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The Western Spring Beauties, *Claytonia lanceolata* (Montiaceae): A Review and Revised Taxonomy For California

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Abstract—The taxonomic history of *Claytonia lanceolata* is fraught with confusion. Poor preservation of diagnostic characteristics on museum specimens and incomplete original descriptions made from limited reference material have resulted in inadequate characterization of morphological features and geographic distributions, particularly for plants in more xeric areas of California. In this paper, we investigate populations previously thought to belong to *C. lanceolata* and provide an updated taxonomy for Californian taxa based largely on morphological observations and geographic records. These data are corroborated by evidence of genetic polymorphisms and ecological divergence. *Claytonia obovata* was synonymized with *C. lanceolata* in 1966 and remained unrecognized until now because previous treatments misinterpreted morphological variation in *C. lanceolata* s. s. ***Claytonia peirsonii*** is a new combination for a species comprising four subspecies endemic to the Desert Southwest, three of which are new to science. Two new species are described here: ***Claytonia panamintensis***, known in California only from the Panamint Mountains but ranging more widely across southern Nevada, and ***Claytonia serpenticola***. The latter species shares a similar geographic range with *C. obovata* in the Klamath-Siskiyou region of northern California and southwestern Oregon, and these two occur in close sympatry through much of their respective distributions. We also provide molecular evidence to support retention of the name *C. lanceolata* for populations in California that do not fall into any of the aforementioned new species or combinations. Taxa accepted in this paper are best distinguished from each other by their habitat (many are apparently edaphic endemics), betalain pigmentation, inflorescence architecture, and morphology of cauline leaves, subterranean stems, and flowers.

Keywords—Edaphic endemism, morphology, natural history, species complex, statistical ordination.

The taxonomic history of *Claytonia lanceolata* Pursh (western springbeauty, lanceleaf springbeauty) is fraught with confusion. This geographically widespread species was considered the most morphologically variable of all tuberous, perennial *Claytonia* L. (Montiaceae) by Davis (1966). This sentiment was echoed by Chambers (1993) and later by Stoughton and Jolles (2013). Stoughton and Jolles (2013) suggested that molecular data taken in combination with morphological and natural history observations would help elucidate evolutionary history and clarify long-standing taxonomic problems associated with this enigmatic taxon (See Davis 1966, but also Miller and Chambers 2006). Studies relying on a small number of 'exemplar' specimens inevitably underestimate the overall range of morphological variation for a geographically widespread taxon. This seems to be the primary reason why application of the name *C. lanceolata* s. s. (i.e. sensu Pursh 1814; s. s.) has been uncertain.

Pursh's (1814) original description of *C. lanceolata* encompasses only a fraction of the morphological variation more recently observed in the species by Miller and Chambers (2006), and Pursh (1814) did not provide measurements or proportions of any kind beyond the general shape of a few key plant parts (i.e. cauline leaves, sepals, and petals). Pursh (1814) designated a type specimen from the Rocky Mountains and provided an illustration of a plant meeting the vague description of *C. lanceolata*. Otherwise, he provided no information about the existence or location of additional, representative collections but did suggest that material collected from eastern Siberia matched *C. lanceolata* perfectly (Pursh 1814). Presumably, the material from Siberia referenced by Pursh (1814) is now considered *C. tuberosa* Pallas ex Willdenow or *C. czukczorum* Volkova. These species exhibit similar morphology to *C. lanceolata* but are not treated as conspecific (Miller and Chambers 2006). Recent taxonomic circumscriptions for *C. lanceolata* do not include plants from Siberia. Unfortunately, most of the infraspecific taxa previously ascribed to *C. lanceolata* s. l. were originally described from few specimens (in some cases only the type collection). As a first step toward understanding this taxonomically enigmatic group across all of western North America, and due to the complexity of the situation, we limit our focus in this paper to taxa occurring in California and treated as *C. lanceolata* by Miller and Chambers (2006).

Morphological variation has been inadequately captured by type specimens and paratypes in taxonomic diagnoses resulting in a proliferation of taxonomic names associated with *C. lanceolata* (Stoughton and Jolles 2013). These taxa have been taxonomically treated in different ways for a variety of regional floras (Table 1). For example, *C. lanceolata* var. *rosea* (Rydberg) R. J. Davis was described as a unique species by Rydberg (1904) from three specimens collected at the type locality in Colorado. This example represents a case where further systematic study clarified at least one small part of the clouded taxonomy of *C. lanceolata* s. l. Although *C. rosea* Rydberg was an available name early in the 20th century (Rydberg 1904), it was not until the extensive field observations and cytological work of Halleck (1963) and Halleck and Wiens (1966) that *C. rosea* was generally accepted as distinct from *C. lanceolata*. Similarly, taxonomic issues persist in California concerning infraspecific taxa previously treated as part of *C. lanceolata*. First, two taxa previously treated as varieties of *C. lanceolata* (*C. l.* var. *sessilifolia* (Torrey) A. Nelson and *C. l.* var. *peirsonii* Munz and Johnston; Table 1) have type localities in California but have recently been treated as synonyms of *C. lanceolata*. A third taxon, *C. obovata* Rydberg, synonymized with *C. lanceolata* by Davis (1966), has a type locality in Oregon but Californian populations in Mendocino County are specifically mentioned in the protologue by Rydberg (1932).

Claytonia lanceolata, as circumscribed by Miller and Chambers (2006), ranges in distribution from Canada to near Mexico and encompasses the variation associated with all three of these taxa (*C. obovata*, *C. lanceolata* var. *peirsonii*, and *C. lanceolata* var.

Table 1. Taxa of the *Claytonia lanceolata* species complex as treated by earlier authors and in the present treatment. An 'X' indicates that a taxon was accepted under the name listed in the leftmost column. No entry indicates that the taxon had not yet been described when the work was published. Not treated indicates that a taxon was either not accepted, or unaddressed (e.g. in a regional flora where that taxon does not occur).

Taxa	Rydberg 1932	Hitchcock 1964	Davis 1966	Chambers 1993	O'Quinn 2005	Miller and Chambers 2006	This treatment
C. lanceolata var. *chrysantha*	not treated	X	*C. lanceolata*	not treated	not treated	*C. lanceolata*	*C. lanceolata*
C. lanceolata var. *flava*	*C. flava*	X	X	not treated	*C. multiscapa*	*C. m.* subsp. *multiscapa*	*C. m.* subsp. *multiscapa*
C. lanceolata var. *idahoensis*			X	not treated	not treated	*C. lanceolata*	*C. lanceolata*
C. lanceolata var. *lanceolata*	*C. lanceolata*	X	X	*C. lanceolata*	X	*C. lanceolata*	*C. lanceolata*
C. lanceolata var. *pacifica*				not treated	not treated	*C. m.* subsp. *pacifica*	*C. m.* subsp. *pacifica*
C. lanceolata var. *peirsonii*	not treated	not treated	X	*C. lanceolata*	X	*C. lanceolata*	*C. piersonii* subsp. *peirsonii*
C. lanceolata var. *rosea*	*C. rosea*	not treated	X	not treated	*C. rosea*	*C. rosea*	*C. rosea*
C. lanceolata var. *sessilifolia*	*C. sessilifolia*	not treated	X	*C. lanceolata*	not treated	*C. lanceolata*	*C. lanceolata*
C. multiscapa	X	*C. l.* var. *multiscapa*	*C. lanceolata*	not treated	X	*C. m.* subsp. *multiscapa*	*C. m.* subsp. *multiscapa*
C. obovata	X	not treated	*C. lanceolata*	not treated	not treated	*C. lanceolata*	*C. obovata*
C. panamintensis							*C. panamintensis*
C. piersonii subsp. *bernardinus*							*C. piersonii* subsp. *bernardinus*
C. piersonii subsp. *californacis*							*C. piersonii* subsp. *californacis*
C. piersonii subsp. *yorkii*							*C. piersonii* subsp. *yorkii*
C. serpenticola							*C. serpenticola*

sessilifolia), but currently no infraspecific taxa are recognized. In California, plants conforming to Miller and Chambers' (2006) interpretation of *C. lanceolata* (Consortium of California Herbaria 2015; T. Stoughton pers. obs.) can be found on a broad spectrum of substrates with vast compositional differences falling into three main categories: (1) those rich in mafic minerals (e.g. gabbro, peridotite, and serpentinite), (2) those rich in alkali minerals (e.g. gneiss, granite, rhyolite, schist, and slate), and (3) siliciclastic or carbonate-dominated (meta)sedimentary rocks (e.g. greywacke, limestone, marble, sandstone, and shale). Further complicating the matter, *C. lanceolata* s. l. grows in California at a wide range of elevations, from ca. 575 m to near 2750 m (Consortium of California Herbaria 2015), and it is found in a wide range of habitat types from transmontane pinyon-juniper and oak woodland habitats to montane or cismontane mixed-conifer forest, subalpine forest, and mesic meadow habitats (Chambers 1993; Stoughton and Jolles 2013; Consortium of California Herbaria 2015).

Two key factors appear to have had a substantial influence on application of the name *C. lanceolata* to plants in California and elsewhere in western North America. First, most members of the *C. lanceolata* species complex (Table 1) appear above ground and vanish quickly in a number of weeks (Miller and Chambers 2006; Stoughton and Jolles 2013). This ephemeral snowmelt ecology likely contributes to the modest number of collections for the group, which in turn limits material available for taxonomists. At least in southern California, plants representing *C. lanceolata* s. l. generally flower and completely disappear during the spring season well before the 'peak' period of botanical collecting (T. Stoughton pers. obs.). The dearth of *C. lanceolata* s. l. specimens in the pooled records of 35 herbaria available through the Consortium of California Herbaria (only 226 records, including duplicates, as of 14 Nov 2015) suggests that an early blooming period hinders full understanding of the taxa, geographic distribution, and overall range of morphological variation. *Claytonia perfoliata* Donn ex Willdenow, a lower elevation, annual species that is part of an equally perplexing group of closely related species, has more than nine times as many collections served on the Consortium of California Herbaria (maximum of 2000 records returned, including duplicates, as of 14 Nov 2015). Second and more substantially, the succulent nature of *Claytonia* poses a challenge to preserving diagnostic morphological characteristics in this group. *Claytonia* plants have relatively high saturated water content (Ogburn and Edwards 2012) which causes specimens to wilt quickly following removal from the ground. The fluids in *Claytonia* tissues cause newspaper and blotters used for collecting to stick to the plants, obliterating many morphological features during the drying process (T. Stoughton pers. obs). Other alternatives for preserving morphological features, such as pickling *Claytonia* tissues in spirits, tend not to be common practice for most general collectors and can often be precluded by site accessibility issues (e.g. space requirements when backpacking to multiple, remote sites).

In this study, we revisit and address taxonomic uncertainty for the Californian members of the *C. lanceolata* species complex using morphometric analyses of key morphological characters. We provide a revised taxonomic treatment for *C. lanceolata* s. l. in California using these data in combination with preliminary molecular phylogenetic data and information about natural history (including substrate association). Our revised taxonomic treatment includes recognition of *C. lanceolata* and *C. obovata* in addition to three new species, *C. panamintensis* T. R. Stoughton, *C. peirsonii* (Munz and Johnston) T. R. Stoughton (including four subspecies), and *C. serpenticola* T. R. Stoughton.

Materials and Methods

Sampling—Going forward in this manuscript, we use '*Claytonia lanceolata* s. l.' to refer specifically to the treatment of *C. lanceolata* by Miller and

Chambers (2006), whereas *C. lanceolata* s. s. refers to the concept of Pursh (1814) and '*C. lanceolata* species complex' refers to the taxa listed in Table 1. Over the course of four field seasons (between February and July, 2011–2014), hundreds of plants resembling *C. lanceolata* s. l. were examined and collected in California (Fig. 1), Oregon, Idaho, and Montana as part of a broader study on phylogenetic relationships of tuberous, perennial *Claytonia* (T. Stoughton unpubl. data). To better understand variation in plants of *C. lanceolata* s. l. (sensu Miller and Chambers 2006), specimens previously identified as *C. lanceolata* from throughout the western U. S. A. held at BABY, CAS/DS, HSC, NSMC, NY, OSC, RSA/POM, UC/JEPS, UNLV, and UNR herbaria were examined.

***Phylogenetic Analysis*—**To investigate patterns of genetic differentiation in *C. lanceolata* s. l. (i.e. as treated by Miller and Chambers 2006), we conducted Bayesian phylogenetic inference using gene sequences available on GenBank (http://www.ncbi.nlm.nih.gov/genbank/; see Benson et al. 2005). GenBank sequences were supplemented with new sequences generated at Rancho Santa Ana Botanic Garden (RSABG) for *C. lanceolata* s. l. collected from populations both within and outside of California (Appendix 1). Samples used for this study were freshly collected material dried in silica from the 2011–2014 field seasons. Exhaustive geographic sampling was not conducted for *C. lanceolata* s. l., given its wide distribution and the diversity of habitat types it occupies, but samples from all Californian taxa

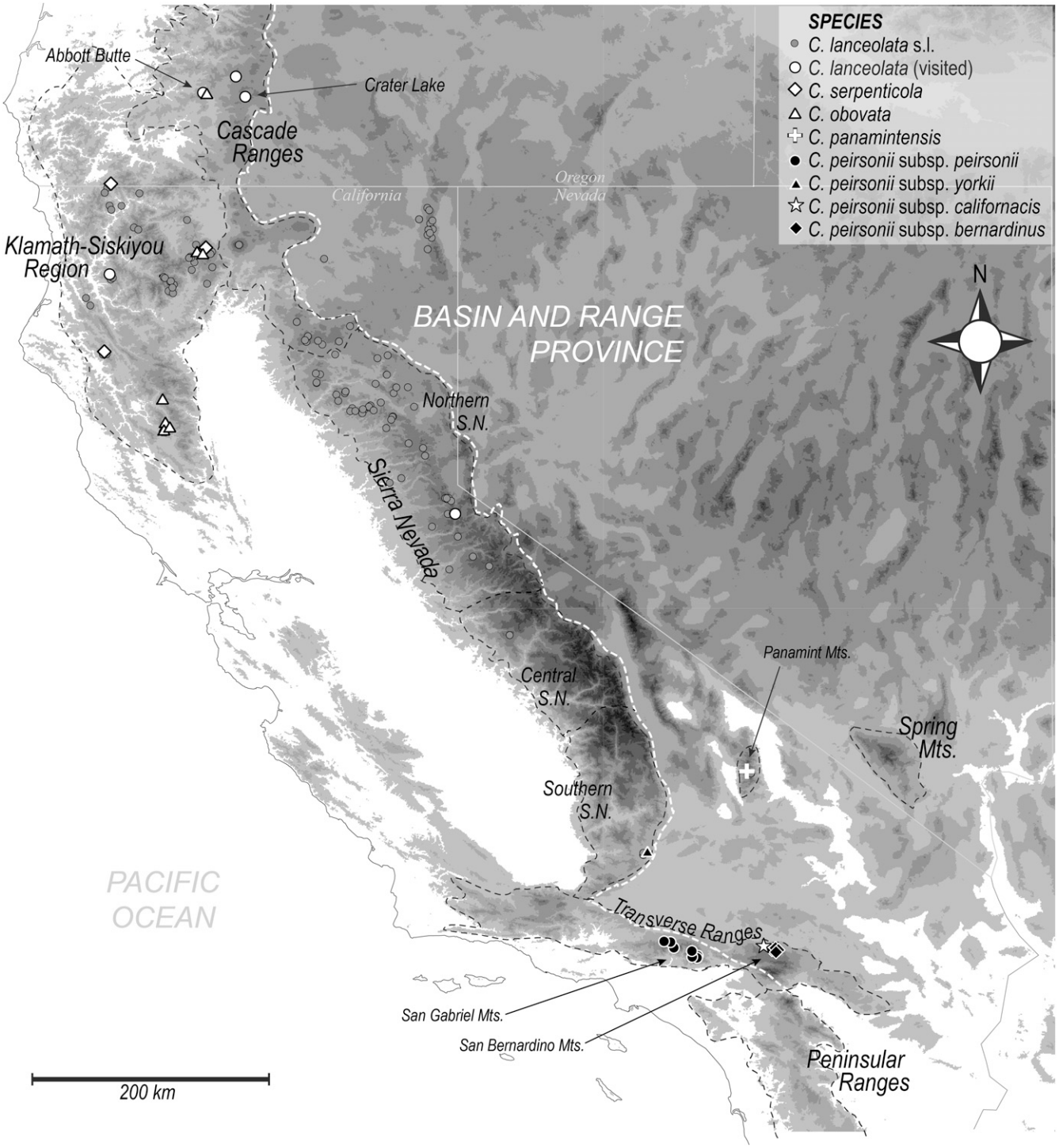

FIG. 1. Map of locations in California and Oregon visited during 2011–2014 field seasons and referenced in text. Georeferenced specimens from the Consortium of California Herbaria (CCH 2015) are gray circles labeled as *C. lanceolata* s. l.

