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DISCOVERY OF *CLAYTONIA LANCEOLATA* VAR. *PEIRSONII* IN THE SAN BERNARDINO MOUNTAINS PERPETUATES A HISTORY OF TAXONOMIC UNCERTAINTY

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ABSTRACT

Claytonia lanceolata is a widespread perennial herb that typically blooms in areas where snow persists, occurring along mountain corridors from Canada to southern California. Numerous varieties have been described for this species, but most are not recognized under current taxonomic treatments. The discovery of new populations of C. lanceolata in southern California is reported, and the taxonomic uncertainties associated with the C. lanceolata species complex and the southern California var. peirsonii are discussed. Subtle characters for distinguishing the southern populations of C. lanceolata may be obscured during the process of making herbarium specimens. We clarify some of the distinguishing morphological features and associated ecology of C. lanceolata var. peirsonii. Based on detailed field observations in southern California, information is collated for populations across the entire known range of the variety. Recommendations are made regarding opportunities for further investigation, and information pertinent to the conservation of C. lanceolata var. peirsonii in California is updated.

Key words: biogeography, California, *Claytonia lanceolata*, conservation, ecology, Montiaceae, San Bernardino Mountains, species complex, taxonomy.

NOTEWORTHY COLLECTION

Claytonia lanceolata Pursh var. peirsonii Munz & I.M.Johnst. (Montiaceae).—USA. California: San Bernardino Co. Thomas Stoughton 1077 with Scott Eliason and Emma Williams (RSA), 22 Apr 2011. Transverse Ranges; San Bernardino Mountains: North slope of Bertha Ridge, ridge between Holcomb and Bear valleys (Fawnskin 7.5' USGS: 34.28289°N, 116.88575°W; T2N R1E S4). Alt.: 2338 m/7669 ft. Growing in open and shaded sites on northeast aspect of slope in sandy soils among dolomite rocks and relatively dense pine duff. Slope dominated by Pinus monophylla, P. flexilis, and Juniperus occidentalis var. australis. Other associates include Caulanthus major, Euphorbia palmeri, Stipa hymenoides, Penstemon sp., Salvia pachyphylla, Phlox diffusa, Abronia nana var. covillei, Eriogonum microthecum var. corymbosoides, and Physaria kingii subsp. bernardina. Blooming near patches of melting snow. Approximately 100 individuals found within five square meters at this location, with over 500 individuals found in a patchy distribution between the collection locality and the upper limit of the population not more than 100 meters up the hill at 34.28259°N, 116.88577°W. Anthers yellow, becoming pinkish with age as the stigma matures and the anthers reflex outward against the petals. Stems occasionally two from one tuber. Bee fly observed visiting flowers.

Previous knowledge (expanded).—Claytonia lanceolata is described as a widespread perennial herb bearing globose tubers and typically flowering very early in the spring months, particularly where snow persists (Miller 2003; CNPS 2013; Miller and Chambers 2013). It exists in a number of different habitats from 500 to 3000 m in elevation and has been reported from as far north as the southwestern Canadian provinces of British Columbia, Alberta, and Saskatchewan to as far south as northern New Mexico, Arizona, and southern California in the US (Miller 2003). Claytonia lanceolata was described by

Davis (1966) as the most variable of all species in genus *Claytonia*, perhaps relating to its large and heterogeneous range over most of western North America. Up to ten subspecific taxa in the *C. lanceolata* complex (Davis 1966) have been recognized in previous treatments (for details on synonymy, see Miller and Chambers 2006), but the only one known from southern California is var. *peirsonii* (Fig. 1), a sub-umbellate taxon originally considered to be restricted to the higher ridges of the eastern San Gabriel Mountains (Munz and Johnson 1922). The taxon was subsequently found in the area of Cross Mountain in the southern Sierra Nevada of Kern Co. (*York and Shevock 2079*, CAS), the Panamint Mountains of Inyo Co. (*York 2630*, RSA), and was recently collected for the first time in the San Bernardino Mountains of San Bernardino Co. (*Stoughton 1077*, RSA).

