

## **A New, Large-Flowered Variety of *Eremocarya micrantha* (Boraginaceae)**

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A NEW, LARGE-FLOWERED VARIETY OF *EREMOCARYA*  
*MICRANTHA* (BORAGINACEAE)

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ABSTRACT

*Eremocarya* (Boraginaceae), a resurrected segregate of the genus *Cryptantha*, has recently been recognized as containing two species: *E. lepida* and *E. micrantha*. These two species differ in nutlet shape, nutlet size, and features of the corolla, including limb width, presence or absence of a prominent yellow coloration at the fornices of the corolla center, and, perhaps most importantly, presence or absence of distinctive “fornix bodies” at the corolla mouth. Here we present evidence for a large-flowered form of *E. micrantha* that we argue should be treated as a new taxonomic variety, which we call *E. micrantha* var. *pseudolepida*. In nutlet morphology, *E. micrantha* var. *pseudolepida* is very similar to *E. micrantha* var. *micrantha* and different from *E. lepida*. *Eremocarya micrantha* var. *pseudolepida* differs from *E. micrantha* var. *micrantha* and is similar to *E. lepida* in corolla limb diameter and in having a tendency to possess a prominent yellow coloration in the corolla throat. However, *E. micrantha* var. *pseudolepida* lacks the distinctive fornix bodies of *E. lepida*. This new variety of *E. micrantha* is generally geographically discrete and allopatric relative to *E. micrantha* var. *micrantha*, with virtually all known populations occurring in Baja California, Mexico, between approximately 28° and 32° north latitude. However, two contiguous populations of a large-flowered *E. micrantha* were discovered in southeastern Arizona. In addition, one population of *E. micrantha* var. *pseudolepida*, in the central part of its range in Baja California, appears to be sympatric with a disjunct population of *E. micrantha* var. *micrantha*. We feel that the morphological distinctiveness and near geographic discontinuity of this entity warrants its status as a new taxon. Future molecular studies will be needed to evaluate the phylogeographic history of this intriguing complex of plants in order to evaluate both character evolution and taxonomic delimitation.

Key Words: Boraginaceae, *Cryptantha micrantha*, *Eremocarya lepida*, *Eremocarya micrantha*, *Eremocarya micrantha* var. *micrantha*, *Eremocarya micrantha* var. *pseudolepida*, fornix bodies, taxonomy.

*Eremocarya* Greene (Boraginaceae), a resurrected segregate of the genus *Cryptantha* Lehm. ex G. Don (see Hasenstab-Lehman and Simpson 2012), has recently been recognized to comprise two species: *E. lepida* (A. Gray) Greene and *E. micrantha* (Torrey) Greene (Simpson et al. 2014). *Eremocarya lepida* differs from *E. micrantha* in having a significantly wider corolla limb and a significantly greater nutlet length, maximum nutlet width, and maximum nutlet width:apical nutlet width (Simpson et al. 2014). In addition, *Eremocarya lepida* always has prominent, yellow fornices at the upper corolla throat and clusters of unique “fornix bodies,” which are tiny (ca. 0.1 mm long), transparent, stalked, ellipsoid, sac-like structures. In contrast, *E. micrantha* lacks any evidence of fornix bodies and generally lacks or has reduced fornices. The two species also differ in distribution, elevation, and associated plant community/vegetation type (see Simpson et al. 2014).

In their 2014 study of *Eremocarya*, Simpson et al. stated that “[o]bservation of *Eremocarya micrantha* specimens from Baja California, Mex-

ico reveals some lower elevation populations with relatively large corollas, but lacking fornix bodies and having a nutlet morphology typical of this taxon, these identified as *E. micrantha* but not included in our quantitative analyses. These unusual populations will be the subjects of a future study.” In fact, the great majority of specimens from this region had previously been identified or annotated as *Cryptantha micrantha* (Torr.) I.M. Johnst. var. *lepida* (A. Gray) I.M. Johnst. (= *Eremocarya lepida*), but nutlet morphology and absence of fornix bodies convinced the authors that they belonged to *E. micrantha*.

After a detailed quantitative study of all specimens of *Eremocarya* from Baja California known by us, and of many specimens from adjacent regions (including mainland Mexico), we conclude here that this large-flowered form should be recognized as a new taxon (based on phenetic discontinuities; see Cronquist 1978, 1988), which we treat as a variety of *E. micrantha*. We choose the rank of variety (over subspecies) by convention, as variety is used for infraspecific taxa in the closely related genus *Cryptantha*

almost exclusively (see Hamilton and Reichard 1992 for a synopsis of concepts of infraspecific classification.)

#### TAXONOMIC TREATMENT

***Eremocarya micrantha*** (Torrey) Greene var. ***pseudolepida*** M.G.Simpson, L.M.Simpson, & Rebman, var. nov. — Type (Fig. 1): MEXICO, BAJA CALIFORNIA, 24 km NW by air from turn off of HWY 1 to Bahía de los Angeles. (29.23787° N, 114.26573° W). Alt.: 515 m. [Note: latitude/longitude and elevation indicated on specimen labels.] Granitic boulder fields and associated flats with *Agave shawii* subsp. *goldmaniana*, *Acalypha californica*, *Bursera microphylla*, *Euphorbia tomentulosa*, *Fouquieria columnaris*, *Pachycereus pringlei*, *Stenocereus gummosus*. Roots staining the new paper purple. *Benjamin T. Wilder 10-116*, 19 March 2010. With Jon P. Rebman, Ian Andrew Happle, and Sara Isabel Enciso Contreras. (holotype: SD218101; isotypes: ARIZ408970, RSA782708-0013360).

Diagnosis: *Eremocarya micrantha* var. *pseudolepida* is similar to *E. micrantha* var. *micrantha* in vegetative morphology, inflorescence structure, and fruit nutlet size and shape, the former differing in having a corolla with a larger (1.5–3.8 mm) limb width, with prominent yellow fornicies. *Eremocarya micrantha* var. *pseudolepida* is similar to *E. lepida* in having a relatively large corolla limb diameter, the former differing in having smaller, acute nutlets and in lacking fornic bodies at the corolla mouth.

Paratypes (arranged alphabetically by collector. Note: latitude, longitude, and/or elevation that are estimated from specimen label locality information are indicated with an asterisk (\*); otherwise, these are listed verbatim from label information. See Figs. 6–8 for map of localities.): MEXICO, BAJA CALIFORNIA; base of mesa, near Village of San Simon, overlooking plain and Bay of San Quintin, 31.53102\*, –115.71678\*, 1,000 m\* elev., 24-Mar-1949, *Bacigalupi 3059* (UC917090); 31 km south of Bahía San Luis Gonzaga, 29° 30', –114° 16', 100 m elev., 9-Mar-1973, *Carter 5705* (UC1443877); Bahía de Los Angeles, talus slope north and south of village, 28.94373\*, –113.56246\*, 50–200 ft elev., 9-Feb-1963, *Cowan 2266* (SD127080); km 35 San Felipe-Ejido Morelia, 30° 52', –115° 7', 470 m elev., 14-Mar-1995, *Delgadillo s.n.* (BCMEX011336, SD165073); Mina Desengaña, ca. 16 miles north of Punta Prieta, 29.18004\*, –114.14174\*, 1,600–2,000 ft elev., 30-Mar-1950, *Gentry 8897* (ARIZ274028, DES00009191, SD86410); 3.5 miles south of Punta Prieta, 28.87567\*, –114.13421\*, 170 m\* elev., 4-May-1939, *Harbison s.n.* (SD25137); 26 miles north of Punta Prieta, 29.27623\*, –114.20582\*, 560 m\* elev., 5-May-1939,

