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ABSTRACT

*Calyptridium parryi* (Montiaceae, formerly Portulacaceae) putatively comprises four varieties: *arizonicum*, *hesseae*, *nevadense*, and *parryi*. We performed a detailed phenetic analysis of seed, fruit, and sepal morphology in order to assess the distinction and rank of these varieties. We treated the San Pedro Martir Mountains, Baja California populations of *C. parryi* as a separate taxonomic unit in these studies, given their great disjunct distribution. In addition, we included the very similar and largely sympatric *C. monandrum* in these analyses. Results from ANOVA and principal components analysis indicate that the six entities examined are, to various degrees, morphologically diagnosable. *Calyptridium parryi* varieties *hesseae*, *nevadense*, and *parryi* show some overlap in features, and we propose keeping these as varieties. Populations from the San Pedro Martir Mountains are distinct from other varieties of *C. parryi*, possibly warranting varietal status, but further studies with more samples are needed to confirm this. However, we conclude that *C. parryi* variety *arizonicum* is different enough in several features and geographic range to warrant species status, by a taxonomic/morphologic species concept. *Calyptridium monandrum* should be retained as a separate species.

Key Words: *Calyptridium*, *Calyptridium monandrum*, *Calyptridium parryi*, Montiaceae, Portulacaceae, species, taxonomy.

*Calyptridium* Nutt. ex Torr. & A. Gray (Fl. N. Am. 1: 198 [1838]) is a genus of the family Montiaceae (formerly Portulacaceae *s.l.*; see Nyffeler 2007; Nyffeler et al. 2008; Ogburn and Edwards 2009; APG III 2009; Nyffeler and Eggl 2010). *Calyptridium* is currently recognized to have eight species (Guilliams 2009), one of which has four varieties, for a total of eleven taxa (Table 1; see Hinton 1975 for a nomenclatural history of the group). The genus is distinguished from closely related taxa in having a two-valved, dehiscent capsule. Many other related genera (e.g., *Calandrinia*, *Cistanthe*) have dehiscent capsules with three valves, or in *Philippiamra* [*Cistanthe*] an indehiscent capsule of two carpels. Members of *Calyptridium*, like some other Montiaceae, have petals (2–4 in this case) that become apically coherent after anthesis, forming a persistent cap-like structure covering the fruit tip (accounting for the etymology of the name: Greek *kaluptra*, veil, cap + *-idion*, little).

Based on evidence from morphology and anatomy, Hershkovitz (1990) transferred the species of *Calyptridium* to section *Calyptridium* (Nutt.) Hershkovitz of an expanded genus *Cistanthe s.l.* However, in subsequent molecular analyses of the “portulacaceous alliance,” *Cistanthe s.l.* is paraphyletic (Applequist and Wallace 2001; Hershkovitz and Zimmer 2000; Hershkovitz 2006). Although these studies stop short of making any definitive nomenclatural changes, it

is clear that *Cistanthe s.l.* must be reevaluated, and Hershkovitz (2006), in a study of the western American Portulacaceae, suggested that *Calyptridium* be again classified as a genus distinct from *Cistanthe*. Based on these studies, we have chosen to recognize *Calyptridium* at the genus level (in contrast to the treatment in *Flora of North America*; see Packer 2003).

The eight species of *Calyptridium* have been sorted into two groups, based on plant habit and morphological features of the flower, fruit, and seed (Hinton 1975; Guilliams 2009). One group, comprised of annual plant species with reduced flowers, consists of *C. monandrum* Nutt., *C. parryi* A. Gray, *C. pygmaeum* Parish ex Rydb., *C. quadripetalum* S. Watson, and *C. roseum* S. Watson. These five species are similar in lacking a style and in having a fruit that ranges from ovate to narrowly oblong (Table 1). The other group, corresponding to the “*Calyptridium umbellatum* complex” of Hinton (1975), consists of one annual and two perennial species: *C. monospermum* Greene, *C. pulchellum* (Eastw.) Hoover, and *C. umbellatum* (Torr.) Greene. These three species are similar in having filiform styles and an elliptic to orbicular fruit shape (Table 1). Some authors have chosen to recognize the genus *Spraguea* Torr. (Smithson. Contrib. vi. [Pl. Fremont.] [1854] 4. t. 1.) for this “*Calyptridium umbellatum* complex” in recognition of these putative morphological differences. However, the validity of *Spraguea* as a genus distinct from *Calyptridium* was called into question by Watson (1885), Greene (1886), and Hoover (1940). These authors argue that some of these morphological features

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TABLE 1. MORPHOLOGICAL FEATURES OF *CALYPTRIDUM* TAXA, ARRANGED BY DIAGNOSTIC FEATURES. Abbreviation: marg. = marginally; narr. = narrowly.

Taxon	Plant duration	Flower attachment	Petal number	Style shape/ presence	Fruit shape	Seed sculpturing
<i>C. monandrum</i> Nutt.	annual	sessile	3	absent	ovate - narr. oblong	marg. papillate
<i>C. parryi</i> A. Gray var. <i>arizonicum</i> J. T. Howell	annual	sessile	3-4	absent	ovate - narr. oblong	smooth
<i>C. parryi</i> A. Gray var. <i>hesseae</i> J. H. Thomas	annual	sessile	3-4	absent	ovate - narr. oblong	marg. papillate
<i>C. parryi</i> A. Gray var. <i>nevadense</i> J. T. Howell	annual	sessile	3-4	absent	ovate - narr. oblong	marg. papillate
<i>C. parryi</i> A. Gray var. <i>parryi</i>	annual	sessile	3-4	absent	ovate - narr. oblong	papillate
<i>C. pygmaeum</i> Parish ex Rydb.	annual	pedicellate	4	absent	ovate - narr. oblong	smooth
<i>C. quadripetalum</i> S. Watson	annual	pedicellate	4	absent	ovate - narr. oblong	papillate
<i>C. roseum</i> S. Watson	annual	pedicellate	2	absent	ovate - narr. oblong	marg. papillate
<i>C. pulchellum</i> (Eastw.) Hoover	annual	sub-sessile	4	filiform	elliptic - orbicular	smooth
<i>C. monospermum</i> Greene	perennial	sub-sessile	4	filiform	elliptic - orbicular	marg. papillate
<i>C. umbellatum</i> (Torr.) Greene	perennial	sub-sessile	4	filiform	elliptic - orbicular	marg. papillate

are not fully diagnostic for the group. Most recent treatments (e.g., Wilken and Kelley 1993) of the group follow Greene (1886) in lumping members of *Spraguea* within an expanded genus *Calyptridium* (or *Cistanthe* in Packer 2003).

The interrelationships of the species of *Calyptridium* have only recently been the subject of molecular phylogenetic studies. In an analysis using molecular data from the nrDNA internal transcribed spacer (ITS) and *ycf3-trnS* chloroplast DNA intergenic spacer, Hershkovitz (2006) showed that *Calyptridium* (as defined here) is weakly supported as a monophyletic group. The "*C. umbellatum* [former genus *Spraguea*] complex" is strongly supported as monophyletic, with *C. monospermum* and *C. umbellatum* weakly supported as sister taxa and these sister to *C. pulchellum*. The other five species are weakly supported as a monophyletic group as well, but with little resolution among them. *Calyptridium roseum* and *C. pygmaeum* are weakly supported as sister taxa. Three investigated varieties of *C. parryi* and *C. monandrum* form a weakly supported monophyletic group but with no resolution among them.

Guilliams (2009), using ITS, ETS, and three non-coding chloroplast regions, obtained results similar to those of Hershkovitz (2006), including the resolution of a monophyletic complex consisting of the four varieties of *C. parryi* plus *C. monandrum*, but with no resolution of relationships within this complex. However, in a combined molecular-morphological study, in which previously named taxa were a priori assumed to be monophyletic, he obtained support for a clade

in which *C. parryi* var. *hesseae* J. H. Thomas is sister to *C. monandrum*, with these two taxa sister to a clade consisting of a basal *C. parryi* var. *arizonicum* J. T. Howell sister to *C. parryi* var. *nevadense* J. T. Howell (including *C. parryi* populations from the San Pedro Martir Mountains, Baja California, Mexico) and *C. parryi* var. *parryi* (Guilliams 2009).

*Calyptridium parryi* (see Fig. 1A–C for habit and general morphology) has four varieties, which have been separated from one another primarily based on the size and sculpturing pattern of the seeds (Thomas 1956): variety *arizonicum* having smooth seeds (Fig. 1D); variety *hesseae* having relatively small, marginally papillate seeds (Fig. 1E); variety *nevadense* with marginally papillate seeds (Fig. 1F); and variety *parryi* with seeds papillate over the entire surface (Fig. 1G). Features of the pedicel ("articulate" in *C. parryi* var. *arizonicum*, not in the others) and flower duration ("persistent" in *C. parryi* var. *parryi*, not in *C. parryi* vars. *hesseae* or *nevadense*) have also been used to separate the varieties (Thomas 1956; Wilken and Kelley 1993), but we found these features difficult to evaluate from herbarium material. *Calyptridium monandrum* has been separated from *C. parryi* primarily on fruit morphology (e.g., Wilken and Kelley 1993), the former having fruits longer than 2× the (abaxial) sepal length, the latter <2×.