Previous to the mid-1990s, C. lanceolata var. peirsonii was known from five populations along the high elevation ridges of the eastern San Gabriel Mountains in southern California between Mt. San Antonio (Mt. Baldy) and Ontario Peak (Fig. 2; Krantz 1980; CPC 2010; CNPS 2013). These five populations are disjunct by 120 air-km from more recently (i.e., 1998) documented populations of C. lanceolata var. peirsonii to the north in the southern Sierra Nevada, Kern Co. (Fig. 1; York and Shevock 2079, CAS; Stoughton 1705, RSA). Populations in Kern Co. are, in turn, located approximately 350 km from the nearest documented occurrence of C. lanceolata in the Sierra Nevada in Tuolumne Co. (CCH 2013), but only about 145 km from other desert mountain populations of C. lanceolata in the Panamint Mountains of Death Valley National Park (Fig. 1; York 2630, RSA; Stoughton 1711, RSA). Plants from the Panamint Mountains fit the relatively ambiguous description C. lanceolata var. peirsonii of Munz and Johnson (1922). Furthermore, isolated populations of C. lanceolata have been documented approximately 145 km to the east of the Panamint Mountains in the Spring Mountains outside of Las Vegas,

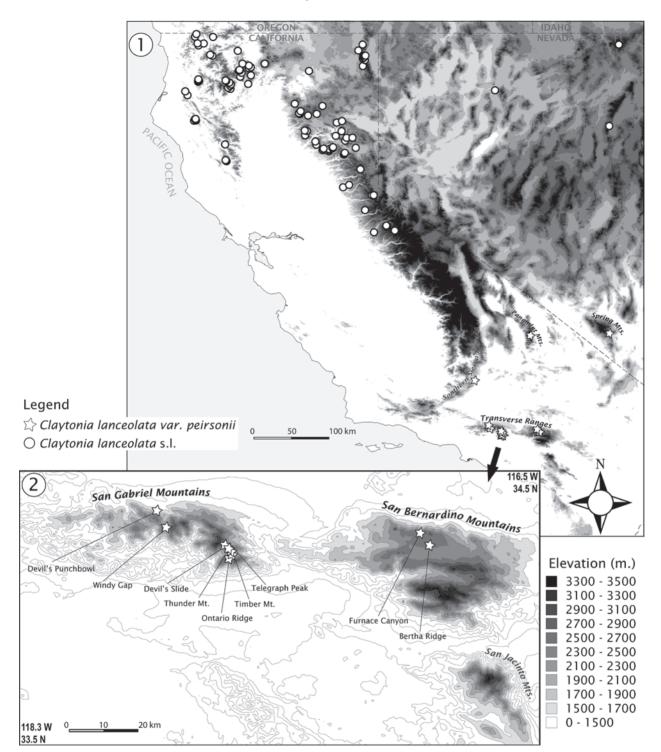


Fig. 1–2. Distribution of Claytonia lanceolata sensu lato in California and Nevada: circles denote C. lanceolata excluding var. peirsonii, and stars denote C. lanceolata var. peirsonii in the southern portion of both states.—2. Inset showing the Transverse Ranges and all known occurrences of C. lanceolata var. peirsonii in the San Gabriel and San Bernardino Mountains of southern California. Maps generated by the second author in QGIS (QGIS Development Team 2013) using Shuttle Radar Topography Mission elevation data aggregated to 30 arc second spatial resolution (Hijmans et al. 2005).

Nevada (A. Pinzl 6409, NY). Examination of specimens of C. lanceolata var. peirsonii at the Niles Herbarium (University of Las Vegas, Nevada) strongly suggests that populations of C. lanceolata in the Spring Mountains of Nevada are also var. peirsonii, a variety that was previously described as a narrowly

restricted, Californian variety of the widespread and extremely polymorphic *C. lanceolata*. Field observations and information gathered from herbarium specimens at RSA, CAS/DS, UC/JEPS, UNLV by the first author, in addition to earlier reports (Krantz 1980; Mistretta and Brown 1987; Allan et al.



