

Baja California (Fig. 4A, C) have the characteristic sculpturing pattern of the type specimen (Fig. 2A–C), being smooth and glossy in the lower half and densely tuberculate in the upper half, on both dorsal (abaxial) and ventral (adaxial) surfaces. Nutlets of the other population of coastal, northwestern Baja California (Fig. 4B) are less densely tuberculate in the apical region. Those of four of the five Santa Catalina Island, Los Angeles Co. vouchers (Fig. 4D–G) are also less densely tuberculate than the type material, but otherwise appear to belong to this species. However, one recent collection (*Simpson 3682*, SDSU), found in the same general region as a 1931 collection (*Fosberg 4934*, POM), is quite different in having nutlets with numerous, but much less dense, tubercles extending to the base, with the extreme basal region glabrate (Fig. 4H). This specimen also has a slightly larger calyx, 4–5 mm long, as opposed to 3–4 mm long in typical *C. wigginsii*. This collection, which is in all other respects like typical *C. wigginsii* and fits no other known species in the genus, we refer to here as *C.* aff. *wigginsii*. Further investigations will be needed to determine if this should be treated as a separate taxon.

Distribution maps (Figs. 5, 6) show that almost all populations of *C. wigginsii* are near

the coast, with the exception of the Riverside Co. voucher. The substrate for five of the nine known populations of *C. wigginsii* is a clay soil, described as "red clay soil, very rocky," "gabbro substrate," "heavy clay soil," "heavy crumbly clay soil," "dark gray sandy diablo clay," "brownish-red rocky clay soil," "gray-brown sandy/gravelly diablo clay," "bare, clayey openings," "upper margin of clayey vernal pool," or "adobe soil." The substrates of other populations are described as "rocky, dry," "silt," "silty sand," "rocky, tan, silty soil," or "gravelly, brown silty-sand soil." Two collections lack substrate descriptions. Thus, a common substrate appears to be clay, suggesting that *C. wigginsii* may preferentially grow on clay, but other substrate types occur. The surrounding community type for *C. wigginsii*, where documented, is a "closed mixed coastal succulent scrub community," "maritime succulent scrub," or "coastal sage scrub or opening of coastal sage scrub." Elevation ranges from 6–274 m (20–900 ft); Table 1.

Cryptantha wigginsii can be readily distinguished from other members of the genus. In recent keys to California taxa of *Cryptantha s.l.* (e.g., Simpson and Hasenstab 2009; Kelley et al. 2012), *C. wigginsii* would correspond to the group with ebracteate flowers and nutlets (at least one) that are rough, homomorphic, and with rounded margins. *Cryptantha wigginsii* is distinctive and unique within this group in having nutlets that are basally smooth and apically tuberculate, generally densely so. The rediscovered species requires an addition to the key of the *Cryptantha s.l.* of California of Kelley et al. (2012) as follows (abbreviated with addition in bold):

1. Bracts present; generally annual, generally wider than tall, often rounded to cushion-like; root generally red-purple, staining
1′ Bracts generally 0; annual or perennial herb, generally taller than wide (rounded or cushion-like); root generally not red-purple
7. Biennial to perennial herb; leaves generally basal or tufted; nutlet wide-rounded to obtuse at tip; tip of attachment scar groove well below nutlet tip
7′ Generally annual; leaves generally cauline; nutlet narrow-acute to acuminate at tip; tip of attachment scar groove ± to nutlet tip
23. Nutlets ± smooth
23′ Nutlets, or at least 1, rough
46. At least 1 nutlet with all or part of margin a ± flat rim (occasionally seeming sharp-angled) or wing
46′ All nutlets with margin rounded or sharp-angled, not a ± flat rim or wing
55. Nutlets 2–4, dissimilar in 1 fruit, 1 more persistent, >other(s), of similar textures or not
55′ Nutlets 1–4, generally of similar persistence, size, texture
Nutlets basally smooth, apically tuberculate. . . . . ***C. wigginsii***
Nutlet sculpturing uniform at base and apex

Given that collections of *C. wigginsii* are known to date from only 13 populations (Table 1; Figs. 5, 6), despite our search in major California herbaria, we conclude that this taxon is rare. An attempt in April 2012 to find the species on Santa Catalina Island was successful in only one of the three localities known from vouchers (this population is the morphologically different *C.* aff. *wigginsii*, cited earlier), and one new population was located (Fig. 6). An attempt, also in April 2012, to re-locate the species in the area known from a voucher in Riverside Co. was unsuccessful, although it should be pointed out this was a relatively dry year. With regard to current protection, all Carlsbad populations are under management (Contract and Conservation Easement) by the Center for Natural Lands Management (CNLM) and can therefore be considered protected. However, two of the Carlsbad populations straddle developed edge, and therefore risk extirpation from fuel-clearance activities, over-irrigation/seepage, landscape dumping, and erosion, and will therefore require regular visitation in perpetuity (McConnell personal observation). The Riverside Co. population ("Southwestern Perris Basin: Hill W of Skunk Hollow," in an unincorporated area north of Temecula called French Valley) is on land owned and managed by CNLM and is protected in perpetuity under a Conservation Easement. Threats to the Riverside Co. population are unlikely, but can only be assessed when and if individuals of the population are relocated. The three known populations at Santa Catalina Island are most likely protected, given they are within the land holdings of the Catalina Island Conservancy (2012). The conservation status of the Baja California populations of *C. wigginsii* is unknown. However, the two known populations near Colonet are potentially in danger, given the proposal by the Mexican government for the construction of a massive port nearby (Clark et al. 2008; Harper et al. 2011).

Additional populations of *C. wigginsii* may yet be discovered in Mexico and the United States, especially given the now heightened awareness of this taxon. However, we feel that the rarity of this species justifies listing in the California Native Plant Society (CNPS) Inventory of Rare and Endangered Plants (2012), a process underway. Subject to further field studies in the near future, *C. wigginsii* may warrant listing at the California state and/or federal level. Appropriate measures should be taken to preserve existing populations

of this species. It is hoped that future studies will also evaluate the morphological variation, phylogenetic relationships, and specificity of this taxon to a clay substrate.

Lastly, this discovery highlights the need for active collection of plant specimens, their storage and maintenance in herbaria, and their continued study by scientific experts. Half of the discovered populations of *C. wigginsii* were identified from specimens in existing herbarium collections, having been mistaken as other species. This constitutes yet another example of the "thousands of plant species undiscovered in cupboards" (Bowdler 2010).

Acknowledgments

We wish to acknowledge Steven Boyd for relaying information about the Riverside Co. population of *C. wigginsii*; the Catalina Island Conservancy, Linda Farley, John Clark, and Kim Klementowkski for help in logistics with field work; Jorge Montiel, Michael Park, Nicole Beasley, Gavin Bridgeman, Emma Clohessy, Chris Orosz, and Lori L. Simpson for help in field collecting; Lee M. Simpson and Regina Dowdy for help with photography; and the herbaria at RSA, SD, SDSU, and UC-JEPS for access to their specimens used to verify the identity *C. wigginsii* vouchers.

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A NEW SPECIES OF *CRYPTANTHA* (BORAGINACEAE) FROM THE SIERRA DE SAN PEDRO MÁRTIR, BAJA CALIFORNIA, MEXICO

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Abstract

Cryptantha martirensis M. G. Simpson & Rebman is described as new, being endemic to high elevations of the Sierra de San Pedro Mártir of Baja California, Mexico. It is sparse to common in the understory of coniferous woodland and in montane arroyos, slopes, and ridges in sandy to gravelly granitic substrates. This new species is similar to *C. muricata* (Hooker & Arnott) A. Nelson & J. F. Macbride in having nutlets with a shallow, dorsal ridge. It differs from the three recognized varieties of *C. muricata* in having a combination of tall and virgate primary stems with short and clustered inflorescence units; stems with mostly appressed and a few sparse, fine, spreading trichomes; a small corolla limb; and relatively large nutlets with dorsal tubercles that are low, rounded, and few per area. Quantitative evidence justifying these differences is summarized.

Key Words: Baja California, Boraginaceae, *Cryptantha*, *Cryptantha martirensis*, *Cryptantha muricata*, Mexico, Sierra de San Pedro Mártir.

Upon observing all known specimens of what had been identified as *Cryptantha* sp., *C. muricata* (Hooker & Arnott) A. Nelson & J. F. Macbride, or *C. muricata* var. *denticulata* I. M. Johnst. from high elevations of the Sierra de San Pedro Mártir, Baja California, we noticed several distinctive differences between these plants and any other *Cryptantha* species, including *C. muricata* and its known varieties (see below). We propose that these differences are sufficient to recognize these populations as a new species of *Cryptantha,* utilizing a taxonomic (morphologic) concept (Cronquist 1978, 1988) in which taxa are circumscribed based on the discontinuity of features.

Taxonomy

Cryptantha martirensis M. G. Simpson & Rebman, sp. nov. (Figs. 1–4). —TYPE: MEXICO, Baja California, Sierra de San Pedro Mártir, SE of Vallecitos and approximately 3 mi (4.8 km) s of the Observatory, along the highest ridge en route to Pedro's Dome (Fig. 4), conifer forest with *Pinus jeffreyi, Abies concolor, Eriogonum wrightii* var. *oresbium, Philadelphus microphyllus,* and *Hesperocyparis montana*, mostly granitic substrates, 2630 m elev., 31.00803°N, 115.43591°W, 30 September 2008, *J. Rebman 15993*, with V. Marshall and M. Dykens (holotype: SD; isotypes: BCMEX, RSA, SDSU, UC).

Plant a terrestrial, annual, herb. **Root** a taproot, staining herbarium paper purple in some specimens. **Primary** stem erect, virgate, 35–70 cm tall, giving rise to several, elongate, inclined secondary (lateral) branches, those near the base often very thin; stem trichomes ca. 0.5–1.5 mm long, whitish, thin, tapered, straight to slightly curved, mostly appressed, a few sparse, fine horizontal to ascending, all often with minute bulbous base. **Leaves** simple, basal and cauline, sessile, spiral; basal leaves narrowly oblanceolate, 12–30 mm long, withered at anthesis; cauline leaves narrowly oblanceolate to linear, 15–40 mm long, 2 mm wide; all leaves with similar vestiture on both surfaces, trichomes ca. 1 mm long, whitish, thin, tapered, straight to slightly curved, inclined to appressed, those near leaf apex often with prominent, white, swollen base surrounded by tessellated rosette of often whitish, radially-oriented cells. **Inflorescence** unit a tightly clustered (often spheric) to elongate scorpioid cyme, 5–10 mm long, arising at nodes along length of primary axis or apex of primary and lateral branches, often with subtending inclined to reflexed, straight to recurved bracts, similar to cauline leaves. **Flowers** ebracteate, inclined to appressed, pedicellate. **Pedicels** ca. 0.5 mm long. **Calyx** appearing valvate at maturity, basally synsepalous, ca. 3.0 mm long, adaxially glabrous, abaxially hirsutulous along lobe margins and scattered on surface, trichomes straight to slightly curved, mostly appressed to ascending (ca. 0.5–2 mm long), midrib raised/ridged, hirsute, bearing straight, mostly inclined, bulbous-based bristles ca. 1–1.8 mm long. **Calyx lobes** lance-ovate, narrowly acute. **Corolla** rotate-salverform, sympetalous, white, tube ca. 1.5 mm long, limb ca. 1 mm wide. **Stamens** uniseriate, 5, epipetalous,

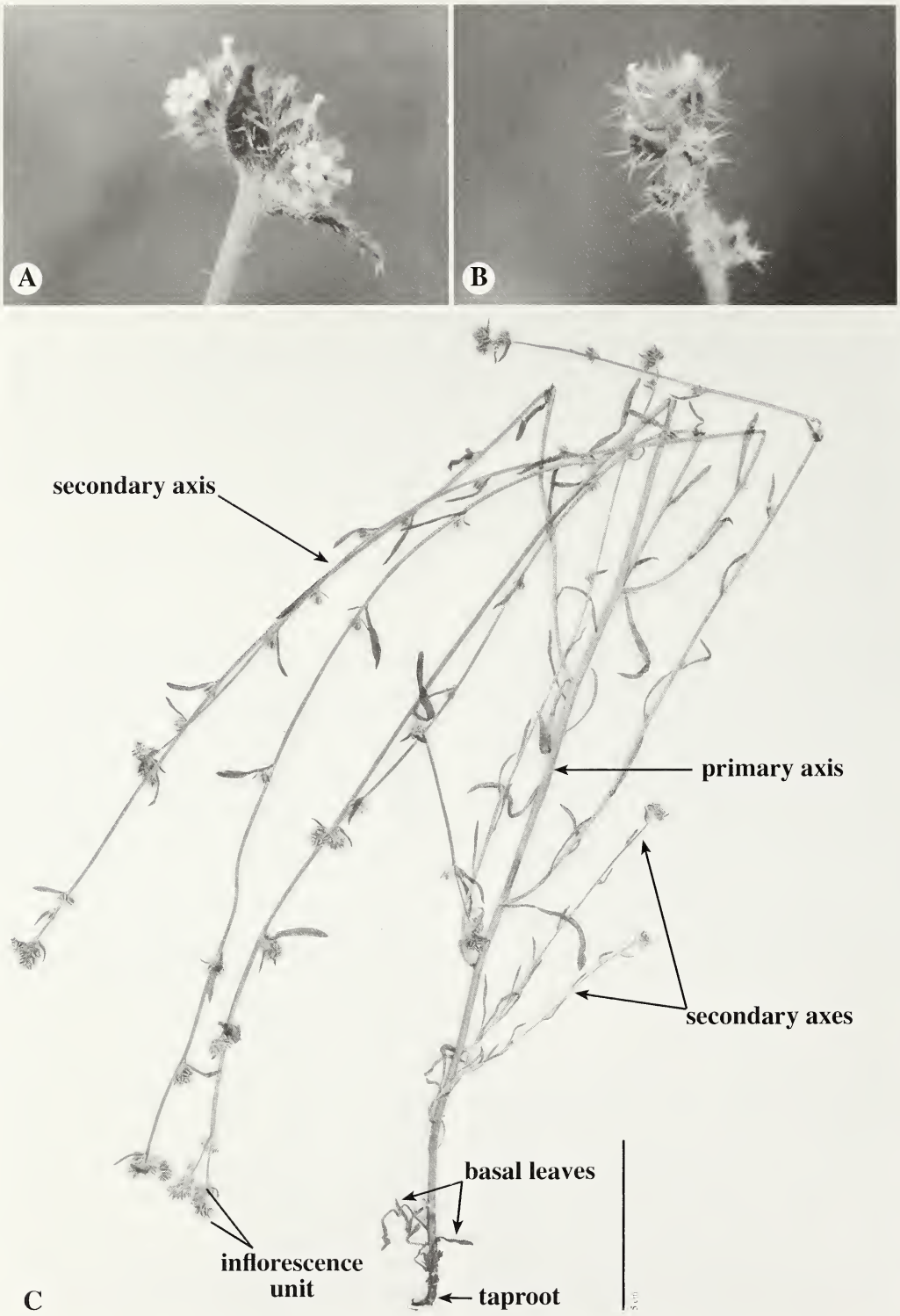

FIG. 1. *Cryptantha martirensis*. A–B. Photographs in native habitat (*Rebman 16022*). A. Inflorescence unit in flower. B. Inflorescence unit in fruit. C. Pressed specimen (*Rebman 15993,* type specimen), showing elongate (virgate) primary axes and short inflorescence units.