The purpose of this study is to investigate the taxonomy of *C. parryi* in order to evaluate the delimitation, taxonomic ranking, and biogeography of its infraspecific taxa. Because of the similarity of *C. monandrum* to *C. parryi* in a

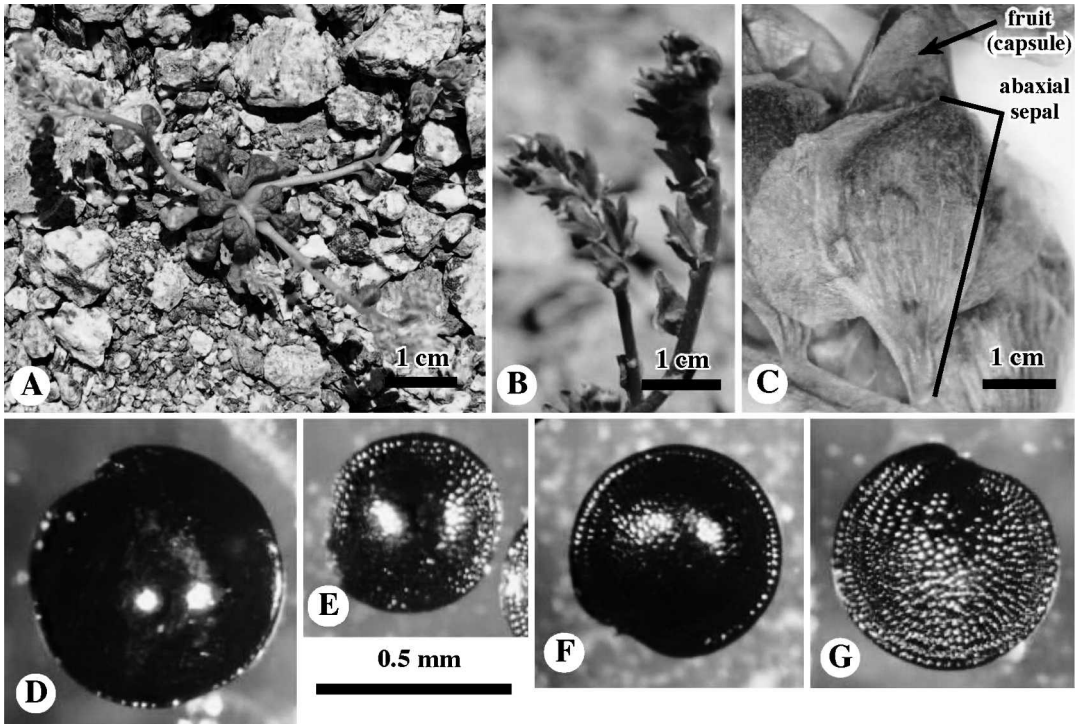


FIG. 1. A–B. Photographs of *Calyptridium parryi* var. *parryi*, showing plant habit in the wild (Simpson 2766, SDSU 18974). C. Close-up of fruit and abaxial sepal from herbarium specimen (RSA 225930). D–G. Seeds of the four varieties of *Calyptridium parryi*, all to scale. D. *C. parryi* var. *arizonicum*; E. *C. parryi* var. *hesseae*; F. *C. parryi* var. *nevadense*; G. *C. parryi* var. *parryi*.

number of features (Table 1) and because these two taxa are nested together in recent molecular analyses, *C. monandrum* was included in all comparative analyses.

#### MATERIALS AND METHODS

A total of 109 specimens of *Calyptridium parryi* and *C. monandrum* from nine herbaria (ARIZ, ASU, CAS-DS, RSA, SD, SDSU, UC-JEPS, UCR, UTC) were studied, with permission granted to remove seed material for this study. Accession numbers (Appendix 1) were recorded and latitude/longitude recorded or inferred from label information. Seeds were removed from individual plant specimens having mature fruits and mounted on double-stick tape on microscope slides, labeled with the specimen accession number.

Seeds were photographed using a Nikon 990 digital camera on a Wild dissecting microscope. Measurements were made using Image J software (Rasband 1997–2007; see Abramoff et al. 2004) on a Macintosh computer. Seeds are lenticular in shape and have a small notch at the hilar end; a line from this notch through the seed center forms an approximate sagittal section, dividing the seed into two mirror image halves (Fig. 2A).

Depending on available material and proper developmental stage, 10–25 seeds per specimen were analyzed. For each seed, the sagittal diameter (SD, including notch length), transverse diameter (TD), notch length (NL), and distance from the perimeter to the central-most extent of papillae (if present) along both the transverse plane (TP) and sagittal plane (SP) were measured from digital images (Fig. 2A).

In addition, approximately 5–10 fruits and their corresponding persistent, abaxial sepals (Fig. 2B) were photographed (intact) for each specimen (see Fig. 3 for variation among taxa). In some cases, fewer than five fruits and sepals were measured if suitable material could not be located on the specimen. Fruit outlines could be seen behind the abaxial sepal or determined with minimal manipulation. The abaxial sepal has a distinctive scarios margin. From the images acquired we measured fruit length (FL), maximum fruit width (FW), sepal blade length (SBL), sepal stalk length (SSL), sepal width at widest point (SW), scarios sepal margin width (SM, measured on one side only, the one most intact), and distance from the sepal blade base to the point of greatest sepal width (SB-SW) (Fig. 2B).



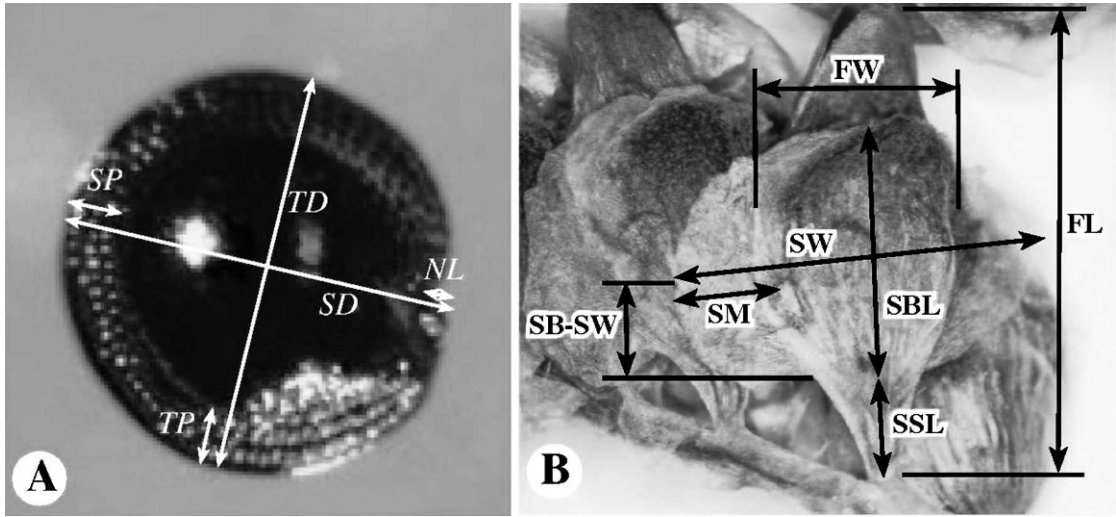


FIG. 2. A. Seed image illustrating features measured: sagittal diameter (SD), transverse diameter (TD), notch length (NL), distance from perimeter to the central-most extent of papillae (if present) along both the transverse (TP) and sagittal (SP) planes. B. Fruit and sepal, illustrating features measured: fruit length (FL), fruit width (FW), sepal blade length (SBL), sepal width at widest point (SW), sepal stalk length (SSL), sepal scarious margin width (SM), distance from sepal base to sepal maximum width (SB-SW).

Highly disjunct populations of *C. parryi* from the San Pedro Martir Mountains of Baja California, Mexico were initially identified as *C. parryi* var. *nevadense*. However, to investigate possible differences between these Mexican populations with those of the U.S. populations of *C. parryi* var. *nevadense*, these two groups were separated in the analyses, the former labeled *C. parryi* "martirensis."

To visualize character distributions by taxon, box plots showing the median and the four quartiles of distribution were prepared for 1) average seed papillation; 2) average seed diameter (mm); 3) fruit length (mm); 4) fruit width at widest point (mm); 5) sepal length (mm); 6) ratio of fruit length:total sepal length; 7) sepal width (mm); 8) ratio of total sepal length:sepal width; 9) relative width of scarious margin region of sepal; and 10) distance from the sepal blade base to the widest point (mm). Average seed papillation was quantified as the relative distance that papillae extend from the seed margin to its center =  $2(SP + TP)/(SD + TD)$ . A bivariate plot of sepal width versus total length was prepared to visualize trends in these features. Average seed diameter was calculated as  $(SD + TD)/2$ . Relative width of the scarious margin region was calculated as  $SM*2/SW$ . Each of these morphological characters were evaluated for statistically significant differences by taxon using analysis of variance (ANOVA), with multiple comparisons made between the taxon means using the Tukey post hoc test. Taxa that were statistically different from all other taxa in a particular character are indicated as such (at probabilities  $<0.01$  and

$<0.05$ ) in the box plot diagrams and in a table, summarizing the mean values of these characters.