Fig. 3. Habitat of *Claytonia lanceolata*. Photo taken on the north slope of Bertha Ridge in the San Bernardino Mountains, southern California, near the initial discovery site of *C. lanceolata* var. *peirsonii*. White dolomite rocks characterize the landscape that is dominated by open woodland of both *Pinus flexilis* and *P. monophylla*, along with *Juniperus grandis*. Plants occur in dense populations on these steep hillsides underneath the shade of trees in heavy duff as well as in open sun amongst rocks. Photo by first author.

1995; Soza and Boyd 2000; CPC 2010; CNPS 2013) suggest that *C. lanceolata* var. *peirsonii* is typically found blooming next to melting patches of snow on north-facing slopes, often in open sun amongst rocks (Fig. 3) or in shady areas with dense conifer litter (not pictured). At a more inclusive level, this taxon is described as occurring on unstable talus below ridgelines in lodgepole forest or upper montane, mixed coniferous forest habitats. *Claytonia lanceolata* var. *peirsonii* is on CNPS list 3.1, which means "needs review, but seriously endangered in California" (CNPS 2013). The purpose of this manuscript is to provide a review of the literature and draw together observations made in the field and from herbarium specimens so a more appropriate conservation status can be formulated for populations in southern California that meet the description of *C. lanceolata* var. *peirsonii*.

Significance.—The collection from Bertha Ridge (above) is the first of *C. lanceolata* var. *peirsonii* from the San Bernardino Mountains, a range extension of about 65 km from the nearest known occurrences atop Timber Mountain in the San Gabriel Mountains to the west (Fig. 2). It also is the first population of this taxon documented on limestone substrates in southern California (Fig. 4–8), and in the time since this discovery var. *peirsonii* has also been collected at the head of Furnace

Canyon on carbonates (Fig. 8; Stoughton 1516, RSA). Plants in the Panamint Mountains of Death Valley National Park (Fig. 6) and in the Spring Mountains of Nevada are also known from calcareous substrates, while those in the southern Sierra Nevada are found on rhyolitic gravel (Fig. 5). In the San Gabriel Mountains these plants can be found with both igneous (Fig. 4) and metamorphic rocks. Previously undocumented in the literature, the populations of *C. lanceolata* in the San Bernardino Mountains contribute greatly to our understanding of the geographic distribution and wide edaphic tolerances of var. *peirsonii*. In addition, the high risk of extirpation of all of the southern California populations is reviewed.

METHODS AND RESULTS

Field observations.—Observations in the field include three years of visits to all but one of the known localities in the San Gabriel and San Bernardino Mountains of southern California, as well as the southern Sierra Nevada and Panamint Mountains, and the southern Spring Mountains in Nevada, made between March and May 2011–2013. Five sites were visited in the San Gabriel Mountains in 2012 (Fig. 2),