*Harbison s.n.* (SD25138); in sandy wash, 36 miles west of Bahía de Los Angeles, 29.04959\*, –113.94653\*, 420 m\* elev., 10-Mar-1979, *McLaughlin 2063* (ARIZ215596); 27.2 miles west of junction of Mexico 3 at roadside cleared area by Mexico 3, 31.30272\*, –115.42470\*, 640 m\* elev., 10-May-1980, *McLaughlin 2463* (ARIZ239724); Sierra San Borja, 28° 45', –113° 36.5', 1,100 m elev., 28-Mar-1960, *Moran 8112* (ARIZ158791, SD60715, UC298136); north of Cerro San Luis, 29° 19', –114° 7', 1,250 m elev., 2-Mar-1963, *Moran 10317.5* (SD54531); Sierra San Pedro Martir, Rancho San Matias, 31° 17', –115° 33', 1,050 m elev., 6-May-1963, *Moran 10859* (SD53783); outwash slope near the village, Bahía de Los Angeles, 28° 56', –113° 35', 10 m elev., 21-Feb-1966, *Moran 12311* (ARIZ165392, SD65317); La Bocana, 28° 28', –113° 25', 250 m elev., 10-Mar-1966, *Moran 12496* (SD65316); Rancho Las Palomas, 28° 13', –113° 26', 400 m elev., 17-Mar-1966, *Moran 12717* (SD65315, UC1345885); 2 miles south of El Crucero, 29° 14', –114° 11', 530 m elev., 1-Feb-1973, *Moran 19624* (SD92326); 8 miles northwest of Sauzalito, 30° 12', –115° 27', 350 m elev., 7-May-1973, *Moran 20886* (SD88930); mouth of Arroyo Taraizo, 31° 20', –115° 25.5', 800 m elev., 1-May-1976, *Moran 22958* (SD95519); Cañon el Saladito, 14 km southeast of San Vicente, 31° 14.75', –116° 8', 170 m elev., 11-Apr-1982, *Moran 30352* (SD110836); 14 miles west of San Felipe and Rte 5 along the road to Santa Clara, 31° 2', –115° 8', 720 m elev., 11-Mar-1993, *Rebman 1484* (BCMEX06250, SD137251); dirt road from Highway 1 just south of mile marker 171, then ca. 0.6 mile west, then along path ca. 500 feet northwest from dirt road, 29.77881, –114.78226, 623 m elev., 7-Mar-2015, *Simpson 3847* (SDSU 21205); head of San Matias Pass, Highway 3, 31° 8.5', –115° 30', 920 m elev., 19-Apr-1985, *Thorne 60111* (SD124982); sandy fields 2.8 km east of Rancho Pénjamo, 29° 59', –115° 6', 300 m elev., 20-Apr-1958, *Turner 20* (UC112443); La Bocana, 29.7167, –114.75, 300 m elev., 18-Mar-2003, *Vinton s.n.* (SD182664); San Felipe Valley, 28 miles northwest of San Felipe, 31° 8', –115° 15', 430 m\* elev., 28-Mar-1973, *Webster 18216* (SD95971); vicinity of Bahía de los Angeles ca. 4.0 miles south of Las Flores, 28° 47', –113° 34', 150 m\* elev., 13-Feb-1962, *Wiggins 262* (SD94536); between San Augustin and Rancho Cataviña, 31.82882\*, –116.51687\*, 730 m\* elev., 13-Apr-1931, *Wiggins 5311* (UC660809); 40 miles NE of Pozo Aleman, 28.05770\*, –113.39243\*, 340 m\* elev., 28-Feb-1935, *Wiggins 7813* (UC651114); El Potrero, about 10 miles south of Rancho San Jose (Meling's Ranch), 31.75653\*, –116.23410\*, 2,300 ft elev., 20-May-1941, *Wiggins 10043* (UC718753); partially stabilized sand dunes 6 miles south of San Felipe, 30.91265\*, –114.72640\*, 40\* m elev., 18-Mar-1960, *Wiggins*

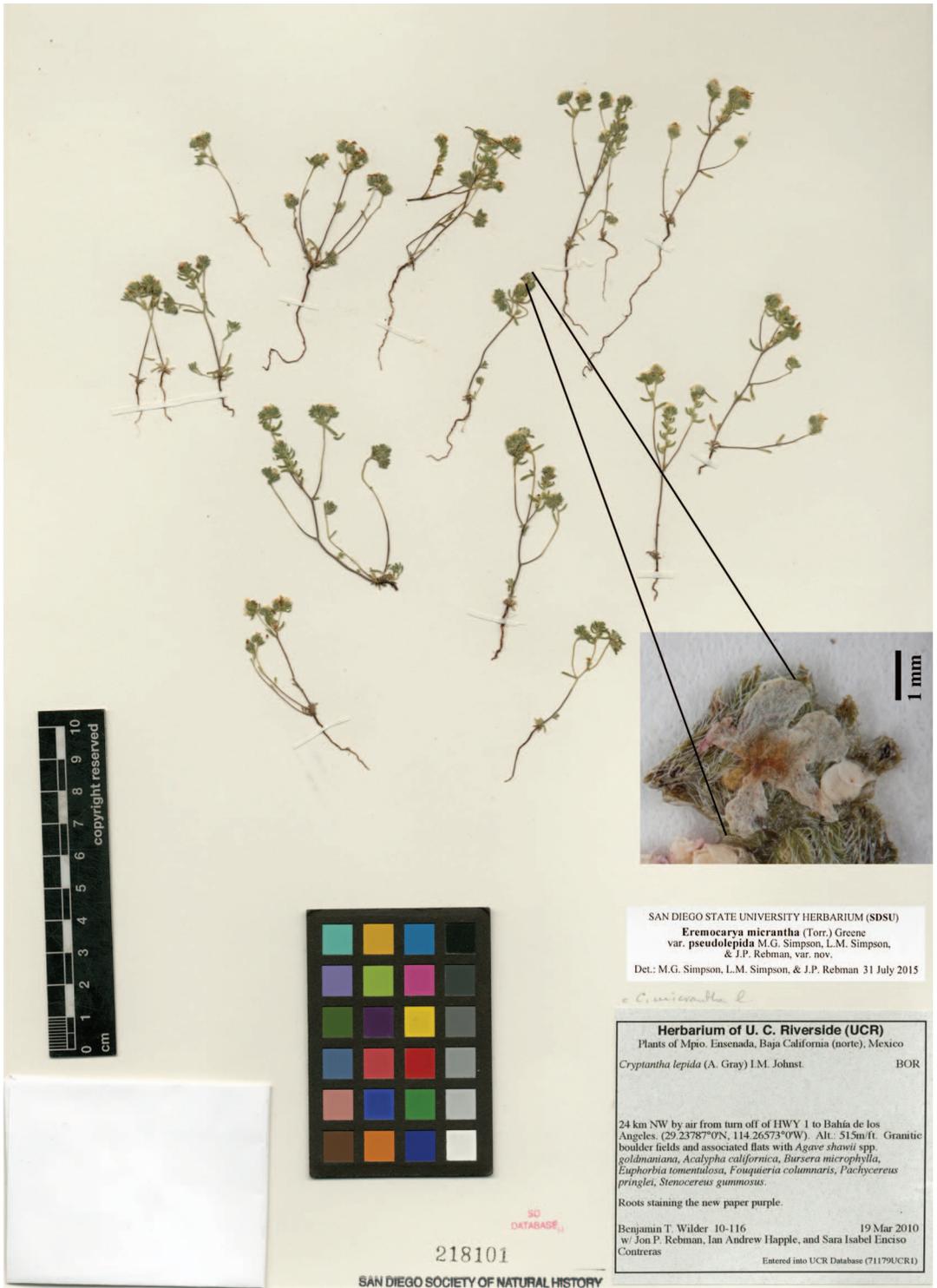


FIG. 1. Holotype specimen of *Eremocarya micrantha* var. *pseudolepida* (Wilder 10-116, SD218101). Inset shows magnified image of corolla.