we recognize in this paper were analyzed. This set includes material from the San Bernardino Mountains, San Gabriel Mountains, and Panamint Mountains of southern California, the Klamath-Siskiyou region (including North Coast Ranges) of northern California, and the Sierra Nevada. Additional samples of *C. lanceolata* s. l. were included from the mountains of Idaho, Nevada (on GenBank), Oregon, and British Columbia, Canada to represent the extremes of its geographic range. Pre-existing sequence data on GenBank sampled from across the genus *Claytonia* (O'Quinn and Hufford 2005; M. Hershkovitz unpubl. data) were added for comparisons and to provide phylogenetic context for the gene sequences developed at RSABG. This phylogenetic comparison included more than half (5/9) of the tuberous, perennial *Claytonia* species recognized by Miller and Chambers (2006), but in no way represents an attempt to resolve the phylogeny of *Claytonia.* Rather, we include a phylogenetic estimate as corroboration of taxonomic concepts, which are based principally on morphology.

Genomic DNA was isolated at RSABG from leaf material of 12 *C. lanceolata* s. l. samples (classified in Vegetative Morphology analysis below) using a protocol modified from the CTAB-method of Doyle and Doyle (1987). Two or more individuals per taxon were used to sample multiple exemplars in the *C. lanceolata* species complex (15 total samples). Nine samples of other tuberous, perennial *Claytonia* were included as outgroups with respect to *C. lanceolata* s. l. Thirty-one total samples were used for the phylogenetic analysis, including more distant outgroups from *Claytonia* and *Lewisia* (Appendix 2).

Sequence data of the internal transcribed spacers (ITS1, ITS2) flanking the nuclear ribosomal 5.8*S* exon (nrITS) were obtained from all samples following manufacturer's instructions for Phusion® High-Fidelity DNA Polymerase (New England Biolabs, Ipswich, Massachussetts). The nrITS gene region was amplified on a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, California) in a single reaction using the plant-specific primer pair ITS5a (Prince and Kress 2006) and 26SR (Prince 2010). Reaction conditions for all amplifications were: 98°C for 30 s; 35 cycles of 98°C for 10 s, 48°C for 20 s, and 72°C for 20 s; an extension cycle for 7 min at 72°C followed the 35 cycles, and samples were held at 4°C until removed and stored at -20°C. Amplification products were then purified using a polyethylene glycol (PEG) precipitation. Purified PCR products were processed using a BigDye Terminator (Applied Biosystems) cycle sequencing reaction with the same primers (albeit at lower concentrations) following the manufacturer's instructions. Cycle sequencing products were purified using Sephadex columns (Amersham Biosciences, Piscataway, New Jersey) and analyzed on an automated sequencer (3130*xl*, Applied Biosystems).

Geneious v. 6.1.2 (Biomatters Ltd., Auckland, New Zealand) was used to edit, assemble and align sequences, resulting in an alignment 639 base pairs long. Bayesian inference (BI) was conducted using MrBayes v. 3.1.2 (Huelsenbeck and Ronquist 2001), and posterior probability values (PP) are reported for all nodes ≤ 0.95. One replicate of BI was conducted using flat priors. The BI analysis was run for ten million generations, with four chains, and sampled every 1000 generations. The final average standard deviation of split frequencies was less than 0.01. Inspection of the resulting parameter files using Tracer v. 1.6. (Rambaut et al. 2014) indicated that effective sample sizes were sufficiently high to meet statistical assumptions. The first 25% of trees were discarded from the final tree set as burn-in; remaining trees were used to determine the PP distribution for the nrITS gene region. Information on vouchers and GenBank numbers are included in Appendix 1, and data are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.qm344 (Stoughton et al. 2017).

Geomorphic Context—Because *C. lanceolata* s. l. is known to occur on a broad diversity of rock types, substrate affinity was identified from parent rock material that was collected from around *Claytonia* plants at selected field sites in California and southern Oregon (Appendix 1). Slope aspect, geomorphic landform, elevation, associated species, and other local site information was also recorded in the field at these sites and is included on herbarium labels for all collections.

Vegetative Morphology—Five morphological characters (stem length [measured from proximal end of stem at tuber apex to attachment point of the cauline leaf pair], cauline leaf length [measured from stem-petiole attachment to leaf apex], cauline leaf width [measured at widest point of blade], cauline leaf length/width ratio, and peduncle length [measured from attachment point of cauline leaf pair to base of proximal-most pedicel]) were measured and used in morphometric analyses comparing all of the plants occurring in California treated as *C. lanceolata* by Miller and Chambers (2006). Characters were selected because they exhibit variation within and among species and are easily measured; the drying process does not appear to distort leaves and stems as much as tubers and floral parts (T. Stoughton pers. obs.). Measurements were taken from 19 pre-existing RSA/POM herbarium specimens collected in California and from an additional 89 specimens (including duplicates) collected in California and Oregon contributed by this study (108 total herbarium specimens; Appendix 1). Measurements provided in the current study were made from dried herbarium specimens specifically for the enhanced identification and curation of specimens already existing in herbaria.

To best capture variation within a single population, measurements were taken from all measurable plants on a given herbarium specimen and averaged for each character to obtain one set of character means per specimen. Herbarium specimens were then identified using the taxonomic concepts presented in this study (see Taxonomic Treatment below), a limited number of samples were assayed using molecular phylogenetic data (see Phylogenetic Analysis above), and the taxonomically sorted morphometric data were ultimately used for principal components analysis (PCA) and discriminant analysis (DA) to characterize variation. Prior to multivariate analyses, morphological characters were examined for independence, multinormality and outliers. In a few cases, outlying measurements were given the maximum or minimum quartile value for that taxon/character combination depending on which extreme of the first and third quartiles they fell, and missing data was filled with average values for that taxon/character combination. Peduncle length was correlated with stem length and was therefore omitted from multivariate analyses. The remaining characters were log-transformed to achieve normality. Subsequently, both PCA and DA were conducted in R v. 3.1.2 (R Core Team 2014) using the STATS::princomp and MASS::lda functions (Ripley 1996; Venables and Ripley 2002), respectively. The STATS::predict function in R was also used to determine how effectively specimens were classified in the DA using our a priori taxonomic categorization by dividing the number of correctly predicted samples by the total number of samples for that taxon. A χ^2 test was used to determine whether the DA diagnosed the taxonomic identity of our samples with greater accuracy based upon the morphological characters measured compared with random assignment. These analyses (i.e. both the PCA and DA) were conducted including all samples listed in Appendix 2 in a single analysis (eight taxa, n = 108) and separately for each geographic region (i.e. north California [three taxa, n = 42] and south California [5 taxa, n = 66]).

Results and Discussion

Phylogenetic Analysis—Multiple unique lineages attributed to *C. lanceolata* are uncovered in the nrITS gene tree with strong PP support (i.e. PP = 1.0 for *C. lanceolata*, *C. obovata*, *C. panamintensis*, and *C. peirsonii* clades), all of which are circumscribed in the Taxonomic Treatment below. However, monophyly of *C. lanceolata* s. l. (i.e. as treated by Miller and Chambers 2006) cannot be rejected based on the PP distribution of our BI analysis (Fig. 2). Results are inconclusive (regarding monophyly of *C. lanceolata*) due largely to an unresolved backbone separating major lineages within a clade that includes all tuberous, perennial *Claytonia* sampled in this study.

Claytonia caroliniana Michaux, *C. virginica* L. and *C. tuberosa* are inferred as paraphyletic in our BI analysis, but these results are not surprising considering the historic work on *C. virginica* by Doyle (1981, 1983, 1984a, b), Doyle et al. (1984), and Doyle and Doyle (1988). These results also support a recent effort by Yatskievych et al. (2013) to incorporate natural history information in recognizing a new species of *Claytonia* from Arkansas that is part of this primarily arctic species complex (the *C. virginica* complex, including *C. tuberosa* and *C. caroliniana*). Furthermore, monophyly of sect. *Claytonia* L. is called into question based on the position of two *C. serpenticola* samples together in a trichotomy that includes *C. acutifola* Pallas ex Willdenow and the rest of the tuberous, perennial *Claytonia* (Fig. 2). *Claytonia acutifolia* is a caudicose perennial and has been traditionally treated in another section. Miller and Chambers (2006) suggested abandonment of the sectional classification in *Claytonia* until further study can elucidate the morphological and anatomical transitions to perennial habit.

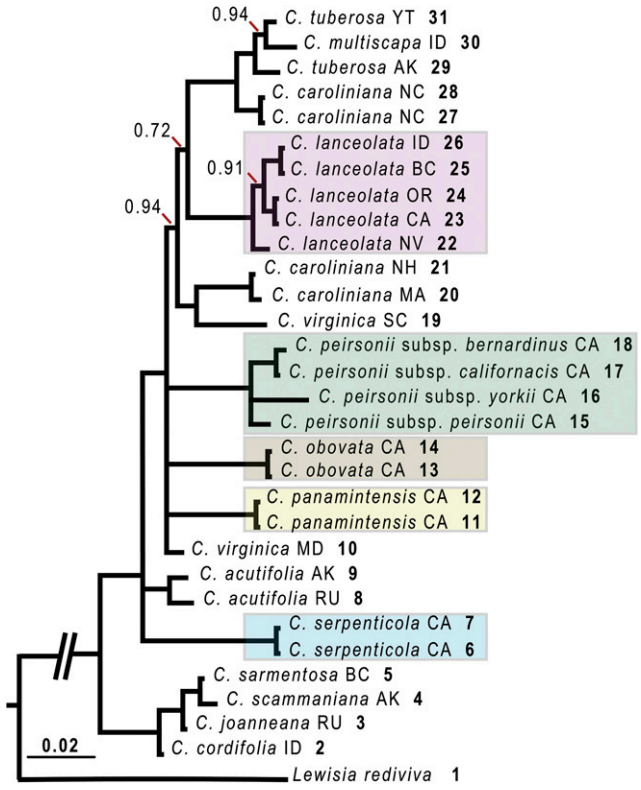

FIG. 2. Bayesian 70% consensus phylogeny of *Claytonia lanceolata* s. l. estimated using data collected from the nrITS gene region. Branches are unlabeled where PP support is ≥ 0.95, support values are specified for branches with PP ≥ 0.70 but < 0.95, and branches are collapsed where PP support is < 0.70. Numbers associated with each terminal correspond with a list of GenBank accession numbers in Appendices 1 and 2. Highlighted taxa were treated as *C. lanceolata* by Miller and Chambers (2006).

Use of nrITS in this study may be problematic, considering the possibilities of concerted evolution and multiple copies (especially in polyploid plants, of which there are many in *Claytonia*), but we do not believe its use detracts significantly from our main conclusions. We used different PCR primers than O'Quinn and Hufford (2005) and M. Hershkovitz (unpubl. data), yet samples corresponding to our morphological concept of *C. lanceolata* s. s. are resolved as a clade with samples from these other studies, providing no evidence that different copies of nrITS were amplified. The results of this preliminary analysis do not permit new inferences regarding relationships among tuberous *Claytonia*, but this was not a specified goal of this study. Instead, our phylogenetic results fully complement our morphological analyses of Californian taxa (see below). Given our discovery of strongly supported lineages (Fig. 2), at minimum the results are suggestive that the current treatment of *C. lanceolata* by Miller and Chambers (2006) should be reconsidered. The phylogenetic status of sect. *Claytonia* (implying a single origin of the tuber), and relationships of tuberous species within that putative clade, are the subjects of our continuing research using high-throughput sequencing.

Geomorphic Context—Both in the field and in herbaria we observed edaphic differences (habitat differences) that are correlated with morphological differences among taxa in both northern and southern California. Several clear ecological differences were observed within *C. lanceolata* s. l. in northern California and southwestern Oregon where plants grow on mafic rocks (e.g. gabbro, serpentinite, peridotite) and siliciclastic or carbonate-dominated sedimentary substrates (e.g. greywacke, limestone, shale) in comparison to sites where populations occur in the same vicinity on more alkali-rich lithologies (e.g. granite, rhyolite). Ecological differentiation was also observed between populations of *C. lanceolata* s. l. in southern California where it grows on alkali-rich lithologies (e.g. gneiss, granite, rhyolite, schist) in comparison to sites in the same vicinity where populations are found on siliciclastic or carbonate-dominated (meta)sedimentary rocks (e.g. limestone, marble, sandstone, shale, slate). In general, a combination of character differences were observed among plants growing in northern California (i.e. the Klamath-Siskiyou region; Fig. 3A–B), those in the Northern and Central Sierra Nevada regions (Fig. 3C), and those from southeastern California (Fig. 3D–H). Observed morphological differentiation among populations on different substrates reflects changes in betalain pigmentation, inflorescence architecture, and morphology of cauline leaves, subterranean stems, and flowers (Fig. 3). Ecological differences correspond with changes in parent rock material, soil type, and water availability, all of which are generally reflected by vegetation associations.

Morphological and ecological differences among taxa are summarized in the Taxonomic Treatment below. Explicit consideration is given as to whether a taxon's occurrence on a given substrate in a given region indicates a physiological/ecological requirement, or rather mere happenstance (e.g. a particular substrate type is common in the region where a taxon is known). With so few populations identified, particularly for the southern Californian taxa, edaphic constraints on species distributions are still unclear for most of the *C. lanceolata* species complex.