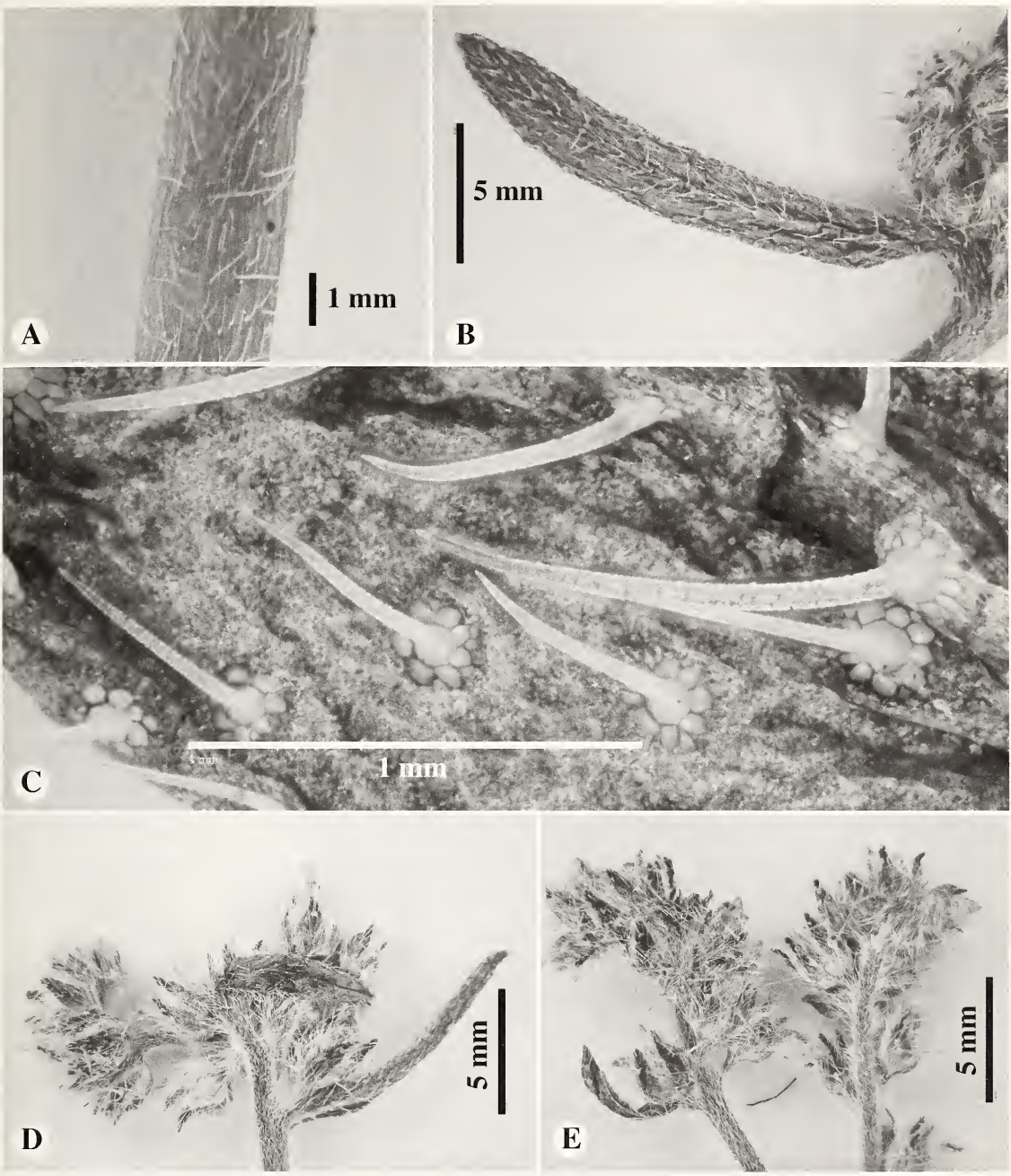

FIG. 2. *Cryptantha martirensis* (*Rebman 15993,* type specimen). A. Aerial stem close-up, showing thin, tapered, straight to slightly curved, mostly appressed trichomes. B–C. Inflorescence unit bract, similar to cauline leaf. B. Whole view. C. Close-up, adaxial surface, showing tapered trichomes with swollen base surrounded by tessellated rosette of radially-oriented cells. D. Inflorescence unit, in flower. E. Inflorescence unit, fruiting stage.

whorled, alternipetalous, distinct. **Gynobase** 4-flanged, narrowly oblong to oblanceolate in outline, ca. 1.4 mm long. **Style** terete, slightly ridged, ca. 0.7 mm long beyond gynobase, slightly surpassing fruit at maturity. **Stigma** minute, sub-capitate. **Fruit** a schizocarp of usually 4 nutlets with the surrounding calyx accessory. **Nutlets** 1.8–2.0 mm long, 1.2–1.4 mm wide, light tan-gray to brown, mottled, ovate, base truncate, margin angled (ca. 45°) in cross-section, sometimes slightly ridged and/or minutely tuberculate or scalloped, apex acute, ventral surface papillate and sparsely tuberculate, dorsal surface densely papillate and sparsely to moder-

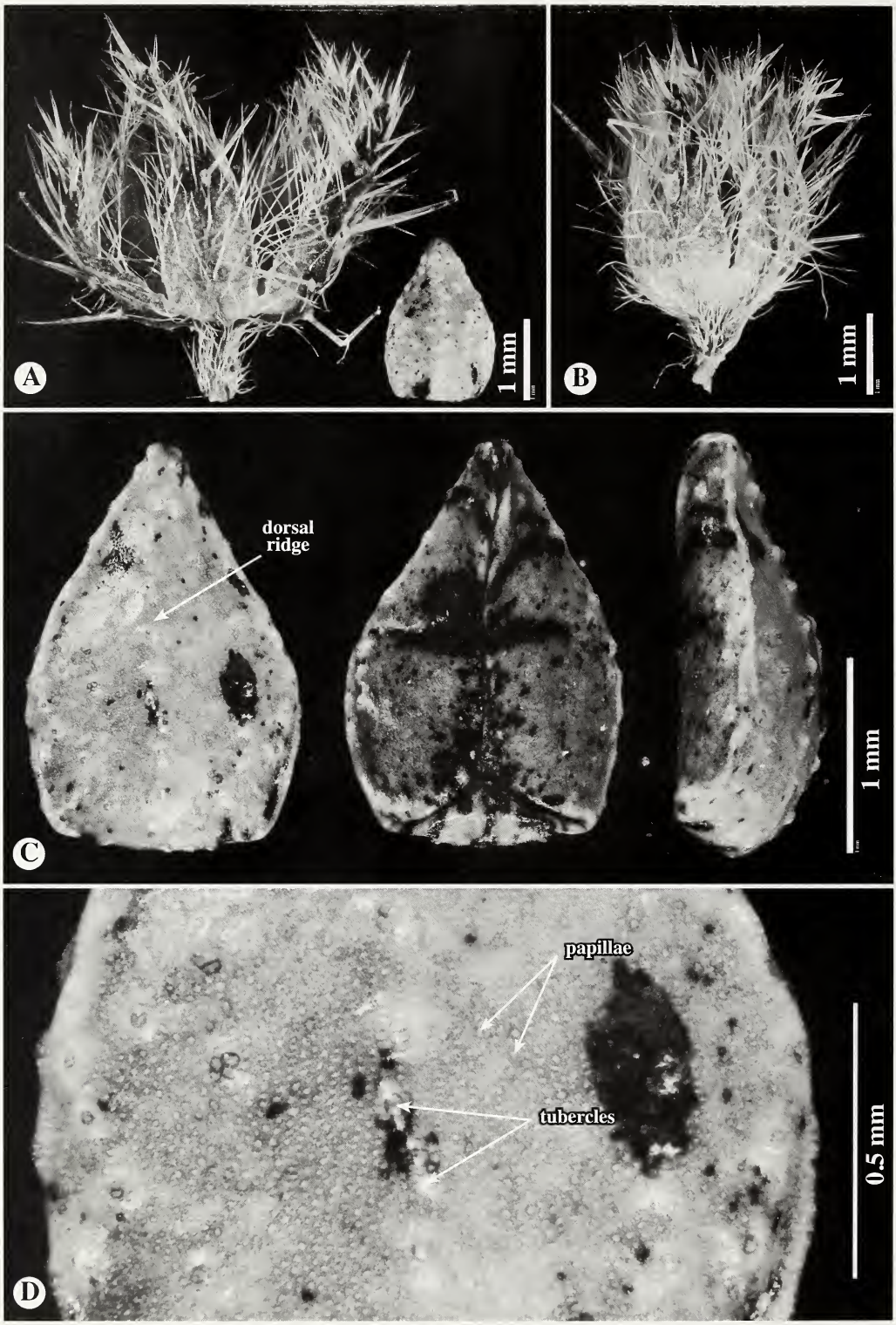

FIG. 3. *Cryptantha martirensis*. A. Calyx in fruit, with one of four nutlets (*Rebman 16022*). B–D. (*Rebman 15993*, type specimen). B. Calyx in fruit. C. Nutlet, in dorsal (left), ventral (middle) and lateral (right) views. Note dorsal ridge. D. Nutlet dorsal surface, close-up. Note numerous papillae and low tubercles.

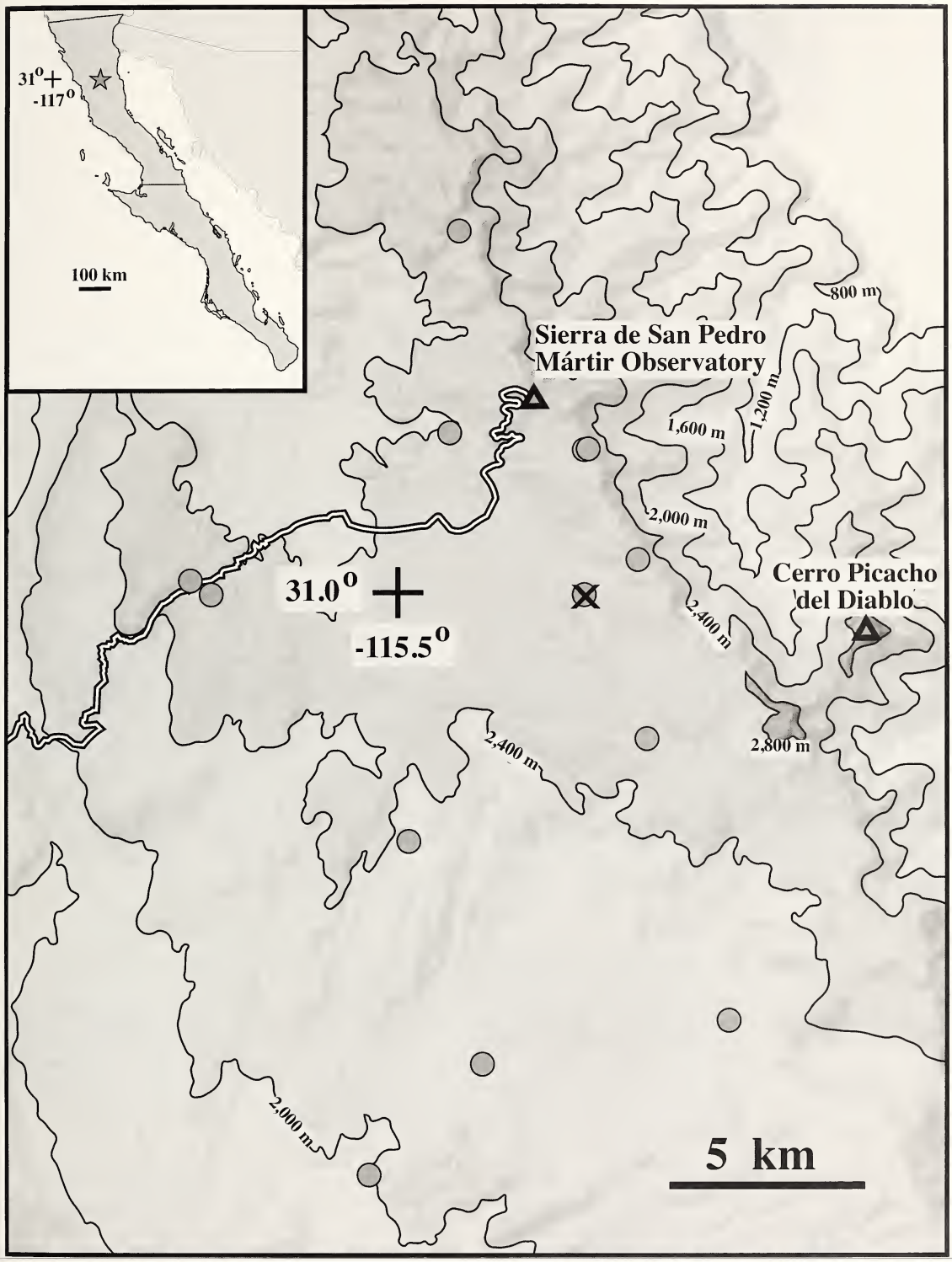

FIG. 4. Map showing the geographic distribution of the 13 known collections (circles) of *Cryptantha martirensis* from the Sierra de San Pedro Mártir. Locality indicated with "X" is that of the type specimen, *Rebman 15993*.