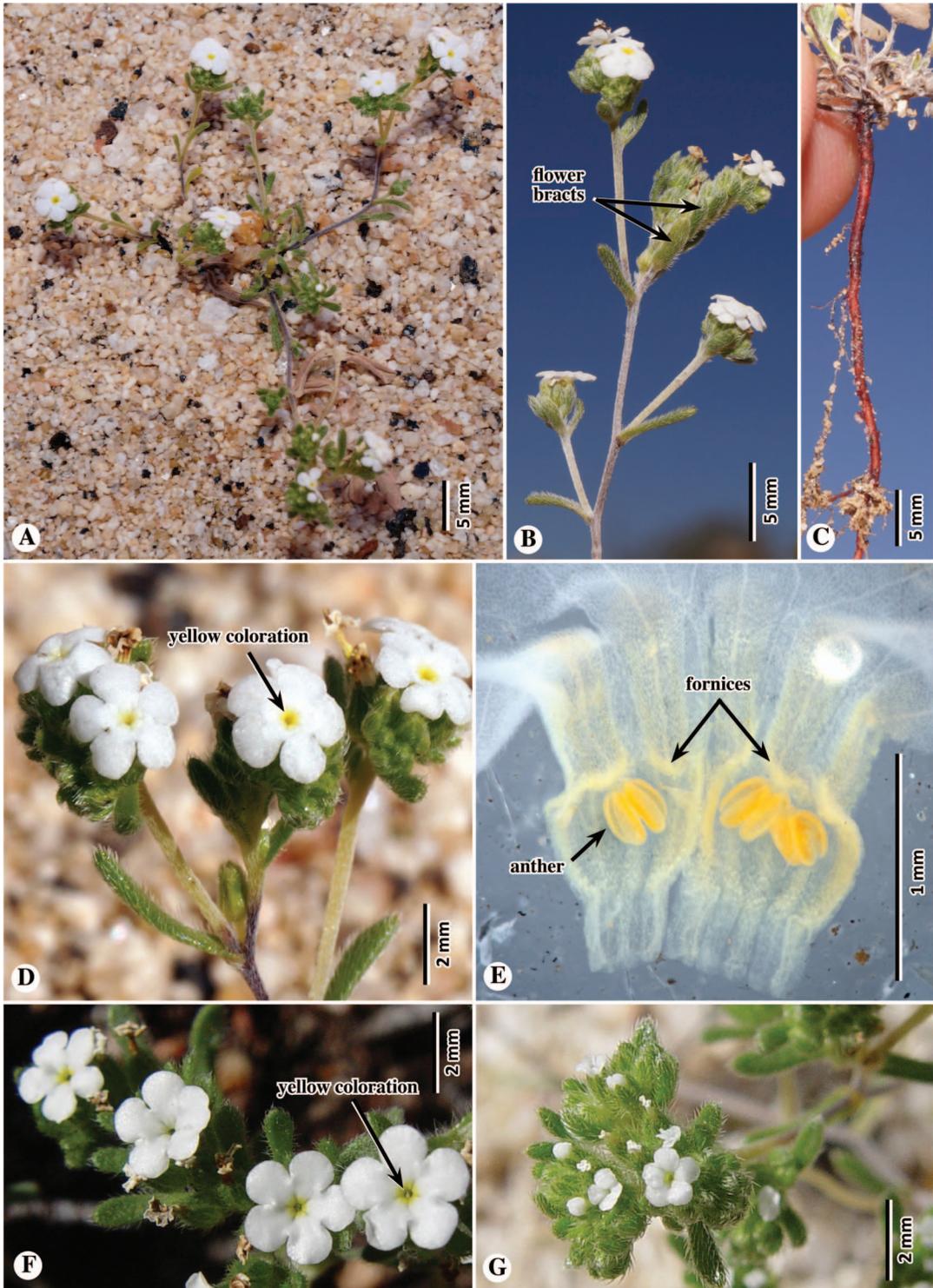


FIG. 2. A–E. *Eremocarya micrantha* var. *pseudolepida* (Simpson 3847, SDSU 21205). A–D. Field photographs, showing whole plant (A), floral bracts (B), red-pigmented root (C), and corollas with prominent yellow coloration at throat center D. E. Single flower longitudinally sectioned and opened, showing anthers (two detached) and inner surface of corolla tube with fornicies present but fornix bodies absent. F. *Eremocarya lepida* field photograph (Simpson 2816, SDSU17572), showing similarly large corollas with prominent yellow centers. G. *Eremocarya*

15799 (ARIZ169992, UC1303271); sandy bajada 2 miles NE of junction of Gulf road with western road, 20 miles N. of Punta Prieta, 29.27090\*, -114.12354\*, 700 m\* elev., 16-Mar-1960, *Wiggins 15961* (ARIZ176981); sandy desert 18 miles north of Punta Prieta, 1/2 mile south of road to San Felipe, 29.23754\*, -114.13853\*, 600 m\* elev., 26-Mar-1960, *Wiggins 15972* (ARIZ169970); granitic hillside 1.5 miles northwest of the village of Valle Trinidad, 31.4\*, -115.7833\*, 790 m\* elev., 3-Apr-1960, *Wiggins 16067* (ARIZ169969); ca. 35 km E of El Rosario by air and ca. 5 km N by air of Hwy 1, 30° 7' 12.5", -115° 22' 20.8", 400 m elev., 22-Mar-2010, *Wilder 10-248* (ARIZ408961, SD218100, UCR) [Note: ARIZ and UCR specimens of *Wilder 10-248* are mixed collections of *Eremocarya micrantha* var. *pseudolepida* and *E. micrantha* var. *micrantha*].

We are excluding the following two Arizona populations as paratypes, given their disjunct distribution and ambiguous identity (see Discussion). Latitude/longitude of these two specimens were estimated from label locality information, indicated by asterisks (\*); however, elevations were indicated on original labels. USA, ARIZONA, **Pima Co.**: annual, moist soil near streambed in riparian woodland, along Miller Creek, east side of the Rincon Mountains, 32.1576\*, -110.4944\*, 1,310 m elev., 18-Apr-1982, *Bowers R34* (ARIZ244153); annual, on dry, gravelly slopes in open pine-oak woodland, along Miller Creek, east side of the Rincon Mountains, 32.1600\*, -110.4995\*, 1,560 m elev., 1-May-1983, *Bowers R1152* (ARIZ243542).

*Etymology.* The varietal epithet means “false *lepida*,” because this new variety has most commonly been mistaken for *Eremocarya lepida* (= *E. micrantha* var. *lepida* (A. Gray) I.M. Johnst.; *Cryptantha micrantha* var. *lepida*; *C. m.* subsp. *lepida* (A. Gray) K. Matthew & P.H. Raven) because of its large corolla size.

#### MATERIALS AND METHODS

Field observations of all three taxa of *Eremocarya* were made and documented with photographs. Herbarium specimens were obtained and studied from the following herbaria: University of Arizona (ARIZ), Desert Botanical Garden (DES), San Diego Natural History Museum (SD), San Diego State University (SDSU), and University of California, Berkeley (UC). Acronyms of herbaria are after Thiers (continuously updated). A total of 216 herbarium specimens were sampled, annotated, and recorded for latitude/longitude and elevation (or these esti-

mated from label data). We concentrated our sampling on Mexico, California, and Arizona, with some in New Mexico and Nevada. A dried flower (the largest visible) from each specimen was boiled for 1–2 minutes and placed on a piece of clear, double-stick tape on a microscope slide. Corolla limb width of the boiled, re-expanded flower was measured with a video-interfaced dissecting microscope, using Image J software (Rasband 1997–2007, see Abramoff et al. 2004). (Our observations support the idea that re-expanded corollas are closer in dimensions to fresh flowers than are dried flowers, but we have no direct comparative measurements.) The corolla throat was then slit and opened, followed by staining with a drop of 0.5% toluidine blue. The presence or absence of corolla throat “fornix bodies” was observed and recorded.

From the same specimens, 2–3 mature fruits were detached and the nutlets removed and placed in dorsal (abaxial) view on the same microscope slide. The length, maximum width, and width at 1/4 relative distance from the apex were measured using the same apparatus. Nutlet data were segregated based on fruit heteromorphism. If selected fruits contained heteromorphic nutlets, the single (“odd”) large nutlet was tabulated separately from the three smaller (“consimilar”) nutlets, the latter values averaged. If fruit nutlets were homomorphic, measurements of all four were averaged. All measured nutlet parameters were averaged per herbarium specimen.