Vegetative Morphology—PCA of the morphological variables we measured for herbarium specimens indicates that the first three components summarize 99.7% of the total variation in the dataset with the first component explaining 57.7% (Fig. 3J; Table 2). The highest loadings in the first component indicate that cauline leaf length/width ratio (0.737) and width (-0.655) contribute most to the total variation (Table 2). This is not surprising given that cauline leaf morphology has been given a great amount of attention in nearly all treatments of the *C. lanceolata* species complex (Table 1). Plotted scores for samples of all Californian taxa (8 taxa, n = 108; Fig. 3I) showed differentiated clustering of samples assignable to each taxon we circumscribed, with the vast majority of overlap occurring among taxa in different regions of California rather than among taxa in the same geographic area. In other words, the PCA indicates that morphological similarity for the characters measured is shared mostly among northern and southern Californian taxa but not among the collective taxa within either geographic area. One exception is the substantial overlap between two taxa in southern California belonging to the *C. peirsonii* species complex (Fig. 3E–H, and see Taxonomic Treatment below).

Regional analyses show comparable (but greater) separation of discrete clusters, particularly for the taxa in southern California. In the northern California regional PCA (three taxa, n = 42, Fig. 3L), the first three components summarize 99.8% of the total variation with the first component explaining 66.6% and the strongest loading contributed by cauline leaf length/width ratio (0.819; Table 2). In the southern California regional PCA (five taxa, n = 66, Fig. 3M), the first three components summarize 99.6% of the total variation with the first

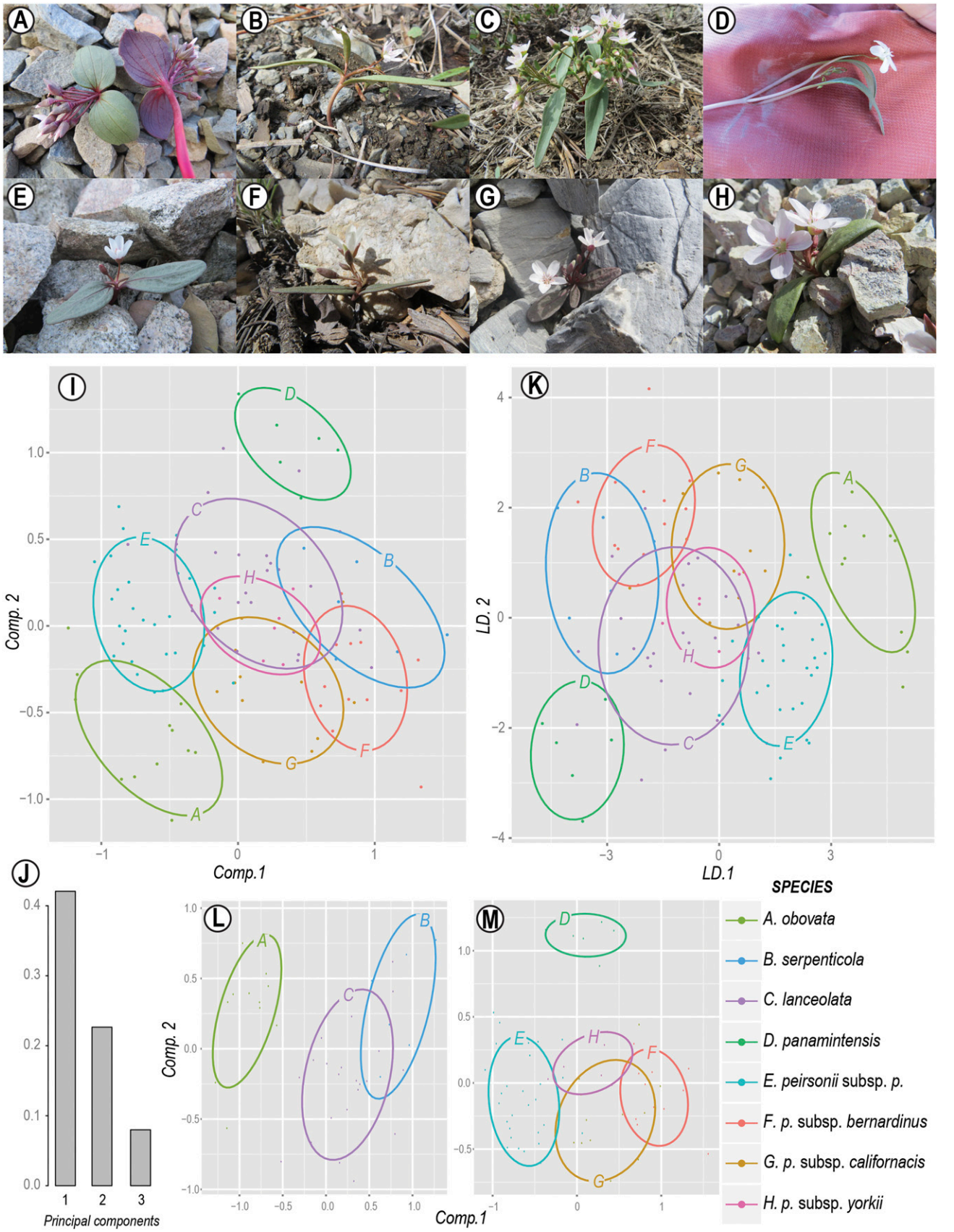

FIG. 3. Morphology of *Claytonia lanceolata* s. l. in California. A–C. Northern Californian taxa. A. *C. obovata*. B. *C. serpenticola*. C. *C. lanceolata*. D–H. Southern Californian taxa. D. *C. panamintensis*. E. *C. peirsonii* subsp. *peirsonii*. F. *C. peirsonii* subsp. *bernardinus*. G. *C. peirsonii* subsp. *californacis*. H. *C. peirsonii* subsp. *yorkii*. I–M. Results from morphometric analyses. I. PCA scatter and J. scree plot showing proportions of explained variance for all taxa accepted in California analyzed together; K. DFA scatter plot for the same, and PCA scatter plots for regional analyses of L. northern and M. southern Californian taxa analyzed separately. Confidence interval (95%) ellipses are included on all scatter plots.

TABLE 2. Results of the principal components analyses for Californian *Claytonia lanceolata* s. l. North taxa and South taxa respectively refer to separate geographic analyses run on plants in northern and southern California, whereas All taxa refers to an analysis including all taxa we treat as part of this group in California. Bold is used to draw the reader's eye to cumulative variation explained by three principal components and to signify those characters with the highest loadings on each of the components.

Variances	Comp. 1	Comp. 2	Comp. 3
All taxa			
Proportion of Variance	0.577	0.311	0.110
Cumulative Proportion	0.577	0.887	**0.997**
North taxa			
Proportion of Variance	0.666	0.268	0.063
Cumulative Proportion	0.666	0.934	**0.998**
South taxa			
Proportion of Variance	0.609	0.280	0.107
Cumulative Proportion	0.609	0.889	**0.996**
Loadings	Comp. 1	Comp. 2	Comp. 3
All taxa			
Mean stem length	−0.145	0.585	**0.798**
Mean cauline lf length	-	**0.656**	−0.468
Mean cauline lf width	−0.655	0.333	−0.361
Cauline lf length/width ratio	0.737	0.343	−0.115
North taxa			
Mean stem length	-	−0.473	**0.881**
Mean cauline lf length	0.437	−0.596	−0.335
Mean cauline lf width	−0.372	**-0.648**	−0.334
Cauline lf length/width ratio	**0.819**	-	-
South taxa			
Mean stem length	−0.253	**0.755**	0.605
Mean cauline lf length	−0.144	0.467	**-0.642**
Mean cauline lf width	**-0.743**	-	−0.344
Cauline lf length/width ratio	0.603	0.459	−0.323

component explaining 60.9% and the strongest loading contributed by cauline leaf width (-0.743; Table 2). Furthermore, we found, as expected, that the four lineages identified within the *C. peirsonii* species complex from southern California (treated as subspecies of *C. peirsonii*, see Taxonomic Treatment below) cluster closely together but are distinct from *C. panamintensis*. The results from both PCA analyses suggest strong morphological divergence on a regional scale but convergence at broader levels, as revealed by the analysis of all Californian taxa together (Fig. 3I). Morphological similarity in this group is likely the result of retained ancestral similarity, hybridization, or some other factor(s) not discussed here.

For the DA of all Californian taxa (eight taxa, n = 108), three linear discriminants were important for maximal differentiation of species (LD1 = 0.7394, LD2 = 0.2212, LD3 = 0.0389) explaining 99.9% of the total variation in the morphological dataset. Factors that best discriminated among taxa were the length (-5.417) and width (3.813) of the cauline leaves. The graph of optimized discriminants (Fig. 3K) indicates that all factors taken in combination separate discrete clusters of samples for most taxa. Essentially, these results are comparable to those of the PCA in showing distinct clustering of specimens assignable to each taxon we circumscribed with the majority of overlap occurring among species in different portions of California (i.e. northern or southern California) rather than among species within the same geographic area.

Additionally, taxonomic predictions from the DA were fairly accurate (78.7%, 85 of 108 correctly predicted; Table 3) but indicate that classification accuracy based on the morphological characteristics we measured varies among taxa (*C. lanceolata*, 12/24 = 50% correct; *C. obovata*, 11/12 = 91.7% correct; *C. panamintensis*, 6/6 = 100% correct; *C. peirsonii* subsp. *bernardinus*, 12/12 = 100% correct; *C. peirsonii* subsp. *californacis*, 9/12 = 75% correct; *C. peirsonii* subsp. *peirsonii*, 29/29 = 100% correct; *C. peirsonii* subsp. *yorkii*, 3/7 = 42.9% correct; *C. serpenticola*, 3/6 = 50% correct). For the northern California regional DA (three taxa, n = 42), cauline leaf length (-4.108) discriminates best among taxa and predictive accuracy was high (*C. obovata*, 12/12 = 100% correct; *C. lanceolata*, 21/24 = 87.5% correct) for all but one taxon, *C. serpenticola* (3/6 = 50% correct). In comparison, for the southern California regional DA (five taxa, n = 66), cauline leaf width (5.646) and length (-5.470) discriminate best among taxa and predictive accuracy was also high (*C. panamintensis*, 6/6 = 100% correct; *C. peirsonii* subsp. *bernardinus*, 12/12 = 100% correct; *C. peirsonii* subsp. *californacis*, 11/12 = 91.7% correct; *C. peirsonii* subsp. *peirsonii*, 29/29 = 100% correct) for all but one taxon, *C. peirsonii* subsp. *yorkii*, (5/7 = 71.4% correct). It should be noted that these prediction accuracies all increase (or stay the same) in individual regional analyses compared with the analysis for all Californian taxa (Table 3). This result suggests that actual misclassification rates in the field using the treatment provided below should be lower than we observed using the DA for four continuous morphological characters. Furthermore, additional discontinuous characters facilitate easy recognition of the two taxa identified least successsfully by the DA. The alternate leaf arrangement and venation of *C. serpenticola* readily distinguish it from *C. lanceolata* and the limited betalain pigmentation of *C. peirsonii* subsp. *yorkii* is diagnostic for that taxon with respect to other members of the *C. peirsonii* complex. Results of the χ^2 test from the predictive DA of all Californian taxa strongly reject the null hypothesis of statistical independence between taxon and measured morphological characters for samples included in this study (All Californian taxa: X-squared = 435.2407, df = 49, $p < 0.001$; North Californian taxa: X-squared = 47.9062, df = 4, $p < 0.001$; South Californian taxa: X-squared = 228.8473, df = 16, $p < 0.001$). As with the PCA discussed above, these findings suggest both strong morphological differentiation on the regional scale and convergence across California.

The inferences made from the data we collected have clear taxonomic implications for California: 1) recognition of species status for a southern Californian taxon formerly subsumed within *C. lanceolata* s. l. and further delimitation of four subspecies, three of these being newly described taxa, 2) reinstatement with modified circumscriptions for previously recognized taxa in California treated as *C. lanceolata* by Miller and Chambers (2006), and 3) circumscription of two newly discovered species from the Klamath-Siskiyou region of California and Oregon and the Transmontane habitats of California and Nevada, respectively. Using a taxonomic concept originally proposed by Cronquist (1978), we argue that observed and statistically significant morphological differences are sufficient to recognize populations in southern California and southern Nevada discussed by Stoughton and Jolles (2013) as two new species of *Claytonia, C. panamintensis*, and *C. peirsonii*. Drawing from discourse concerning species concepts communicated by several authors over the years (e.g. Baum 2009; Johnson and Cairns-Heath 2010; Stoughton et al. 2014), information about the natural histories included below and molecular divergence included above provides additional support for the recognition of four morphologically and

TABLE 3. Results of the descriptive discriminate analyses for Californian *Claytonia lanceolata* s. l. North taxa and South taxa, respectively, refer to separate geographic analyses run on plants in northern and southern California, whereas All taxa refers to an analysis including all *C. lanceolata* s. l. taxa we treat as part of this group in California. Percent of incorrect samples predicted as geographic impossibility refers to situations when northern Californian taxa are misclassified as southern Californian taxa, or vice versa. Measurements denoted by [1] indicate group means.

All taxa	*C. pe. bernardinus*	*C. pe. californacis*	*C. lanceolata*	*C. obovata*	*C. panamintensis*	*C. peirsonii pe.*	*C. serpenticola*	*C. pe. yorkii*
Prior probabilities of groups	0.11	0.11	0.22	0.11	0.06	0.27	0.06	0.06
Stem length[1] (cm)	4.07	5.13	6.84	5.78	11.57	7.29	5.30	7.84
Cauline lf length[1] (mm)	20.87	17.53	27.85	12.81	42.29	22.44	25.73	19.35
Cauline lf width[1] (mm)	2.80	3.98	5.42	6.50	5.43	8.24	3.08	4.33
Leaf length/width ratio[1]	7.58	4.67	5.59	2.05	7.97	2.81	8.79	4.62
Peduncle length[1] (mm)	0.56	0.27	1.83	0.17	12.31	0.57	0.82	0.79
% samples correctly predicted	67	83	54	83	83	79	33	43
% incorrect samples predicted as geographic impossibility	50	100	91	100	100	67	75	50
North Taxa only								
Prior probabilities of groups			0.57	0.29			0.14	
% samples correctly predicted			88	100			50	
South Taxa only								
Prior probabilities of groups	0.18	0.18			0.09	0.44		0.11
% samples correctly predicted	100	92			100	100		71

genetically diagnosable subspecies of *C. peirsonii* endemic to the North American Desert Southwest.

We here present a new taxonomic circumscription of tuberous, perennial *Claytonia* in California based on these results and information included in the Taxonomic Treatment below. We cannot overemphasize that the diagnostic characters presented in the current treatment are best observed from several plants while in the field (Stoughton and Jolles 2013). *Claytonia* specimens that will be most useful for subsequent taxonomic work should include an image of a live plant and should be made by quickly and carefully pressing plants in the field. Finally, we invite researchers who locate and collect these plants to communicate with us (images and vouchers ideal) toward further advancing our knowledge of this challenging group.