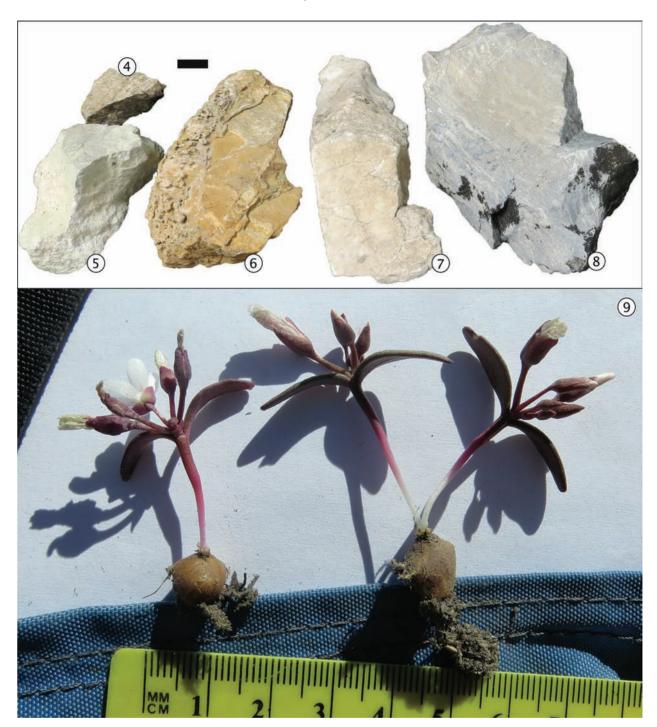


Fig. 4–9. The common substrates and overall plant form of *Claytonia lanceolata* var. *peirsonii.*—4–8. Rocks collected from each of the five disjunct mountain ranges where *C. lanceolata* var. *peirsonii* occurs in southern California. Scale bar = 1 cm.—4. Metamorphic rock, near Devil's Punchbowl County Park, San Gabriel Mountains.—5. Rhyolite (tuff), north slope of Cross Mountain, Jawbone Canyon, southern Sierra Nevada.—6. Limestone, Johnson Canyon, Panamint Mountains.—7. White dolomite (or low-grade marble), Bertha Ridge, San Bernardino Mountains.—8. Gray dolomite, head of Furnace Canyon, San Bernardino Mountains.—9. Entire plants of *Claytonia lanceolata* var. *peirsonii* showing the characteristic sub-umbellate inflorescence, collected from gray dolomite at the head of Furnace Canyon in the San Bernardino Mountains. Plants were photographed shortly before being dried and prepared for herbarium specimens. Note that the short internodes give the inflorescence its sub-umbellate appearance, in contrast to the primarily elongate inflorescence of other members of the *C. lanceolata* complex (not shown). Photos by first author.

excluding the Devil's Backbone locality but including a new population discovered by Jane Tirrell just west of Mt. San Antonio along the Pacific Crest Trail in the area of Windy Gap (Stoughton 1539, RSA). This new site is about 20 km west of the plants growing on the Devil's Backbone, which was previously thought to be the western-most occurrence of this taxon (Krantz 1980; CPC 2010; CCH 2013; CNPS 2013). A population even further to the west (Stoughton 1706, RSA), near Devil's Punchbowl County Park, was visited in 2013 after another discovery by Jane Tirrell, who found the plants during surveys related to a comparative phenology study in the San Gabriel Mountains (Tirrell et al. in press). Two sites separated by about 7 km were visited in the San Bernardino Mountains in 2012. The Furnace Canyon locality to the north was identified as suitable habitat (i.e., presence of Pinus flexilis E.James at low elevation on limestone), and plants were documented for the first time during the 2012 visit (Fig. 2). The discovery at Furnace Canyon was made immediately following a revisit to populations further south at Bertha Ridge in 2012, almost exactly one year after initial documentation of var. peirsonii in the San Bernardino Mountains at that locality in 2011 (label information shown above). Both localities were revisited in 2013, along with first-time visits to the populations at Jawbone Canyon in the southern Sierra Nevada and at Johnson Canyon in the Panamint Range. Suitable habitat was visited in 2013 in the southern portion of the Spring Mountains near the reported locality of C. lanceolata just west of Jean, Nevada (Fig. 1), but no plants were found. Future expeditions will be made to this area to evaluate whether the absence of var. peirsonii in 2013 was the result of poor snowpack from the previous winter's precipitation in the areas searched. That same year, second-time site visits to the Thunder Mountain population and the type locality of var. peirsonii on Ontario Ridge in the San Gabriel Mountains (Fig. 2) proved to be fruitless expeditions even though the plants are definitely present there.