To visualize character distributions by taxon, box plots showing the median and the four quartiles of distribution were prepared for all three taxa for: (1) corolla limb width (mm); (2) nutlet length (mm); (3) nutlet maximum width (mm); and (4) the ratio of nutlet maximum width:width 1/4 from apex (see Simpson et al. 2014). For specimens with heteromorphic nutlets, only the largest nutlet was tabulated in these comparisons (see also Simpson et al. 2014). In addition, the extrinsic character of elevation was plotted (not illustrated). Each of these variables was evaluated for statistical difference (at probabilities <0.05 and <0.01) using analysis of variance (ANOVA), with multiple comparisons made between the taxon means using the Tukey post hoc test. Taxa that were statistically different from all other taxa in a particular character are indicated as such (at probabilities <0.01) in illustrated box plot diagrams. Note that the two large-flowered Arizona populations were omitted from these calculations because of their uncertain taxonomic status; however, the values of these specimens were indicated on the boxplots.

←

*micrantha* var. *micrantha* field photograph (Simpson 3126, SDSU19604), showing small corollas, generally with white or obscurely yellow centers.

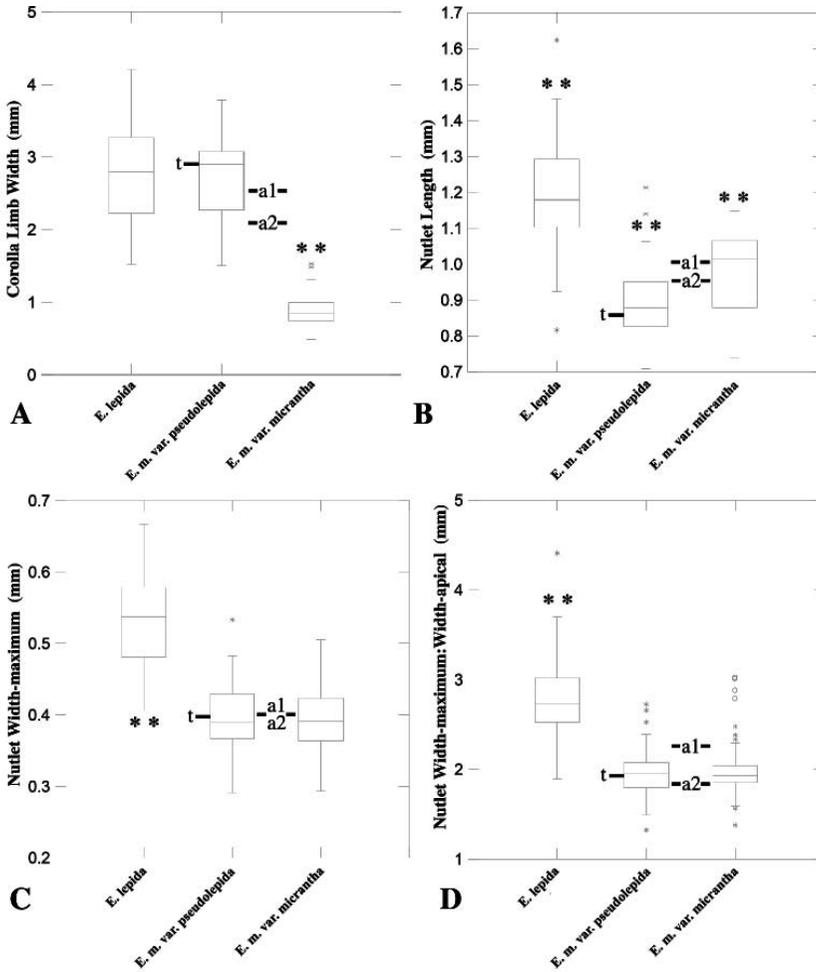


FIG. 3. Box plots of single characters analyzed for *E. lepida*, *E. micrantha* var. *pseudolepida*, and *E. micrantha* var. *micrantha*. A. Corolla limb width (mm). B. Nutlet length (mm). C. Nutlet maximum width (mm). D. Ratio of nutlet maximum width:width at apex (ca. 1/4 distance from tip). Statistical difference between a given taxon and all other taxa (via ANOVA Tukey post hoc test) indicated as: \*\* =  $p < 0.01$ . Note: box plots show median (horizontal line), first and third quartiles (boxes above and below median), and second and fourth quartiles (vertical lines); outliers indicated by small, single asterisk-like symbol (\*) and extreme outliers ( $> 1.5\times$  the distance from the median to the outer quartile boundary) by small circles. Holotype measurements indicated by "t". The placement of the two large-flowered Arizona specimens, not included in these analyses, indicated by "-a1-" (ARIZ244153) and "-a2-" (ARIZ243542).

A principal components analysis (PCA) was conducted on all samples (including the large-flowered Arizona populations) having complete data for five characters: (1) corolla limb width; (2) nutlet length; (3) nutlet maximum width; (4) nutlet width 1/4 relative distance from the apex; and (5) presence/absence of fornx bodies. A second PCA was conducted using these characters but without (5) presence/absence of fornx bodies (not illustrated). Variables were standardized by subtracting the total mean for a feature from each individual measurement, then dividing by the total 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, 2nd versus 3rd components, and 1st versus 3rd components. The component loadings and percent of total variance explained by each axis are listed in Table 1. All statistical analyses were performed in SYSTAT, Version 11 (Systat Software, Inc., San Jose, CA, USA, <http://www.systat.com>).

Several topographic maps of all measured specimen collections were prepared, showing the distributions of specimens annotated to variety. In addition, maps were prepared of Baja California, Mexico showing more detailed representations of plant community and vegetation types.