Taxonomic Treatment

Key to the Claytonia lanceolata Species Complex in California

1. Cauline leaves 1-nerved, distinctly petiolate, petioles generally > 5 mm and distinct from blade; developing flower buds nodding; Transmontane (desert) habitats and on variable (meta)sedimentary substrates (e.g. marble, sandstone, shale/slate) ..... 1. *C. panamintensis*
1. Cauline leaves 3- or 1-nerved, sessile to indistinctly petiolate (sometimes distinctly short-petiolate), petioles generally < 5 mm, often tapered into blade when present; developing flower buds erect to spreading or nodding; not strictly in desert habitats, and on a variety of rock types including but not limited to (meta)sedimentary substrates ..... 2.
    2. Inflorescence an elongate raceme often with some internodal elongation among pedicels by fruiting stage, peduncle generally present and > 3 mm, flower buds nodding to spreading in early development; 1° veins (midribs) of cauline leaves generally greenish at base of blade on adaxial surfaces, blades generally similar in color on ab/adaxial surfaces (occasionally dissimilar in *C. lanceolata* from Central and Northern Sierra Nevada, see 3.); Northern California Mtns. (including Central Sierra Nevada region). ..... 3.
        3. Cauline leaves 2–4, alternate to sub-opposite and 1-nerved; cauline leaves generally > 5 × longer than wide, blades narrowly elliptic to lance linear; terminal inflorescences often appearing branched with axillary inflorescences developing in the axils of the proximal-most cauline leaves; generally found on substrates dominated by mafic minerals (e.g. gabbro, peridotite, serpentinite), or on sedimentary substrates (e.g. shale), occurring in Klamath-Siskiyou region (including North Coast Ranges) ..... 2. *C. serpenticola*
        3. Cauline leaves 2, opposite and 3-nerved (sometimes midrib more prominent than lateral veins); cauline leaves generally < 5 × as long as wide, blades ovate to lance ovate to lance linear; inflorescences terminal and solitary, generally lacking axillary inflorescences; generally not found on mafic or sedimentary substrates but instead occurs in Klamath-Siskiyou and Central and Northern Sierra Nevada regions on more alkali-rich lithologies (e.g. granite, rhyolite) ..... 3. *C. lanceolata*
    2. Inflorescence axis not elongate, raceme generally lacking internodal elongation among pedicels even in fruit (sometimes appearing umbellate), peduncle generally absent or < 3 mm, flower buds erect to ascending or spreading in early development; 1° veins (midribs) of cauline leaves generally reddish at base of blade on adaxial surfaces (sometimes pigmentation weak or lacking in *C. peirsonii* subsp. *yorkii*), blades generally dissimilar in color on ab/adaxial surfaces with purple coloration abaxially (pigmentation faint or lacking in *C. peirsonii* subsp. *yorkii* from the southern Sierra Nevada); Southern California Mtns. (except *C. obovata* from Klamath-Siskiyou region, including North Coast Ranges, see 4.) ..... 4.
        4. Cauline leaves generally 3-nerved with parallel veins equal in length (or nearly so), lateral veins converging with midrib at apex; adaxial surfaces of cauline leaves lacking raised veins; Klamath-Siskiyou region (including North Coast Ranges), generally on siliciclastic or carbonate-dominated sedimentary rocks (e.g. greywacke, limestone, shale), or substrates dominated by mafic minerals (e.g. gabbro, peridotite, serpentinite) ..... 4. *Claytonia obovata*
        4. Cauline leaves generally 1-nerved or with branched veins not equal in length and not converging with midrib at apex; adaxial surfaces of cauline leaves with raised veins generally present (sometimes weak or lacking in *C. peirsonii* subsp. *bernardinus*, see 5.); Transverse Ranges and Southern Sierra Nevada region, on a variety of substrates except those dominated by mafic minerals ..... 5.
            5. Cauline leaves often ≥ 6 × longer than wide, linear to lanceolate, sessile; 2° veins of cauline leaves weakly if at all raised on the adaxial surfaces; petals white (generally with pink veins), with a yellow to orange-colored (generally not pink) spot at base of blade above claw; San Bernardino Mtns., on carbonate-dominated (meta)sedimentary substrates (e.g. limestone, marble) ..... 5b. *Claytonia peirsonii* subsp. *bernardinus*
            5. Cauline leaves generally < 6 × longer than wide, variously shaped but not linear-lanceolate, short-petiolate to sessile; 2° veins of cauline leaves generally noticeably raised on the adaxial surfaces; petals pink to white (generally with pink veins), with a pink or yellow to orange-colored spot (not always present) at base of blade above claw; Southern California Mtns. (including Southern Sierra Nevada region), on a variety of substrates including but not limited to carbonate rocks ..... 6.

6. Sepals generally green (sometimes with reddish-tinged apices) in bud; cauline leaves generally weakly pigmented on abaxial surfaces (reddish to purplish pigmentation often absent except in stem and pedicels); Southern Sierra Nevada region, generally on alkali-rich substrates (e.g. rhyolite) ..... 5d. *Claytonia peirsonii* subsp. *yorkii*
6. Sepals generally entirely purplish to brownish but not green in bud; cauline leaves generally purple on abaxial surfaces; Transverse Ranges, on a variety of substrates including alkali-rich and carbonate-dominated lithologies ..... 7.
   7. Cauline leaves generally $< 3.5 \times$ as long as wide, blades (3–)3.5–11.5(–18) mm wide, variously shaped but generally not oblanceolate; petals white (generally with pink veins) with a yellow to orange-colored spot at base of blade above claw; San Gabriel Mtns., generally on alkali-rich lithologies (e.g. gneiss, granite, schist) ..... 5a. *Claytonia peirsonii* subsp. *peirsonii*
   7. Cauline leaves generally $> 3.5 \times$ as long as wide, blades (1–)2–5.5(–9) mm wide, generally oblanceolate to elliptic; petals pink to white (generally with pink veins) with a pink-colored spot (rarely yellow or absent) at base of blade above claw; San Bernardino Mtns., generally on carbonate-dominated (meta)sedimentary (e.g. limestone, marble) substrates ..... 5c. *Claytonia peirsonii* subsp. *californacis*

1. **Claytonia panamintensis** T. R. Stoughton, sp. nov.—TYPE: U. S. A. California: Inyo Co., upper Johnson Canyon, Panamint Mountains, 6 April 2013, *T. R. Stoughton 1711* (holotype: RSA!; isotypes: UCR!, JEPS!).

Perennial; tuberous root 0.5–2.5 cm in diameter, globose, sometimes with a distinctly narrowed area at tuber apex where the aerial stems emerge; rhizomes absent. Stems (7–)11–14 (–20) cm long; foliage dark green adaxially, often at least weakly beet-red abaxially. Basal leaves absent to 1 (rarely more than 1), absent at flowering time, up to 15 cm long, petioles tapered or sometimes indistinct from blades; blades ca. 25 × ca. 2.5 mm, lanceolate, apex acute to acuminate. Cauline leaves 2–4, opposite at least proximally, 1-nerved, (20–)30–60(–80) × (2.5–)4–9 mm, elliptic to oblanceolate, distinctly petiolate, petioles generally ≥ 5 mm long. Inflorescences 1–3, terminal and often also axillary, pedunculate, unibracteate, bracts 1–3 mm long, membranous. Flowers 16–20 mm in diameter, developing buds nodding; sepals 2–4 × 1–4 mm; petals 8–10 × 2.5–4.5 mm, white, generally with at least faintly-colored pink veins, generally with a yellow-colored blotch at base of blade above claw, apices entire to irregularly toothed distally. Ovules 6. Seeds unknown. Chromosome number unknown. Figures 3D, 4C.

Distribution—Found in southeastern California in the Panamint Mountains (Fig. 1) east at least to the Spring Mountains of southern Nevada, on north-facing, stony and talus slopes comprised of primarily (meta)sedimentary substrates (e.g. marble, shale/slate, sandstone) mixed with decomposing organic material. Found most often in openings of *Pinus-Juniperus* and *Quercus* woodland habitats; 1,825 m +/− ca. 500 m elevation.

Notes—*Claytonia panamintensis* is only superficially similar to the broad interpretation of *C. lanceolata* by Miller and Chambers (2006). Plants treated here as *C. panamintensis* are distinctly petiolate and therefore should not be confused for the sessile-leaved *C. lanceolata* s. s. *Claytonia panamintensis* differs from the entire *C. peirsonii* species complex (discussed below) in having nodding flower buds (as opposed to the spreading to erect buds present in *C. peirsonii*) and an elongate peduncle. *Claytonia panamintensis* also differs from *C. lanceolata* s. l. in California by its ecological setting (*C. panamintensis* is associated with transmontane habitats and a mixture of variable sedimentary or metasedimentary substrates), shape, arrangement, and venation of the cauline leaves, longer stems, and a racemose inflorescence that retains an elongate peduncle with little to no internodal elongation among pedicels by the time of fruiting.

Given its distinctly petiolate cauline leaves, betalain pigmentation on abaxial surfaces of the foliage, and near sympatric distribution, *C. panamintensis* may be easily confused with *C. umbellata* S. Watson in the Great Basin. *Claytonia panamintensis* can be readily distinguished from *C. umbellata*

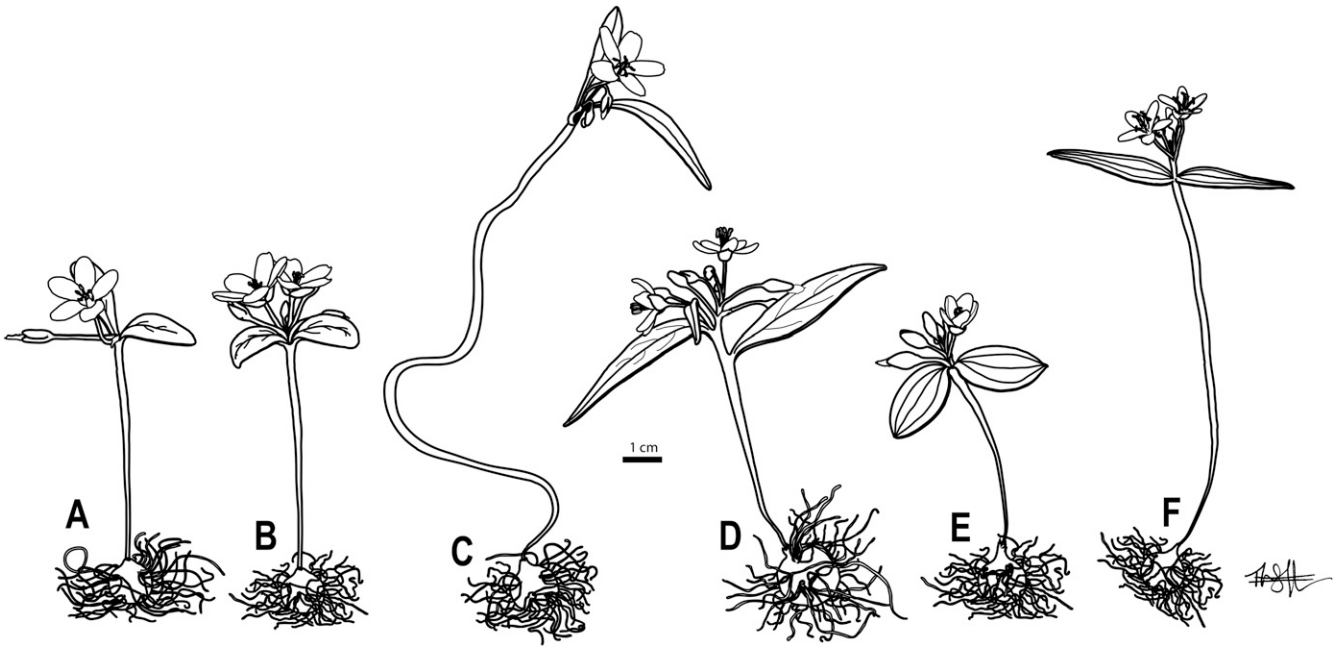

FIG. 4. Illustrations of Californian plants. A. *C. peirsonii* subsp. *californacis*. B. *C. peirsonii* subsp. *yorkii*. C. *C. panamintensis*. D. *C. serpenticola*. E. *C. obovata*. F. *C. lanceolata*.

because it lacks a taproot extending from below the tuber (consistently present in *C. umbellata*), it tends to have larger (longer) leaves and flowers than *C. umbellata,* and the shape of their leaf blades are different. Tuberous, perennial *Claytonia* plants in the Panamint Mountains (i.e. *C. panamintensis*) were previously identified as *C. lanceolata* (Miller and Chambers 2006) or *C. lanceolata* var. *peirsonii* (Stoughton and Jolles 2013; i.e. *C. peirsonii* in this treatment), the latter of which has sessile to only short-petiolate or indistinctly petiolate leaves (Stoughton and Jolles 2013). The distribution (Fig. 1), habitat, DNA data (Fig. 2), and morphology (Figs. 3D, 4C) of these *Claytonia* in the Panamint Mountains indicate that *C. panamintensis* is a distinct species worthy of recognition. *Claytonia panamintensis* should be sought out in additional areas throughout southeastern California, particularly in (meta)sedimentary habitats of the *Pinus-Juniperus* and *Quercus* belts in mountainous areas adjacent the Panamint Mountains, and east toward the Spring Mountains in southern Nevada. Collections held at CAS/DS, NSMC, and UNLV from the Bristol Range and Mormon Mountains in Lincoln Co., Nevada, approach *C. panamintensis* in gross morphology but may represent a distinct taxon and therefore are not included as representative here. More field and molecular work are needed to address these outstanding questions.

The specific epithet, *panamintensis*, refers to the type locality for the species in the Panamint Mountains. The suggested common name for the species is Panamint spring beauty.

***Representative Specimens Examined*—**U. S. A. California, Inyo Co.: Panamint Mountains, upper Johnson Canyon, 17 Mar 2014, *T. Stoughton 1844* (RSA, JEPS); Johnson Canyon, 1.8 km NW of Hungry Bills Ranch, 23 May 2001, *D. York 2630* (RSA812089). Nevada, Clark Co.: Spring Mountains, 1.75 mi E of Red Rock Summit, 19 Apr 1974, *J. Holland 141* (UNLV7576); Northern Red Rock Canyon Recreation Area, 28 Apr. 1990, *A. Leary 3938* (UNLV32952); Wilson Pass Rd, NE slope below ridge, 2 Apr 1985, *A. Pinzl 6409* (NSMC8104, UNLV19821).

2. **Claytonia serpenticola** T. R. Stoughton, sp. nov.—TYPE: U. S. A. California: Trinity Co. (near Humboldt Co. line), North Coast Ranges, Lassics Botanical Area, north slope of Signal Peak (Mount Lassic), 28 May 2013, *T. R. Stoughton 1759.* (holotype: RSA!; isotype: JEPS!).

Perennial; tuberous root 0.5–2.0 cm in diameter, globose; rhizomes absent. Stems (1.5–)3–7(–10) cm long; foliage dark to light green ab/adaxially. Basal leaves absent to 1 (rarely more than 1), absent at flowering time, (2–)7–12 cm long, petioles tapered or indistinct from blades; blades (1–)2–5 × (1–)2–5 mm, linear-lanceolate to oblanceolate, apex acute to acuminate. Cauline leaves 2–4, alternate to subopposite, 1-nerved, (10–)12–34(–45) × (1–)2–4.5(–8) mm, linear to lanceolate or narrowly elliptic, sessile, base of blade sometimes attenuate but not distinctly petiolate. Inflorescences 1–3, terminal and often also axillary, pedunculate, unibracteate, bract 1–2 mm long, membranous. Flowers 10–16 mm in diameter, developing buds nodding to spreading; sepals 3–6 × 1–5 mm; petals 5.5–8 × 1.5–4 mm, white to pinkish, with faintly colored pink veins, generally with a yellow-colored blotch at base of blade above claw, apices entire. Ovules 6. Seeds 1–6, ca. 2 mm long, smooth to very weakly tuberculate; elaiosomes generally < 1 mm, $+/-$ equal to funicular notch at maturity. Chromosome number unknown. Figures 3B and 4D.