Herbarium observations.—Observations were made during visits to the herbarium at Humboldt State University in Arcata (HSC), UC/JEPS in Berkeley and the California Academy of Sciences (CAS/DS) in San Francisco, California, the herbarium at Oregon State University in Oregon (OSC), the Niles herbarium at the University of Las Vegas, Nevada (UNLV), and as part of ongoing work at Rancho Santa Ana Botanic Garden (RSA). Collectively, over 350 specimens representing C. lanceolata, as circumscribed by Miller and Chambers (2006), were examined by the first author at these herbaria. Particular attention was given to cauline leaf morphology, corolla morphology, and inflorescence architecture.

DISCUSSION

Taxonomic recognition of *C. lanceolata* var. *peirsonii* has been uncertain for at least 20 years, evidenced in part by the dismissal of all varieties of *C. lanceolata* in *The Jepson Manual* by Chambers (1993). Chambers (1993) considered variation in the group to be environmentally induced and reported that the species is in need of further study. This came after Davis' (1966) focused research on the perennial species of *Claytonia* in North America, where he emphasized both geographic coherence and morphological discontinuity between most varieties of *C. lanceolata* that were previously described,

including var. *peirsonii*. Referring specifically to var. *peirsonii* in the San Gabriel Mountains, Miller and Chambers (2006) added that, "...the subtle variation among plants of these populations does not warrant taxonomic recognition because they fall within the general morphological range of *C. lanceolata*." This note is in direct conflict with a report from the Center for Plant Conservation (CPC 2010), which states (albeit ambiguously) that the San Gabriel Mountain populations appear to be distinctive.

As originally described, C. lanceolata var. peirsonii is distinguished by both its relative geographic isolation (Fig. 1) and by a primary inflorescence axis that is shortened so as to make the inflorescence appear umbellate (Munz and Johnston 1922; Fig. 9). The description was based on the type specimen, collected by Mabel Peirson near Kelly's Cabin on Ontario Ridge (M. Peirson s.n., RSA), and from one other specimen collected along the ridge just east of Mt. Harwood known as the Devil's Backbone (F. W. Peirson 2151, RSA), both from the eastern San Gabriel Mountains. Given that these populations were at least 450 km away from other known conspecific populations (discovery of the species in the southern Sierra Nevada and desert mountains came later), Munz and Johnston (1922) likely considered geographic isolation in recognizing var. peirsonii as a distinct taxon. Davis (1966) thought that the variety was not highly distinct, but he recognized it nevertheless specifically because of its geographic isolation. However, Davis (1966) notes that he, too, examined only two specimens, the type and one other representing var. peirsonii. These are the same (and only) two herbarium specimens upon which the variety was described! The distinguishing morphological character (sensu Munz and Johnston 1922), a shortened inflorescence axis (Fig. 9), is readily observed in the field but can be subtle in herbarium specimens where it is most often obscured by the leaves. Having examined the entire collection of C. lanceolata specimens at RSA (including the holotype of var. peirsonii) and additional specimens at CAS/DS, HSC, UC/JEPS and UNLV, there is reason to believe that the southern populations of C. lanceolata in California, including those in Kern and Inyo Cos. and in the Spring Mountains of Nevada, are unique and distinct from other so-called conspecific populations in northern California and adjacent populations in northern Nevada (Fig. 1). This claim is additionally supported by detailed field observations of the new populations discovered in the San Bernardino Mountains, and all but two of the known localities in the San Gabriel Mountains, southern Sierra Nevada, and Panamint Range. Preliminary evidence indicates that this morphological variation has a genetic basis (T. Stoughton, unpubl.).

Confusion regarding the varieties of *C. lanceolata* is further evidenced by an example of duplicate specimens of *York and Shevock 2079* at RSA and UCR. Collected from the southern tip of the Sierra Nevada at Cross Mountain in Kern Co., the UCR specimen has been determined by A. C. Sanders to be var. *peirsonii* (CCH 2013). This would represent a 120-km northerly range extension for the variety previously thought to be restricted only to the San Gabriel Mountains. The RSA specimen was determined by Steve Boyd as var. *pacifica* in 2003, and as var. *lanceolata* in 2005, but our studies lead us to think that this collection represents var. *peirsonii*. Observations of *C. lanceolata* s.l. by the first author in both northern and southern California support this claim, as do key herbarium holdings representing the entire range of the species complex.