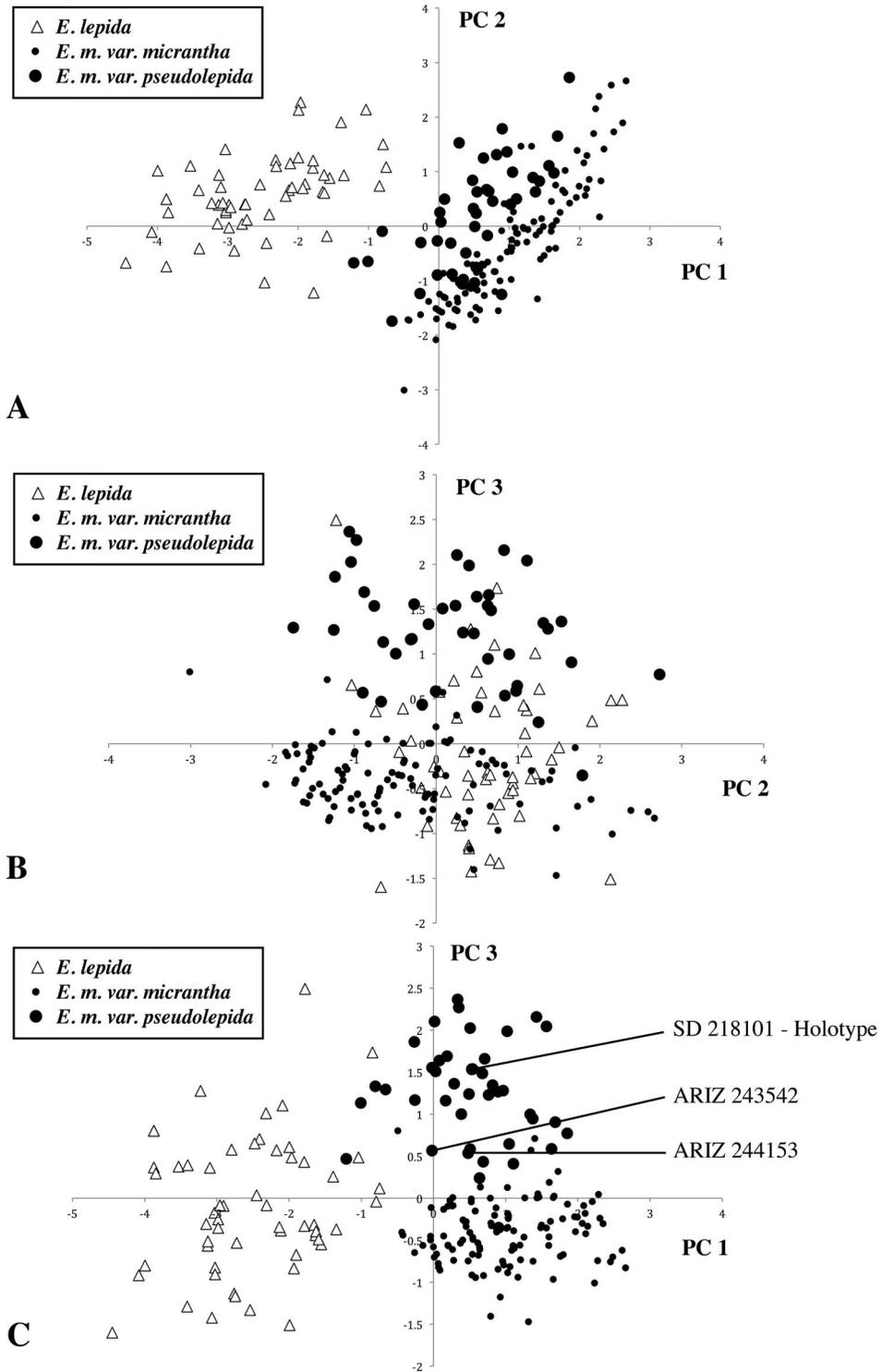


FIG. 4. Principal Components Analysis (PCA) plots. A. First (PC1) and second (PC2) factors, showing general separation of *Eremocarya lepida* from the two varieties of *E. micrantha* with overlap of the two varieties. B. Second (PC2) and third (PC3) factors, showing general separation of *E. micrantha* var. *pseudolepida* from *E. m. var. micrantha*, but with overlap of *E. lepida* with both of these. C. First (PC1) and third (PC3) factors, showing general separation of all three taxa, but with some overlap. Holotype (SD218101) and two large-flowered Arizona populations (ARIZ244153, ARIZ243542) indicated by lines.



FIG. 5. Nutlet images of three taxa. A. *Eremocarya micrantha* var. *pseudolepida* (holotype: *Wilder 10-116*, SD218101), showing typical heteromorphic morphology with one odd, minutely tuberculate nutlet (left) and three consimilar, smooth nutlets (right). B. *Eremocarya micrantha* var. *micrantha* (*Purer 4943*, SD39196), showing nutlets very similar to *E. micrantha* var. *pseudolepida*, but odd nutlet slightly longer. C. *Eremocarya lepida* (*Simpson 2816*, SDSU17572), with homomorphic (rarely heteromorphic), larger, minutely tuberculate nutlets with an acuminate apex.

RESULTS

Field photographs of *Eremocarya micrantha* var. *pseudolepida* show most corollas having a yellow coloration at the corolla mouth (Fig. 2A, 2B, 2D). It also has floral bracts (Fig. 2B) and red-pigmented roots (Fig. 2C), which are typical of all *Eremocarya* taxa. In all specimens of *E. micrantha* var. *pseudolepida* that we examined, corolla fornicies were present, but fornic bodies were absent (Fig. 2E). Similarly,

a yellow coloration in the corolla mouth regularly occurs in *E. lepida* (Fig. 2F). In *E. micrantha* var. *micrantha*, fornicies are not evident (see Simpson et al. 2014) and the corolla mouth is generally white, occasionally obscurely yellow (Fig. 2G).

The corolla limb width of *Eremocarya micrantha* var. *pseudolepida* and of *E. lepida* are very similar (statistically indistinguishable), with both of these taxa significantly larger (with almost no overlap) from *E. micrantha* var. *micrantha* (Fig. 3A).



FIG. 6. Topographic map showing distribution of all measured specimens, with flower diagrams scaled to relative sizes: *Eremocarya lepida* (white flowers), *E. micrantha* var. *pseudolepida* (larger gray flowers), and *E. micrantha* var. *micrantha* (smaller gray flowers). Note two samples of *E. micrantha* var. *pseudolepida* in Arizona (arrows). Map from ©Google 2013, INEGI Data.

Nutlet lengths of all three taxa are significantly different, with *E. lepida* having larger nutlets and with *E. micrantha* var. *pseudolepida* having the smallest nutlets but the latter having considerable overlap with *E. micrantha* var. *micrantha* (Fig. 3B). Nutlet width of *E. lepida* is significantly greater than both *E. micrantha* varieties (Fig. 3C), as is the ratio of maximum nutlet width:nutlet width at 1/4 distance from the nutlet apex (Fig. 3D); for both nutlet features the two *E. micrantha* varieties are statistically indistinguishable from one another. The values for the

measurements of the two large-flowered Arizona populations generally correspond to those of *E. micrantha* var. *pseudolepida*; values for the holotype specimen of *E. micrantha* var. *pseudolepida* are quite close to the mean for that taxon (Fig. 3A–D).

The PCA derived from analysis of all five characters shows some separation between all three forms of *Eremocarya*. A plot of the 1st and 2nd components shows a fairly discrete separation of *E. lepida* from the two varieties of *E. micrantha*, with some separation of the latter (Fig. 4A). A plot of the 2nd and 3rd components shows a fairly discrete separation of *E. micrantha* var. *pseudolepida* from *E. micrantha* var. *micrantha*, but with *E. lepida* overlapping both of these (Fig. 4B). A plot of the 1st and 3rd components shows discrete separation of all three taxa; in this plot the values for the two large-flowered Arizona populations largely correspond to those to *E. micrantha* var. *pseudolepida* (Fig. 4C). The first principal component, explaining 57% of the overall variance, corresponds to nutlet size (and shape when ratios are considered), with three characters (nutlet length, nutlet maximum

TABLE 1. PRINCIPAL COMPONENTS ANALYSIS LOADINGS FOR CHARACTERS USED IN ANALYSIS: Percent of total variance explained: axis 1 = 57%, axis 2 = 22%, and axis 3 = 14%.

Character	Component loadings		
	1	2	3
Corolla limb width	0.66	-0.34	-0.65
Nutlet length	0.84	0.23	0.42
Nutlet maximum width	0.94	0.15	0.10
Nutlet apical width	0.20	0.91	-0.34
Fornix body presence	0.88	-0.32	-0.06