***Distribution*—**Found in the Klamath-Siskiyou region of northwestern California in the North Coast Ranges up to the Siskiyou Mountains in southern Oregon (Fig. 1), on xeric, stony slopes (generally north-facing) comprised of mafic substrates (e.g. gabbro, peridotite, serpentinite), sometimes mixed with sedimentary rocks (e.g. shale), and in soils derived from these parent materials. Most often found in openings of mixed-conifer and subalpine forest habitats from 1,000 to ca. 2,450 m.

Notes*—Claytonia serpenticola* is morphologically similar to the broad interpretation of *C. lanceolata* by Miller and Chambers (2006). However, *C. serpenticola* differs in its ecological setting (it is primarily associated with mafic rocks), by its alternate leaf arrangement, and by the shape, number, and venation of its cauline leaves. At least in northern California, *C. serpenticola* is diagnosable by its propensity to have inflorescences that emerge from the axils of its cauline leaves. This diagnostic feature has been observed to occur only rarely in populations of *C. lanceolata* or *C. obovata,* and only in areas where these taxa grow in sympatry with *C. serpenticola* (T. Stoughton pers. obs.). Some morphological variation was observed within and among populations identified here as *C. serpenticola,* perhaps reflecting morphological evidence of hybridization with close congeners, particularly in areas of sympatry with *C. obovata*. Nevertheless, *C. serpenticola* is a diagnosable taxon worthy of recognition at the rank of species. *Claytonia serpenticola* is morphologically most similar to *C. peirsonii* subsp. *bernardinus*, based on the results of our morphological study, sharing lance-linear leaves with a single vein (and a propensity for development of axillary inflorescences), but the two do not co-occur geographically and the latter typically has purple pigmentation on the abaxial surfaces of its leaves. The distinctive, beet-red colored pigmentation of *C. peirsonii* is absent from the abaxial surfaces of the leaves of *C. serpenticola*. Our molecular results also suggest these two are highly divergent at the nrITS gene region (Fig. 2), if they are at all closely related.

The discovery of a distinct lineage of *Claytonia* in the Klamath-Siskiyou region occurred during preliminary molecular analyses when DNA sequences for *C. lanceolata* generated by M. Hershkovitz (unpubl. data on GenBank) did not resolve as sister to other sequences acquired by O'Quinn and Hufford (2005). Upon examining the specimen sampled by M. Hershkovitz, *B. W. Klipfel 318* (HSC41230), the diagnostic feature of this lineage became immediately evident: these plants have alternate cauline leaves and axillary (as opposed to strictly solitary/terminal) inflorescences. The more common condition for *C. lanceolata* s. l. is to have an opposite pair of cauline leaves and Pursh (1814) mentions specifically in the original description that *C. lanceolata* has a solitary inflorescence.

The alternate phyllotaxis of *C. serpenticola* is significant not only because it is an easy morphological character to use and makes the taxon an outlier for the *C. lanceolata* species complex, but also because the leaf blades of *C. serpenticola* otherwise might be considered to resemble in shape and size those of geographically co-occurring *C. lanceolata* (see treatment below). *Claytonia serpenticola* differs also from *C. lanceolata* by having single-nerved cauline leaves with pinnate venation. In contrast, *C. lanceolata* has tri-nerved cauline leaves with (sometimes inconspicuous) parallel venation.

The specific epithet, *serpenticola*, refers to a propensity for this species to be associated with serpentine soils. The suggested common name for the species is Serpentine spring beauty.

Representative Specimens Examined—U. S. A. California: Humboldt Co., 3/4 mi N of Alder Spring near Lassics Lookout, 30 Jun 1982, *D. K. Imper s.n.* (HSC79323); Horse Mountain, 8 May 1974, *B. W. Klipfel 318* (HSC41230); Horse Mountain, 30 May 1975, *B. W. Klipfel 648* (HSC44425); 2 miles south of intersection with Forest Service Road 5N09, 2 Jun 2008, *C. Witte 663* (HSC98784); Shasta Co., ca. 2 miles N of Slate Mountain, 22 May 1993, *D. W. Taylor 13465* (JEPS101969); Siskiyou Co., E slope of Kangaroo Mtn., above Toehead Lake, 3 Jul 1972, *J. P. Smith 5708* (HSC27336); Ridge between Durney Lake and Little Crater Lake, 17 Apr 1976, *J. Whipple 1030* (HSC92978); Trinity Co., Black Lassic along W side, 13 Jun 1972, *D. E. Anderson 5546* (HSC31833); N side of Red Lassic, 14 Jun 1972, *D. E. Anderson 5583* (HSC31422); Big Flat, 6 Jun 1967, *W. J. Ferlatte 502* (HSC4434); E side of Packers Peak, 28 Jun 1967, *W. J. Ferlatte 544* (HSC4433); Head of Union Creek, 7 Jul 1967, *W. J. Ferlatte 654* (HSC4435); Swift Creek at SE end of Parker Meadow, 28 May 1979, *D. L. Goforth 144* (HSC64957); Red Lassic, 20 May 1973, *T. W. Nelson 914* (HSC32862); Along Mule Ridge SE of Red Lassic, 30 May 1973, *T. W. Nelson 992* (HSC32904); E side of Black Lassic along S side of branch off Shanty Creek, 23 May 1976, *T. W. Nelson 2547* (HSC39535); Shores of Diamond Lake, 28 Jun 1974, *J. O. Sawyer 2635* (HSC38970); Upper Bowerman Meadows on trail to Lake Anna, 14 Jun 1981, *J. O. Sawyer 4132* (HSC75606); Big Bear Lake trail, N of Eagle Creek Campground, 21 Apr 1973, *J. P. Smith 6241 (*HSC28802); Mt. Eddy trail above Deadfall Lakes, 31 May 2014, *T. R. Stoughton 1899* (RSA, JEPS); Lassics Botanical Area, north slope of Signal Peak (Mount Lassic), 1 Jun 2014, *T. R. Stoughton 1900* (RSA, JEPS); Deadfall Creek drainage in the vicinity of Deadfall Lakes, 11 Jun 1976, *J. Whipple 959* (HSC92977); Oregon: Jackson Co., Observation Peak, Siskiyou Mtns, 16 Jun 1994, *K. L. Chambers 5816* (OSC209262); Red Mountain W. from Siskiyou Peak, 14 June 1899, *J.B. Leiberg 4068* (ORE29125 at OSC); Observation Peak, Siskiyou Mtns, 28 May 2014, *T. R. Stoughton 1896* (RSA, JEPS).

3. CLAYTONIA LANCEOLATA Pursh, Flora Americae Septentrionalis: 175. 1814.—TYPE: U. S. A. Idaho: Clearwater Co., headwaters of Kooskooski, 27 Jun 1806, *Lewis s.n.* (holotype: PH, [photos] POM! OSC!).

Claytonia caroliniana Michaux var. *sessilifolia* Torrey, Pacific Railroad Survey Reports 4(5): 70. 1857. *Claytonia lanceolata* Pursh var. *sessilifolia* (Torrey) A. Nelson, Bulletin of the Torrey Botanical Club 27: 259. 1900. *Claytonia sessilifolia* (Torrey) Henshaw, Mountain Wild Flowers of America: 28. 1906.—TYPE: U. S. A. California: Sierra Co., Downieville, 2 May 1854, *Bigelow s. n.* (holotype: NY!; isotypes: GH, US).

Claytonia chrysantha Greene, Leaflets of Botanical Observation and Criticism 2: 45. 1910. *Claytonia lanceolata* f. *chrysantha* (Greene) St. John, Research Studies of the State College of Washington 1: 97. 1929. *Claytonia lanceolata* subsp. *chrysantha* (Greene) Ferris in Abrams, Illustrated Flora of the Pacific States 2: 122. 1944. *Claytonia lanceolata* var. *chrysantha* (Greene) C. L. Hitchcock, Vascular Plants of the Pacific Northwest 2: 229. 1964. *Claytonia caroliniana* var. *chrysantha* (Greene) Boivin, Phytologia 16: 323. 1968.—TYPE: U. S. A. Washington: Whatcom Co., Mt. Baker, E side of Deming Glacier, moist sandy slopes, 5,500 ft, 6 Aug 1909, *M. W. Gorman 2809* (holotype: NDG; isotypes: ORE! [at OSC], WS).

Claytonia lanceolata var. *idahoensis* R. J. Davis, Brittonia 18: 294. 1966.—TYPE: U. S. A. Idaho: Bannock Co., at Justice Park, 14 mi S of Pocatello, *R. J. Davis 6029* (holotype: [photo] ISC!; isotypes: ASU, BRY, DS!, NY!, UTC).

Perennial; tuberous root 0.2–2.5 cm in diameter, globose or sometimes with a narrowed area at tuber apex where the aerial stems emerge; rhizomes absent. Stems (3–)4.5–13.5(–16) cm long; foliage generally green throughout, sometimes beet-red on abaxial surfaces in the Sierra Nevada. Basal leaves absent to 1 (rarely to 6), generally absent at flowering time, 3.5–9.5 cm long, petioles tapered or indistinct from blades; blades 10–35 × (1.5–)3.5–7(–12) mm, generally lanceolate to elliptic to oblanceolate, apex acute to obtuse. Cauline leaves 2(3), opposite, 3-nerved (sometimes lateral veins indistinct), (10–)17–43(–70) × (1.5–)3–7(–12) mm, lance-linear to lance-ovate to narrowly elliptic, sessile (rarely winged-petiolate), blades sometimes widest above middle but generally not appearing petiolate. Inflorescences generally 1(2), terminal (axillary inflorescences rarely present), pedunculate, unibracteate, bracts 1–5 mm long, membranous. Flowers 10–18 mm in diameter, developing buds nodding; sepals 1.5–6 × 1–4 mm; petals 5–9 × 1.5–4.5 mm, white to pinkish, with faintly to strongly-colored pink veins, with a yellow-colored blotch at base of blade above claw, apices strongly to weakly notched or entire. Ovules 6. Seeds 1–6, 1.5–2 mm long, smooth; elaiosomes < 1 mm, $+/-$ equal to funicular notch at maturity. Chromosome number unknown, likely $n = 8$ based on reports by Lewis (1967) made from samples collected in Washington (Kittitas Co.) and Oregon (Baker Co.). Figures 3C, 4F.

Distribution—Found from Northern California in the Central Sierra Nevada and Klamath Regions (Fig. 1), northward to Canada (Alberta, British Columbia, and Saskatchewan) primarily on the east side of the Cascade Ranges, and eastward in the mountains to Colorado, New Mexico, and Wyoming. In California, on mostly north-facing, stony slopes comprised of more alkali-rich substrates (e.g. granite, rhyolite) and in soils derived from a combination of these parent rocks and some organic material. Most often found in protected, mesic openings of mixed conifer or subalpine forest habitats from ca. 600 to ca. 2,750 m.

Notes—Our concept of *C. lanceolata* is morphologically similar to *C. peirsonii* subsp. *bernardinus* and *C. serpenticola*, but differs in the shape, venation, and arrangement of its leaves, and by its ecological setting (*C. lanceolata* is primarily associated with mesic, montane and subalpine habitats). It differs also by its larger overall plant and smaller flower size, often (at least weakly) notched petals, and by having an elongate inflorescence that often exhibits elongation of the peduncle and internodal elongation among pedicels by the time of fruiting.

Claytonia lanceolata is most likely to be mistaken for *C. serpenticola* in the field because the two taxa tend to have lance-linear cauline leaf blades that are similar in size. The alternate phyllotaxis and propensity for axillary infloresence development in *C. serpenticola* make it distinguishable from *C. lanceolata* in most cases. However, these features can be complicated in *C. serpenticola* by aborted axillary inflorescence development, resulting in solitary inflorescences, and by the occasional presence of cauline leaf pairs appearing to be sub-opposite rather than distinctly alternate. In California, *C. lanceolata* has a geographic range that is primarily east of *C. serpenticola.* Aside from phyllotaxis, the primary character distinguishing these two taxa is the venation of the cauline leaf pair: *C. lanceolata* is tri-nerved (sometimes appearing as single-nerved without use of a microscope or hand lens) whereas *C. serpenticola* is distinctly single-nerved. *Claytonia lanceolata* also does not appear to occur on the same substrate types as *C. serpenticola,* at least in California.

Discovered in the early years of territorial and botanical exploration, *C. lanceolata* var. *sessilifolia* was originally described as a variety of the eastern *C. caroliniana* from material collected in the Sierra Nevada during surveys for the Pacific Railroad. This taxon was originally characterized as having single-nerved cauline leaves, but closer inspection of this character reveals that the tri-nerved nature of the cauline leaf pair is often obscured in dried herbarium specimens because

the midrib is thicker than the lateral veins in Californian populations of *C. lanceolata* (especially those in the Sierra Nevada). After being transferred to *C. lanceolata* as a variety, *C. sessilifolia* (Torr.) Henshaw was treated as a distinct species only a few years later but venation of the cauline leaf pair was not further addressed for the basionym. Davis (1966) later taxonomically treated *C. lanceolata* var. *sessilifolia* (Table 1), but he apparently confused some specimens of the tri-nerved *C. obovata* with this taxon. For example, *Wiggins 12393* (DS327493) collected from Siskiyou Co., California, was listed as a representative specimen for *C. lanceolata* var. *sessilifolia* by Davis (1966). The two are easily distinguished except in cases where diagnostic characteristics have been overlooked or obscured by their poor preservation on herbarium specimens. The cauline leaf blades of *C. obovata* are generally less than three times longer than wide and obtuse to rounded at the apex whereas those of *C. lanceolata* in California are generally greater than three times as long as wide and have acute to acuminate (rarely obtuse) apices. Due to the wide range of morphological variation observed in *C. lanceolata,* and for the lack of molecular resolution or exhaustive sampling of lineage diversity in the species, we conservatively lump infraspecific taxa contained within *C. lanceolata* until outstanding questions can be addressed in the context of the full distribution of the species and its closest relatives.