In addition to comparisons of one character, a principal components analysis (PCA) was conducted using 12 characters: 1) seed sagittal diameter; 2) seed transverse diameter; 3) sagittal seed papillation; 4) transverse seed papillation; 5) sepal length; 6) sepal width; 7) distance from sepal blade base to widest point; 8) extent of sepal scarious margin; 9) fruit length; 10) fruit width; 11) fruit length:sepal length; and 12) sepal stalk length. Variables were standardized by subtracting the variable mean from each individual measurement, then dividing by the variable standard deviation. This transformation results in all variables having a mean of zero and a standard deviation of 1. The resulting factor scores of this PCA were plotted for the 1st versus 2nd components and 2nd versus 3rd components. Only samples with complete data sets were used in the PCA analyses. All statistical analyses were performed in SYSTAT, Version 11 (Systat Software, Inc., San Jose, CA USA, <http://www.systat.com>).

Maps were prepared showing the distribution of the four varieties of *C. parryi* and the *C. parryi* "martirensis" populations. Circles denote relative seed size and shading represents relative papillation of the seed surface (white = smooth region, black = papillate region). The latter was diagramed in clock fashion, with, e.g., shading from 12 to 3 o'clock representing 25% average papillation, meaning that the band of papillation extends 25% from the seed periphery to the seed center.

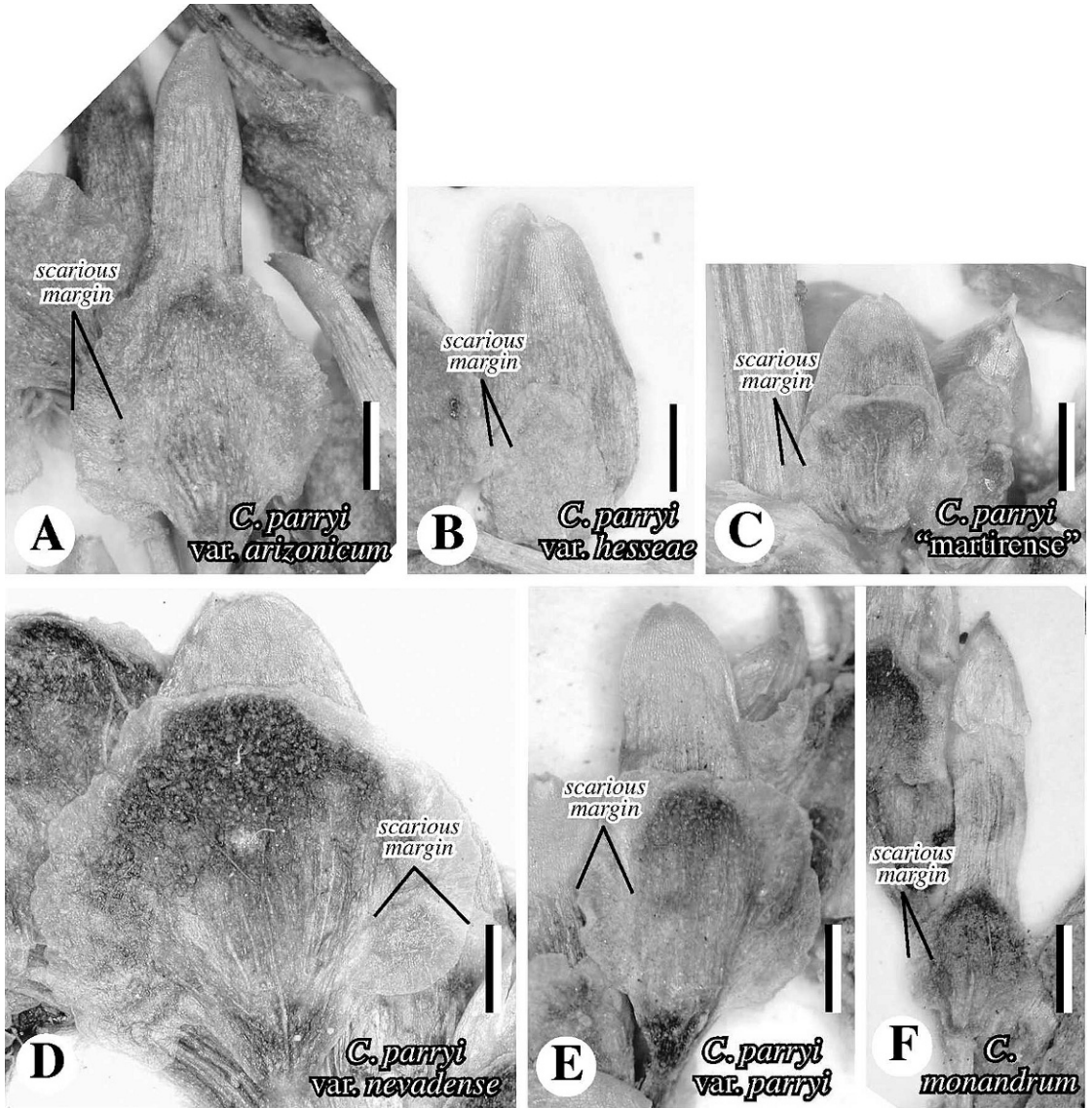


FIG. 3. Images, showing examples of fruits with subtending abaxial sepal (scarious margin indicated), all to scale. A. *Calyptridium parryi* var. *arizonicum* (ARIZ 200373). B. *C. parryi* var. *hesseae* (DS 266493). C. *C. parryi* "martirensis" (SD 97873). D. *C. parryi* var. *nevadense* (CAS 318495). E. *C. parryi* var. *parryi* (RSA 13478). F. *C. monandrum* (JEPS 48483). Scale bar = 1 mm.

## RESULTS

Three of the four varieties of *Calyptridium parryi*, plus the *C. parryi* "martirensis" populations from the San Pedro Martir Mountains and *C. monandrum*, exhibit statistically significant differences for one or more variables examined using ANOVA ( $P$ -values  $<0.05$  and  $<0.01$ ). Tukey HSD post hoc tests indicate which, if any, of the taxon means are statistically different. Mean values with statistical differences for characters examined are listed in Table 2.

The seed sculpturing of *C. parryi* var. *arizonicum* and *C. parryi* var. *parryi* are confirmed to be different from all other taxa examined in having, respectively, totally smooth versus totally papillate surfaces (both  $P < 0.01$ ; Fig. 4A). *Calyptridium monandrum*, *C. parryi* var. *hesseae*, *C. parryi* "martirensis," and *C. parryi* var. *nevadense* are very similar in seed sculpturing, having between 25–55% papillation (Fig. 4A). The seed size of *C. parryi* var. *hesseae* is overlapping but significantly smaller than all other taxa ( $P < 0.05$ ), whereas that of *C. parryi* var. *arizonicum* is

TABLE 2. MEAN VALUES FOR CALYPTRIDIMUM TAXA OF CHARACTERS EXAMINED USING ANOVA. \* = <0.05; \*\* = <0.01.

Taxon	Average seed papillation (%)	Average seed diameter (mm)	Fruit length (mm)	Fruit width (mm)	Sepal length (mm)	Fruit length:sepal length	Sepal width (mm)	Sepal length:width	Sepal scarious margin (%)	Distance sepal base to widest (mm)
<i>C. monandrum</i>	35.4	0.624	4.384	0.894**	1.771**	2.501**	1.419	1.129	16.1	0.633*
<i>C. parryi</i> var. <i>arizonicum</i>	0.0**	0.754**	6.689**	1.742	4.165*	1.611	3.942	0.785	41.5	0.885
<i>C. parryi</i> var. <i>hesseae</i>	32.5	0.540*	4.468	1.449	2.777*	1.620	1.838	1.265	16.0	0.894
<i>C. parryi</i> var. <i>nevadense</i>	34.5	0.685	4.643	1.481	3.249	1.445	3.723	0.751	51.5	1.089
<i>C. parryi</i> var. <i>parryi</i>	99.7**	0.677	4.666	1.574	3.249	1.447	2.814	0.983	61.1	1.119
<i>C. parryi</i> "martirensis"	35.9	0.599	3.252**	2.227*	3.515	0.925**	2.882	0.932	42.9	1.122

overlapping but significantly larger ( $P < 0.01$ ; Fig. 4B). The other four taxa, although showing some variation, generally overlap in seed size, with no significant differences between them (Fig. 4B).

Fruits show significant differences in both length and width among investigated taxa. The fruits of *C. parryi* var. *arizonicum* are significantly longer than, and (barely) non-overlapping with any other taxon ( $P < 0.01$ ; Fig. 4C). In contrast, fruits of *C. parryi* "martirensis" are significantly shorter ( $P < 0.01$ ), although overlapping in range with those of *C. monandrum*, *C. parryi* var. *nevadense*, and *C. parryi* var. *parryi* (Fig. 4C). Fruit width is significantly smaller ( $P < 0.01$ ) in *C. monandrum* and significantly larger ( $P < 0.05$ ) in *C. parryi* "martirensis" (Fig. 4D).

Abaxial sepals show significant differences in total length. The sepal length of *C. monandrum* is significantly shorter ( $P < 0.01$ ) than that of all other taxa, with virtually no overlap in range (Fig. 5A). Sepal length of *C. parryi* var. *hesseae* is generally smaller than the remaining taxa (both  $P < 0.05$ ), and that of *C. parryi* var. *arizonicum* is generally greater than all taxa, but both with considerable overlap of ranges (Fig. 5A).

In comparing fruit:sepal length the fruits of *C. monandrum* are 2.1–3.0× longer than the total abaxial sepal length, significantly greater ( $P < 0.01$ ) than any other taxon (Fig. 5B). This is due not to its having longer fruits (Fig. 4C), but to its having smaller sepals (Fig. 5A). In contrast, the fruit length of *C. parryi* "martirensis" is <1.1× longer than the abaxial sepal length, significantly less ( $P < 0.01$ ) than any other taxon (Fig. 5B). This is due to its significantly smaller fruit length (Fig. 4C), and a relatively large sepal length (Fig. 5A). The three other taxa examined overlap in fruit:abaxial sepal length ratio (Fig. 5B).