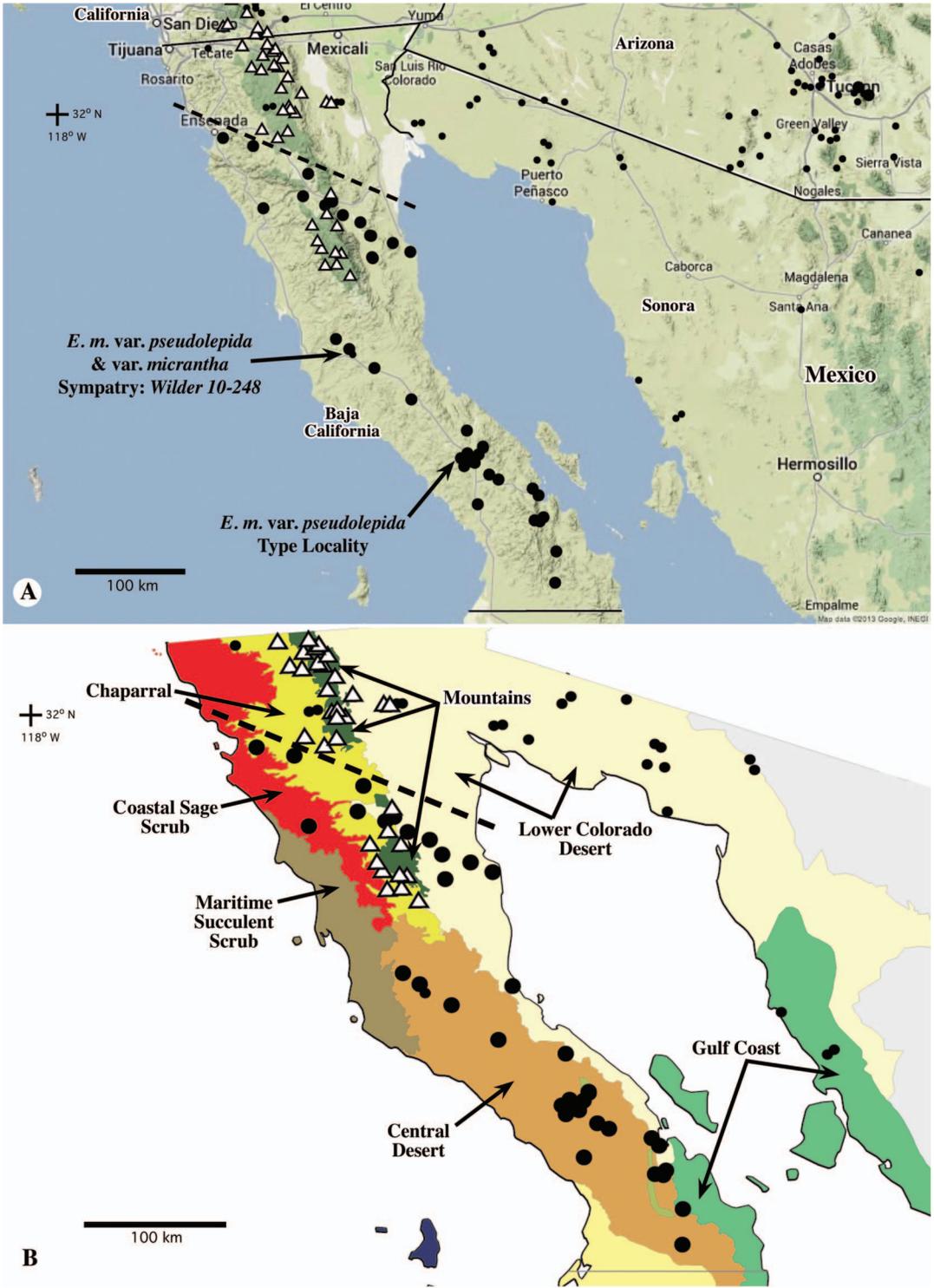


FIG. 7. Distribution maps of *Eremocarya lepida* (white triangles), *E. micrantha var. pseudolepida* (large black circles), and *E. micrantha var. micrantha* (small black circles), focusing on Baja California and mainland Mexico. A. Topographic map, showing most *E. lepida* specimens in higher elevation regions of the peninsular range and *E. micrantha var. pseudolepida* generally south of 32° north latitude at generally lower elevations. Arrows show locality of type specimens and of sympatric populations (from Wilder 10-248) of *E. micrantha var. pseudolepida* and

width, and fornix body presence) loading heavily, at 0.84–0.94 (Table 1). The second component, explaining 22% of the overall variance, corresponds to nutlet apical width, loading at 0.91. The third component, accounting for 14% of the overall variance, corresponds to corolla limb width, loading negatively at –0.65 (Table 1).

## DISCUSSION

These quantitative analyses support our qualitative observations that *Eremocarya micrantha* var. *micrantha* and *E. micrantha* var. *pseudolepida* differ from one another discretely in corolla limb width, with almost no observed overlap (Fig. 3A). In contrast, *E. micrantha* var. *pseudolepida* and *Eremocarya lepida* have a very similar corolla limb width (Fig. 3A; see Fig. 2D, 2F). As cited earlier, only *Eremocarya lepida* has ever been observed to possess fornix bodies (Simpson et al. 2014); the two varieties of *Eremocarya micrantha* consistently lack them (Fig. 2E; see Simpson et al. 2014). Corolla size, measured here as limb diameter, can be difficult to measure from herbarium material; it can vary significantly within an individual, and corollas can shrink approximately 10% after being dried (see [http://tchester.org/plants/analysis/cryptantha/barbigera\\_fergusoniae.html](http://tchester.org/plants/analysis/cryptantha/barbigera_fergusoniae.html)). However, we believe that this character, combined with others and considered with geographic range, is enough to warrant recognition of this new taxon. The general separation of the three taxa in the principal components analysis supports this conclusion (Fig. 4).

Nutlets of *Eremocarya lepida* are significantly different from both varieties of *E. micrantha* in length, maximum width, and ratio of maximum width:width 1/4 from nutlet apex (Fig. 3B–D; see Fig. 5). *Eremocarya micrantha* var. *pseudolepida* has nutlets very similar to those of *E. micrantha* var. *micrantha* (Fig. 5A, 5B), with no significant difference in nutlet maximum width or ratio of maximum width:width 1/4 from nutlet apex (Fig. 3C, 3D). However, var. *pseudolepida* does appear to have a slightly smaller nutlet length than *E. micrantha* var. *micrantha* (see Fig. 5A, 5B) although with considerable overlap between the two varieties (Fig. 3B). Our observations indicate that both varieties of *E. micrantha*

usually have heteromorphic nutlets, with one slightly larger, minutely tuberculate nutlet and three smaller, smooth nutlets (Fig. 5A, 5B). In contrast, *E. lepida* almost always has homomorphic nutlets, with all four the same size and minutely tuberculate (Fig. 5C).

A significant piece of evidence for our recognition of this new taxon comes from geographic range data (Figs. 6–8). Variety *pseudolepida* is found only (or largely; see below reference to Arizona populations) in Baja California, Mexico, a little below 32° north latitude (Fig. 6–8). Most populations of var. *pseudolepida* occur in the Central Desert region of the Sonoran Desert, but several are found in the southern Lower Colorado Desert region, as well as in the southern regions of both the Chaparral and Coastal Sage Scrub regions of the California Floristic Province (Fig. 7B). We struggled with the appropriate rank for this new taxon but chose the rank of variety to be consistent with past treatments for other members of this taxonomic complex. For example, in the closely related genus *Cryptantha*, *C. barbigera* var. *barbigera* (A. Gray) Greene and *C. barbigera* var. *fergusoniae* J.F. Macbride are virtually identical except for a small versus large corolla limb width (see Kelley et al. 2012). Given that the two *E. micrantha* forms are very similar in nutlet morphology and that both lack the fornix bodies of *E. lepida*, we think that varietal status is appropriate at this time. However, we reiterate that *E. micrantha* var. *pseudolepida* has an almost separate geographic range, whereas the ranges of *E. m.* var. *micrantha* and *E. lepida* partially overlap (although generally separated by elevation).

From our study of herbarium specimens, we discovered two unusual Arizona specimens of *Eremocarya*: *Bowers R34*, 18 Apr 1982, ARIZ244153 and *Bowers R1152*, 1 May 1983, ARIZ243542. Both of these specimens have a nutlet morphology and absence of fornix bodies similar to *E. micrantha* (Fig. 3B–D), but they have a large corolla size that fits the range of *E. micrantha* var. *pseudolepida* (Fig. 3A; see Fig. 4C). These large-flowered specimens (reportedly located very near one another) are restricted to the east side of the Mica Mountain/Rincon Peak region just east of Tucson in southeastern Arizona (Fig. 6). Although the corolla morphology of these fits our circumscription of

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*E. m.* var. *micrantha*. Map from ©Google 2013, INEGI Data. B. Vegetation map, showing (1) *E. lepida* largely restricted to the mountains of the peninsular range; (2) *E. micrantha* var. *pseudolepida* occurring in the Central Desert and Lower Colorado Desert regions, with some populations in coastal sage scrub and chaparral regions; and (3) *E. micrantha* var. *micrantha* occurring in the Lower Colorado Desert of Baja California and adjacent Sonora, Mexico, with some populations in the northern Chaparral region of Baja California and Gulf Coast region of mainland Mexico and one sympatric population in the Central Desert of Baja California. Dashed line in both maps indicates boundary separating almost all specimens of the two varieties of *E. micrantha* in Baja California.