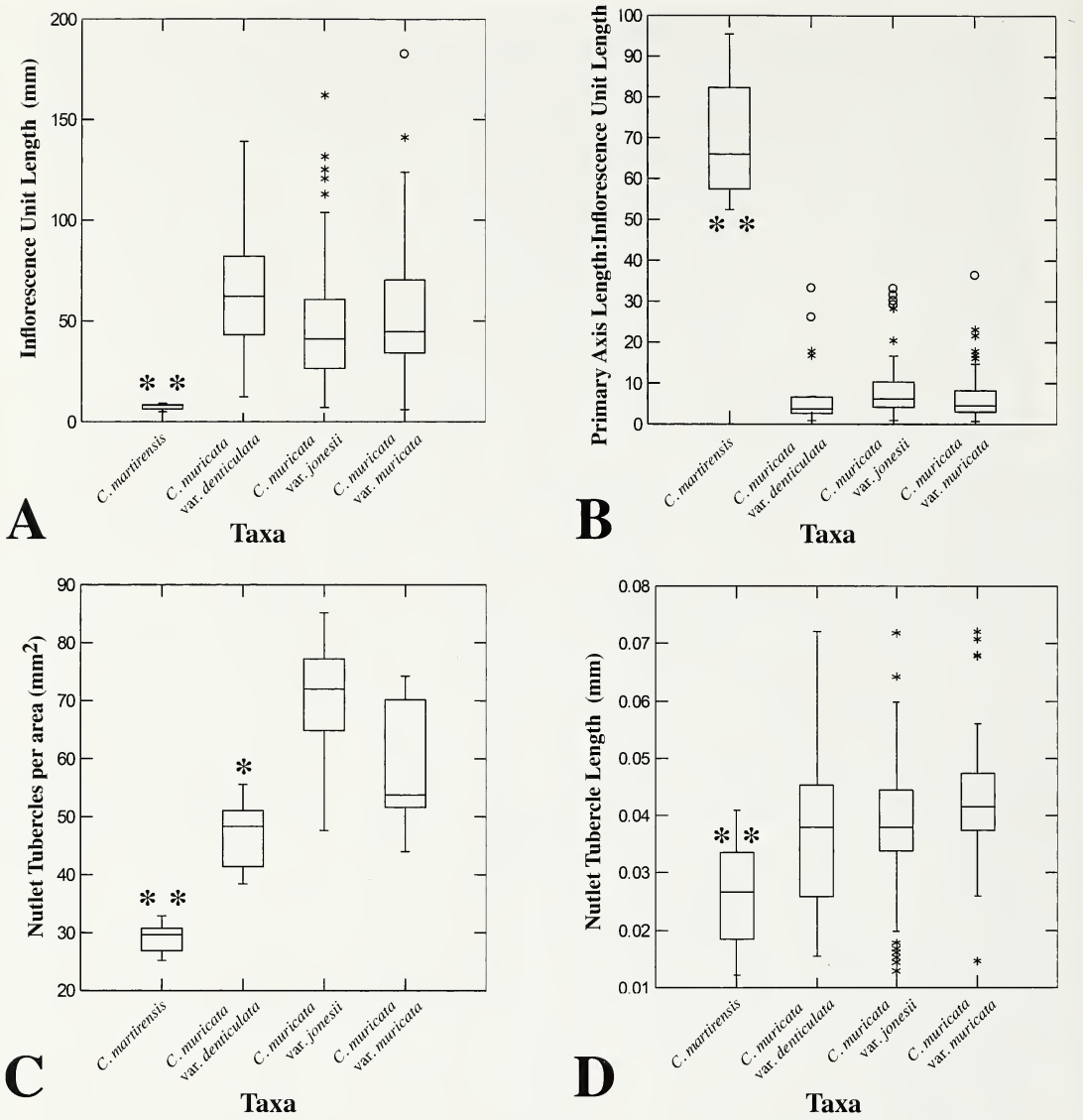

FIG. 5. Box plots of single characters, comparing *C. martirensis* with the three varieties of *C. muricata*. A. Inflorescence unit length (mm), that of *C. martirensis* significantly shorter ($P < 0.01$). B. Ratio of primary axis length:inflorescence unit length, that of *C. martirensis* significantly greater ($P < 0.01$). C. Nutlet tubercle number per area, dorsal face, that of *C. martirensis* significantly smaller ($P < 0.01$). D. Nutlet tubercle length, that of *C. martirensis* significantly smaller ($P < 0.01$), but with overlap of range. Note: box plots show median (middle horizontal line), first and third quartiles (lower and upper horizontal lines, respectively), and the range of the data outside the first and third quartiles (vertical lines). Outliers represented by "x," "*," and small circles. Statistical difference between a given taxon and all other taxa (via ANOVA Tukey post hoc test) is indicated as: ** = $P < 0.01$, * = $P < 0.05$ (probability that difference between groups due to chance alone).

ately tuberculate (tubercles denser at apex); median ridge present, low (obscure), often lighter-colored, sparsely tuberculate; ventral groove narrow, closed near apex, slightly open below, 2-forked at base, forks horizontal to slightly reclined; groove borders prominent, rounded, slightly up-curved basally. See Figs. 1–3.

Cryptantha martirensis is similar to *C. muricata* and varieties, differing in having a combination of elongate, virgate primary stems; axes with mostly appressed and a few sparse, fine, spreading trichomes; small corollas (limb ca. 1 mm wide); short (5–10 mm long) inflorescence axes; and relatively large (1.8–2.0 mm long) nutlets with dorsal tubercles that are low, rounded, and relatively few per area.

Cryptantha martirensis is found in usually sandy or gravelly soil and/or soil and rocks of granitic origin. Most records describe it in the understory of conifer or mixed conifer forest

(*Pinus jeffreyi, Abies concolor*, occasionally *Populus tremuloides*) with mixed shrubs and herbs (including *Ceanothus cordulatus, Eriogonum wrightii* var. *oresbium, Salvia pachyphylla, Silene laciniata*, and *Symphoricarpos* sp.), although some records describe the habitat as an arroyo, meadow margin, slope, or summit ridge. The species is cited as being scarce to common in different localities and habitats. *Cryptantha martirensis* is known only from high elevation (1900–2800 m) locations in the Sierra de San Pedro Mártir of Baja California, Mexico. Plants flower from as early as May to as late as early August and develop mature fruits from June to September.

The specific epithet, *martirensis*, is after the Sierra de San Pedro Mártir, ("mountains of Saint Peter the martyr"), to which this species is endemic. The suggested common name for the species is the Sierra de San Pedro Mártir cryptantha.

Paratypes (all from the Sierra de San Pedro Mártir and arranged alphabetically by collector; see Fig. 4 for map of localities): MEXICO, Baja California, Yerba Buena, scarce, in sandy soil of arroyo, 31.00°N, 115.45°W, 2500 m elev., 16 August 1967, *Moran 14161* (SD 79684); Los Llanitos, 30.967°N, 115.433°W, 2550 m elev., 17 August 1967, *Moran 14272* (RSA, SD 79685); La Grulla, scarce, under pines, 30.893°N, 115.478°W, 2100 m elev., 22 August 1967, *Moran 14493* (SD 79676); east slope of Cerro "2828", on east rim, occasional on east slope, 31.033°N, 115.45°W, 2800 m elev., 24 August 1968, *Moran 15412* (SD 68921); north slope of Cerro "2828", occasional in gravelly soil, 31.033°N, 115.45°W, 2800 m elev., 14 September 1968, *Moran 15624* (SD 69127); south summit ridge, Cerro Venado Blanco, occasional in gravelly granitic soil, 31.083°N, 115.483°W, 2750 m elev., 15 September 1968, *Moran 15635* (SD 69098); El Alto de Corona, fairly common under pines, 31.00°N, 115.55°W, 2400 m elev., 28 July 1970, *Moran 17909* (SD 76440); La Víbora, Arroyo la Grulla 4.0 km SW of La Grulla, occasional in sand by stream, 30.867°N, 115.508°W, 1900 m elev., 10 August 1977, *Moran 24465* (SD 97701); La Tasajera region, SW of Observatory, approx. 7 mi (11.3 km) S of the Observatory Road, *Pinus jeffreyi, Abies concolor, Populus tremuloides*, granite rocks and sand, annual, flowers white, 30.94389°N, 115.49722°W, 2285 m elev., 15 September 1998, *Rebman 5569* (SD 152066); along the road to Venado Blanco, N of Vallecitos and the main road to the Observatory, conifer forest with *Pinus jeffreyi, Abies concolor, Eriogonum wrightii* var. *oresbium, Silene laciniata*, and *Symphoricarpos*, annual, flowers white, rare. 31.03694°N, 115.48556°W, 2400 m elev., 29 September 2008, *Rebman 15973* (SD 191478, SDSU 18625); in vicinity of the campground along the road to Proyecto Condor approximately 0.25 mi (400 m) NE of the SSPM office and formal entrance, about 4 mi (6.4 km) W of Vallecitos and about 6 mi (9.7 km) SW of the Observatory, conifer forest with *Pinus jeffreyi, Abies concolor, Ceanothus cordulatus, Salvia pachyphylla*, and *Eriogonum wrightii* var. *oresbium*, mostly granitic substrates, annual, common, 31.00302°N, 115.55461°W, 2500 m elev., 30 September 2008, *Rebman 16022* (SD 191477); La Encantada, about rocks at margins of meadow, 30.9030°N, 115.4116°W (lat./long. estimated from locality data), 2200 m elev., 18 September 1930, *Wiggins 4880* (SD 67578).

Taxonomic Relationships

Cryptantha martirensis appears to be a close relative of *Cryptantha muricata* (Hooker & Arnott) A. Nelson & J. F. Macbride, Botanical Gazette 61:42, 1916, a species of subtribe Cryptanthinae (Hasenstab-Lehman and Simpson 2012) of the Boraginaceae. *Cryptantha muricata* occurs in California, Nevada, and Arizona in the U.S. (Kartesz 2011; Kelley et al. 2012) and in Baja California and Sonora of Mexico (BajaFlora 2012; SEINet 2012). This species is the sole member of section Muricatae (Johnston 1925; cited in Abrams 1951). Johnston diagnosed section Muricatae as "Nutlets 4, verrucose or coarsely tuberculate, triangular-ovate, decidedly homomorphous, back obtuse, and bearing a suggestion of a medial ridge, with sides evidently angled and beaded; style usually surpassing the nutlets though rarely only equaling them." Given that *C. martirensis* also has four homomorphic nutlets per fruit that are tuberculate with a medial ridge, we propose that it may be tentatively placed in section Muricatae; however, molecular phylogenetic studies are needed to verify the monophyly of this group.

Johnston (1925) treated *C. muricata* as having three, intergrading varieties (a view upheld in recent treatments, e.g., Kelley et al. 2012): var. *denticulata* (Greene) I. M. Johnston, var. *jonesii* (A. Gray) I. M. Johnston, and var. *muricata*. Variety *muricata*, which is found mostly in the central-western mountains and Transverse Ranges of California, is distinctive in having a large corolla limb, a stout and well-differentiated central (primary) aerial stem axis, and relatively large nutlets with a sculpturing that is muricate (having radially elongate, rounded processes that are longer than broad, accounting for the epithet name, *muricata*). Variety *denticulata*, which occurs in higher elevation regions of the Sierra Nevada, Tehachapi, Transverse, and White/Inyo mountains of California, and in western Arizona and Nevada, differs in having primary and secondary axes not well differentiated, a small corolla, and large nutlets with generally low, rounded tubercles (with rounded processes shorter

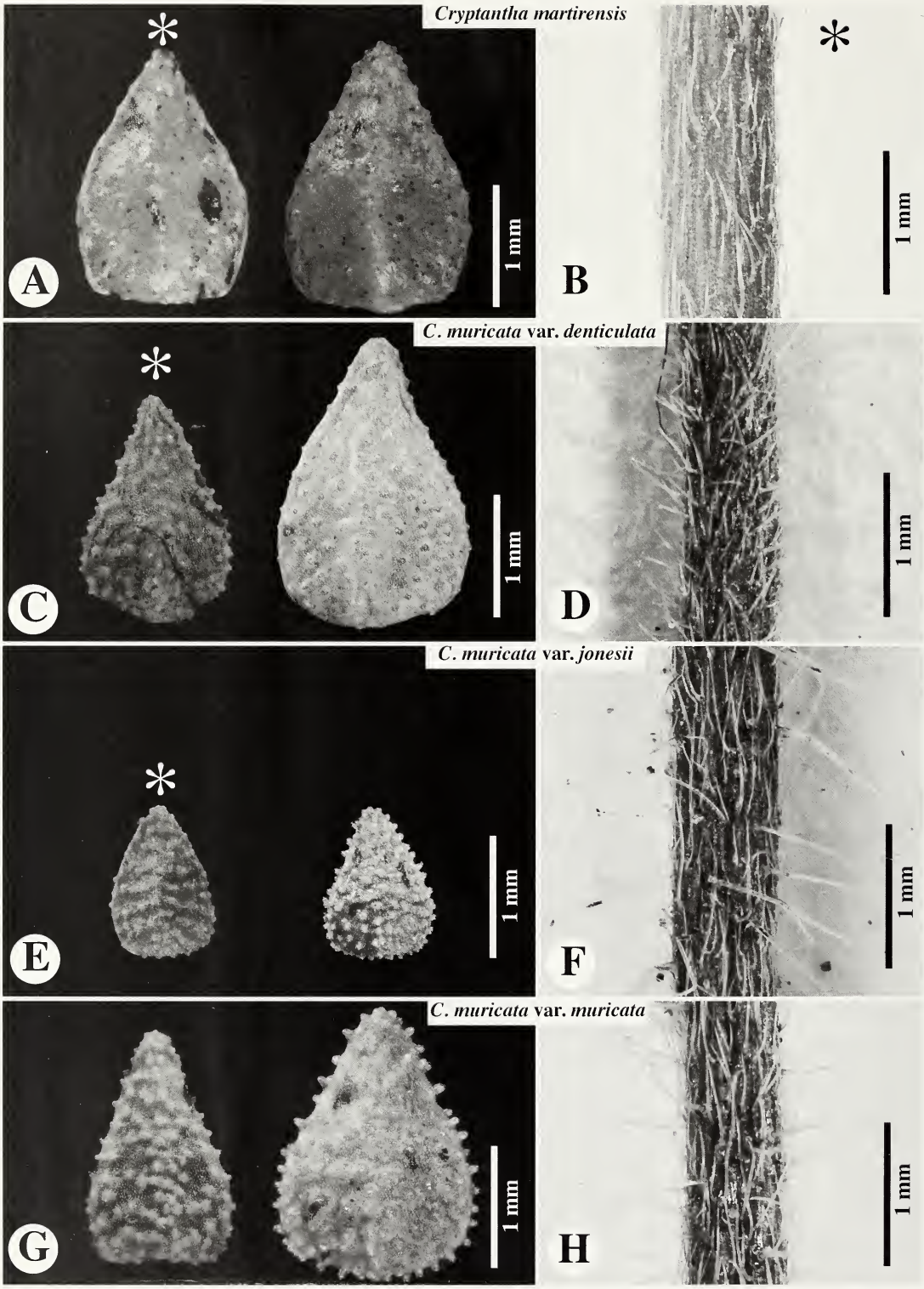

FIG. 6. Comparisons of nutlets and inflorescence axis of investigated taxa. A–B. *Cryptantha martirensis*. A. Nutlets (left = *Rebman 15993;* right = *Rebman 15973*). B. Inflorescence axis (*Rebman 15993*). C–D. *Cryptantha muricata* var. *denticulata*. C. Nutlets (left = *Curran s.n.,* CAS 123277; right = *Simpson 2910*). D. Inflorescence axis (*DeDecker 3354*). E–F. *Cryptantha muricata* var. *jonesii*. E. Nutlets (left = *Jones 79* [GH 97680]; right = *Howe 996*).

than broad). Variety *jonesii*, which occurs in the North and South Coast Ranges, Transverse and Peninsular ranges and adjacent coastal areas, the eastern Sierra Nevada foothills of California, western Arizona, and as far south as the central desert of Baja California, resembles var. *muricata* in aerial stem morphology but resembles var. *denticulata* in corolla size and has nutlets that are usually smaller than either variety with a muricate sculpturing (Kelley et al. 2012).