Abaxial sepals are also variable among taxa with regard to width (at widest point), length:width ratio, relative width of the scarious margin region, and distance from the sepal blade base to the widest point. No taxa are significantly different from all other taxa in sepal width (Fig. 5C). However, both *C. monandrum* and *C. parryi* var. *hesseae* are similar in having relatively narrow sepals, each significantly narrower ( $P < 0.01$ ) than the other four taxa (Fig. 5C). A plot of abaxial sepal length to width ratio (Fig. 5D) shows that *C. parryi* var. *nevadense* has the (relatively) widest abaxial sepals and *C. parryi* var. *hesseae* has the (relatively) narrowest sepals. However, there is considerable overlap among taxa, and no taxon is significantly different from any other, although *C. monandrum* and *C. parryi* var. *hesseae* have generally greater ratios, indicating that their sepals are relatively narrow (Fig. 5D). A bivariate plot of sepal length versus width (Fig. 6A) shows a general grade with respect to these features, but with definite trends in the complex. *Calyptridium monandrum* has



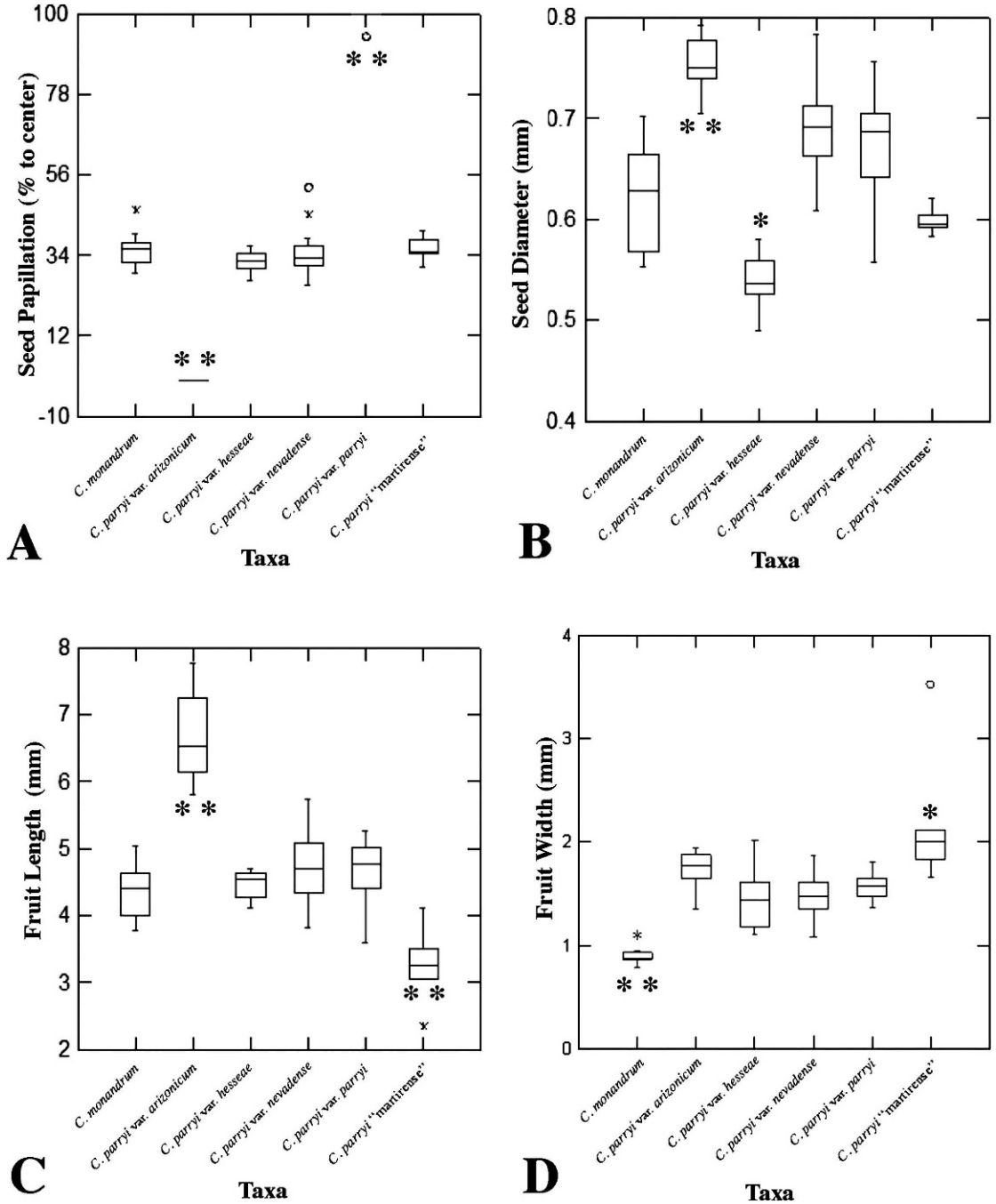


FIG. 4. Box plots of single characters. A. Percentage seed papillation. B. Seed diameter (mm). C. Fruit length (mm). D. Fruit width (mm). Note: box plots show median (horizontal line), first and third quartiles (boxes above and below median), and second and fourth quartiles (vertical lines); x = outliers; *C. parryi* "martirensis" = San Pedro Martir Mountains populations of *Calyptridium parryi*. Statistical difference between a given taxon and all other taxa (via ANOVA Tukey post hoc test) indicated as: \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ .

relatively small sepals (in length and width) as does *C. parryi* var. *hesseae*, the two taxa overlapping in these two features. *Calyptridium parryi* var. *nevadense* and *C. parryi* var. *arizoni-*

*cum* have a relatively large sepal length and width. *Calyptridium parryi* var. *parryi* and *C. parryi* "martirensis" are intermediate in these two sepal metrics.

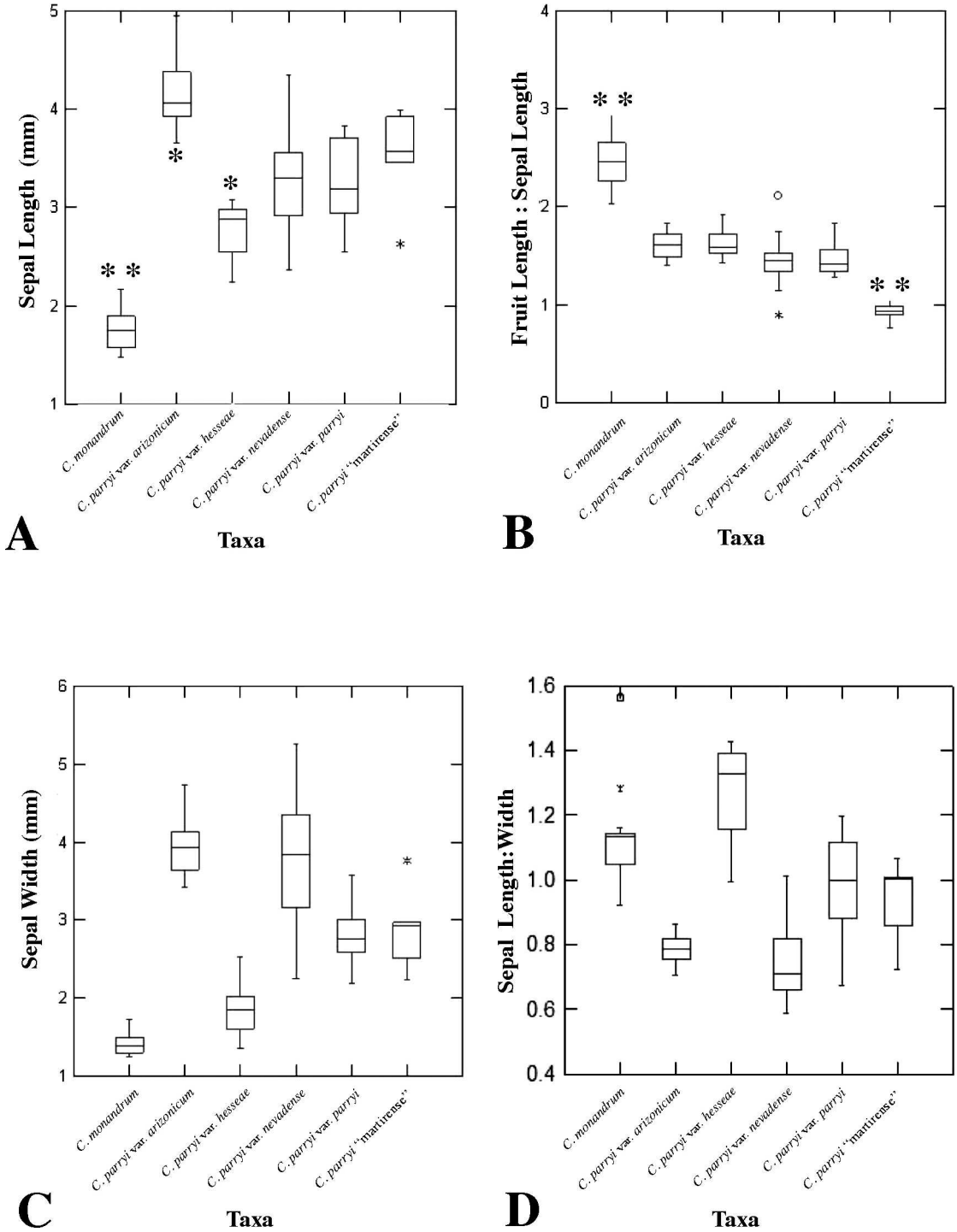


FIG. 5. Box plots of single characters. A. Sepal length (mm). B. Fruit length:sepal length ratio. C. Sepal width (mm). D. Sepal length:width ratio. Symbols as in Fig. 4.