*E. micrantha* var. *pseudolepida*, their highly disjunct distribution from the Baja California concentration of var. *pseudolepida* is puzzling. An examination of these two Arizona collections indicates some possible differences in leaf shape and calyx vestiture; however, we caution that these features largely fall into the range of features of the Baja California specimens and may simply represent local phenotypic variation. We hesitate at this time to list these two Arizona collections as paratypes of our new variety described here. The fact that the label of one of the two collections (*Bowers R34*) records the habitat as “moist soil near streambed in riparian woodland” may lead credence to the possibility that the local environment influenced an atypical floral morphology, as members of *Eremocarya* are not generally found in a habitat with appreciable long-term moisture as implied here. In addition, during the years of collection (1982 and 1983), the area was heavily impacted by cows, both in terms of grazing and manure deposition (George Ferguson, University of Arizona Herbarium, personal communication, April 2015), these altered conditions possibly influencing a phenotypic shift in corolla size. The other possibility is that these are indeed members of our new variety and that these populations arrived from the main Baja California populations by long distance dispersal (perhaps via bird migration, this possibly supported given the riparian habitat as a potential resource for a bird stop-over of at least one Rincon Mountain population) or that they are vestiges of an ancestral vicariant event.

Phylogenetic analyses using molecular data are needed to resolve whether these Arizona populations are part of the Baja California var. *pseudolepida* complex or represent a case of convergent evolution. Such a study, involving extensive sampling of all three taxa, is planned for the near future. However, the large-flowered Arizona herbarium specimens are too old to extract good quality DNA or grow plants from seed. A rigorous attempt in April 2015 to relocate these Arizona populations was unsuccessful, but we will keep trying. Until that is done, the status and relationships of these large-flowered Arizona populations may remain a mystery.

The three taxa of *Eremocarya* have significantly different elevations (boxplot not shown), although with considerable overlap. *Eremocarya lepida* has the highest average elevation, at 1,315 m (200–2,200 m, SD  $\pm$ 436 m). This correlates well with our knowledge of these taxa, with *E. lepida* found at higher elevation in mountainous and desert transition regions of the Peninsular Range (Simpson et al. 2014) (Fig. 6, 7). The average elevation of *E. micrantha* var. *micrantha* is 759 m (9–2,131 m, SD  $\pm$ 492 m). That of *E.*

*micrantha* var. *pseudolepida* (not including the two Arizona populations) is lowest at 510 m (range 10–1,250 m, SD  $\pm$ 303 m). Thus, even though the ranges of *E. lepida* and *E. micrantha* var. *pseudolepida* interdigitate to some degree (Fig. 6–8), they would not be expected to be sympatric, given these differences in elevation and vegetation regions. The two disjunct Arizona populations have elevations higher than any *E. micrantha* var. *pseudolepida* populations in Baja California, the former at 1,560 m (ARIZ243542) and 1,310 m (ARIZ244153). Although not considerably higher than the highest Baja California collection of var. *pseudolepida* (1,250 m), the relatively high elevation of these large-flowered Arizona populations underscores their aberrant nature.

Aside from the anomalous Arizona populations, *Eremocarya micrantha* var. *pseudolepida* is almost entirely allopatric from *E. micrantha* var. *micrantha*, the latter occurring north of about 32° latitude on the Baja peninsula, although there are a few small populations much further south in Sonora on the Mexican mainland (Figs. 6, 7). The one exception we discovered is a single collection in the middle of the range of *E. micrantha* var. *pseudolepida* (*Wilder 10-248*, ARIZ408961, SD218100, UCR; locality indicated in Fig. 7A), two sheets of which (ARIZ and UCR) contain a mixture of both varieties of *E. micrantha* (personal observation of UCR specimen by Andy Sanders). Interestingly, we saw no evidence of introgression between the two varieties in this limited sampling. The fact that they can grow together in at least one population without apparent interbreeding may be supportive of their having genetic differences. However, nothing is known of the breeding system in this genus. We are hypothesizing that *E. m.* var. *pseudolepida* is outcrossing, given its relatively large corolla size. *Eremocarya m.* var. *micrantha* may well be selfing, given its very small corolla size. But, this is all speculation in the absence of observational or experimental studies of reproductive biology.

One interesting facet of the biogeography of *Eremocarya micrantha* var. *pseudolepida* is its distribution across what we term the “Baja California Trans-Peninsular gap,” a lower elevation zone between the Sierra de San Pedro Martir and the Sierra de Juarez (Fig. 8). In this area a mapped desert “arm” extends westward from the Colorado Desert well into the more Mediterranean region of the California Floristic Province, potentially enabling desert-adapted species to disperse from east to west into these lower elevation cismontane habitats without traversing the high elevation mountains. Additional species typical of the Colorado/Sonoran Desert that occur both in the Baja California Trans-Peninsular gap and in pockets of more arid microhabitats

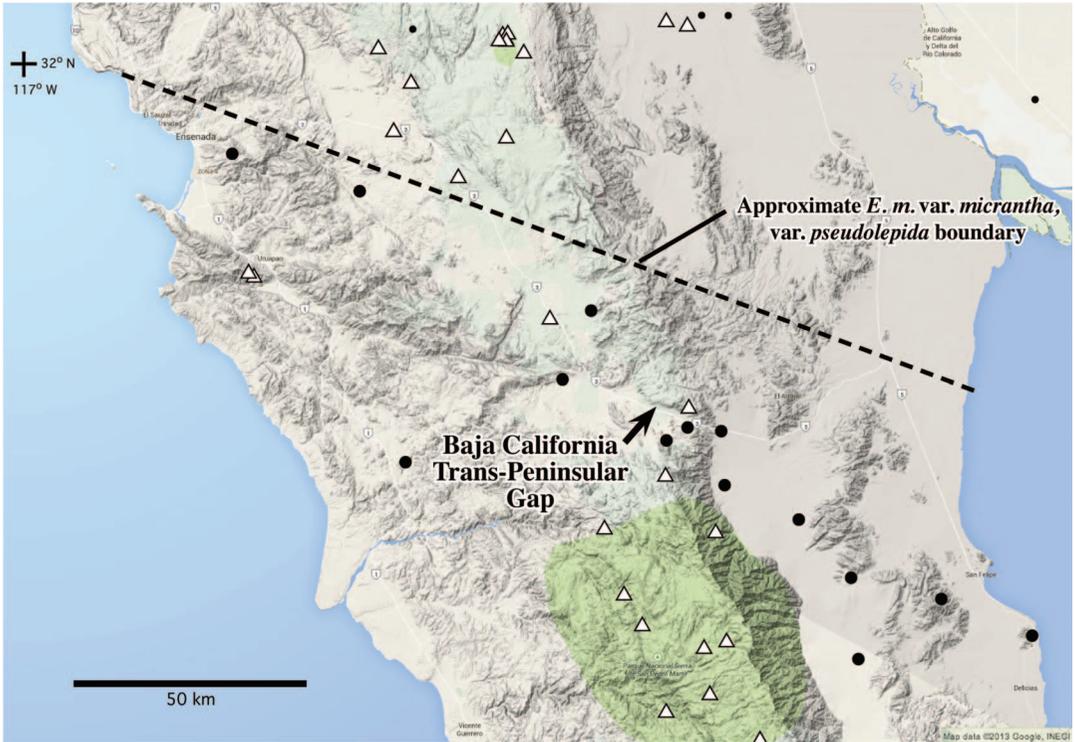


FIG. 8. Topographic map of *Eremocarya lepida* (white triangles), *E. micrantha* var. *pseudolepida* (large black circles), and *E. micrantha* var. *micrantha* (small black circles), focusing on northern Baja California. Note boundary (dashed line) separating almost all specimens of the two varieties of *E. micrantha* in Baja California. Arrow shows location of Baja California Trans-Peninsular Gap, a possible dispersal corridor across the peninsular range. Map data from ©Google 2013, INEGI Data.

in northwestern Baja California include *Palafoxia arida* B.L. Turner & M.I. Morris var. *arida* (Asteraceae), *Enneapogon desvauxii* P. Beauv. (Poaceae), *Eriogonum fasciculatum* Benth. var. *flavoviride* Munz & I.M. Johnst. (Polygonaceae), *Nicotiana obtusifolia* M. Martens & Galeotti (Solanaceae), and *Boerhavia coccinea* Mill. (Nyctaginaceae). Although we cannot know definitively without perhaps detailed molecular studies, we hypothesize that the direction of dispersal of our new taxon occurred from east to west across this gap, allowing for the movement of this desert-adapted taxon into arid microhabitats of chaparral and coastal sage scrub.