Quantitative Analyses and Classification

Specimens of *Cryptantha muricata* and *C. martirensis* from herbaria at IRVC, RENO, RSA-POM, SBBG, SD, SDSU, UC-JEPS, and UNLV were studied as part of a larger project (Simpson et al. unpublished; Appendix 1) evaluating the taxonomic validity of the recognized varieties of this species. Twenty-three specimens of *C. muricata* var. *denticulata*, 97 specimens of *C. muricata* var. *jonesii*, and 83 specimens of *C. muricata* var. *muricata*, and eight of the 13 known specimens of *C. martirensis* were included in this larger morphometric study. A statistical analysis of primary axis length, inflorescence unit length, corolla width, nutlet tubercle length, and nutlet tubercle number dorsal face (both per nutlet and per area of the dorsal face) was conducted. To visualize character distributions by taxon, box plots showing the median and the four quartiles of distribution were prepared for these characters. Each of these was evaluated for statistically significant differences by taxon using analysis of variance (ANOVA), with multiple comparisons made between the taxon means using the Tukey post hoc test. Taxa that were statistically different from all other taxa in a particular character are indicated as such (at probabilities <0.01) in the box plot diagrams. All statistical analyses were performed in SYSTAT, Version 11 (Systat Software, Inc., San Jose, CA).

Qualitative observations and quantitative measurements from all known populations of *C. martirensis* confirm that the species is distinctive in the length of the inflorescence unit (a scorpioid cyme), which in *C. martirensis* is significantly shorter ($P < 0.01$) than the three varieties of *C. muricata* (Fig. 5A). *Cryptantha martirensis* has an elongate primary axis, but this is not significantly longer than other varieties (not shown). However, the correlated ratio of primary axis:inflorescence unit length in *C. martirensis* is significantly greater than the three varieties of *C. muricata* (Fig. 5B). Nutlet length of var. *martirensis* overlaps with those of the other three varieties (not shown), although *C. muricata* var. *jonesii* tends to have smaller nutlets. However, both the number of tubercles per area (Fig. 5C) and the nutlet tubercle length (Fig. 5D) of *C. martirensis* is significantly smaller than that of the three *C. muricata* varieties, the former without and the latter with overlap of range.

We considered treating this new taxon as a variety of *C. muricata*, given its similarity in nutlet morphology, being four per fruit, homomorphic, tuberculate to muricate, and with a median ridge. *Cryptantha martirensis* does resemble and overlap with varieties of *C. muricata* in several features. The branching pattern of *C. martirensis* is similar to that of *C. muricata* vars. *jonesii* and *muricata*, although the primary (and often secondary) axes are generally longer and thinner, being more virgate ("wand-like"). The range of corolla size of *C. martirensis* is very similar to that of *C. muricata* vars. *denticulata* and *jonesii*. Nutlet size of *C. martirensis* is very similar to that of *C. muricata* vars. *denticulata* and *muricata*. However, *C. martirensis* is distinctive from the varieties of *C. muricata* in having: 1) a significantly shorter inflorescence cyme unit, with no overlap (Fig. 5A, B); 2) nutlets with significantly fewer tubercles per area (Fig. 5C) and significantly shorter tubercles, though overlapping with those of *C. muricata* var. *denticulata* (Fig. 5D; see Fig. 6); and 3) stem axis trichomes mostly appressed, with qualitatively sparser and finer spreading trichomes (Fig. 6). We believe that these three distinctive morphological features of *C. martirensis*, along with its isolated geographic distribution having no known intergradation with *C. muricata*, warrant its species status by a taxonomic (morphologic) species concept (Cronquist 1978, 1988).

We speculate that *C. martirensis* may represent the descendant of a past relictual population or the product of long-distance dispersal. Its isolation in the Sierra de San Pedro Mártir region has perhaps resulted in barriers to gene flow and the evolution of a unique combination of morphological features. However, we know nothing about the phylogenetic relationships within this complex; that is the goal of future molecular studies.

←

F. Inflorescence axis (*Boyd 6316,* SBBG 101675). G–H. *Cryptantha muricata* var. *muricata*. G. Nutlets (left = *Smith 4697*; right = *Simpson 3034*). H. Inflorescence axis (*Simpson 3034*). * = Type specimen. (Note: the type specimen of *C. muricata* var. *muricata,* D. Douglas *s.n.* (GH 00097575) is immature and lacks nutlets.)

Taxonomic Key to *Cryptantha Martirensis* and Varieties of *Cryptantha Muricata* (modified from Kelley et al. 2012)

1. Corolla limb 3–8 mm in diameter . . . . . ***C. muricata*** var. ***muricata***
1′ Corolla limb 1–3.5 mm in diameter
   2. Nutlets 1.1–1.3(1.9) mm long, muricate, tubercles generally elongate . . . . . ***C. muricata*** var. ***jonesii***
   2′ Nutlets 1.8–2.0 mm long, tuberculate, tubercles generally low, rounded
      3. Primary stem axis 11–53 cm long, not obviously different from secondary axes; inflorescence unit, including stalk, 12–140 mm long. . . . . ***C. muricata*** var. ***denticulata***
      3′ Primary stem axis 35–68 cm long, prominent, elongate, virgate; inflorescence unit, including stalk, 5–10 mm long. . . . . ***C. martirensis***

Geography

The geographic range of *Cryptantha martirensis* is one of the most restricted of any species of *Cryptantha s.s.* (*sensu* Hasenstab-Lehman and Simpson 2012), with known populations occupying an area less than 200 km^2 (80 mi^2; Fig. 4). Elevation range of specimen collections is 1900–2800 m. Wiggins (1980) cited *C. muricata* as occurring in Baja California but recognized no varieties for the species. Based on our current knowledge, *C. muricata* var. *jonesii* is the only variety of this species known to occur in Baja California, found in mountainous and coastal regions of the northwestern portion of the state to as far south as the central desert (BajaFlora 2012). In the Sierra de San Pedro Mártir region, we have discovered only one collection of *C. muricata* var. *jonesii* in an adjacent canyon (Cañón del Diablo) at a lower (1550 m) elevation (*Moran 25642*, 6 May 1978, SD 100241). Other *Cryptantha s.l.* taxa in this area include *Eremocarya micrantha* (Torrey) Greene var. *lepida* J. F. Macbride [*Cryptantha m.* (Torrey) I. M. Johnston var. *l.* (A. Gray) I. M. Johnston] and *C. simulans* Greene (Thorne et al. 2010; BajaFlora 2012).

The Sierra de San Pedro Mártir is a floristically diverse region of great botanical importance, having a natural fire regime and being the southern continuous limit of the California Floristic Province (Riemann and Ezcurrra 2007; Thorne et al. 2010). The higher elevations comprise the Parque Nacional Sierra de San Pedro Mártir, established in 1947. Thorne et al. (2010) reviewed the vascular plant flora of the "high" Sierra de San Pedro Mártir, defined as being greater than 1800 m in elevation. These authors cited 453 species native to this region. Of these taxa, 23 species and two varieties (including the recently described *Calyptridium parryi* var. *martirense*; see Guilliams et al. 2011) are endemic to the Sierra de San Pedro Mártir, slightly over 5%. To this we add yet another species, increasing the endemic flora of this interesting region.

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Appendix 1

List of voucher specimens of *Cryptantha martirensis* and varieties of *C. muricata* examined for the morphometric analysis, in order by collector within each taxon.

C. martirensis: *Moran 14161* (SD 79684); *Moran 14272* (SD 79685); *Moran 15412* (SD 68921); *Moran 15624* (SD 69127); *Moran 15635* (SD 69098); *Rebman 15993* (SD 191476); *Rebman 16022* (SD 191477); *Rebman 5569* (SD 152066). ***C. muricata* var. *denticulata***: *Anonymous 1225* (SDSU 5401); *Batholomew s.n.* (SBBG 63779); *Clokey 7001* (POM 255821); *Clokey 7001* (RSA 19960); *Curran s.n.* (CAS 123277); *DeDecker 2988* (RSA 273709); *DeDecker 3354* (SBBG 47796); *DeDecker 3576* (RSA 618916); *DeDecker 4878* (RSA 620298); *DeDecker 5229* (RSA 624848); *Gross 1282* (RSA 699885); *Higgins 25402* (RENO 405345); *Honer 1218* (RSA 682027); *Honer 1245* (RSA 682014); *Honer 1275* (RSA 682033); *Honer 338* (RSA 682639); *Howell 40157* (RSA 595061); *Kennedy 1917* (RENO 13686); *Munz 15086* (POM 229454); *Secrest s.n.* (SBBG 37365); *Simpson 2908* (SDSU 17552); *Simpson 2910* (SDSU 17554); *Spalding s.n.* (POM 368165); *Tiehm 1754* (RENO 34423). ***C. muricata* var. *jonesii***: *Abrams 3418* (POM 156385); *Ackley* (SBBG 63609); *Anderson 43B* (SDSU 13783); *Beauchamp 3301* (SBBG 92221); *Beauchamp 3301* (SD 128345); *Betzler 502* (IRVC 277); *Betzler 502* (IRVC 27758); *Boughey 204* (IRVC 15122); *Boyd 4032b* (RSA 524238); *Boyd 6316* (RSA 543848); *Boyd 6316* (SBBG 101675); *Brandegee s.n.* (POM 64391); *Brandegee s.n.* (POM 71557); *Brandegee s.n.* (RENO 31260); *Brandegee s.n.* (RENO 31261); *Burch 8V96C* (SDSU 12174); *Cain 725* (SDSU 18490); *Chandler 2416* (SBBG 45326); *Chandler 2418* (SBBG 23094); *Chandler 2426a* (RSA 321805); *Chandler 2426a* (SBBG 22707); *Chandler 2632* (SBBG 25522); *Chandler 2656a* (SBBG 25484); *Clokey 5818* (RENO 15621); *Dearing 4851* (SBBG 6266); *Elvin 2695* (IRVC 28285); *Estrella 59* (SDSU 15671); *Fosberg 10679* (POM 338000); *Fosberg 10686* (UNLV 25687); *Gallup 224* (SDSU 5395); *Glenn 20* (RSA 656912); *Gross 1775* (RSA 711527); *Gross 1817* (RSA 711556); *Guillians 312* (SDSU 17357); *Guilliams 357* (SDSU 17539); *Guilliams 366* (SDSU 17542); *Haid s.n.* (SBBG 34216); *Hardham 10430* (SBBG 19499); *Hardham 1389* (SBBG 109613); *Hasenstab 22* (SDSU 18328); *Hoffmann* (SBBG 63782); *Hoffmann* (SBBG 63808); *Hoffmann* (SBBG 63809); *Hoffmann* (SBBG 63810); *Hoffmann* (SBBG 63811); *Hoffmann* (SBBG 63776); *Hoffmann s.n.* (SBBG 63807); *Howe 1522* (SDSU 5407); *Howe 4700* (SDSU 5411); *Howe 996* (SD 27675); *Howe 996* (SDSU 5422); *Johnston s.n.* (RSA 499834); *Jones* (SBBG 63778); *Jones 3405* (POM 71371); *Jones 79* (GH 97680); *Jones 79* (GH 97681); *Jones s.n.* (POM 71537); *Karnes 71* (SDSU 16304); *Karnes 71* (SDSU 16305); *Kraebel s.n.* (SBBG 11222); *Lauri 404* (SDSU 16714); *Marsh s.n.* (IRVC 19460); *Marsh s.n.* (SDSU 5413); *Myrick 833* (SBBG 28428); *Parish 11118* (RSA 499713); *Piehl 63544* (SBBG 19075); *Pollard s.n.* (SBBG 37255); *Reed 4124* (POM 96629); *Reiser 4-II-88* (SDSU 14567); *Roberts 5787* (IRVC 28143); *Roos 4732* (RSA 662061); *Ross 2854* (RSA 525098); *Sanders 26481* (IRVC 26327); *Sanders 6537* (UNLV 23020); *Sanders 9036* (UNLV 30634); *Simpson 12III88C* (SDSU 5428); *Simpson 2263* (SDSU 19322); *Simpson 2462* (IRVC 30815); *Simpson 2462* (SDSU 17210); *Simpson 2790* (SDSU 19296); *Simpson 2794* (SDSU 17573); *Simpson 2885* (SDSU 17512); *Simpson 2894* (SDSU 17551); *Simpson 3822* (SDSU 18310); *Smith 4786* (SBBG 83057); *Smith 8323* (SBBG 83070); *Spalding s.n.* (RSA 499833); *Taylor 17263* (JEPS96822); *Thorne 38079* (RSA 633326); *Thorne 52830* (RSA 309664); *Tucker 2720* (RSA 115221); *Twisselmann 9930* (SBBG 21646); *Wheeler 2527* (RSA 611443); *Whittaker SJ-2* (IRVC 283); *Whittaker SJ-28* (IRVC 279); *Whittaker SJ-345* (IRVC 276); *Zabriskie s.n.* (SBBG 53352). ***C. muricata* var. *muricata***: *Beauchamp 2265* (SBBG 92228); *Blakley 4036* (SBBG 13155); *Blakley 7340* (SBBG 85224); *Blakley 7341* (SBBG 85223); *Boyd 9395* (RSA 599821); *Boyd 9554* (RSA 599530); *Boyd 9820* (RSA 600065); *Chandler 2426a* (SBBG 22803); *Chandler 2475* (SBBG 22915); *Chandler 3671* (RSA 535943); *Chandler 3671* (SBBG 97609); Clokey 5667 (RENO 15620); *Davidson 2810* (RSA 499708); *Denslow 1084* (RSA 679206); *Donahue* (RSA 499693); *Douglas s.n.* (GH 97575); *Gross 442* (RSA 660818); *Hardham 12750* (SBBG 107289); *Hardham 18247* (SBBG 109273); *Hardham 918* (SBBG 106802); *Hardham 995* (SBBG 106799); *Hasenstab 31* (SDSU 18343); *Helmkamp 5496* (IRVC 28175); *Hoffmann* (SBBG 63786); *Hoffmann* (SBBG 63787); *Hoffmann s.n.* (SBBG 63781); *Hoffmann s.n.* (SBBG 63788); *Hoffmann s.n.* (SBBG 63793); *Hoffmann s.n.* (SBBG 63795); *Hoffmann s.n.* (SBBG 63796); *Hoffmann s.n.* (SBBG 63798); *Hoffmann s.n.* (SBBG 63799); *Hoffmann s.n.* (SBBG 63800); *Hoffmann s.n.* (SBBG 63801); *Hughes 7855* (SBBG 119335); *Johnston 1950* (POM 3905); *Johnston s.n.* (POM 7910); *Jones s.n.* (POM 72218); *Junak 4211* (SBBG 94000); *Marsh s.n.* (IRVC 19457); *Meinke 352* (UNLV 25262); *Mulroy 2979* (IRVC 22526); *Mulroy 3625* (IRVC 21516); *Niles 4752* (UNLV 37537); *Niles 4795* (UNLV 37585); *Philbrick s.n.* (SBBG 42677); *Pollard s.n.* (SBBG 63785); *Purer 6553* (SD 39203); *Roberts 4939* (RSA 599646); *Ross 2499* (RSA 517128); *Ross 3512* (RSA 597275); *Ross 3520* (RSA 597266); *Ross 3772* (RSA 597401); *Ross 3914* (RSA 567176); *Ross 7628* (RSA 578276); *Ross 7685* (RSA 578246); *Ross 7941* (RSA 580301); *Ross 8038* (RSA 579449); *Ross 8440* (RSA 596019); *Ross 8521* (RSA 596911); *Sanders 21993* (IRVC 28524); *Sanders 25987* (IRVC 26334); *Sanders 26051* (IRVC 26363); *Sanders 26095* (IRVC 28379); *Sanders 26609* (IRVC 26233); *Simpson 3034* (SDSU 19185); *Simpson 3035* (SDSU 19186); *Smith 1127* (SBBG 85060); *Smith 1569* (SBBG 6265); *Smith 1983* (SBBG 95323); *Smith 3658* (SBBG 85063); *Smith 4037* (SBBG 85062); *Smith 4697* (SBBG 85061); *Smith 5565* (SBBG 85056); *Smith 6096* (SBBG 85050); *Smith 6392* (SBBG 86451); *Smith 983* (SBBG 6262); *Swinney 7281* (RSA 730260); *Thompson 3178* (IRVC 4840); *Twisselmann 12985* (SBBG 28572); *Wheeler 754* (SBBG 45092); *White 7855* (RSA 674776); *Whittaker SJ-13* (IRVC 281).