With regard to relative width of the scarious abaxial sepal margin, *C. parryi* var. *hesseae* and *C. monandrum* have very similar, relatively thin scarious margins (Fig. 6B). These two taxa are

not significantly different from each other in this feature, but each is significantly different ( $P < 0.01$ ) from the other four taxa (*C. parryi* var. *arizonicum*, *C. parryi* var. *nevadense*, *C. parryi*

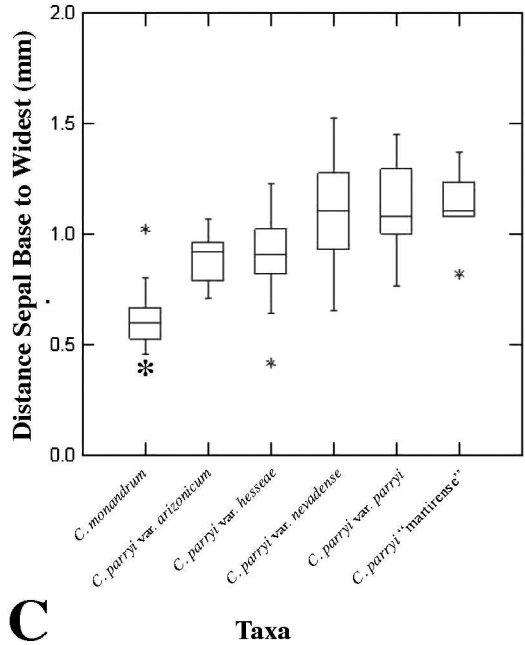
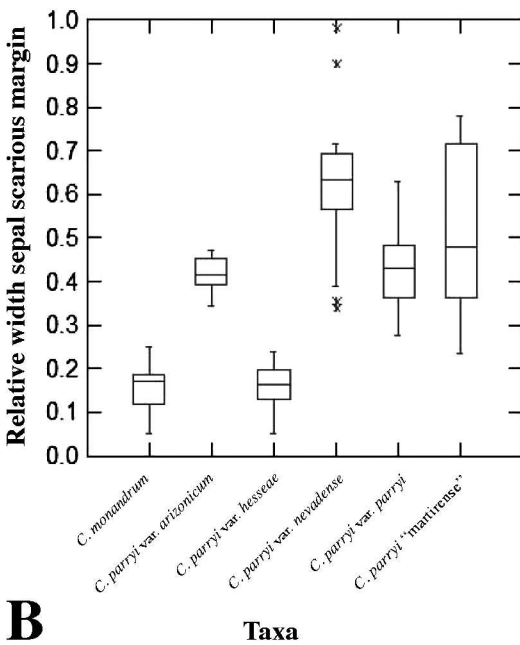
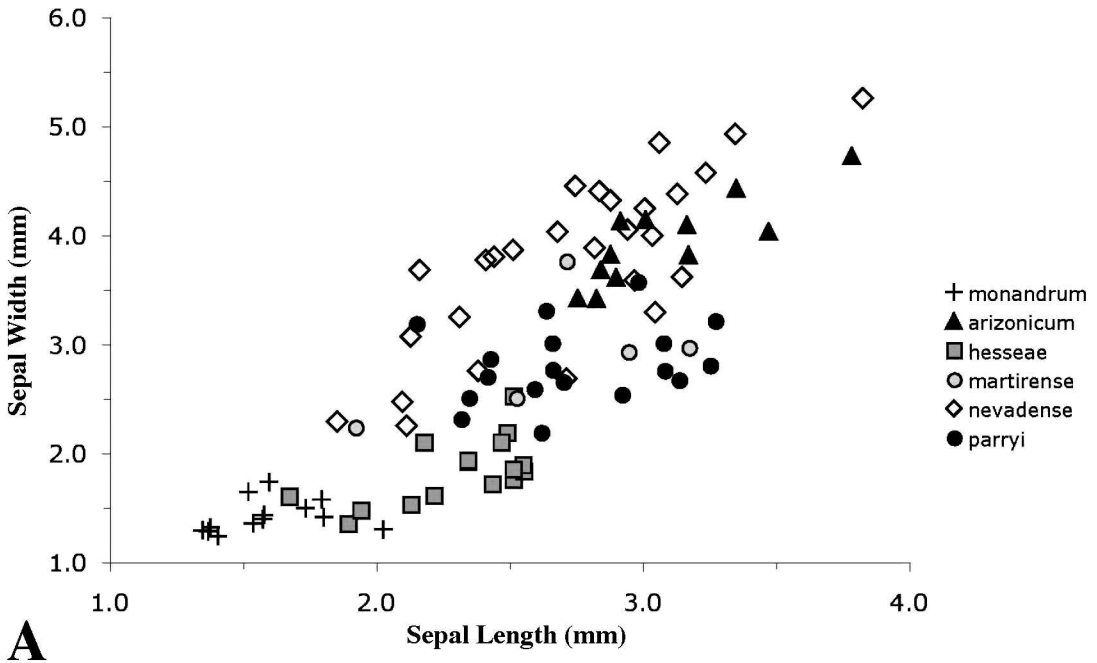
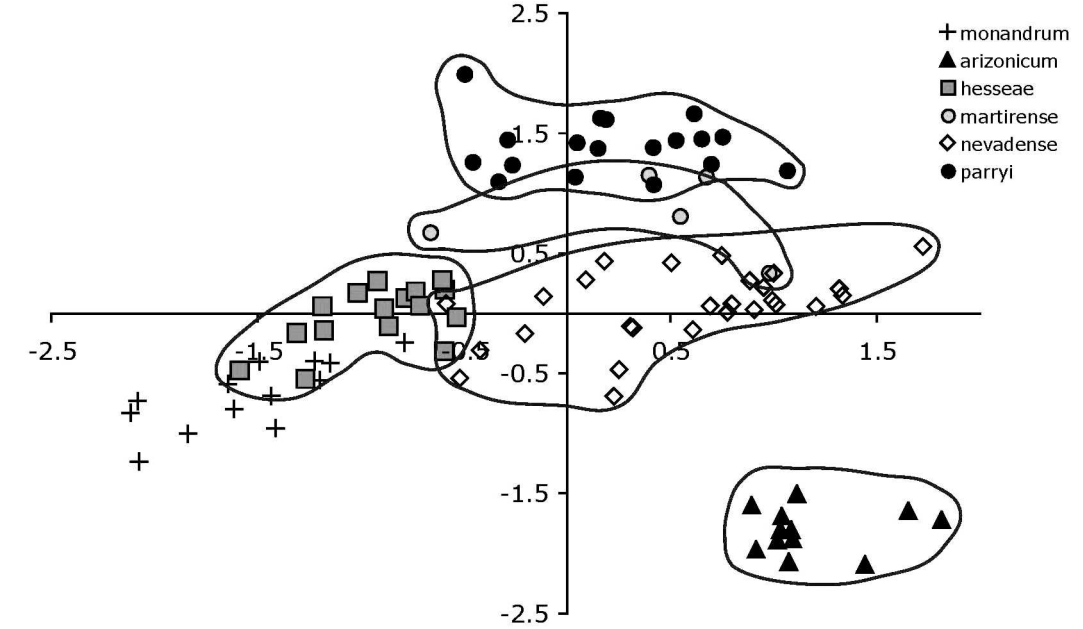


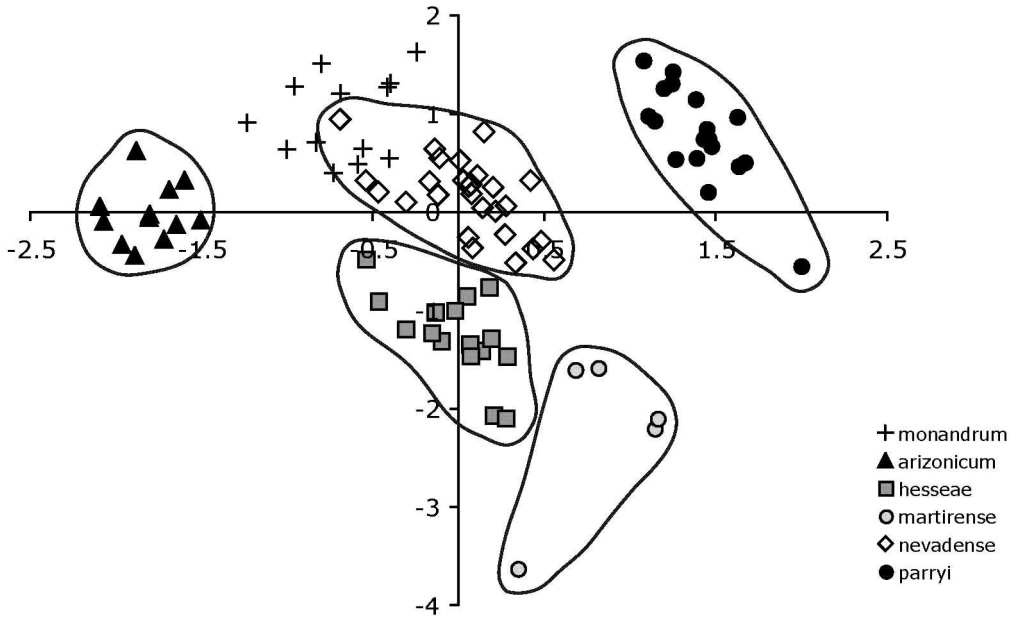
FIG. 6. A. Bivariate scatter plot of abaxial sepal blade length versus maximum sepal width. B–C. Box plots of single characters. B. Relative width of sepal scarious margin. C. Distance from sepal base to widest point (mm). Symbols as in Fig. 4.

var. *parryi*, and *C. parryi* “martirensis”). In the comparison of distance from the sepal base to the widest point, taxa generally overlap and show no significant differences, except for *C. monandrum*, which is significantly less in this feature (but at the  $P < 0.05$  level).