Fig. 10. Line drawing of *Claytonia lanceolata* var. *peirsonii*. Note the short above-ground stem, and variation in leaf shape. The variety differs from many members of the *C. lanceolata* complex by having entire (as opposed to notched) petals, but in common with other members its flowers have pink veins and yellow spots at the base of the petals. Generally, plants in the San Bernardino Mountains have narrower leaves than those in the San Gabriel Mountains from which the variety was originally described. All scale bars = 1 cm. Line drawing by first author.

Given the various issues in taxonomic research more broadly discussed by Venu (2002), we think that some subtle, yet informative, taxonomic characters exist for the southern populations of *C. lanceolata* that may be obscured during the process of making herbarium specimens. Aside from the ecological setting, the majority of characters most readily used to distinguish this species are undoubtedly best observed in the field, including inflorescence architecture, floral morphology, and cauline leaf shape.

Claytonia lanceolata var. peirsonii is readily distinguished from other members of the C. lanceolata complex by having succulent, lance-ovate to lance-linear leaves with a prominent midrib and betalain pigmentation on the above-ground stem and abaxial side of the deeply green cauline leaf pair, in addition to its shortened peduncle and inflorescence internodes (Fig. 9-10). Claytonia lanceolata var. peirsonii is generally associated with a variety of rock types, predominantly in habitats characterized by exposed limestone substrates or on other metamorphic rocks (Fig. 4-8). In contrast, var. lanceolata is generally a taller, less succulent and lighter green plant that has generally lance-ovate to narrowly elliptic to oblanceolate leaves lacking a midrib more prominent than the outer veins (which converge at the leaf apex), and lacks betalain pigmentation on the above-ground stem or abaxial side of the cauline leaf pair. Claytonia lanceolata s.l. (excluding var. peirsonii) generally has a pronounced raceme and expanded internodes in the inflorescence, which may or may not be dependent on seasonal conditions. Claytonia lanceolata s.l. has affinities to a variety of substrates, including distinct ecological and morphological races identified on ultramafic rocks and other unusual substrates in California (T. Stoughton, unpubl.).

All of the southern populations of *C. lanceolata* in California are at risk of extirpation regardless of which taxonomic organization is observed. Southern populations have been found in highly insular patches, about 350 km away from the nearest populations in Tuolumne Co. (Fig. 1; CCH 2013). With almost 120, 145, and 160 air-km separating plants

in the southern Sierra Nevada from populations in the San Gabriel, Panamint, and San Bernardino Mountains, respectively (Fig. 1), it is unlikely that there is any gene flow occurring among these widely separated populations. High levels of genetic polymorphisms and the presence of private alleles among populations in the San Gabriel Mountains, as supported by Mistretta and Liston's (1992) isozyme analyses and preliminary analyses of nuclear ribosomal DNA sequences (T. Stoughton, unpubl.) suggest that these populations are genetically isolated at an even finer scale. Bee flies (Bombyliidae) have been observed transferring pollen among plants in the southern populations of C. lanceolata (Mistretta and Brown 1987; pers. obs.), but it is not clear if this is the primary means of pollen movement or how frequent pollen transfer is. Small insects have also been implicated as mechanisms for seed dispersal for closely related species (Turnbull et al. 1983). Both of these observations support the idea of limited gene flow among the southern populations of C. lanceolata inhabiting these widely separated mountain ranges (i.e., Transverse Ranges, Southern Sierra Nevada, Panamint Mountains, and Spring Mountains), considering the shortest pairwise distance between the sites investigated by Mistretta and Liston (1992) in the San Gabriel Mountains is ca. 1.5 km and the longest distance is only ca. 6.5 km. Reproductive isolation and subsequent reduction of the gene pool in these small populations may lead to a reduction in fitness (i.e., inbreeding depression) of the southern populations of C. lanceolata. Although inbreeding coefficients calculated by Mistretta and Liston (1992) were not statistically significant, the observed number of heterozygous individuals was less than expected for all of the five occurrences of C. lanceolata var. peirsonii sampled in the San Gabriel Mountains, a sign that nonrandom gene flow (probably inbreeding, given population sizes and isolation) is affecting these populations.