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MONARDELLA EPLINGII, A NEW SPECIES FROM THE BLACK MOUNTAINS OF NORTHWESTERN ARIZONA, USA

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Abstract

Monardella eplingii Elvin, A. C. Sanders, & J. L. Anderson (Lamiaceae), a new species from the Black Mountains of northwestern Arizona is described and illustrated. This new species is similar to *M. arizonica* Epling, *M. eremicola* A. C. Sanders & Elvin, *M. robisonii* Epling, *M. mojavensis* Elvin & A. C. Sanders, *M. boydii* A. C. Sanders & Elvin, *M. linoides* A. Gray subsp. *linoides*, and *M. linoides* subsp. *erecta* (Abrams) Elvin & A. C. Sanders. It differs from these taxa in leaf and bract morphology, pubescence on the stems and calyces, soil and geologic affinities, and distribution. A key is included for the *Monardella* of the eastern Mojave Desert region.

Key Words: Arizona, Black Mountains, Epling, Lamiaceae, Mojave Desert, *Monardella*.

Monardella Bentham (Lamiaceae) is a complex genus that occurs throughout western North America in Mexico, the United States, and Canada. There are over 30 species of annuals and perennials with more than 50 taxa currently recognized. Since first being described in 1834 (Bentham 1834), 215 names and combinations have been published in *Monardella* and the synonymous genus *Madronella* Greene (IPNI 2012). During recent taxonomic work for the publication of *The Jepson Manual, 2nd ed.* (Baldwin et al. 2012), nine new taxa were described from California (Elvin and Sanders 2009). We noted at that time that there are additional undescribed taxa throughout the range of this genus that we were unable to address because of the timeline for publication. Many specimens have been unavailable for review and analysis by us during the past several years; therefore, this manuscript will only address one new species from Arizona for which we were able to acquire a sufficient quantity of material, and which was out of the range of those taxa treated in *The Jepson Manual.* An additional impetus for the timing of this description is that areas within the entire range of this new species are being considered for renewable energy development.

Within the genus as a whole, there is a cluster of closely related, perennial taxa distributed throughout the Mojave Desert region characterized by branched inflorescences bearing multiple, small glomerules (a cyme condensed into a head-like cluster) on each stem (in contrast to the perennial, non-desert *Monardella* taxa characterized by unbranched inflorescences bearing larger, solitary, terminal glomerules).

The desert taxa occur as isolated populations within discrete mountain ranges. These populations appear to represent incipient speciation and tend to differ in relatively small but consistent traits such that all individuals from a particular mountain range can readily be identified as having come from that range and not another. One hypothesis to explain this divergence of taxa is that they may all be recent products of the breakup of a more widespread population system across the Mojave Desert during the Pleistocene, when pinyon woodlands covered much of the lowland Southwest (Van Devender et al. 1985).

The desert taxa tend to be isolated in the higher elevations associated with mountains and are surrounded by large expanses of relatively low, flat, hot deserts where perennial *Monardella* have never been documented. The expansion of deserts over the past 11,000 years may have disrupted gene flow in a formerly continuous population. Allopatric or peripatric populations may have developed and diverged in response to isolation, genetic drift, and directional selection for survival on differing substrates. It has long been noticed that some *Monardella* appear to be specialized for

[1] The findings and conclusions in this article/publication are those of the author and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

particular substrates (Epling 1939; Hardham and Bartel 1990; Elvin and Sanders 2003, 2009). Two other theories that may explain the unresolved relationships between the *Monardella* in the deserts are: 1) reticulation of taxa (as indicated by cladograms) over one or more climatic change events, and 2) convergent evolution. The reticulation/multiple expansions theory could help explain the difficulty that botanists have determining what and how many taxa exist throughout the genus.

Taxonomically Important Characters in *Monardella*

The taxonomy of and relationships in the genus *Monardella* have been difficult to understand, and there has been a great deal of confusion regarding the validity and circumscription of the taxa over the past 179 years. Morphological characters that have regularly been used to distinguish taxa in *Monardella* include plant habit; leaf, bract, and inflorescence morphology; and pubescence (Gray 1876, 1886; Abrams 1912a, b, 1951; Epling 1925, 1939; Jepson 1925, 1943; Munz 1935, 1959, 1974; Jokerst 1993; Elvin and Sanders 2003, 2009). Of the 215 published names, only 50 to 60 taxa are currently recognized, which illustrates some of the difficulties that all botanists studying this genus have had. Determining the circumscription of taxa in *Monardella* is not simple or obvious.

Some characters in the genus are highly variable, but can still assist in identification (e.g., leaf morphology, petiole length, flower and bract color, stem length). Other characters are variable in some taxa, but more consistent in others (e.g., calyx length, bract morphology), while still other traits have no observable variation within a species (e.g., stem, calyx pubescence). In the perennial desert *Monardella*, the stem and calyx pubescence is very consistent and is among the most reliable of morphologic characters for identification. The trichomes on the stems and calyces of these *Monardella* do not form a gradient from short to long, but instead fall into discrete categories, whether they are on new growth or mature stems and calyces. Some types are gland-tipped while others are nonglandular.

The four types of trichomes on the stems of the desert *Monardella* include: very minute, gland-tipped 0.01–0.03 mm; minute, nonglandular 0.03–0.05 mm; short, nonglandular 0.1–0.25 mm; and long, spreading, nonglandular 0.3–0.5 mm. The five types of trichomes on the calyces of the desert *Monardella* include: very minute, gland-tipped 0.01–0.02 mm; minute, gland-tipped 0.06–0.1 mm; minute, nonglandular 0.03–0.05 mm; short, nonglandular 0.2–0.3 mm; and long, spreading, nonglandular 0.3–0.6 mm. Unfortunately, most of these trichomes cannot be seen well with a standard 10× hand lens, but, instead, require the use of a microscope. While this does not lend itself to easy identification in the field, it does provide for accurate identification.

Taxonomy

Monardella eplingii Elvin, A. C. Sanders, & J. L. Anderson, sp. nov. (Figs. 1 and 2).—TYPE: USA, Arizona, Mohave Co., Black Mountains, canyon ca. 2.0 km SSE Sitgreaves Pass, volcanic soils, 35 d 01.685 m -114 d 21.148 m, 1125 m elevation, 4 September 2009, *M. A. Elvin 6379* with G. L. Clifton and M. Glenn (holotype: ASU; isotypes: ARIZ, ASC, DES, GH, GMDRC, JEPS, RSA, UCR).

Subshrub to shrub; similar to *Monardella arizonica* Epling, but differs in having bracts shorter and narrower, leaves narrower; similar to *M. eremicola* A. C. Sanders & Elvin, but differs in lacking conoideus glands on stems and having some sparse, long, spreading, nonglandular trichomes on stems longer than 0.3 mm.

Subshrub to shrub, (12)15–30(35) cm tall, erect, stems visibly woody at base; pubescence sparse to dense, stem trichomes four types: very minute, gland-tipped 0.01–0.03 mm; minute, nonglandular 0.03–0.05 mm; short, nonglandular 0.1–0.25 mm; and sparse, long, spreading, nonglandular 0.3–0.5 mm. Leaves 12–20 × 2–5 mm, length:width = 3–5:1, narrowly elliptic, apex acute (rarely obtuse), pale or grayish green, base acute, subglabrous to sparsely puberulent above and sparsely puberulent below, especially on the veins, subsessile, petioles (0)1–2 mm. Inflorescence generally an open compound cyme (occasionally solitary), multiple stems per plant. Glomerules (1)3–5 per main stem, 7–12 mm wide. Bracts 4–7 × 1.5–2(3) mm, green to purple tinted, narrowly elliptic to narrowly lanceolate, apex acute, apices less than or equaling apices of the calyces. Calyx 5–6 mm, green to purple tinted, trichomes two types: minute, gland-tipped 0.06–0.1 mm and short, nonglandular 0.2–0.3 mm. Corolla 9–10 mm, weakly bilaterally symmetrical, white with purple markings, appearing lavender. Nutlets light brown, oblong, 1.5 mm long.

All known occurrences and collections of *M. eplingii* are from the Black Mountains of Mohave Co., Arizona at the eastern edge of the Mojave Desert (Fig. 3). The westernmost mountain range in northwestern Arizona, the Black Mountains, lie immediately east of the Colorado River and differ from the surrounding mountain ranges and desert floor in Arizona, Nevada, and California by the volcanic nature of their geology. This provides a distinct, edaphic habitat for *M. eplingii* and essentially forms a desert "sky island." The Black Mountains are of mid-Tertiary origin, whereas other nearby mountain ranges, the Cerbat, Hualapai, and Mohave Mountains in Mohave Co., Arizona, and the Newberry Moun-

FIG. 1. *Monardella eplingii*. Habit (center) typical plant in spring. Glomerule (upper right).

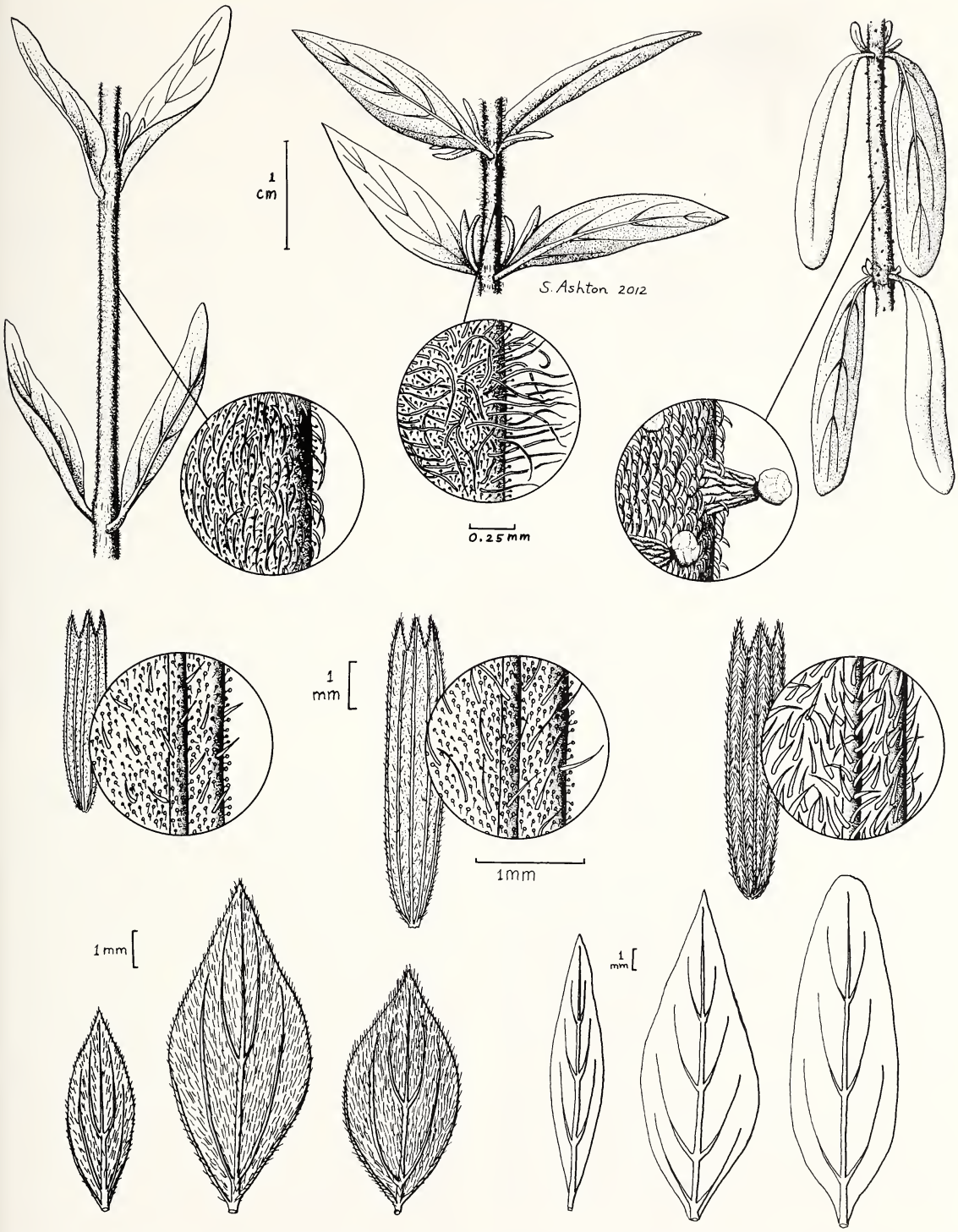

FIG. 2. Comparison of characters between *Monardella eplingii* (left), *M. arizonica* (center), *M. eremicola* (right). Top: stem internodes, stem pubescence in roundel. Center: calyces, calyx pubescence in roundel. Bottom: left, bracts; right, leaves.