The multivariate principal components analysis (PCA) using twelve quantified features (Fig. 7) accounts for ca. 44% of the variation explained by the first loading, ca. 23% by the second loading, and ca. 13% by the third loading (Table 3). A plot of the first and second factors



**A**



**B**

FIG. 7. Graph of results of a Principal Components Analysis. A. Plot of first and second factors. Note clear separation of *C. parryi* var. *arizonicum*. B. Plot of second and third factors. Note separation of all *C. parryi* taxa, overlap of *C. monandrum* and *C. parryi* var. *nevadense*.



TABLE 3. PRINCIPAL COMPONENTS ANALYSIS LOADINGS FOR TWELVE CHARACTERS USED. Percent of total variance explained: axis 1 = 44.365, axis 2 = 23.348, and axis 3 = 12.759.

Character	Component loadings		
	1	2	3
Seed sagittal diameter	0.726	-0.293	0.540
Seed transverse diameter	0.742	-0.150	0.580
Sagittal seed papillation	-0.068	0.870	0.362
Transverse seed papillation	-0.096	0.867	0.348
Sepal length	0.914	0.126	-0.126
Sepal width	0.911	-0.069	0.043
Distance from sepal base to widest point	0.656	0.524	-0.137
Extent of sepal scarious margin	0.795	0.218	0.128
Fruit length	0.545	-0.577	0.188
Fruit width	0.619	0.153	-0.542
Fruit length:sepal length	-0.577	-0.611	0.383
Sepal stalk length	0.701	-0.336	-0.350

shows non-random clusters for all taxa. There is some overlap of taxa clusters with the exception for *C. parryi* var. *arizonicum* (Fig. 7A). *Calyptrididium monandrum* overlaps with *C. parryi* var. *hesseae*. A plot of the second and third factors shows a separation of all *C. parryi* taxa from one another; *C. monandrum* overlaps with *C. parryi* var. *nevadense* (Fig. 7B).

A distribution map shows minimal overlap in range among the five *C. parryi* taxa (Fig. 8). *Calyptrididium parryi* var. *parryi* is found mainly in the transverse range and northern peninsular range, with one known outlier in the South Coast Ranges. *Calyptrididium parryi* var. *nevadense* is found in the Sierras, Inyo, White and desert ranges of California (with one outlier in the transverse range) and in the adjacent mountains of western Nevada, with a couple of outliers in more eastern states. *Calyptrididium parryi* var. *hesseae* is restricted to a few localities in the Santa Lucia, Diablo, and Santa Cruz ranges of the Central Coast, California. *Calyptrididium parryi* var. *arizonicum* is found both in southern Arizona and in north-central Baja California, Mexico (with two examined outliers in Sonora, Mexico). As mentioned earlier, the “martirensis” populations of *C. parryi* are restricted to high elevations of the San Pedro Martir Mountains of Baja California, Mexico. Finally, the distribution of *C. monandrum* overlaps with that of most varieties of *C. parryi* (not shown; see Consortium of California Herbaria 2009), although *C. monandrum* generally occurs at lower elevations.

#### DISCUSSION

The results of these analyses suggest that the four varieties and “martirensis” populations of *Calyptrididium parryi* and the presumed closely

related *C. monandrum* each show various differences in sepal, fruit, and seed morphology.

*Calyptrididium parryi* var. *arizonicum* is perhaps the most distinctive of the taxa examined (Table 2). Its seeds are totally smooth, lacking any evidence of papillation (Fig. 4A), and are significantly larger in size (both  $P < 0.01$ ), although overlapping in size range with *C. parryi* var. *nevadense* and *C. parryi* var. *parryi* (Fig. 4B). Fruits of *C. parryi* var. *arizonicum* are significantly longer ( $P < 0.01$ ; Fig. 4C) and sepals are generally longer ( $P < 0.05$ ) but greatly overlapping with those of other taxa (Fig. 5A). Both PCA component plots show a marked separation of *C. parryi* var. *arizonicum* in the combination of 12 characters examined (Fig. 7A, B).

*Calyptrididium parryi* var. *hesseae* has significantly smaller seeds ( $P < 0.05$ ), although overlapping slightly with two other taxa, particularly with *C. monandrum* (Fig. 4B). Variety *hesseae* has sepals shorter than all other taxa except *C. monandrum* ( $P < 0.05$ ; Fig. 5A). Variety *hesseae* is also similar to *C. monandrum* in having narrow sepals (Fig. 5C) and a relatively narrow sepal scarious margin (Fig. 6B), each significantly different ( $P < 0.01$ ) from the other four taxa. The sepal length to width ratio of these two taxa is also greater than that of the other four *Calyptrididium* taxa (Fig. 5D; see also Fig. 6A), but without statistical significance.

*Calyptrididium parryi* “martirensis” was surprisingly different in some respects from any of the known varieties of that species. The seed sculpturing of this group is very similar to that of *C. monandrum* and *C. parryi* varieties *hesseae* and *nevadense* (Fig. 4A), and its seed size is somewhat intermediate (Fig. 4B). However, the fruit length of *C. parryi* “martirensis” is significantly smaller than any of the other five taxa examined ( $P < 0.01$ ; Fig. 4C), as is its fruit:sepal ratio (Fig. 5B). In the PCA analysis *C. parryi* “martirensis” shows overlap with other taxa in the plot of the 1st and 2nd factors (Fig. 7A), but is discontinuous in the plot of 2nd and 3rd factors (Fig. 7B).

*Calyptrididium parryi* var. *parryi* was confirmed to be discontinuous with respect to seed papillation; all seeds examined had ca. 95–100% papillation (Fig. 4A). The few seeds that were problematic in our study proved to be shrunken, due we think to immaturity or abortion during development. In all other features *C. parryi* var. *parryi* shows overlap with one or more taxa. However, in the PCA analysis it shows a discontinuous clustering in the plot of factors 2 and 3 (Fig. 7B).

*Calyptrididium parryi* var. *nevadense* is the only taxon that lacks any unique character states. It is very similar to *C. monandrum*, *C. parryi* var. *hesseae*, and *C. parryi* “martirensis” in seed sculpturing (Fig. 4A) and to *C. parryi* var. *parryi*