Representative Specimens Examined—U. S. A. California: Alpine Co., Meiss Ridge, 24 May 2014, *T. R. Stoughton 1884* (RSA, CAS, JEPS, UCR, UNR); El Dorado Co., Echo Lakes Divide, 7 Jul 1925, *F. W. Peirson 6314* (RSA65732); Humboldt Co., Near Bret Hole, 19 Jul 1980, *M. A. Baker 3035* (HSC73821); Grogan's Hole near N Trinity Mountain, 27 May 1973, *B. W. Klipfel 30* (HSC48838); S of Trinity Summit Station, 15 Jun 1971, *J. O. Sawyer 2385* (HSC24076); Trinity Summit Area, Trinity Alps, 30 May 2013, *T. R. Stoughton 1762* (RSA, JEPS); Lassen Co., 0.5 mi W of Predonyer Pass, Highway 36, 23 May 1952, *M. S. Baker 12429* (RSA74140); Madera Co., Iron Lake Ridge, 2 Aug 1938, *M. V. Hood s.n.* (RSA464475); 1.4 km NE of Iron Mountain, 10 Jul 1998, *D. York 2191* (RSA696304); Modoc Co., Ca. 1 km NW of Bald Mountain, E side of the Warner Mountains, 24 Jun 2002, *B. Bartholomew 8839* (CAS1032034); Deep Creek, 15 Jun 1946, *A. M. Alexander 4773* (POM275200A); Sierra Co., Nine woods near Yuba Pass, 3 Jul 1927, *R. C. Bacigalupi 1601* (POM161630); Gold Lake, 22 Jun 1927, *H. A. Barker 720* (RSA8013); 15 mi west of Portola, 5 May 1929, *M. Canby 128* (POM220759); Siskiyou Co., Baldy Mountain ca. 6 mi W of Happy Camp, 2 Jul 1952, *P. A. Munz 17896* (RSA78818); Ridge west of Baldy Mountain, 6 mi W of Happy Camp, 2 Jul 1952, *P. A. Munz 17908* (RSA78830); Along Happy Camp-O'Brien Rd above Louse Creek, May 1977, *P. Stekel 239B* (HSC48274); Poker Flat, 9 Jul 1959, *R. Van Deventer s. n.* (HSC61811, HSC61812); Tuolumne Co., Eagle Peak, 20 Jun 1936, *R. F. Hoover 1354* (UC766152); Canyon opening N head of Emigrant Lake, 22 Jul 1941, *R. F. Hoover 5513* (UC765758); Oregon: Douglas Co., N of Crater Lake National Park, 15 Jul 2012, *D. Jolles 512* (RSA, JEPS); N of Crater Lake National Park, 26 May 2014, *T. R. Stoughton 1890* (RSA, JEPS); Trail to Abbott Butte Lookout, 27 May 2014, *T. R. Stoughton 1895* (RSA, JEPS); Klamath Co., near Crater Lake National Park, 16 Jul 2012, *D. Jolles 515* (RSA, JEPS); Crater Lake National Park, 29 Jun 1962, *J. Rockwell 113* (HSC17656); near Crater Lake National Park, 26 May 2014, *T. R. Stoughton 1889* (RSA); Linn Co., Monument Peak, 17 Jun 1948, *H. M. Gilkey s. n.* (OSC65157); Ca. 10 mi W of the junction of FS Rd 11 and State Highway 22, 2 Jun 2009, *R. G. Halse 7635* (OSC223100).

4. CLAYTONIA OBOVATA Rydberg, North American Flora 21: 299. 1932.—TYPE: U. S. A. Oregon: Douglas Co., Abbott Butte, 1,600 m, 6 July 1899, *J. B. Leiberg 4262* (holotype: [photo] US!; isotype: ORE! [at OSC]).

Perennial; tuberous root 0.7–2(–3) cm in diameter, globose or sometimes with a narrowed area at tuber apex where the aerial stems emerge; rhizomes absent. Stems (2–)3.5–8.5(–13) cm long; foliage dark green adaxially, beet-red abaxially. Basal leaves absent to 1 (rarely more than 1), absent at flowering time, 6–11(–16) cm long, petioles tapered or indistinct from blades; blades 10–25(–40) × (2–)4–9 mm, widely lanceolate to lance-ovate or narrowly elliptic, apex acute to obtuse. Cauline leaves 2(3), opposite, 3-nerved (sometimes more), (5–)7.5–22 (–30) × (3–)4–9.5(–15) mm, blades lance-ovate to elliptic to ovate or obovate, sessile, base generally asymmetric, rarely narrowed at base but not distinctly petiolate. Inflorescences 1 (2), terminal (rarely also axillary), sessile to short-pedunculate, unibracteate, bracts 1–3 mm long, membranous. Flowers 10–15 mm in diameter, developing buds spreading to ascending; sepals 2–6 × 1–5 mm; petals 5–7.5 × 1.5–5 mm, white to pinkish, with faintly colored pink veins, generally with a yellow blotch at base of blade above claw, apices entire. Ovules 6. Seeds 1–6, 2–2.5 mm long, smooth; elaiosomes < 1 mm, +/− equal to funicular notch at maturity. Chromosome number unknown. Figures 3A, 4E.

Distribution—Found in the Klamath-Siskiyou region of northwestern California in the North Coast Ranges to southwestern Oregon at Abbott Butte (Fig. 1), generally on north-facing, stony and talus slopes comprised of siliciclastic or carbonate-dominated (meta)sedimentary rocks (e.g. greywacke, limestone, shale), or mafic substrates (e.g. gabbro, peridotite, serpentinite), and in soils derived from these parent materials. Most often found in openings of subalpine forest habitats from ca. 1,200 to ca. 2,200 m.

Notes—*Claytonia obovata* is morphologically similar to the broad interpretation of *C. lanceolata* by Miller and Chambers (2006), but differs primarily in its ecological setting (*C. obovata* is primarily associated with cismontane, subalpine habitats) and by the presence of sunken, red veins on the cauline leaves that diverge near the base of the leaf blade and generally converge near the apex. It differs also by the shape of the cauline leaf pair, its smaller overall plant size, and in having a sub-umbellate inflorescence that generally lacks a peduncle and exhibits little to no internodal elongation among pedicels by the time of fruiting. *Claytonia obovata* most notably resembles *C. peirsonii* subsp. *peirsonii* but the two do not co-occur geographically and should not be confused. *Claytonia obovata* lacks raised (appearing thickened) veins of any kind on the adaxial surfaces of the cauline leaves, which are always present in *C. peirsonii* subsp. *peirsonii.*

Davis (1966) did not recognize *C. obovata*, but described visiting the type locality at Abbott Butte, Oregon, where he encountered plants matching the descriptions of *C. obovata* as well as *C. multicaulis* Nelson (currently treated as a synonym of *C. multiscapa*), *C. chrysantha* Greene, and *C. lanceolata*. Essentially, Davis (1966) recounted seeing plants showing a wide range of intermediate characters at Abbott Butte. Davis (1966) mentioned also growing plants in the greenhouse that maintained a broad cauline leaf morphology at flowering and subsequently used his findings to justify *not* recognizing *C. obovata*. We interpret Davis' observations differently: the broad leaves of *C. obovata* are not likely the result of phenotypic plasticity in a polymorphic *C. lanceolata,* but instead the expression of fixed genetic changes in populations assignable to *C. obovata*, a closely related species. It is true that the type specimen and live plants from Abbott Butte do not have obovate cauline leaves (i.e. ovate with the narrower end positioned proximally), as Davis (1966) points out, but Rydberg (1932) also cites plants from the North Coast Ranges of California at Hull Mountain in the original description of *C. obovata*. The plants at Hull Mountain tend to have obovate cauline leaves, although sometimes only weakly so (T. Stoughton pers. obs.). We have been in the field at both Abbott

Butte and Hull Mountain (and localities in between, Fig. 1) to observe these tuberous, perennial *Claytonia* in their native habitats. Davis (1966) gives no indication of visiting other sites where *C. obovata* grows or seeing material from Hull Mountain in Mendocino Co., California. As for the possible hybrid swarm at Abbott Butte mentioned above, we observed a vast and variable (perplexing!) population of *C. lanceolata* there and only scattered remnants of a few plants at lower elevations that resemble the type specimen of *C. obovata*. More than 40 yr later, we did not observe any yellow-flowered plants assignable to *C. chrysantha*, reported to be present by Davis (1966). We have, however, observed what appears to be natural interspecific hybridization involving *C. obovata* and *C. serpenticola* at one sympatric locality near Mount Shasta in northern California, in addition to what appears to be hybridization between *C. obovata* and *C. lanceolata* at Abbott Butte. We suspect a similar scenario to what has been observed by Doyle and Doyle (1988) with closely related tuberous *Claytonia* on the east coast, or possibly a similar situation to what was observed by Stewart and Wiens (1971) with close relatives in the Mountain West, in addition to what Davis (1966) mentioned he observed at Abbott Butte. We do not believe that a low frequency of hybridization with close relatives is grounds for sinking a diagnosable taxon that maintains morphological and genetic coherence across a broad range (T. Stoughton et al. unpubl. data).

We found scant collections in existing herbaria (not listed as representative) but several plants collected from the same general area in the Central Sierra Nevada (Tuolumne Co., Bald Mountain, *L.R. Heckard 4741*) approach both *C. obovata* and *C. peirsonii* in their leaf morphology. We consider these plants to represent a range extension for *C. obovata* but suspect these populations represent a new, pedunculate subspecies of either *C. obovata* or *C. peirsonii* that may be worthy of later taxonomic recognition. Additional field and molecular research are required to address outstanding questions concerning these geographically and morphologically outlying populations.

Representative Specimens Examined—U. S. A. California: Mendocino Co., Anthony Peak, east of Lookout, 14 Jul 1944, *M. S. Baker 10808* (CAS378247); Near Monkey Rock, 27 May 2012, *H. A. Bartosh 588* (RSA); Windy Point, 0.2 rd mi north of Hull Mountain, 4 Jul 1967, *R. Gankin 907* (RSA202422); Below Hull Mountain Lookout, 25 Jun 1969, *Hamann & Dearing* s. n. (HSC17659); Leech Lake Mountain, northeast of Covelo, 20 Jun 1952, *G. D. Hanna & G. C. Gester s. n.* (CAS515388); Mt. Hull, Jun 1894, *C. A. Purpus 867* (UC82747); Along road to summit, Anthony Peak, 17 Jun 1980, *G. L. Smith 5942* (CAS927960); Ridge NW of Hull Mountain, 5 June 1974, *S. Smith s. n.* (JEPS74662); near Calamese Rock, 26 May 2013, *T. R. Stoughton 1751* (RSA); Road to Hull Mtn. S of Monkey Rock, 26 May 2013, *T. R. Stoughton 1757* (RSA, JEPS); ridge E of Hull Mtn, 26 May 2013, *T. R. Stoughton 1758* (RSA, JEPS); ridge below and E of lookout tower on Anthony Peak, 1 Jun 2014, *T. R. Stoughton 1902* (RSA, JEPS); 0.5 mi N of Hull Mountain, 22 Apr 1972, *D. Toren s.n.* (CAS567326); Forest Road 20n02 between Calamese Rock and Hells Half Acre, 21 Jun 1983, *C. R. Wheeler 3429* (CAS911596); Windy Gap, on spur ridge to N of Hull Mountain proper, 24 Jun 1956, *H-M. Wheeler s. n.* (JEPS14708); Siskiyou Co., 0.5 mi E of Highway 3 on the dirt road heading E at Scott Mountain Pass, 30 May 1981, *D. Renwick 162* (HSC73412); N facing slopes in the Eddy Creek drainage, 19 Jun 1976, *J. Whipple 1068* (HSC92962); 0.3 miles west of Carmen Lake, 28 May 1950, *I. L. Wiggins 12393* (DS327493); Tehama Co., Anthony Peak, east side, 14 Jul 1944, *J. T. Howell 19764* (CAS322563); Trinity Co., Along the Limestone Ridge Trail 0.5 mi S of Rattlesnake Lake, 29 May 1974, *E. Carter 773* (CAS1129584); 0.5 mi W of Cory Peak, 29 May 2014, *T. R. Stoughton 1897* (RSA, JEPS); hills on S side of upper Deadfall Lakes, 30 May 2014, *T. R. Stoughton 1898* (RSA, JEPS); Oregon: Curry Co., Chetco Divide Trail, between Red Mountain and Chetco Peak, 5 May 1980, *V. Stansell s. n.* (OSC158534).

5. **Claytonia peirsonii** (Munz & Johnston) T. R. Stoughton, stat. et comb. nov.—*Claytonia lanceolata* Pursh var. *peirsonii* Munz & Johnston, Bulletin of the Torrey Botanical Club 49: 352. 1923. *Claytonia caroliniana* var. *peirsonii* (Munz & Johnston) Boivin, Phytologia 16: 323. 1968.—TYPE: U. S. A. California: San Bernardino Co., near Kelley's Cabin, Ontario Ridge, San Antonio [San Gabriel] Mountains, 29 May 1920, *F. W. & Mabel Peirson s.n.* (holotype: POM!; isotype: NY!).

Distribution—Found in montane to transmontane habitats of the Transverse Ranges (San Gabriel and San Bernardino Mountains) to the southern Sierra Nevada in southern California (Fig. 1), generally on north-facing, stony and talus slopes comprised of igneous, sedimentary, and metamorphic rocks, and growing in soils derived from these parent rock materials. Most often found in openings of subalpine forest down to pinyon-juniper and oak woodland habitats from ca. 1,350 to ca. 2,600 m in elevation.

Notes—*Claytonia peirsonii*, which we also refer to as the *C. peirsonii* species complex, is a highly variable taxon that includes multiple unnamed lineages (Figs. 3E–H, 4A–B) discussed in some detail by Stoughton and Jolles (2013). It was originally described by Munz and Johnston (1923) as a variety of *C. lanceolata* based upon only a few specimens, and persisted through multiple taxonomic re-circumscriptions of *C. lanceolata* until it was subsumed as a synonym (along with all other varieties of *C. lanceolata* in California) by Chambers (1993).

We maintain a conservative taxonomic approach which recognizes the collective of southern populations identified as *C. lanceolata* var. *peirsonii* by Stoughton and Jolles (2013), excluding those treated as *C. panamintensis* (see above), as a unique and variable lineage recognized here at the rank of species with at least four easily recognizable subspecies. Based on evidence presented in this paper, we assign for the first time additional infraspecific ranks to populations assignable to *C. peirsonii* in the southern Sierra Nevada and San Bernardino Mountains. The nominate taxon is the most widespread and morphologically polymorphic of all of the subspecies and is known from the most populations, all of which are restricted to the San Gabriel Mountains. As reported by Stoughton and Jolles (2013), plants of this species flower early in the spring months (February–May) and therefore may be present but still unaccounted for in the conifer and oak belts of the higher mountains in the eastern Mojave Desert (i.e. the Clark, Kingston, and New York Mountains) where in-depth floristic studies are lacking.

5a. Claytonia peirsonii subsp. peirsonii

Perennial; tuberous root 0.3–2.1 cm in diameter, globose, sometimes with a narrowed area at tuber apex where the aerial stems emerge; rhizomes absent. Stems (2.5–)5–18(–25) cm long; foliage dark green adaxially, generally with heavy, beet-red coloration abaxially. Basal leaves absent to 2 (rarely more than 2), absent at flowering time, (8–)10–15(–19) cm long, petioles tapered or indistinct from blades; blades 10–35 × (2–)5–7 mm, elliptic to oblanceolate, apex acute to obtuse. Cauline leaves 2–4, opposite at least proximally, 1-nerved (sometimes more than one but lateral veins not all developed fully or converging at leaf apex), (6–)14–35(–42) × (3–)3.5–11.5(–18) mm, blades ovate or lance-ovate to elliptic, sometimes rounded, rarely lanceolate or oblanceolate, generally sessile to distinctly short-petiolate or with blade attenuate into indistinct

petiole, base often asymmetric, adaxial surfaces generally with reddish, sunken 1° veins and strongly thickened (appearing raised), green-colored 2° veins. Inflorescences 1–3, terminal and often also axillary, sessile to short-pedunculate, unibracteate, bracts 1–3 mm long, membranous. Flowers 14–22 mm in diameter, developing buds erect to ascending or spreading; sepals 2–7 × 1.5–6 mm; petals 7–11 × 2–6 mm, white with lightly colored pink veins, generally with a yellow to orange-colored blotch at base of blade above claw, apices entire (rarely weakly notched). Ovules 6. Seeds 1–6, 1.5–2.5 mm long, smooth to very weakly tuberculate; elaiosomes generally < 1 mm, $+/-$ equal to funicular notch at maturity. Chromosome number unknown. Figure 3E.