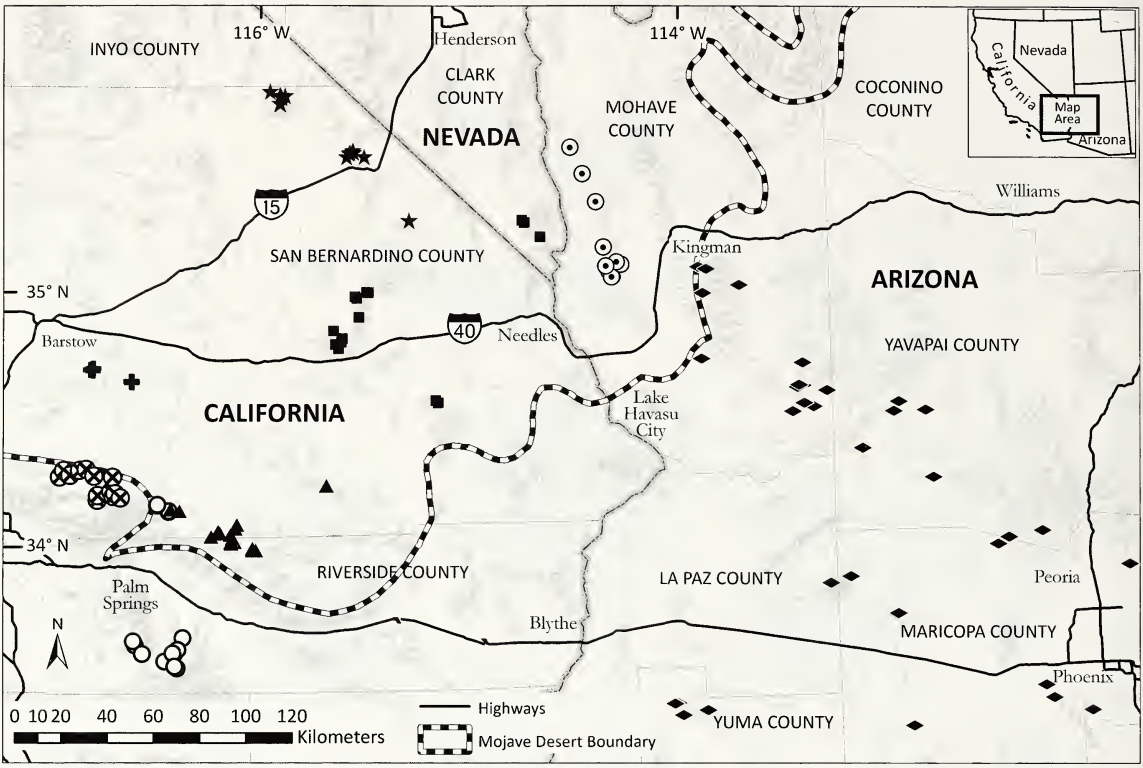

FIG. 3. Distribution of *Monardella eplingii* (⊙), *M. arizonica* (◆), *M. eremicola* (★), *M. robisonii* (▲), *M. mojavensis* (■), *M. boydii* (+), *M. linoides* subsp. *linoides* (○), and *M. linoides* subsp. *erecta* (⊗). The Mojave Desert boundary was developed by the U.S. Environmental Protection Agency, Mojave Basin and Range Ecoregion Assessment (U.S. Environmental Protection Agency 2005).

tains in Clark Co., Nevada (locality of the recently described *M. mojavensis* Elvin & A. C. Sanders), are of early Proterozoic granitic and metamorphic origin (Richard et al. 2000). The major geologic unit in the Black Mountains is classified as Middle Miocene to Oligocene volcanic rocks. The compositionally variable, volcanic substrates include andesite, rhyolite, and tuff (Richard et al. 2000). There are extensive ash-flow tuffs throughout this mountain range and it is the major substrate at the type locality. *Monardella eplingii* is found throughout the Black Mountains on these volcanic substrates.

Monardella eplingii occurs in mixed Mojave Desert scrub, desert riparian scrub, and among scattered shrubs of interior chaparral between 850–1100 m elevation. It occurs mostly in the cracks of bedrock and boulders along intermittent drainages, rock outcrops, and cliffs, but also along the bottoms of ephemeral washes and on open, gravelly or rocky slopes. It has been described on herbarium labels variously as "local, not common," "rare shrub," "uncommon," "occasional," and "scarce to locally occasional."

Associated species include *Eriogonum heermannii* Dur. & Hilg., *Senegalia greggii* Britton & Rose, *Salvia mohavensis* Greene, *Larrea tridentata* (DC.) Coville, *Fouquieria splendens* Engelm. subsp. *splendens*, *Hyptis emoryi* Torr., *Scutellaria mexicana* (Torr.) A. J. Paton, *Ephedra aspera* Engelm. ex S. Watson, *Ericameria laricifolia* (A. Gray) Shinners, *Yucca schidigera* Ortgies, *Juniperus californica* Carrière, *Nolina bigelovii* (Torr.) S. Watson, *Keckiella antirrhinoides* (Benth.) Straw, *Sclerocactus johnsonii* (Engelm.) N. P. Taylor, and *Coleogyne ramosissima* Torr. Another local endemic, *Penstemon bicolor* (Brandegee) Clokey & D. D. Keck, is also a common associate.

Based on the phenology of the material on herbarium specimens, *M. eplingii* appears to be on a typical Mojave Desert shrub phenological schedule with the main flowering period occurring in late summer to early fall. It also occasionally flowers into early winter and has been documented producing a few flowers throughout the year (e.g., in December, January, and April), which appear to be opportunistic after rains.

Etymology

The specific epithet refers to Carl Epling who first noted the distinctiveness of the *Monardella* plants in the Black Mountains. He published his

observations regarding their resemblance to *Monardella epilobioides* Greene [*M. linoides* A. Gray subsp. *erecta* (Abrams) Elvin & A. C. Sanders] (endemic to the San Bernardino Mountains) in his description of *M. arizonica* (Epling 1939). He labeled his collection from "Battleship Rock, Ute [Black] Mountains, [Mohave Co.,] Arizona" in 1935 (*C. C. Epling s.n.*, CAS 299247, RSA 580012) as "*M. epilobioides*." In his treatment of the *Monardella* from Arizona (Epling 1951), he noted that "[t]he plant of the Black Mountains may not be conspecific [with *M. arizonica*]." In addition to discussing the distinctiveness of the plants from the Ute [Black] Mountains in his 1951 treatment, he also discussed the distinctiveness of other plants in the *M. linoides s.l.* complex, including plants from the different Mojave Desert mountain ranges (Elvin and Sanders 2009). However, he never described the Black Mountains taxon because he was cautious and wanted to wait to publish it until "further evidence has accumulated as to the range of variation of each [of the desert taxa], as well as their cytology."

We name this taxon in Epling's honor—for his extensive efforts towards creating a better understanding of the taxonomy of *Monardella*, his love of the genus, his caution for waiting for sufficient evidence to publish his theories, and his many years of dedication to botany.

Similar Taxa

Monardella eplingii is most similar to the other *Monardella* in the Mojave Desert: *M. arizonica*, *M. eremicola*, *M. robisonii* Epling, *M. mojavensis*, and *M. boydii* A. C. Sanders & Elvin; but it also has affinities with *M. linoides* subsp. *linoides* and *M. linoides* subsp. *erecta*. Collections of *Monardella* from the Black Mountains have been variously identified and labeled as *M. arizonica* (e.g., *W. Hodgson 9159*; *M. Butterwick H793*), *M. linoides* (e.g., *J. L. Anderson 2006-1*; *J. L. Anderson 95-22*; *S. Braem s.n.*, POM 192565), *M. epilobioides* (e.g., *C. C. Epling s.n.*, RSA 580012), and *M. robisonii* (e.g., *L. N. Goodding 6024*). It is similar to all of these species in general habit, vestiture, and inflorescence structure. All *Monardella* in the Mojave and Sonoran deserts contain multiple glomerules per main stem. However, *M. eplingii* differs from each of these other taxa by multiple characters (Table 1). Certain characters (e.g., leaf size) can vary on individuals within a given *M. eplingii* population and approach the aspects of some of the other desert *Monardella*. For instance, larger leaves of some *M. eplingii* individuals can overlap in size with diminutive leaves of some *M. arizonica* individuals. *Monardella eplingii* is most similar to *M. arizonica* and *M. eremicola* and contains a mixture of characters from both of those taxa (Table 1). *Monardella eplingii* is peripatric with all nearby or similar taxa (Fig. 3).

Most of the *M. eplingii* specimens previously collected were identified as *M. arizonica* (Epling 1925, 1935, 1939, 1951; McDougall 1973; Trauth-Nare 2003). *Monardella eplingii* differs from *M. arizonica* in that it has minute, nonglandular trichomes on the stems; narrower leaves; shorter and narrower bracts; short, nonglandular trichomes on the calyces; shorter corollas; and it lacks the long, spreading, nonglandular trichomes on the calyces. While most *M. eplingii* individuals contain some sparse, long, spreading, nonglandular trichomes on the stems, it lacks the abundance of this type of trichome, which is one of the distinguishing characters for *M. arizonica*. The density of the short, nonglandular trichomes (0.1–0.25 mm) on the stems of *M. eplingii* makes it difficult to see the very minute, gland-tipped trichomes (0.01–0.03 mm) underneath. The short, nonglandular trichomes on the stems of *M. arizonica* are much less dense and it is easier to see the very minute, gland-tipped trichomes underneath. There is overlap in some of the more variable characters between *M. eplingii* and *M. arizonica* (e.g., leaf length), as is the case with many phenotypic characters throughout the genus (Epling 1925; Abrams 1912a, b; Gray 1886; Jepson 1925, 1943; Munz 1935, 1959, 1974; Jokerst 1992, 1993; Hardham 1966a, 1966b; Elvin and Sanders 2003, 2009; Sanders, Elvin, and Brunell 2012). These two species occur on different soil substrates and have different plant associations. While they occur within 30 km of each other, their distributions do not overlap. *Monardella eplingii* is endemic to the Mojave Desert and *M. arizonica* is endemic to the Sonoran Desert (Fig. 3).

Monardella eplingii differs from *M. eremicola* in that it lacks prominent conoideus glands on the stems. Conoideus glands are miniature, stout protuberances that are subcylindrical to conical in shape and resemble miniature volcanoes (Fig. 2; and see Fig. 7 in Elvin and Sanders 2009). *Monardella eplingii* also differs from *M. eremicola* in that it has very minute, gland-tipped trichomes on the stems; narrower leaves and bracts; and minute, gland-tipped trichomes on the calyces. These two species occur on different soil substrates and have different plant associations. Their distributions and elevational ranges do not overlap and they are separated by approximately 70 km.

Some *M. eplingii* collections have been labeled as *M. robisonii*, indicating their general similarity. Both species contain very minute, gland-tipped and short, nonglandular trichomes on the stems. Of the desert *Monardella*, these very minute, gland-tipped trichomes are only found on *M. eplingii*, *M. arizonica*, and *M. robisonii*. The abundance of long, spreading, nonglandular

TABLE 1. COMPARISON OF CHARACTERS BETWEEN *MONARDELLA EPLINGII* AND SIMILAR *MONARDELLA* TAXA.

Monardella taxa (mm unless otherwise noted)	*eplingii*	*arizonica*	*eremicola*	*robisonii*	*mojavensis*	*boydii*	*linoides* subsp. *erecta*	*linoides* subsp. *linoides*
Stem length (cm)	(12)15–30(35)	(15)30–60+	15–55	15–50	30–60	12–40	15–30	18–50
Stem conoideus glands	no	no	yes	no	no	no	no	no
Stem trichomes: gland-tipped 0.01–0.03	yes	yes	no	yes	no	no	no	no
Stem trichomes: nonglandular 0.03–0.05	yes	no	yes	no	yes	yes	yes	yes
Stem trichomes: nonglandular 0.1–0.25	yes	yes	yes	yes	no	no	no	no
Stem trichomes: nonglandular 0.3–0.5	yes (sparse)	yes (abundant)	no	yes (abundant)	no	no	no	no
Leaf length	12–20	12–23	12–27	8–20	8–20	7–15	12–19	10–25
Leaf width	2–5	(3)4–10	3–10	2–6	2–4	1–3(5)	2–4	2–4
Glomerule width	7–12	(7)9–15	7–20	7–20(25)	10–20	10–20	7–18	10–22
Glomerules per stem	(1)3–5	(1)3–7(11)	(1)3–5	3–7	3–7	(1)3–5	1	1(3)
Bract length	4–7	8–10	4.5–9	9–12	10–11	8–9	6–11	10–15
Bract width	1.5–2(3)	3–5	2–4.5	3–5	2–5	2–3	2–4	5–12
Relative bract/calyx apex position	≤	>	+/− =	>	>	≤	=	>
Calyx length	5–6	5–9	5–7	6–9	5–7	6–8	6–9	8–9
Calyx trichomes: gland-tipped 0.01–0.02	no	no	no	no	yes	yes	yes	no
Calyx trichomes: gland-tipped 0.06–0.1	yes	yes	no	no	yes	no	no	no
Calyx trichomes: nonglandular 0.03–0.05	no	no	no	no	no	no	no	yes
Calyx trichomes: nonglandular 0.2–0.3	yes	no	yes	yes	no	yes	yes	no
Calyx trichomes: nonglandular 0.3–0.6	no	yes	no	no	no	no	no	no
Corolla length	9–10	10–13	8–11	9–11	10–11	10–11	10–11	10–14
Geology/substrate	volcanic: tuff, andesite and rhyolite	granitic	limestone	granitic	granitic	volcanic: basalt	granitic	granitic
Elevation (m)	850–1100	550–2000	1500–2100	1100–1350	800–1500	1400–1650	1800–2600	900–2000

trichomes on the stems of *M. robisonii* readily distinguishes it from *M. eplingii*. *Monardella eplingii* further differs from *M. robisonii* in that it has shorter and narrower bracts; shorter calyces; and minute, gland-tipped trichomes on the calyces. These two species occur on different soil substrates and have different plant associations. Their distributions and elevational ranges do not overlap and they are separated by a distance of approximately 140 km.

Monardella eplingii differs from *M. mojavensis* in that it has shorter stems; very minute, gland-tipped and short, nonglandular trichomes on the stems; shorter and narrower bracts; short, nonglandular trichomes on the calyces; and shorter corollas. *Monardella eplingii* lacks the very minute, gland-tipped trichomes that are on the calyces of *M. mojavensis*. These two species occur on different soil substrates, have different plant associations, and their distributions do not overlap.

Monardella eplingii differs from *M. boydii* in that it has very minute, gland-tipped and short, nonglandular trichomes on the stems; generally longer leaves; smaller glomerules; shorter and narrower bracts; shorter calyces and corollas; and minute, gland-tipped trichomes on the calyces. *Monardella eplingii* lacks the very minute, gland-tipped trichomes that are on the calyces of *M. boydii*. These two species occur on different soil substrates and have different plant associations. Their distributions and elevational ranges do not overlap and they are separated by approximately 200 km.

Some specimens of *M. eplingii* have been identified as *M. linoides s.l.,* presumably based on the abundance of short, nonglandular trichomes (0.1–0.25 mm) on the stems. All of the perennial *Monardella* taxa in the eastern Mojave Desert were historically thought to be *M. linoides* subsp. *linoides*. *Monardella linoides* subsp. *linoides* does not occur in the eastern Mojave Desert. *Monardella eplingii* differs from *M. linoides* subsp. *linoides* in that it has very minute, gland-tipped; short, nonglandular; and sparse, long, spreading, nonglandular trichomes on the stems; smaller glomerules; considerably shorter and narrower bracts; shorter calyces and corollas; and minute, gland-tipped and short, nonglandular trichomes on the calyces. *Monardella eplingii* lacks the minute, nonglandular trichomes that area on the calyces of *M. linoides* subsp. *linoides*. These two species occur on different soil substrates and have different plant associations. Their distributions do not overlap and they are separated by approximately 220 km.