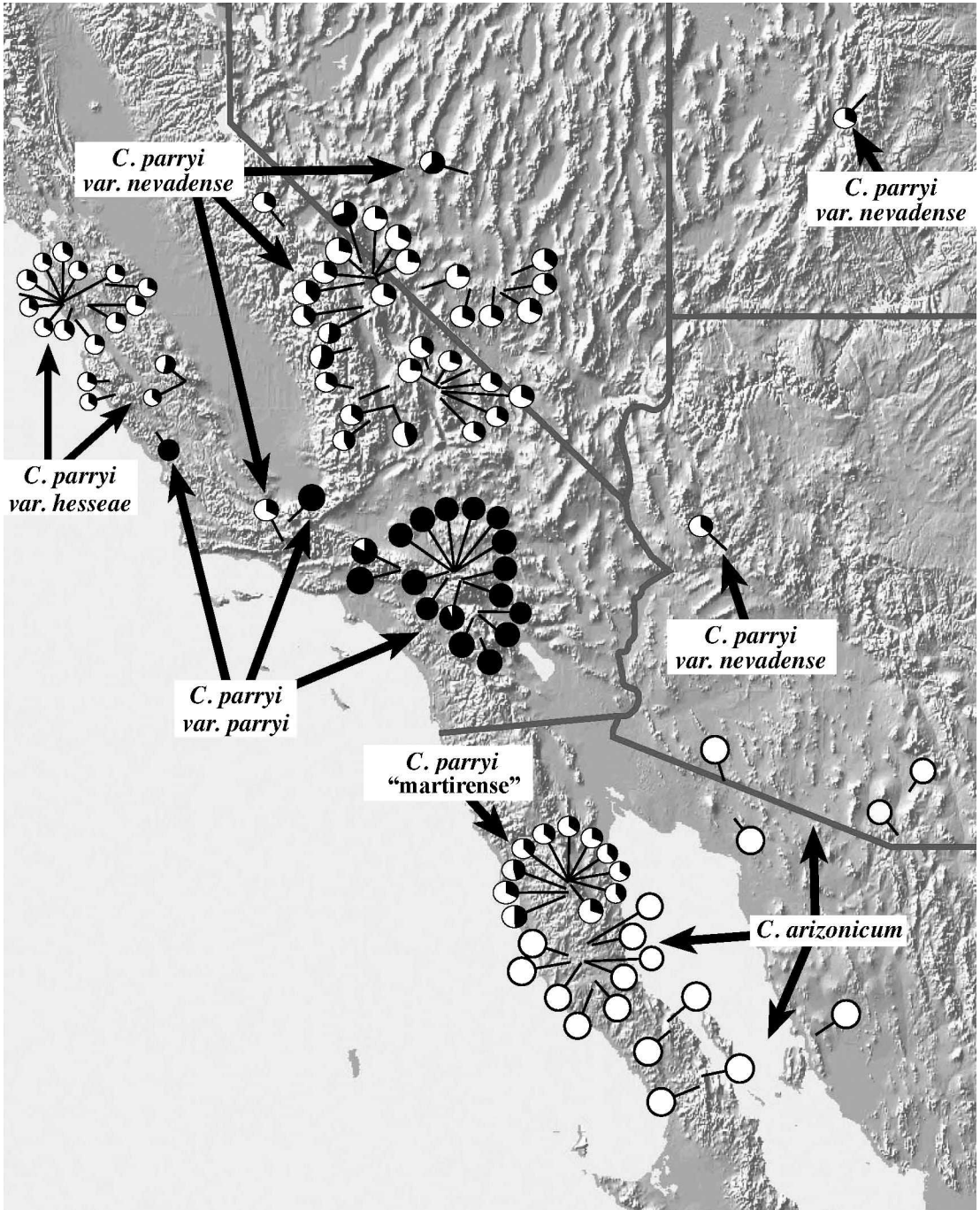


FIG. 8. Detailed map of quantified seed data for the *Calytridium parryi* groups. Circles are proportional to seed diameter. Black coloring is indicative of percentage of distance of papillae from seed periphery to seed center.

in seed size (although also slightly with most other taxa; Fig. 4B). Variety *nevadense* overlaps considerably with other taxa in fruit length (Fig. 4C), fruit width (Fig. 4D), fruit length:sepal length (Fig. 5B), and all sepal features (Figs. 5A, C–D, 6A–C). In the PCA analysis it has a

discontinuous distribution in the plot of factors 2 and 3 among the other *C. parryi* varieties/groups, but overlaps with *C. monandrum* (Fig. 7B).

*Calytridium monandrum* has a significantly smaller fruit width ( $P < 0.01$ ; Fig. 4D) and sepal

length ( $P < 0.01$ ; Fig. 5A) than any *C. parryi* taxon. It also has a significantly greater fruit length:sepal length ( $P < 0.01$ ; Fig. 5B). It is this large fruit to sepal ratio that has been used (Wilken and Kelley 1993; Guillems 2009) to distinguish this species from *C. parryi*. It is interesting, however, that the fruit length of *C. monandrum* is quite similar to that of *C. parryi* vars. *hesseae*, *nevadense*, and *parryi* (Fig. 4C); the greater fruit to sepal ratio is due to *C. monandrum* having shorter sepals, not to having longer fruits. Finally, as already discussed, *C. monandrum* and *C. parryi* var. *hesseae* are similar in having relatively narrow sepals (Fig. 5C) with relatively narrow scarious margins (Fig. 6B).

Biogeographically, the four varieties of *C. parryi* have mostly discontinuous, well-separated ranges (Fig. 8). *Calyptridium parryi* var. *hesseae* is biogeographically unique in being restricted to lower elevations (600–1050 m) in the Santa Cruz, Santa Lucia, and Diablo ranges of the Central Western California Region (biogeographic regions after Hickman 1993). It is interesting that *C. parryi* var. *arizonicum* occurs in two disjunct regions, one in southern Arizona to Sonora, Mexico and the other in north-central Baja California; we note that another population of *C. parryi* var. *arizonicum* was discovered in 2009 in mountains of Anza Borrego Desert State Park, San Diego Co., California (not illustrated; see Consortium of California Herbaria 2009). Thus, *C. parryi* var. *arizonicum* is restricted to habitats of the Sonoran (including Coloradan) and Viscaïno deserts. *Calyptridium parryi* var. *nevadense* and var. *parryi* have fairly discontinuous ranges, with slight overlap. *Calyptridium parryi* var. *parryi* is mostly restricted to mid to high elevations (1400–3500 m) in the transverse range of southern California, whereas *C. parryi* var. *nevadense* is largely restricted to mid to high elevations (1100–3000 m) in the Sierra Nevada mountains of California and adjacent ranges of the Mohave and Great Basin, east into Nevada, with one examined population in Utah and one in Arizona. One sample each of *C. parryi* var. *parryi* and of *C. parryi* var. *nevadense* occurs in the western transverse range of southern California, and one sample of *C. parryi* var. *parryi* occurs in the South Coast Ranges. As pointed out earlier, the “martirensis” populations of *C. parryi*, endemic to the San Pedro Martir Mountains of northern Baja California (2200–2600 m elevation), are quite disjunct from the other populations (Fig. 8).

Of the taxa we studied, only *C. parryi* var. *hesseae* is rare and appears threatened. This variety was previously described as “has not been seen in many years” and “likely extirpated locally and possibly near extinction” (Morgan et al. 2005). In earlier field work (Guillems 2009), we were only able to relocate only one population of

this taxon, warranting subsequent solicitation for a California Native Plant Society Inventory listing of 1B.1 (meaning that it is “rare, threatened, or endangered in California and elsewhere” and “seriously endangered in California, over 80% of occurrences threatened/high degree and immediacy of threat”); see California Native Plant Society (2009) and Guillems (2009).

#### NOMENCLATURE CONSIDERATIONS

Based on the presented quantitative morphological data, our study has demonstrated the existence of six groups – *Calyptridium monandrum*, the four *C. parryi* varieties, and the *C. parryi* “martirensis” populations. The question becomes what to call them and at what rank? In evaluating nomenclatural changes resulting from this study, we here review the concepts for recognizing species and infraspecies (see McDade 1995).

Evaluation of the six entities as “biological species” (Mayr 1969) is currently untestable in this complex because we know nothing about reproductive biology of these species and cannot evaluate whether any particular group might be reproductively isolated from any other. The only *Calyptridium* taxa studied reproductively are *C. monospermum* and *C. umbellatum*, found to be outcrossing or have insect-mediated self-pollination (Hinton 1976). The reduced flowers of the *C. monandrum* - *C. parryi* complex studied here may imply self-pollination, but this is only speculative, and reproductive isolation among its members has not been tested.

Recognition of “phylogenetic species” (e.g., Mishler and Donoghue 1982; de Queiroz and Donoghue 1988), necessitates a phylogenetic analysis and the identification of at least one apomorphy characterizing a lineage. However, the molecular phylogenetic studies of both Hershkovitz (2006) and Guillems (2009) are inconclusive about the monophyly of any of the taxonomic entities of this study. Thus, a phylogenetic taxon concept based on current molecular data alone is unworkable for this group, perhaps because of the lack of fine enough molecular marker or because the entities in this complex have evolved relatively recently.

Thus, we feel that the only viable procedure is to use a “taxonomic” or “morphological” species concept (Cronquist 1978, 1988) in which taxa are circumscribed based on a demonstrated discontinuity of morphological features. Species are sets of populations that are clearly discontinuous from one another in at least one morphological feature, showing no intergradation. Varieties and subspecies (in practice interchangeable; see Hamilton and Reichard 1992) are typically considered to be forms that show differences from one another, but the feature or features that make them different have some intergradation. Varie-



ties could represent genetically distinct ecological variants or populations that have either diverged incompletely or become geographically fragmented from a larger, ancestral population, possibly representing incipient speciation.

Of the six groupings recognized in this study, four – *C. parryi* var. *hesseae*, *C. parryi* var. *nevadense*, *C. parryi* var. *parryi*, and the *C. parryi* “martirensis” populations – are more similar to one another than the other two in the features examined. We feel that the similar seed papillation between varieties *hesseae*, “martirensis,” and *nevadense* and the contiguous geographic ranges (with slight interdigitation) between varieties *nevadense* and *parryi* support the retention of these taxa as varieties at this time. Within this complex, *C. parryi* var. *hesseae* differs from *C. parryi* var. *nevadense* and *C. parryi* var. *parryi* to a greater degree in its moderately ( $P < 0.05$ ) significantly smaller (but overlapping) seed size and, along with *C. monandrum*, its strongly ( $P < 0.01$ ) significantly narrower (but slightly overlapping) sepals and scarious sepal margin. However, because of overlap in these features, we believe that *C. parryi* variety *hesseae* should be retained at the varietal rank, given the uncertainty of recent molecular evidence. In addition, we point out that *C. parryi* var. *parryi* is completely non-overlapping in one feature: having an entirely papillate seed surface. This is not only a morphological distinction, but could represent a possible apomorphy, as the only other *Calyptridium* taxon to have a uniformly papillate seed surface is *C. quadripetalum*, which is more distantly related, having evolved uniform seed papillation independently (Guilliams 2009). However, we choose to retain *C. parryi* var. *parryi* as a variety, given its very slight interdigitation in range (Fig. 8) and otherwise greatly overlapping morphology with *C. parryi* var. *nevadense*.