Distribution—Found in Southern California in the San Gabriel Mountains (Fig. 1), generally on north-facing, stony and talus slopes comprised of primarily alkali-rich lithologies (e.g. gneiss, granite, schist) mixed with moderate to high amounts of decomposing organic material from the surrounding forest. Most often found in openings and under closed canopy of mixed conifer and subalpine forests down to pinyon-juniper and oak woodland habitats from ca. 1,575 to ca. 2,600 m.

Notes—*Claytonia peirsonii* subsp. *peirsonii* is morphologically similar to *C. obovata* and the broad interpretation of *C. lanceolata* by Miller and Chambers (2006) in some respects. However, it differs in its ecological setting (*C. peirsonii* subsp. *peirsonii* is generally associated with alkali-rich rocks in subalpine and transmontane habitats), betalain pigmentation on the abaxial surfaces of its leaves, and the presence of raised 2° veins and a single (sometimes branched), sunken, red 1° vein on the adaxial surfaces. It differs also by the shape, arrangement, and venation of its cauline leaves, smaller overall plant size, and in having a sub-umbellate inflorescence that exhibits an abbreviated peduncle (often absent) with little to no internodal elongation among pedicels by the time of fruiting. *Claytonia peirsonii* subsp. *peirsonii* is also morphologically similar to the other subspecies of *C. peirsonii* but can be distinguished by the strongly thickened 2° veins on the adaxial surfaces of the leaves (often weak in other varieties, if present), wider cauline leaves, and it does not co-occur geographically with any other subspecies in the San Gabriel Mountains. We have observed a great deal of morphological variation within and among populations identified here as *C. peirsonii* subsp. *peirsonii*, particularly among populations in the high elevation, eastern San Gabriel Mountains and those disjunct to the west of Mount Baldy mostly at lower elevations (Fig. 1). Conservatively, we treat these as the same taxon until further morphological and molecular research can be conducted. *Claytonia peirsonii* subsp. *peirsonii* is considered to be fairly uncommon and should be sought after in additional areas in southeastern California, particularly in subalpine and transmontane habitats near and in the San Gabriel Mountains.

The subspecific epithet, *peirsonii*, is the nominate epithet and refers to the original collectors of *Claytonia lanceolata* var. *peirsonii*. The suggested common name for the subspecies is Peirson's spring beauty.

Representative Specimens Examined—U. S. A. California: Los Angeles Co., Just below Pacific Crest Trail to the E of Little Jimmy Campground near Windy Gap, 13 May 2012, *T. R. Stoughton 1539* (RSA812097, UCR, JEPS); Near the Devil's Punchbowl County Park, 1 Apr 2013, *T. R. Stoughton 1706* (RSA812100, UCR, JEPS, CAS); near Devil's Punchbowl County Park, 15 Feb 2014, *T. R. Stoughton 1837* (RSA); PCT near Devil's Punchbowl County Park, 15 Feb 2014, *T. R. Stoughton 1838* (RSA); San Bernardino Co., Ontario Ridge, 25 Jun 1980, *T. P. Krantz s. n.* (RSA509347); N aspect of Thunder Mountain, E of ski run, 5 May 1987, *O. Mistretta s. n.* (RSA505073); 0.5 mi N of Telegraph Peak, 5 May 1987, *O. Mistretta s. n.* (RSA505075, RSA505076); Head of Delker Canyon along trail, 13 May 1987, *O. Mistretta s. n.* (RSA505074); Devil's Backbone Ridge, 19 May 1920, *F. W. Peirson 2151* (JEPS5840, RSA65672); Mt. Baldy Ski area, Gold Ridge north of Thunder Mountain, below FS Road 7W04, 11 Jun 2001, *V. Soza 1274* (RSA679587); N slope of Thunder Mountain on ridges between ski runs, 8 May 2012, *T. R. Stoughton 1532* (RSA812094, UCR, JEPS, CAS); In cirque N of Telegraph Peak, 8 May 2012, *T. R. Stoughton 1533* (RSA812095, UCR, JEPS); N slope of Timber Mountain, switchbacks along trail to summit, 8 May 2012, *T. R. Stoughton 1536* (RSA812096, UCR, JEPS); Ontario ridge trail just W of and below Bighorn Peak near Kelly Camp, 30 May 2012, *T. R. Stoughton 1549* (RSA812098, UCR); Thunder Mountain, 18 May 2014, *T. R. Stoughton 1883* (RSA).

5b. **Claytonia peirsonii** subsp. **bernardinus** T. R. Stoughton, subsp. nov.—TYPE: U. S. A. California: San Bernardino Co., San Bernardino Mountains, north slope of Bertha Ridge (ridge between Bear and Holcomb Valleys), 20 April 2012, *T. R. Stoughton 1514 with S. Eliason & E. Williams* (holotype: RSA!; isotypes: UCR!, JEPS!).

Perennial; tuberous root 0.6–1.7 cm in diameter, globose; rhizomes absent. Stems (1.5–)2.5–5.5(–8) cm long; foliage dark green adaxially, often at least weakly beet-red abaxially. Basal leaves not observed on specimens. Cauline leaves 2–4, opposite at least proximally, 1-nerved, (7–)13–35 (–45) × (1–)1.5–4(–5) mm, linear to lanceolate, sessile, adaxial surfaces generally with reddish, sunken 1° veins, sometimes with greenish, weakly thickened (appearing raised) 2° veins. Inflorescences 1–3, terminal and often also axillary, sessile to short-pedunculate, unibracteate, bracts 1–3 mm long, membranous. Flowers 13–22 mm in diameter, developing buds erect to ascending or spreading; sepals 2–6 × 1.5–4 mm; petals 6.5–11 × 2–5 mm, white, with faintly colored pink veins, generally with a yellow-colored blotch at base of blade above claw, apices entire (rarely weakly notched). Ovules 6. Seeds unknown. Chromosome number unknown. Figure 3F.

Distribution—Found in southern California in the San Bernardino Mountains (Fig. 1), on north-facing, stony and talus slopes comprised of carbonate-dominated (meta) sedimentary substrates (e.g. limestone, marble) often mixed with decomposing organic material from the surrounding forest. Mostly found in openings of a mixture of pinyon-juniper and white fir-limber pine associations around 2,350 m in elevation $+/-$ ca. 500 m.

Notes—*Claytonia peirsonii* subsp. *bernardinus* is morphologically similar to *C. panamintensis*, *C. serpenticola*, and to the broad interpretation of *C. lanceolata* by Miller and Chambers (2006), but differs generally by its ecological setting (*C. peirsonii* subsp. *bernardinus* is associated with variable, carbonate-dominated sedimentary substrates in transmontane habitats), betalain pigmentation on the abaxial surfaces of its leaves, and by the presence of raised 2° veins on the adaxial surfaces. It also differs by shape, arrangement, and venation of its cauline leaves, smaller overall plant size, and in having a sub-umbellate inflorescence that exhibits an abbreviated peduncle (often absent) with little to no internodal elongation among pedicels by the time of fruiting. *Claytonia peirsonii* subsp. *bernardinus* is probably most easily confused with *C. serpenticola*, the two sharing similarly shaped cauline leaves, but they do not co-occur geographically and *C. serpenticola* lacks the betalain pigmentation that *C. peirsonii* subsp. *bernardinus* produces on the abaxial surfaces of its leaves. *Claytonia panamintensis* can be distinguished from *C. peirsonii* subsp.

bernardinus by its nodding flower buds and distinctly petiolate cauline leaves. In contrast, the leaves of *C. peirsonii* subsp. *bernardinus* are unambiguously sessile and its flower buds tend to be erect to ascending in orientation during early development. The weakly thickened (appearing raised) secondary veins, if present, and lanceolate to lance-linear shape of the cauline leaf pair in *C. peirsonii* subsp. *bernardinus,* make it easily distinguished from all other subspecies of *C. peirsonii*.

We have observed a great amount of morphological variation within the population identified here as *C. peirsonii* subsp. *bernardinus*, but even in sympatric situations *C. peirsonii* subsp. *bernardinus* is readily distinguished from *C. peirsonii* subsp. *californacis* by the shape of the cauline leaf pair alone. No intergradation among these subspecies has been observed in the San Bernardino Mountains, which is the only place we currently know these taxa to occur.

Stoughton and Jolles (2013) suggested in their review of *C. lanceolata* that some populations in the San Bernardino Mountains of *C. lanceolata* var. *peirsonii* had considerably narrower leaves than plants in the San Gabriel Mountains and elsewhere, which they illustrated for comparison in figure 10 of their paper. In fact, the plant on the far right side of this figure, and the leaf in the lower left corner, serve perfectly for an illustration of *C. peirsonii* subsp. *bernardinus*: they were drawn from images of plants at the type locality (Bertha Ridge) for this taxon. The rest of the plants in Stoughton and Jolles' (2013) figure 10 are representative of *C. peirsonii* subsp. *peirsonii* and are illustrated from images of plants in the San Gabriel Mountains near (and at) the type locality for *C. peirsonii* subsp. *peirsonii*. Stoughton and Jolles (2013) treated all of these populations as conspecific due to their having access to a limited amount of material and the rather ambiguous protologue in which *C. lanceolata* var. *peirsonii* was first described (Munz and Johnston 1923). *Claytonia lanceolata* var. *peirsonii* was originally diagnosed only by its characteristically 'sub-umbellate' inflorescence architecture and by its southern Californian distribution (Munz and Johnston 1923; Stoughton and Jolles 2013). All of the subspecies of *C. peirsonii* are unified by their sub-umbellate inflorescence architectures (i.e. having little to no peduncle or internodal elongation among pedicels) and their geographic distribution in the mountains of southern California.

Claytonia peirsonii subsp. *bernardinus* is morphologically most similar to *C. serpenticola* (Fig. 3) from northern California and genetically most closely related to *C. peirsonii* subsp. *californacis* (Fig. 2) from the San Bernardino Mountains, based upon our current understanding and evidence presented in this manuscript. *Claytonia peirsonii* subsp. *bernardinus* is considered to be fairly uncommon (known currently from a single population). It should be sought out in additional areas in southeastern California, particularly in transmontane, carbonate-dominated habitats near and in the San Bernardino Mountains, and in similar habitats in the White Mountains of Inyo Co., based on shared species that occur on carbonate substrates in these two mountain ranges.

The subspecific epithet, *bernardinus*, refers to the type locality for this subspecies in the San Bernardino Mountains. The suggested common name for the subspecies is San Bernardino spring beauty.

Representative Specimens Examined—U. S. A. California: San Bernardino Co., N slope of Bertha Ridge, ridge between Holcomb & Bear valleys, 22 Apr 2011, *T. R. Stoughton 1077* (RSA812091, UCR, JEPS, CAS); N slope of Bertha Ridge, ridge between Holcomb & Bear valleys, 20 Apr 2013, *T. R. Stoughton 1717* (RSA812102, UCR, JEPS); N slope of Bertha Ridge, ridge between Holcomb & Bear valleys, 29 Mar 2014, *T. R. Stoughton 1850* (RSA).

5C. **Claytonia peirsonii** subsp. **californacis** T. R. Stoughton, subsp. nov.—TYPE: U. S. A. California: San Bernardino Co., San Bernardino Mountains, Holcomb Valley, head of Furnace Canyon, 20 April 2012, *T. R. Stoughton 1516 with S. Eliason & E. Williams* (holotype: RSA!; isotypes: CAS!, UCR!, JEPS!).

Perennial; tuberous root 0.5–1.5 cm in diameter, globose; rhizomes absent. Stems (2–)3–8(–12.5) cm long; foliage dark green adaxially, often at least weakly beet-red abaxially. Basal leaves absent to 1 (rarely more than 1), absent at flowering time, up to 9 cm long, petioles tapered or indistinct from blades; blades 5–25 × 0.5–3 mm, linear-lanceolate to narrowly elliptic, apex acute to obtuse. Cauline leaves 2–4, opposite at least proximally, 1-nerved, (7–)10–23(–30) × (1–)2–5.5(–9) mm, oblanceolate to elliptic (rarely ovate-elliptic), indistinctly to distinctly short-petiolate (rarely appearing sessile), adaxial surfaces generally with sunken 1° veins that are reddish in color, often with greenish, weakly thickened (appearing raised) 2° veins. Inflorescences 1–3, terminal and often also axillary, sessile to short-pedunculate, unibracteate, bract 1–3 mm long, membranous. Flowers 13–22 mm in diameter, developing buds erect to ascending or spreading; sepals 2–6 × 1–4 mm; petals 6.5–11 × 2.5–5.5 mm, white (rarely light pink), generally with faintly-colored pink veins and a pink (sometimes yellow to orange) blotch at base of blade above claw, apices entire. Ovules 6. Seeds unknown. Chromosome number unknown. Figures 3G, 4A.

Distribution—Found in southern California in the San Bernardino Mountains (Fig. 1), on north-facing, stony and talus slopes comprised of carbonate-dominated (meta)sedimentary substrates (e.g. limestone, marble) mixed with decomposing organic material from the surrounding forest. Mostly found in openings of a mixture of pinyon-juniper and white fir-limber pine associations around 2,300 m in elevation +/− ca. 500 m.

Notes—*Claytonia peirsonii* subsp. *californacis* is morphologically similar to *C. panamintensis* and to the broad interpretation of *C. lanceolata* Pursh by Miller and Chambers (2006). It differs generally by its ecological setting (*C. peirsonii* subsp. *californacis* is associated with variable, carbonate-dominated sedimentary substrates in transmontane habitats), betalain pigmentation on the abaxial surfaces of its leaves, and by the presence of raised 2° veins on the adaxial surfaces. It differs also by the shape, arrangement, and venation of its cauline leaves, its smaller overall plant size, and in having a sub-umbellate inflorescence that exhibits a short peduncle (often absent) with little to no internodal elongation among pedicels by the time of fruiting. *Claytonia peirsonii* subsp. *californacis* is probably most easily confused with other subspecies of *C. peirsonii*, particularly subsp. *peirsonii* and subsp. *yorkii* because of the shape of their cauline leaves, but these do not co-occur geographically and therefore should not be confused. Furthermore, *C. peirsonii* subsp. *yorkii* lacks the betalain pigmentation of *C. p.* subsp. *californacis,* and *C. p.* subsp. *peirsonii* has more strongly thickened (appearing raised) 2° venation on the adaxial surfaces of the cauline leaf pair. *Claytonia panamintensis* can be distinguished from *C. peirsonii* subsp. *californacis* by its nodding flower buds and distinctly

petiolate cauline leaves, although the cauline leaves of *C. peirsonii* subsp. *californacis* are occasionally distinctly short-petiolate (or indistinctly so). The combination of heavy betalain pigmentation, weakly thickened (appearing raised) 2° veins, and the oblanceolate to elliptic shape of the cauline leaves of *C. peirsonii* subsp. *californacis* distinguishes it from all other subspecies of *C. peirsonii*.