Monardella eplingii differs from *M. linoides* subsp. *erecta* in that it has very minute, gland-tipped trichomes; short, nonglandular trichomes; and sparse, long, spreading, nonglandular trichomes on the stems. It also has multiple glomerules per main stem; shorter and narrower bracts; shorter calyces and corollas; and minute, gland-tipped trichomes on the calyces. *Monardella eplingii* lacks the very minute, gland-tipped trichomes that are on the calyces of *M. linoides* subsp. *erecta*. These two species occur on different soil substrates and have different plant associations. Their distributions and elevational ranges do not overlap and they are separated by approximately 230 km.

Paratypes. USA, Arizona, Mohave Co., *J. L. Anderson 95-22* (ASU, herbarium at the Arizona Bureau of Land Management Phoenix District Office [azblm]!); *J. L. Anderson 2006-1* (ASU [digital image!], azblm!); *J. L. Anderson 2012-7* (ASU, azblm!); *S. Braem s.n.*, Dec 1927 (DS 190646!, POM 192565!); *M. Butterwick 8927* (ASU!); *M. Butterwick H793* (ASC, DES 19412 [digital image!], DES 19322 [digital image!]; *G. L. Clifton 39183* (Clifton's personal herbarium!); *T. F. Daniel 4550* (CAS [digital image!]); *T. F. Daniel 4574* (CAS [digital image!]); *M. A. Elvin 6291* (UCR!); *M. A. Elvin 6292* (CIC!, GMDRC!, UCR!); *M. A. Elvin 6293* (OSC!, SBBG!, UCR!); *M. A. Elvin 6294* (OBI!, UCR!, VFWO!); *M. A. Elvin 6295* (LA!, UCR!, WIS!); *M. A. Elvin 6296* (BRY!, CAS!, GH!, K!, MO!, NDG!, NY!, UCR!); *M. A. Elvin 6299* (UCR!, UCSB!); *M.A. Elvin 6300* (RM!, SD!, UCR!, UNLV!, VFWO!); *M. A. Elvin 6301* (GMDRC!, UCR!); *M. A. Elvin 6302* (ASDM!, UCR!, US!); *M. A. Elvin 6303* (CAS!, UCR!); *C. C. Epling s.n.*, 17 June 1935 (CAS 299247!, RSA 580012!), *L. N. Goodding 6024* (RM [digital image!]); *W. C. Hodgson 9159* (ASC, ASU [digital image!], DES [digital image!]); *W. C. Hodgson 9204* (ASC, DES [digital image!]).

Key to the *Monardella* Species of the Eastern Mojave Desert region

1. Stems with conoideus glands, calyx lacking minute gland-tipped trichomes 0.06–0.1 mm. . . . . *M. eremicola*
1′ Stems lacking conoideus glands, calyx with minute, gland-tipped trichomes 0.06–0.1 mm
   2. Stem trichomes ≥0.3 mm abundant, calyx trichomes ≥0.3 mm present . . . . *M. arizonica*
   2′ Stem trichomes ≥0.3 mm sparse or absent, calyx trichomes ≥0.3 mm absent
      3. Bracts >7.5 mm long; corolla ≥10 mm. . . . . *M. mojavensis*
      3′ Bracts <7.5 mm long; corolla ≤10 mm. . . . . *M. eplingii*

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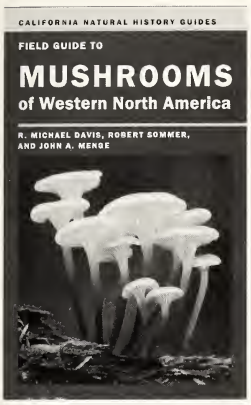
REVIEW



Field Guide to Mushrooms of Western North America. By R. MICHAEL DAVIS, ROBERT SOMMER, AND JOHN A. MENGE. 2012. University of California Press, Berkeley, Los Angeles, London. 459 pp. ISBN 978-0-520-27107-4, $70.00, hardcover; ISBN 978-0-520-27108-1, $26.95, paperback.

Western North America, and California in particular, has a rich mycoflora. This new guidebook with pictures and descriptions of more than 300 species provides a good introduction to this diversity. In general, many western species are still insufficiently known and nameless and more study is desperately needed. The present work gives as many current names as possible, and informs us that the names which are presently in use for many other species might not be the correct ones. To give an example, the well-known fly agaric mushroom with the red cap and white dots, *Amanita muscaria,* is a Eurasian species that also occurs in Alaska, but is as far as known absent from California; the local fly agaric species is North American in its distribution but has not been named yet.

The format of the book follows that of other guidebooks in this series, with an introduction (covering the topics: What is a Mushroom?; Fungal Ecology; and Collecting Mushrooms), a short chapter on classification and keys, followed by the bulk of the book—the species descriptions. At the back we find a chapter on fungal arts and crafts, a glossary, resources, and an index.

Each species is represented by a short description and a photo and is compared with other species that are or are not depicted in the book. In general there is one species per page, which means that the photos are rather small. The quality of the photos varies from stunning to mediocre. Important characters to recognize the species are often, but not always visible, and in some cases the name does not match the photo (e.g., *Entoloma sericeum* and *Lichenomphalia umbellifera*). Very educational and illustrative is the photo of *Russula cremoricolor*, showing the red and the white fruitbodies side by side.

It is always important to know where the descriptions and the photos come from—are the descriptions based on the material that is in the photo? Are they taken from the literature (and if so what is the source), or is it a general description from the authors' experience? This issue is not covered in the introduction, but in some cases it is clear that the description and the photo do not match. This is in particular the case for the photos that were taken in Europe (e.g., *Amanita pantherina*, *Trichoglossum hirsutum*, *Ascocoryne sarcoides*, and *Phallus impudicus*). Furthermore, there is no note in the text saying that these photos were taken outside western North America. As pointed out in the book itself, European names have been and are widely misapplied to western North American species. Using European photos is not helpful and merely adds to the confusion.

The species coverage in the book is fairly comprehensive—the most commonly encountered species in northern California and the Sierra Nevada are represented, where as southern California is less well represented with only a very few desert fungi. However, it is the most up-to-date guidebook for California species available. I recommend it, with the caveats given above, for everybody who is eager to learn more about their local mushrooms. The price is right, and its small size and weight make it easy to take out into the field.

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NOTEWORTHY COLLECTION

CALIFORNIA

Calyptridium pygmaeum Parish ex Rydberg (MONTIACEAE).—San Bernardino Co., Transverse Ranges, San Bernardino Mountains, Bluff Mesa, Castle Rock Trail region, N of Forest Road 2N86, 34.226, −116.963, 8 July 2010, *C. Craig, G. Richmond, K. Day s.n.* (JEPS, RSA); 24 May 2012, *C.M. Guilliams & G. Richmond 1915, 1917, 1920, 1921, 1923* (JEPS, RSA, UCR).

Previous knowledge. Calyptridium pygmaeum is a seldom-collected annual plant in the Montiaceae, formerly in the Portulacaceae. With only 15 documented occurrences, this California endemic is found primarily in the central and southern Sierra Nevada, although three occurrences are in the San Bernardino Mountains approximately 229 km to the south. In this latter region, *C. pygmaeum* was collected at Bear Lake in 1886 (*Parish 1803*), Bluff Lake in 1926 (*Munz 10534*), and Arrastre Flat in 1979 (*Helmkamp & Helmkamp s.n.*). Based only upon the history of collection, this taxon appears to be either very rare throughout its limited range or possibly under-collected due to its small size and ephemeral nature; likely both factors contribute to the paucity of collections of *C. pygmaeum*. Herbarium label habitat descriptions are often wanting for *C. pygmaeum*, but when present, these data suggest that this taxon is often encountered in open areas in pine forest, sometimes in mesic conditions, e.g., meadow and creek margins.

Significance. In October 2008, *C. pygmaeum* was added to the California Native Plant Society's Inventory of Rare and Endangered Plants as a List 1B.2. Following the listing, San Bernardino National Forest (SBNF) botanists began to research the history of the three occurrences on SBNF lands. Through examination of Munz's field records, it was possible for SBNF botanists to narrow the domain of focused searches in the Bluff Lake area to the region surrounding the Castle Rock Trail, approximately 0.3 km north of Forest Road 2N86. A population of *C. pygmaeum* was found in this area in 2010 by SBNF botanists Craig, Richmond, and Day. A subsequent visit in 2012 by Guilliams and Richmond documented numerous other occurrences in the general vicinity (*C. M. Guilliams and G. Richmond 1915, 1917, 1920, 1921, 1923*). These recent collections are confirmation that the species remains extant in the San Bernardino Mountains. This is especially important given that the Bear Valley population from which Parish collected in 1886 was potentially extirpated during the flooding of the valley (initiated in 1884) to create Big Bear Lake. In addition, our limited surveys in the Bluff Lake area appear to support the hypothesis derived from herbarium label data that *C. pygmaeum* occurs in slightly more mesic conditions than other congeners. We often encountered it in slightly lower topographic positions near creeks, in sheltered areas under trees, and in shaded areas on the north sides of shrubs and rocks. It was occasionally found in open, exposed areas as well. In all cases, *C. pygmaeum* was found in sparsely vegetated areas on coarse granitic substrates, and in this way it is similar to close relatives.

Lewisia triphylla (S. Watson) B.L. Robinson (MONTIACEAE).—San Bernardino Co., Bluff Mesa, ca. 60 m N of Forest Road 2N86, yellow pine forest, growing in the bank of a small, ephemeral, unnamed creek; soils wet, of decomposed granite. 34.2238, −116.9627, 24 May 2012, *C. M. Guilliams & G. Richmond 1934* (JEPS, RSA, UCR).

Previous knowledge. Lewisia triphylla is a diminutive (2 to 7 cm) perennial herb in the Montiaceae. Unlike other members of the genus that develop a taproot, this taxon arises from a small, spherical, corm-like structure and produces few basal leaves. As suggested by the specific epithet, this taxon generally bears three leaves, but these are presented in a whorl along the short flowering stem. This widespread taxon is distributed throughout western North America, from southwestern British Columbia in the north to Colorado in the east. Prior to our collection, the southern-most occurrence was from South Fork Meadows in Sequoia National Park (*Ferris and Lorraine 10860,* UC).

Significance. This collection of *L. triphylla* is the southwestern-most occurrence of the species, a new record for the Transverse Ranges (including the San Bernardino Mountains), and a new county record for San Bernardino Co. Interestingly, like *C. pygmaeum*, *L. triphylla* has a disjunct distribution between the southern Sierra Nevada and the San Bernardino Mountains. In the case of *L. triphylla*, this collection is a 280-km southern range extension for the taxon. It seems likely that *L. triphylla* has escaped detection in this area due to its inconspicuous appearance. Additional searches along stream margins following snowmelt in the spring may result in the location of additional populations.

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NOTEWORTHY COLLECTION

CALIFORNIA

Gracilariopsis chorda (Holmes) Ohmi 1958:24 (GRACILARIACEAE).—Monterey Co., attached to a small 5 × 12 m concrete boat launch ramp in the lower intertidal at Kirby Park, Elkhorn Slough, 36°50′ 23.53″N, 121°44′37″W, sterile and cystocarpic, 25 October 2011, *J. R. Hughey s.n.* (UC 1997139); 15 November 2011, *J. R. Hughey s.n.* (UC 1997140, UC 1997141, UC 1997142), and 7 May 2012, *J. R. Hughey s.n.* (UC 1997143, UC 1997144, UC 1997145, UC 1997146).

Previous knowledge. Gracilariopsis chorda (Holmes) Ohmi is a marine red alga that is native to Japan, China, and Korea (Holmes 1896; Kim et al. 2008). The type collection of this species, from Enoura, Shizuoka Prefecture, Japan, was characterized as having a large (up to 1 m), succulent, purple-colored thallus with only three branches off the main axis (Holmes 1896). *Gracilariopsis chorda* was originally assigned by Holmes (1896) to *Gracilaria*, but it was later transferred by Ohmi (1958) to *Gracilariopsis* because it lacked nutritive filaments that extend into the pericarp, one of the defining features of *Gracilaria* (Fredericq and Hommersand 1989). *Gracilariopsis chorda* has coarse, reddish-brown thalli that extend up to 110 cm in length with cylindrical 2–3 mm, sparingly to profusely branched axes and filiform branchlets (Ohmi 1958; Yamamoto 1978; Kim et al. 2008; M. S. Kim et al. 2010). The medullary cells of *G. chorda* are large (612–700 μm) and appear almost empty (Ohmi 1958), with an abrupt transition in cell size from the cortex to the medulla (Kim et al. 2008). On the basis of an analysis of *cox*1 and *rbc*L gene sequences from 22 specimens from Asia, Kim et al. (2008) agreed with Ohmi's placement of *G. chorda* in *Gracilariopsis* at the rank of species.

Significance. First report of *G. chorda* in the northeastern Pacific. The specimens of *G. chorda* collected from Elkhorn Slough are in agreement with published illustrations and descriptions of this species. Anatomical examination of this alga show the cortex to be abbreviated and distinct from the medullary cells, and the medulla to consist of large globular cells (~500 μm in diameter). The cystocarps of *G. chorda* are conspicuous and restricted to the middle thallus. *Gracilariopsis chorda* is red in color when fresh (drying to dark brown or black), while the native species, *Gracilariopsis andersonii* (Grunow) E.Y. Dawson, is straw-colored (Abbott and Hollenberg 1976), and the recently reported invasive seaweed *Gracilaria vermiculophylla* (Ohmi) Papenfuss is dark brown (S. Y. Kim et al. 2010). *Gracilaria vermiculophylla* does not occur on the ramp at the launch facility, but is abundant immediately adjacent to the ramp where it grows on small pebbles and shells partly buried in the mud. It is common throughout the slough. *Gracilariopsis andersonii* is found only near the mouth. Analysis of the *rbc*L gene of *G. chorda* from Elkhorn Slough yielded a DNA sequence (GenBank JX262420) that was identical to eight sequences from South Korea, four from Japan, one from China, and one from an introduced population in the Gulf of Morbihan, Brittany, France (Mineur et al. GenBank, unpublished). Of the five *rbc*L haplotypes reported by S. Y. Kim et al. (2010) for *G. chorda*, the Elkhorn population is assigned to R2, the largest of the haplogroups.

Grateloupia asiatica Kawaguchi & Wang 2001: 435 (HALYMENIACEAE).—San Diego Co., collected from the dock below the Coronado Boathouse Restaurant, Coronado Island, San Diego, 32°40′46.81″N, 117°10′29.30″W, tetrasporangial, 25 June 2012, *J. R. Hughey s.n.* (UC 1997160).

Previous knowledge. Grateloupia asiatica is native to Japan, China, and Korea (Kawaguchi et al. 2001; De Clerck et al. 2005; Lee et al. 2009) (type locality: Tsuyazaki, Fukuoka Prefecture, northern Kyushu, Sea of Japan). It is characterized as having dark red, 10–15 cm high thalli with pinnate branching (Kawaguchi et al. 2001). Although this species has been known in Asia as *G. filicina* (J.V. Lamouroux) C. Agardh (Kawaguchi et al. 2001), morphological and molecular analyses have demonstrated that *G. filicina* is restricted to the Mediterranean basin (Kawaguchi et al. 2001; De Clerck et al. 2005). *Grateloupia asiatica* is said to differ from *G. filicina* by its habit and texture (thin and soft with wider axes), vegetative anatomy (denser medulla), and reproductive structures (scattered and with an large, oval auxiliary cell). *Grateloupia asiatica* and other *Grateloupia* species were recently reported as introduced to Thau Lagoon, Mediterranean, France (Verlaque et al. 2005).