Based on the morphological analyses presented, it is clear that the *C. parryi* “martirensis” populations are different from *C. parryi* var. *nevadense* (to which they were originally identified) within the *C. parryi* complex. Samples of these populations are identical to *C. parryi* var. *hesseae* and *C. parryi* var. *nevadense* in seed sculpturing and intermediate to these two in seed size. However, *C. parryi* “martirensis” has signif-

icantly shorter fruits ( $P < 0.01$ ) and a significantly smaller, but overlapping, fruit:sepal ratio ( $P < 0.01$ ). It also exhibits some discontinuity in the PCA analysis. At this stage, we feel that these populations could be treated as another variety of *C. parryi* (tentatively to be named *C. parryi* var. *martirensis*), but we wish to conduct further analyses with a greater sample size before publishing a new name.

We feel that *C. monandrum* is justified in its continued recognition as a separate species, due its significantly greater fruit:sepal ratio, smaller fruit width, and smaller sepal size. *Calyptridium monandrum* is more widespread and overlaps in range with most members of the *C. parryi* complex. However, as pointed out earlier, it shows some similarity in other features to *C. parryi* var. *hesseae*.

Our strongest conclusion is that *C. parryi* var. *arizonicum* is markedly distinct from all other varieties or forms in its smooth ( $P < 0.01$ , non-overlapping) and significantly larger ( $P < 0.01$ , but overlapping) seeds and its significantly longer ( $P < 0.01$ , essentially non-overlapping) fruits. It has the most discontinuous clustering of any taxa in both plots of the PCA analysis using 12 combined characters (Fig. 7). In addition, the range of this taxon, although split by the Sea of Cortez, is completely non-overlapping with the range of *C. parryi* vars. *hesseae*, *nevadense*, and *parryi* and the “martirensis” populations (Fig. 8), occurring in desert habitats. Thus, based on this study in which seed, sepal, and fruit morphology were quantified, we conclude, based on a taxonomic species concept, that *C. parryi* var. *arizonicum* should be elevated to the rank of species; the necessary new combination is published below, along with a key to this complex of species.

***Calyptridium arizonicum*** (J. T. Howell) M. G. Simpson, M. Silveira, & Guilliams, comb. nov., stat. nov. —Type: USA, Arizona, Pima Co., Pima, hills above Rosemont, 13 March 1903 to 23 April 1903, *D. Griffiths 4125* (holotype: US 00497458, barcode 00103153). Basionym: *Calyptridium parryi* A. Gray var. *arizonicum* J. T. Howell, Leaflet W. Bot. 4: 215. 1945. Synonym: *Cistanthe parryi* var. *arizonica* (J. T. Howell) Kartesz & Gandhi, Phytologia 71: 62. 1991.

Key to the *Calyptridium parryi* Species Complex

- 1. Fruit at maturity gen. <1 mm wide, >2× longer than abaxial sepal; abaxial sepal <2.2 mm long; widespread. . . . . *C. monandrum*
- 1' Fruit at maturity gen. >1 mm wide, <2× longer than abaxial sepal; abaxial sepal 2.2–5 mm long; restricted in range
  - 2. Seeds completely smooth, lacking tubercles; fruit gen. 5–8 mm long . . . . . *C. arizonicum*
  - 2' Seeds not completely smooth, with tubercles at least along the margin; fruit 2–5.7 mm long
    - 3. Seeds with tubercles throughout . . . . . *C. parryi* var. *parryi*
    - 3' Seeds with tubercles only on the margin
      - 4. Fruit ca. 2–4 mm long, ≤1× longer than abaxial sepal; San Pedro Martir Mtns., Baja California, Mexico. . . . . *C. parryi* “martirensis”



- 4' Fruit 3–6 mm long, 1–2.4× longer than abaxial sepal; mostly California and Nevada (rarely Utah, Arizona), USA
5. Seeds >0.6 mm in diam.; abaxial fruiting sepal reniform with a wide scarious margin; mostly Sierra Nevada and Panamint ranges, eastern California to western Nevada (rarely Utah, Arizona) . . . . . *C. parryi* var. *nevadense*
- 5' Seeds <0.6 mm. in diam.; abaxial fruiting sepals usually ovate with a very narrow scarious margin or none; South Coast Ranges, California . . . . . *C. parryi* var. *hesseae*

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## APPENDIX I

## LIST OF VOUCHER SPECIMENS EXAMINED IN THIS STUDY

*Calyptridium monandrum*. *Bettys s.n.* (JEPS 48483); *Gander 1829* (SD 15248); *Gander 3302* (SD 16938); *Gander 7419* (SD 24927); *Gander 7461* (SD 24971); *Gander s.n.* (SD 11394); *King s.n.* (JEPS 52574); *Moran 14874* (SD 67528); *Taylor 14877* (JEPS 105328); *Taylor 14886* (JEPS 100387); *Taylor 18468* (JEPS 100249); *Taylor 6329* (JEPS 101046); *Taylor 6457* (JEPS 101043). *Calyptridium parryi* var. *arizonicum*. *Darrow s.n.* (ARIZ 04242); *Felger 93-230* (ARIZ 368100, RSA 571207); *Moran 12296* (SD 64971); *Moran 12438* (SD 64964, UC 1345807); *Moran 16872* (ARIZ 185335, RSA 231377, SD 76798, UC 1384544); *Moran 16898* (SD 76799); *Moran 16914* (ARIZ 185334, SD 76797); *Moran 20237* (SD 92613); *Moran 20548* (ARIZ 200373, SD 87201); *Moran 20604* (ARIZ 200375, CAS 711439, DS 711439, SD 88866); *Moran 20634* (SD 88867); *Moran 21768* (SD 91249); *Moran 8036* (ARIZ 185333, RSA 231378, SD 61137, UC 1384545); *Moran 8149* (SD 79003); *Peebles 11454* (ARIZ 96164, CAS 324943); *Raven 12549* (CAS 531411, UC 115367); *Rebman 9976* (SD 157331); *Webster 22341* (ARIZ 269658). *Calyptridium parryi* var. *hesseae*. *Boyd 2645* (RSA 519524); *Griffin 3751* (JEPS 73809); *Griffin 3799* (JEPS 73810); *Guilliams 338* (SDSU 17444); *Hesse 1283* (UC 1001290); *Hesse 1288* (DS 370154); *Hesse 1298* (JEPS 6079); *Hesse 1302* (UC 1019332); *Hesse 1360* (DS 583117); *Hesse 1370* (CAS 388412); *Hesse 1942* (DS 583118); *Hesse 972* (DS 344294); *Howitt 1617* (CAS 531410); *McMurphy s.n.* (DS 596821); *Sharsmith 3381* (DS 266493, UC 724493); *Thomas 6001* (CAS 380418, CAS 385058, CAS 408297, DS 380418, DS 385058, DS 587627, UC 1060541); *Thomas 6028* (CAS 393436, DS 393436). *Calyptridium parryi* "martirensis." *Boyd 2706* (RSA 519494); *Moran 14185* (RSA 225157); *Moran 24462* (SD 97873); *Moran 24489* (SD 97766); *Olmsted 4603* (RSA 170797); *Rebman 4174* (SD 142899); *Rebman 5407* (SD 144223); *Rebman 5579* (SD 145561); *Thorne 60834* (RSA 346089); *Witham 384* (SD 74689). *Calyptridium parryi* var. *nevadense*. *Beatley 4079* (DS 611973); *Beatley 4122* (DS 591783); *Beatley 4373* (DS 591784); *Beatley 5732* (UTC 122167); *Bostick 5474* (DS 591786); *Christy 915B* (ASU 200628); *DeDecker 1481* (RSA 618440); *DeDecker 4336* (RSA 273689, RSA 621364); *DeDecker 5448* (RSA 625413); *DeDecker 6244* (RSA 627058); *Duran 1568* (UC 1297315); *Henrickson 17838* (RSA 292001); *Hoffman s.n.* (RSA 466626); *Howell 3912* (CAS 180644); *Howell 42888* (CAS 903599); *Howell 42894* (CAS 911905); *Keck 559* (UC 423468); *Kerr 2* (CAS 318495); *Morefield 3521* (RSA 387582, UC 1535078); *Morefield 4439* (ARIZ 286380, RSA 437274, UC 1545438); *Munez 14802* (RSA 231264); *Munez 14864* (CAS 366672, RSA 231261); *Munez 2630* (RSA 229494); *Pollard s.n.* (CAS 415968); *Romspert 424* (RSA 552078); *Stewart s.n.* (UTC 237486); *Taylor 6429* (JEPS 101044); *Taylor 6507* (JEPS 101042); *Tiehm 13605* (CAS 1013547, RSA 667225); *Wallace K152* (RSA 466627); *Zemba 468* (RSA 274018). *Calyptridium parryi* var. *parryi*. *Duran 1568* (UC 1297315); *Elmer 3948* (CAS 141555, DS 45657); *Guilliams 381* (SDSU 17439); *Hannon s.n.* (SD 135302); *Hardham 1867* (CAS 414369); *Jones s.n.* (DS 154025); *Munz 5726* (RSA 13478, UC 851936); *Munz 6004* (UC 218257); *Parish 10964* (DS 92647); *Parish 1800* (UC 192468); *Parish 3081* (UC 82802); *Parish 3725* (UC 7758); *Parish 800* (DS 92645); *Peirson 3124* (UC 501529); *Peirson s.n.* (RSA 13534); *Peirson s.n.* (RSA 65395); *Roos 3035* (UCR 24222); *Tilforth 41066* (RSA 225930); *Wheeler s.n.* (RSA 620156); *Wilder 942* (UC 130501).