Claytonia peirsonii subsp. *californacis* was first collected during follow-up surveys in 2012 preceding a paper by Stoughton and Jolles (2013) regarding the discovery of *Claytonia lanceolata* var. *peirsonii* in the San Bernardino Mountains. The first author was searching in suitable habitat for new populations of *C. lanceolata* var. *peirsonii* in the San Bernardino Mountains one year after it was first collected there on Bertha Ridge (Stoughton and Jolles 2013). It was noted in the field that plants at Furnace Canyon in Holcomb Valley (i.e. those treated here as *C. peirsonii* subsp. *californacis*) did not perfectly resemble the plants collected earlier in the day at Bertha Ridge (i.e. those treated here as *C. peirsonii* subsp. *bernardinus*). So as not to cloud the taxonomic issue, Stoughton and Jolles (2013) argued for treatment of all populations in southern California and southern Nevada as *C. lanceolata* var. *peirsonii* pending further research. All of these plants approach the vaguely described *C. lanceolata* var. *peirsonii*, mostly due to the lack of a circumscription complete with measurements (until now). Although it was suspected that plants now referable to as *C. peirsonii* subsp. *californacis* were unique the first time they were collected, the molecular and morphological data presented above have fortified the case for recognizing this taxon as a unique subspecies in the *C. peirsonii* species complex.

Claytonia peirsonii subsp. *californacis* is morphologically most similar to *C. peirsonii* subsp. *yorkii* (Fig. 3) from the southern Sierra Nevada and genetically most closely related to *C. peirsonii* subsp. *bernardinus* (Fig. 2) from the San Bernardino Mountains, based on our current understanding and evidence presented here. *Claytonia peirsonii* subsp. *californacis* is considered rare, known only from a single population. It should be sought out in additional areas in southeastern California, particularly in transmontane, carbonate-dominated habitats in and adjacent to the San Bernardino Mountains.

The subspecific epithet, *californacis*, refers to the type locality (Furnace Canyon) for this subspecies in the San Bernardino Mountains. The suggested common name for the subspecies is Furnace spring beauty.

Representative Specimens Examined—U. S. A. California: San Bernardino Co., Head of Furnace Canyon, Apr 2014, *R. O'Quinn s. n.* with D. Jolles (RSA); Ridge running directly E from the Head of Furnace Canyon, N Holcomb Valley, 20 Apr 2013, *T. R. Stoughton 1720* (RSA812103, UCR, JEPS); Ridge running directly E from the Head of Furnace Canyon, N Holcomb Valley, 29 Mar 2014, *T. R. Stoughton 1852* (RSA, UCR, JEPS); Ridge running directly E from the Head of Furnace Canyon, N Holcomb Valley, 20 Apr 2014, *T. R. Stoughton 1882* (RSA).

5D. **Claytonia peirsonii** subsp. **yorkii** T. R. Stoughton, subsp. nov.—TYPE: U. S. A. California: Kern Co., southern Sierra Nevada, north slope of Cross Mountain, 30 March 2013, *T. R. Stoughton 1705 with D. Jolles* (holotype: RSA!; isotypes: UCR!, JEPS!).

Perennial; tuberous root 0.6–2.5 cm in diameter, globose, occasionally with a narrowed area at tuber apex where the aerial stems emerge; rhizomes absent. Stems (3–)6.5–9.5(–15) cm long; foliage generally green on ab/adaxial surfaces. Basal leaves absent to 1 (rarely more than 1), absent at flowering time, up to 11 cm long, petioles tapered or indistinct from blades; blades 10–15 × 1–2 mm, lanceolate to oblanceolate or narrowly elliptic, apex acute to obtuse. Cauline leaves 2–4, opposite at least proximally, 1-nerved, (4–)14–24(–40) × (2–)3–7(–8.5) mm, oblanceolate to narrowly elliptic, sessile to indistinctly petiolate (sometimes distinctly short-petiolate), adaxial surfaces of blades generally with sunken primary veins that are reddish in color (pigmentation sometimes lacking) and weakly thickened (raised) secondary veins that are green in color. Inflorescences 1–3, terminal and often also axillary, sessile to short-pedunculate, unibracteate, bract 1–3 mm long, membranous. Flowers 14–20 mm in diameter, developing buds erect to ascending or spreading; sepals 2–7 × 1.5–5 mm; petals 7–10 × 3–6 mm, light pink (sometimes white), generally with faintly-colored pink veins and a pink or yellow to orange-colored blotch (rarely absent) at base of blade above claw, apices entire or appearing weakly notched. Ovules 6. Seeds unknown. Chromosome number unknown. Figures 3H, 4B.

Distribution—Found in California in the transmontane habitats of the southern Sierra Nevada (Fig. 1), on north-facing, stony and talus slopes comprised of alkali-rich, igneous extrusive substrates (e.g. rhyolite) mixed with decomposing organic material from the surrounding forest. Mostly found in openings of a mixture of *Pinus sabiniana* and *Quercus chrysolepis* associations from around 1,450 m in elevation +/− ca. 500 m.

Notes—*Claytonia peirsonii* subsp. *yorkii* is morphologically similar to *C. panamintensis* and to the broad interpretation of *C. lanceolata* by Miller and Chambers (2006). It differs generally by its ecological setting (*C. peirsonii* subsp. *yorkii* is associated with alkali-rich, igneous extrusive rocks in transmontane habitats) and by the presence of raised 2° veins on the adaxial surfaces of its leaves. It differs also by shape, arrangement, and venation of its cauline leaves, its smaller overall plant size, and in having a sub-umbellate inflorescence that exhibits an abbreviated peduncle (often absent) with little to no internodal elongation among pedicels by the time of fruiting. *Claytonia peirsonii* subsp. *yorkii* is probably most easily confused with other subspecies of *C. peirsonii*, particularly subsp. *peirsonii* and subsp. *californacis*, because of the shape of their cauline leaves. *Claytonia peirsonii* subsp. *yorkii* can be readily distinguished from these two by weak to lacking betalain pigmentation on the abaxial surfaces of its leaves. All other subspecies of *C. peirsonii* have moderate to heavy betalain pigmentation on the abaxial surfaces of their leaves. *Claytonia panamintensis* can be distinguished from *C. peirsonii* subsp. *yorkii* by its nodding flower buds and distinctly petiolate cauline leaves, although the cauline leaves of *C. peirsonii* subsp. *yorkii* are sometimes (indistinctly) short-petiolate.

Claytonia peirsonii subsp. *yorkii* was first collected by Dana York in 1998 (*D. York 2079*, RSA), after which York collected it again (at the same and only known location) two more times in 2001 (*D. York 2530, 2555*). York noted in the field that plants collected at Cross Mountain in the southern Sierra Nevada (i.e. those treated here as *C. peirsonii* subsp. *yorkii*) were growing across a steep slope in loose talus of rhyolite and putatively numbered in the hundreds. York identified these plants as *C. lanceolata* var. *peirsonii.* Also discussed by Stoughton and Jolles (2013), these plants lack an expanded peduncle and internodal elongation among pedicels. They do not co-occur geographically with but are nearly a perfect match for the San Bernardino Mountain endemic *C. peirsonii* subsp. *californacis,* aside from a few minor subtleties in overall morphology and ecology. The two subspecies are known from

different substrates: *C. peirsonii* subsp. *yorkii* is known from collections only on rhyolite while *C. peirsonii* subsp. *californacis* is only known from collections on marble-dominated scree slopes. *Claytonia peirsonii* subsp. *yorkii* is considered to be rare, known only from a single, moderately sized population divided between two subpopulations spaced no more than 0.4 air km from each other. This taxon should be sought out in additional areas in southeastern California, particularly in and around xeric habitats of the southern Sierra Nevada where alkali-rich, igneous extrusive rocks are exposed and associated species are known to occur.

The subspecific epithet, *yorkii*, refers to the first collector of this subspecies in the southern Sierra Nevada, Dana York. The suggested common name for the subspecies is York's spring beauty.

Representative Specimens Examined—U. S. A. California: Kern Co., Jawbone Canyon, N slope just below summit of Cross Mountain, 23 Mar 2014, *T. R. Stoughton 1847* (RSA, UCR); Near the summit of Cross Mountain located in Jawbone Canyon, 21 Mar 1998, *D. York 2079* (CAS1119715, RSA685507); Ca. 24 km NW of California City, Jawbone Canyon, upper slope of Cross Mountain, 8 Apr 2001, *D. York 2530* (RSA683083, RSA812090); Ca. 24 km NW of California City, Jawbone Canyon, upper slope of Cross Mountain, 28 Apr 2001, *D. York 2555* (CAS1127300).

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Appendix 1. List of taxa and voucher specimens examined for this study, sorted by taxon, state, and county. For each specimen, we list the herbarium and accession number, collector and collection number, and GenBank accession numbers with Fig. 2 references for ITS sequences where relevant. An asterisk (*) indicates locations where soil and/or rock collections were made.

Claytonia lanceolata. California: Alpine County—RSA-837948 (CAS, JEPS, UCR, UNR), *T. Stoughton 1884**; El Dorado County—RSA-65732, *F. Peirson 6314*; Humboldt County—RSA-837942 (JEPS), *T. Stoughton 1762*, KX017454 (Fig. 2, #23); Lassen County—RSA-74140, *M. Baker 12429*; Madera County—RSA-464475, *M. Hood s.n.*, 2 Aug 1938; RSA-696304, *D. York 2191*; Sierra County—POM-161630, *R. Bacigalupi 1601*; RSA-8013, *H. Barker 720*; Siskiyou County—RSA-78818, *P. Munz 17896*; RSA-78830, *P. Munz 17908*; Oregon: Douglas County—RSA-837946 (JEPS), *D. Jolles 515*; RSA-837945 (JEPS), *T. Stoughton 1890**; RSA-837943 (JEPS), *T. Stoughton 1895*; Klamath County—RSA-837947 (JEPS), *D. Jolles 512*, KX017452 (Fig. 2, #24); RSA-837944, *T. Stoughton 1889*.

Claytonia obovata. California: Mendocino County—RSA-837941, *Bartosh 588*; RSA-837966, *T. Stoughton 1751*, KX017457 (Fig. 2, #13); RSA-837961 (JEPS), *T. Stoughton 1757*; RSA-837962 (JEPS), *T. Stoughton 1758*, KX017455 (Fig. 2, #14); RSA-837963 (JEPS), *T. Stoughton 1902**; Trinity County—RSA-837965 (JEPS), *T. Stoughton 1897**; RSA-837964 (JEPS), *T. Stoughton 1898**.

Claytonia panamintensis. California. Inyo County. RSA-812101 (JEPS, CAS), *T. Stoughton 1711*, KX017460 (Fig. 2, #11); RSA-837957 (JEPS), *T. Stoughton 1844**; RSA-812089, *D. York 2630*, KX017450 (Fig. 2, #12).

Claytonia peirsonii subsp. ***bernardinus.*** California. San Bernardino County. RSA-812091 (UCR, JEPS, CAS), *T. Stoughton 1077*; RSA-812092 (UCR, JEPS, CAS), *T. Stoughton 1514*; RSA-812102 (UCR, JEPS), *T. Stoughton 1717*, KX017456 (Fig. 2, #18); RSA-837949, *T. Stoughton 1850**

Claytonia peirsonii subsp. ***californacis.*** California. San Bernardino County. RSA-837952, *R. O'Quinn s.n.,* Apr. 2014; RSA-812093 (UCR, JEPS, CAS), *T. Stoughton 1516*, KX017453 (Fig. 2, #17); RSA-812103 (UCR, JEPS), *T. Stoughton 1720*; RSA-837950 (UCR, JEPS), *T. Stoughton 1852**; RSA-837951, *T. Stoughton 1882*.

Claytonia peirsonii subsp. ***peirsonii.*** California: Los Angeles County—RSA-812097 (UCR, JEPS), *T. Stoughton 1539*; RSA812100 (UCR, JEPS, CAS), *T. Stoughton 1706*; RSA-837953, *T. Stoughton 1837*; RSA-837954, *T. Stoughton 1838*; San Bernardino County—RSA-509347, *T.P. Krantz s.n.*, 25 Jun 1980; RSA-505073, *O. Mistretta s.n.*, 5 May 1987; RSA-505075, *O. Mistretta s.n.*, 5 May 1987; RSA-505076, *O. Mistretta s.n.*, 5 May 1987; RSA-505074, *O. Mistretta s.n.*, 13 May 1987; RSA-679587, *V. Soza 1275*; RSA-812094 (UCR, JEPS, CAS), *T. Stoughton 1532*; RSA-812095 (UCR, JEPS), *T. Stoughton 1533*; RSA-812096 (UCR, JEPS), T. *Stoughton 1536*; RSA-812098 (UCR), *T. Stoughton 1549*, KX017449 (Fig. 2, #15); RSA-837955, *T. Stoughton 1883**.

Claytonia peirsonii subsp. ***yorkii.*** California, Kern County. RSA-812099 (UCR, JEPS), *T. Stoughton 1705*, KX017459 (Fig. 2, #16); RSA-837956 (UCR), *T. Stoughton 1847**; RSA-683083, RSA-812090, *D. York 2530*.

Claytonia serpenticola. California: Trinity County. RSA-837960 (JEPS), *T. Stoughton 1759*, KX017458 (Fig. 2, #6); RSA-837958 (JEPS), *T. Stoughton 1899**; RSA-837959 (JEPS), *T. Stoughton 1900**.

APPENDIX 2. List of taxa with Fig. 2 references, location (when known), and GenBank accession numbers for ITS sequences used in phylogenetic analyses.

1. *Lewisia rediviva*, DQ498102. **2. *Claytonia cordifolia***, Idaho, AY764050. **3. *C. joanneana***, Russia, DQ498070. **4. *C. scammaniana***, Alaska, DQ498069. **5. *C. sarmentosa***, British Columbia, DQ498068. **6. *C. serpenticola,*** California, KX017458. **7. *C. serpenticola***, California, DQ498065 [labeled as *C. lanceolata* on GenBank]. **8. *C. acutifolia***, Russia, DQ498063. **9. *C. acutifolia***, Alaska, AY764047. **10. *C. virginica***, Maryland, DQ090125. **11. *C. panamintensis,*** California, KX017460. **12. *C. panamintensis,*** California, KX017450. **13. *C. obovata,*** California, KX017457. **14. *C. obovata,*** California, KX017455. **15. *C. peirsonii* subsp. *peirsonii,*** California, KX017449. **16. *C. peirsonii* subsp. *yorkii,*** California, KX017459. **17. *C. peirsonii* subsp. *californacis,*** California, KX017453. **18. *C. peirsonii* subsp. *bernardinus,*** California, KX017456. **19. *C. virginica***, South Carolina, AY764067. **20. *C. caroliniana***, Maine, AY764049. **21. *C. caroliniana***, New Hampshire, AY764048. **22. *C. lanceolata***, Nevada, DQ498066. **23. *C. lanceolata,*** California, KX017454. **24. *C. lanceolata,*** Oregon, KX017452. **25. *C. lanceolata,*** British Columbia, KX017451. **26. *C. lanceolata***, Idaho, AY764052. **27. *C. caroliniana***, North Carolina, DQ498059. **28. *C. caroliniana***, North Carolina, DQ498058. **29. *C. tuberosa***, Alaska, AY764063. **30. *C. multiscapa***, Idaho, DQ498060 [labeled as *C. lanceolata* var. *flava* on GenBank]. **31. *C. tuberosa***, Yukon Territory, AY764064.