Significance. This is the first report of *G. asiatica* in the eastern Pacific ocean. The single specimen collected at Coronado strongly resembles the illustration of *G. filicina* in Abbott and Hollenberg (1976, fig. 384), a species reportedly rare in California, but occurring on Santa Catalina Island. The morphology and shape of the tetraspores of the Coronado specimen also shows similarities to *G. asiatica* (Kawaguchi et al. 2001; Verlaque et al. 2005). Identification of the Coronado specimen as *G. asiatica* was confirmed with an *rbc*L DNA sequence (GenBank JX307635). The sequence differed by only one bp from two sequences of *G. asiatica* from Fukuoka, Nokoshima; two bp from Fukuoka, Hakata Bay; three bp from Kochi, Sukumo, Minatoura, Japan (Kawaguchi et al. 2001); and seven bp from two specimens from Qingdao, Shandong Province, China (De Clerck et al. 2005). The DNA sequence of the Coronado specimen did not match the nonnative population (i.e., *G. filicina*) in Thau lagoon, differing by three bp (Verlaque et al. 2005). All of these representatives fit comfortably within reported intraspecific sequence divergences (<1% = 0 to 14 bp) for *rbc*L gene sequences in red algae (Freshwater and Rueness 1994). The vector for the Coronado introduction is likely hull fouling, because San Diego Bay is home to a large number of pleasure, commercial, and naval vessels. The appearance of *G. asiatica* was predicted by Miller et al. (2011) based on introduction patterns into the Californias by other nonnative seaweeds. Since the range of *G. filicina* is restricted to the Mediterranean, and *G. asiatica* strongly resembles *G. filicina*, it is probable that previous collections identified as *G. filicina* from southern California are assignable to *G. asiatica*. A genetic study of both recent and historical specimens from California will be

required to assess the distribution of *G. asiatica* in the eastern Pacific Ocean.

ULVA CLATHRATIOIDES L. G. Kraft, Kraft & R. F. Waller 2010:1273 (ULVACEAE).—Monterey Co., covering mud in the upper intertidal at railroad bridge, Elkhorn Slough, 36°51′27.25″N, 121°45′20.75″W, fertile, 29 May 2012, *J. R. Hughey s.n.* (UC 1997147); floating and attached to shells in the upper intertidal at Kirby Park, Elkhorn Slough, 36°50′23.53″N, 121°44′37″W, fertile, 7 May 2012, *J. R. Hughey s.n.* (UC 1997148), and 29 May 2012, *J. R. Hughey s.n.* (UC 1997149); attached to boat launch dock near the marina docks at Elkhorn Slough, 36°48′46″N, 121°47′14″W, fertile, 29 May 2012, *J. R. Hughey s.n.* (UC 1997150, UC 1997151).

Previous knowledge. Ulva clathratioides was described from southern Australia where it grows at 20–30 cm depth at low tide and on rocks on inner-reef flats (type locality: Point Lonsdale, Victoria [Kraft et al. 2010]). It forms small (3–5 cm), dense tufts, that are highly irregular in branching, and typically proliferous. The chloroplasts in this species occupy a narrow, peripheral position in cells. In section, the lateral branches contain cells that are embedded in a thick, extracellular matrix that extends up to 45 μm into the lumen of the branch (Kraft et al. 2010). On the basis of these features, *U. clathratioides* was originally and tentatively identified as *U. clathrata* (Roth) Greville by the authors. However, an analysis of nuclear (internal transcribed spacer) and plastid (*rbc*L) DNA sequences from two specimens showed it to be unrelated to the European *U. clathrata*.

Significance. First report of *U. clathratioides* in the eastern Pacific. Mature thalli are large (up to 35 cm high), pale to dark green in color, and appear hairy. Axes bear many multiseriate branches that vary in length from 200 μm to 1.5 cm. In young plants and branches, the cells are arranged in longitudinal rows, but become disordered as they mature. The chloroplasts are as described by Kraft et al. (2010), however the firm, hyaline matrix reportedly characteristic of this species was not observed in any thalli from Elkhorn Slough. The *rbc*L gene from four specimens from Elkhorn Slough (one near the head, two in the central region, and one at the mouth) was analyzed; the sequences (1171 bp) were identical for all four (GenBank JX262426–JX262429). Comparison of the Elkhorn Slough sequences to those in GenBank showed an exact match to a specimen labeled *Ulva* sp. 2 from North Island, Bay of Islands, Russell, New Zealand (Heesch et al. 2007), but there was only 81% sequence coverage. The missing 19% of sequence near the 3′ end of the *rbc*L gene contains two polymorphic sites that are unique to the Elkhorn Slough specimens. It is therefore not possible to assume that the Elkhorn population is identical in sequence to *Ulva* sp. 2 from New Zealand. *Ulva* sp. 2, like *U. clathratioides* in Australia, forms unbranched or branched tubular blades up to 3 cm high that grow in high intertidal tide pools on rocks, shells, or other algae (Heesch et al. 2007). It was characterized, but not named, as native to New Zealand in a technical report to the Ministry of Primary Industries (Heesch et al. 2007). Comparison against complete sequences revealed that Elkhorn specimens differed by three bp from two specimens from Point Lonsdale, Victoria, Australia (=*U. clathratioides* type locality, Kraft et al. 2010) and two specimens from Maili Point, Oahu Island, USA (O'Kelly et al. 2010). The Oahu specimens (OTU 5) are short (1–3 cm high) unbranched plants, that superficially resemble *Ulva* sp. 2. The Elkhorn Slough material also differed by four bp from one specimen from Okinawa, Ishigaki Island, Japan (Horimoto et al. GenBank, unpublished), and ten specimens from South and North Islands, New Zealand (Heesch et al. 2009). Since interspecific sequence divergence for the *rbc*L gene in *Ulva* ranges from zero to five bp (Kraft et al. 2010), these results indicate that these specimens from New Zealand, Australia, Japan, and California belong to the same species. The status of *U. clathratioides* in California as a native or nonnative species requires further investigation. Additional field and molecular study will likely reveal that *U. clathratioides* occurs in other brackish water habitats in the eastern Pacific Ocean.

ULVA PERTUSA Kjellman 1897:4 (ULVACEAE).—Marin Co., covering the shoreline on rocks and on shells in the upper intertidal at Marshall, Tomales Bay, 38°09′42.70″N, 122°53′37.54″W, fertile, 20 July 2011, *J. R. Hughey s.n.* (UC 1997152); Monterey Co., on shells buried in the mud near boat launch ramp and boat dock in the middle intertidal at Kirby Park, Elkhorn Slough, 36°50′23.53″N, 121°44′37″W, fertile, 25 October 2011, *J. R. Hughey s.n.* (UC 1997153, UC 1997155); on rocks under foot bridge at South Marsh Loop, Elkhorn Slough, 36°49′11.64″N, 121°44′13.59″W, fertile, 3 May 2012, *J. R. Hughey s.n.* (UC 1997156); attached to boat launch facility near the marina docks at Elkhorn Slough, 36°48′46″N, 121°47′14″W, fertile, 29 May 2012, *J. R. Hughey s.n.* (UC 1997157); attached to floating dock in the Monterey Marina, Monterey Harbor, Monterey, 36°36′07″N, 121°53′25″W, fertile, 20 September 2011, *J. R. Hughey s.n.* (UC 1997158, UC 1997159).

Previous knowledge. Ulva pertusa is native to Asia (syntype localities: Hakodate, Yenoshima, and Yokohama, Japan (Kjellman 1897). This species is a known exotic (Verlaque et al. 2002) that occurs worldwide (Guiry and Guiry 2012). *Ulva pertusa* was recently documented from four localities in Baja California (Aguilar-Rosas et al. 2008) and three in southern California (Mission Bay, La Jolla, Newport Bay) (Hayden and Waaland 2004). The thallus is characterized as 1) lobed, perforated, and lacking tooth-like protuberances on the margins; 2) wrinkled in the basal portion; 3) of variable thickness, approximately 500 μm thick above the holdfast, 90–156 μm in the lower parts, and 34–50 μm on the margins; 4) composed of unordered, round cells with 1–3 pyrenoids; 5) forming a broad, linear reproductive rim (Verlaque et al. 2002).

Significance. This is the first report of *Ulva pertusa* in central and northern California. The specimens of *U. pertusa* collected from Tomales Bay, Elkhorn Slough, and the Monterey Marina are in good morphological agreement with the description above. *Ulva pertusa* grows intermixed with native *U. rigida* C. Agardh at the mouth of Elkhorn Slough and *U. lobata* (Kützing) Harvey in the Monterey Marina. Compared to the native species, *U. pertusa* differs most notably in texture (the native species is fleshy and lax while *U. pertusa* is waxy and very rigid, appearing plastic) and cell shape (those of the the native species are bullet-shaped to quadrate while those of *U. pertusa* are rounded). Identification of *U. pertusa* was confirmed using *rbc*L DNA sequences (GenBank JX262421-JX262425). The sequence from the Tomales Bay specimen did not match any accessions deposited in GenBank, and differed by 1 bp from the Monterey Marina and three Elkhorn Slough sequences, which were identical. The specimens from central California were the same as sequences of *U. pertusa* from La Jolla and Newport

Bay, and plants from Australia, China, Japan (excluding a few ambiguous nucleotides), New Zealand, and Spain. All of the above specimens differed by 2 bp from the plant from Mission Bay, California.

To determine if historical collections from the Monterey Marina are assignable to *U. pertusa*, four specimens resembling this species from the Gilbert M. Smith Herbarium at Hopkins Marine Station, Pacific Grove, California, were analyzed. The four plants included isotype material of *U. expansa* (*Ulva fasciata* forma *expansa* Setchell, P.B.-A LXXVII, GMS 8034, 1901) and blades identified by I. A. Abbott as *U. expansa* (GMS 7779, GMS 8025) and *U. lobata* (GMS 8043) collected from the Monterey Harbor in 1965. All four specimens (these data deposited in www.boldsystems.org) were identical to each other and to two others deposited in GenBank under the name *U. lobata*. The four sequences differed from those of *U. lactuca* and *U. rigida* by three bp, and *U. pertusa* by four bp. These data support the merging of *U. expansa* with *U. lobata*, a view implied by Hayden and Waaland (2004). Based on these results, however, it is not possible to pinpoint the time of the introduction of *U. pertusa* to Monterey.

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NOTEWORTHY COLLECTION

WYOMING

Luzula subcapitata (Rydb.) H. D. Harr. (JUNCACEAE).—Albany Co., wet meadow at lake's edge, W side of Lost Lake, Medicine Bow Mountains, 3350 m, 19 Jul 1989, *J. Haines & C. Regan 7602A* (RM); wet meadow by lake and stream, S side of western lobe of Lost Lake, Medicine Bow Mountains, 3335 m, 26 Aug 1991, *J. Haines and M. Hille 10027* (RM).

Previous knowledge. Colorado woodrush, native in the mountains of Colorado, was considered a state endemic (Weber 1990). Kartesz (2003, updated 2012) recorded *Luzula subcapitata* in 15 Colorado counties, with a continuous range from San Juan Co. north through the mountains to Larimer Co., on the Wyoming border. Dorn (2001) did not include *L. subcapitata* in his Wyoming flora.

Significance. A native addition to the flora of Wyoming. The Lost Lake population of *L. subcapitata* is only 40 air km N of Larimer Co., Colorado, constituting a short extension of its known range.

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ANNOUNCEMENT

IN MEMORIAM

DR. JOHN O. SAWYER, JR. 1939–2012

With deep admiration and loss, we reflect upon the passing of Dr. John O. Sawyer, Jr. (1939–2012), California plant ecologist extraordinaire. He died peacefully at his home amongst the redwoods on August 19, 2012, after battling cancer for over seven years. John was born in Chico, California, into the farmer's family of John and Barbara Sawyer. He is survived by his devoted wife Roberta Jane Cole, sister Dorothy Erickson, two sons Kevin and Jeffrey, and their mother Judy Sawyer. In addition, John was a "father" to many former students, and he was close friends with many of his colleagues, especially Dr. James P. Smith, Jr., his best friend.

Dr. Sawyer completed a B.A. at California State University, Chico, and then an M.S. and Ph.D. at Purdue University, where he studied the ecology of tropical ecosystems. John joined the faculty at Humboldt State University in 1966. During more than 40 years as Professor of Botany, John became a nationally recognized authority on conifers, plant ecology, and the vegetation of California, especially that of the Klamath Mountains ecoregion. He has contributed greatly to our knowledge of California plants and plant ecology with over 40 scientific publications. These include taxonomic treatments of *Ribes* and Rhamnaceae in California and three books—*Trees and Shrubs of California, Northwest California: A Natural History*, and *A Manual of California Vegetation* (in two editions), which has been adopted as the state's standard for vegetation classification.

In supporting over 50 graduate students and scores of undergraduates, he fostered rigorous field-based and theoretical investigations of plant species and ecological systems across California, from the local Humboldt Bay area to the Klamaths, the Sierra Nevada, and the Mojave

John Sawyer backpacking along Stoney Ridge Trail, Trinity Alps. Photo by J. M. Evens.

and Sonoran deserts. His students and colleagues knew him as a teacher, mentor, scientist, author, and editor. John was a passionate theorist and classifier of nature, and he seemed to understand equally well relationships amongst his "people" as well as his "plants." He shaped the lives and pursuits of many of his past students, who now hold laudable positions at state and federal agencies, conservation organizations, consulting firms, and colleges and universities around the world.

Among his many awards and accolades, John was recognized in 1997 as Humboldt State University's Scholar of the Year, in 2008 by the California Botanical Society's dedication of Volume 55 of *Madroño* to him, and in 2010 as one of the recipients of Santa Barbara Botanic Garden's Conservation Award for the year's most influential contribution to botanical literature. He actively participated in several organizations, including the California Native Plant Society (CNPS), the Ecological Society of America's Vegetation Panel, and Save the Redwoods League. For CNPS, John was a past President and Fellow and a founding member of the Vegetation Committee; he was also a founding member and first president of the North Coast Chapter. In his free time, John was an avid backpacker; he also traveled extensively and loved music and art. He was instrumental in the protection of the Lanphere Dunes along the Humboldt Bay and the Russian Wilderness, an area that contains the richest concentration of conifer species in the Klamath Mountains.

John believed that instruction in the field was always the most informative. With that thought in mind, the John O. Sawyer, Jr. Endowment has been established at HSU to continue supporting field studies in botany and plant ecology. For more details about his life, accomplishments, and ways to contribute in his memory, please see the following link: http://www.cnps.org/cnps/about/memorial/johnsawyer/index.php.

—Julie M. Evens, Vegetation Program Director, California Native Plant Society; Todd Keeler-Wolf, Ph.D., Senior Vegetation Ecologist, California Department of Fish and Wildlife.

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