The extreme spatial discontinuity among only a handful of known populations in southern California and the implications of inbreeding should be reasons alone to raise the conservation status of populations of C. lanceolata var. peirsonii, but these are not the only concerns. Foot traffic, recreational activities, and proposed ski area expansion in the Angeles National Forest (Krantz 1980; CPC 2010; CNPS 2013) are also legitimate threats. A warming climatic trend puts the southern populations at further risk because of their high-elevation habitat associations (Lenoir et al. 2008). Claytonia lanceolata var. peirsonii is thought to be a relict of cooler climates during the Pleistocene Epoch (Mistretta and Liston 1992; Krantz 1994; Miller and Chambers 2006), and it strictly inhabits high-elevation sites today. The persistence of these southern populations may be due to the relative east-west orientation of the mountainous regions in which var. peirsonii occurs. This orographic phenomenon may have generated north-facing "refugia" in which this cold-adapted species could persist in a warming climate, a hypothesis proposed to explain the Arctotertiary disjunction exhibited by several other plant taxa occurring in the Transverse Ranges (Raven and Axelrod 1978; Krantz 1994). The effects of habitat limitation due to climate change (Lenoir et al. 2008), potentially low within- and among-population genetic diversity, and anthropogenic effects on highly discontinuous and potentially relictual populations of C. lanceolata are cause for concern.

Opportunities for further study.—To the best of our knowledge, no chromosome counts have been made for *C. lanceolata* var. peirsonii despite the complex patterns of hybridization and polyploidy reported in the genus *Claytonia* (see Miller and Chambers 2006 for a detailed review) and both the euploidy and aneuploidy documented in the *C. lanceolata* species complex (Stewart and Wiens 1971; Miller and Chambers 2006). This information will be vital to understanding taxonomy and biogeography in the *C. lanceolata* species complex.

Monitoring surveys and further study are recommended for C. lanceolata, including var. peirsonii. Chuckwalla Mountain in Kern Co. is noted as having potential habitat for additional populations of var. peirsonii due to its elevation and close proximity to the Cross Mountain occurrence in the southern Sierra Nevada. The area has yielded relatively few plant collections (CCH 2013), especially around the peak and the north slopes where C. lanceolata var. peirsonii is most likely to occur. Further surveys are also recommended (1) at additional sites along Bertha Ridge near the newly discovered San Bernardino Mountain occurrence, (2) along other higher ridges and limestone outcrops in the San Bernardino Mountains, and (3) in carbonate habitats of the eastern Mojave Desert mountains, such as the Clark Mountains or Kingston Range, during the early spring months when Claytonia is typically blooming. The previous study by Mistretta and Liston (1992) should be expanded to include new genetic markers and these newly discovered populations. A study of the entire C. lanceolata species complex and close relatives is justified, especially considering the genetic and phylogenetic tools now available to the scientific community. Along with the recent discovery of these new populations of C. lanceolata in the San Bernardino Mountains of southern California, useful morphological characters and ecological affinities that support the recognition of var. peirsonii as a unique species (T. Stoughton, in prep.) are only pieces of a larger puzzle. Sampling of the enigmatic C. lanceolata in the context of the entire group of tuberous perennial Claytonia will

likely yield answers to age-old questions about the roles of hybridization, polyploidization, dispersal, and vicariance in the evolution of spring beauties.

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