Future molecular studies will be needed to evaluate the evolutionary history of *Eremocarya* entities with respect to their taxonomic status and character state changes. These studies will, we hope, help to assess the taxonomic rank of the three entities as recognized here, perhaps based on branch lengths and assessment of reciprocal monophyly. Current phylogenetic analyses (Hansenstab-Lehman and Simpson 2012) indicate that *Eremocarya* is the sister taxon to the genus *Oreocarya* Greene, whose members are high elevation perennials, many with relatively large flowers. If this relationship continues to be

supported, a fascinating question will be the morphology of the common ancestor of these two genera. This may help to answer the ancestral corolla size in *Eremocarya* and what possible selective pressures might have influenced a subsequent shift in size. How has habitat, particularly as related to elevation, influenced this evolutionary shift? How does this relate to reproductive biology and possible pollinator shifts? We presume that the distinctive fornix bodies of *E. lepida* are derived; work is underway to elucidate their possible function.

Chromosome counts of both *Eremocarya lepida* (*Cryptantha micrantha* subsp. *lepida* in their paper) and *E. micrantha* var. *micrantha* (*C. m.* subsp. *micrantha* in their paper) were done by Mathew and Raven (1962), who determined a count of  $n = 12$  for both taxa. There are no known chromosome counts for *E. micrantha* var. *pseudolepida*, so possible polyploidy or aneuploidy in the latter cannot be assessed at this time. We hope to obtain a count of *E. micrantha* var. *pseudolepida* in the near future. Finally, as pointed out, nothing is known of the breeding system of members of this genus. We hope to at least determine if the three entities are capable of selfing or outcrossing.

KEY TO THE TAXA OF *EREMOCARYA*

The following revised key to the two species of *Eremocarya* including infraspecies (modified from Simpson et al. 2014, Kelley and Simpson in prep.) may be used to more effectively identify them.

- 1. Corolla limb 0.5–1.5 mm diam., center white, rarely obscurely yellow ..... *E. micrantha* var. *micrantha*
- 1. Corolla limb 1.5–4.8 mm diam., center generally prominently yellow, rarely white
  - 2. Nutlets usually homomorphic, minutely tuberculate, 1.2–1.4 mm long, apex acuminate; corolla fornicies each with a basal cluster of tiny (ca. 0.1 mm long), pendant, ellipsoid “fornix bodies;” southern California to northern Baja California, Mexico ..... *E. lepida*
  - 2. Nutlets usually heteromorphic, with one slightly larger, minutely tuberculate nutlet and three smaller, smooth nutlets, the largest ca. 1–1.1 mm long, apex narrowly acute; corollas lacking “fornix bodies;” mostly from Baja California south of 32° north latitude ..... *E. micrantha* var. *pseudolepida*

Note in proof: We have recently become aware of a specimen (*Schmidt 2649*, 18 April 1998, MO04884946) that appears quite similar to the two large-flowered Arizona specimens (ARIZ244153 and ARIZ243542) examined in our study, having a corolla limb diameter of 2.5–3.4 mm (measured from an herbarium sheet scan). This MO specimen has a locality (32° 08' 14" N, 110° 28' 52" W, 1250–1380 m. elev., all information indicated on the label) approximately 1.7 mi (2.7 km) south-southeast of the two ARIZ specimens. It may provide sufficiently recent material for future DNA studies. We plan to search for this population in future field work.

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## APPENDIX 1

VOUCHER SPECIMENS OF *EREMOCARYA* USED IN THIS STUDY (MINUS THE *E. MICRANTHA* VAR. *PSEUDOLEPIDA* TYPES AND LARGE-FLOWERED ARIZONA SPECIMENS CITED EARLIER), LISTED ALPHANUMERICALLY BY COLLECTOR AND COLLECTION NUMBER; DATE LISTED FOR COLLECTIONS WITHOUT A COLLECTION NUMBER (S.N.). ALL SPECIMENS WERE VERIFIED AND MEASURED IN ONE OF BOTH OF THE QUANTITATIVE STUDIES.

*Eremocarya lepida*: Abrams 2904 (UC407303); Alameda 6544 (CAS831263); Anderson 26 (SDSU10277); Bourell 2980 (CAS741818); 9 June 1951, Brattstrom s.n. (SD44489); Breisch 270 (SD194947); Breisch 449 (SD201471); Clemons 1289 (SD118945); Copp 14 (CAS840487, SD134020); 1 May 1933, Cota s.n. (SD15615); Eastwood 9422 (CAS26923); Eastwood 9539 (CAS26924); Gander 5123 (SDSU5412); 10 June 1933, Gander s.n. (SD4195); 11 June 1933, Gander s.n. (SD4194); Grimmell 282 (CAS26926); Hendrickson 1953 (SD196338); 17 June 1971, Howell s.n. (CAS862225); 18 June 1922, Jaeger s.n. (DH140398); Levin 1674 (SD119269); Macias 463 (BCMEX011181, SD165072); Marsden 491 (SD205615); Marsden 578 (SD205614); McGill 8726 (DES00004221); Moran 3430 (SD48056); Moran 10923 (SD53840); Moran 11126 (SD54693); Moran 13869 (SD64660); Moran 13898 (SD64661); Moran 14381 (SD79677); Moran 14475 (SD79678); Moran 14906 (SD72336, UC1361697); Moran 15001 (SD69225); Moran 21288 (SD86898); Moran 22039 (SD91906); Moran 22063 (SD91864); Moran 22143 (SD91487); Moran 23334 (SD96974); Moran 24086 (SD97110); Moran 27342 (SD103646); Moran 27427 (SD103440); Moran 27448 (SD103457); Moran 28894 (DES00024907, SD105525); Moran 30665 (SD111068); Nenow 1103 (SD221038); Otis 7 (SD201473); Rebman 7210 (SD155824); Rebman 17601 (SD197223); Rebman 21146 (SD213030); Reeder 7193 (ARIZ216244); 17 June 1971, Roos s.n. (CAS905666); Ross 2598 (UC 1584224); Shevock 1074 (CAS713389); Simpson 2369 (SD180702); Simpson 2369 (SDSU17281); Simpson 2816 (SDSU17572); Simpson 3109 (SDSU18628); Simpson 3184 (SDSU19533); Simpson 3320 (SDSU19612); Simpson 6VI91AB (SDSU5418); Simpson 6VI91AC (SDSU5388); Suttikus 73-23-14 (DES00065387); Sweet 266 (SD178709); Thorne 55789 (SD124127); Thorne 55937 (SD124128); Thorne 60451 (SD124983); Thorne 61669 (SD124981); 29 May 1983, Thorne s.n. (BCMEX001288); 15 March 2003, Vinton s.n. (SD182665); 16 May 2003, Vinton s.n. (SD182666); Wedberg 909 (SDSU5046); Wiggins 9808 (UC718873); Wiggins 11809 (SD47301); Wolf 8019 (ARIZ142056); Wolfinger 133 (SD217612).

*Eremocarya micrantha* var. *micrantha*: Howe 2625 (SDSU5400); Barth 407 (SD169356); Beatley 3715 (DH595377); Beauchamp 2192 (SD85416); Benson 9972 (ARIZ13871); Benson 10029 (ARIZ13870); Bowers 3127 (ARIZ259823); Burgeas 6850 (ARIZ259530); Butterwick 4513 (DES00020253); Butterwick 6442 (ARIZ228881); Christian 819 (ARIZ161721); Clemons

1634 (SD120961); Clemons 2020 (SD122612); Clokey 5926 (CAS380904); Clokey 8731 (ARIZ417391, CAS380903); Cronquist 10192 (DH592832); Crooks 7081 (ARIZ417366); 19 April 1938, Crooks s.n. (ARIZ417367); Devender 934 (ARIZ235363); Devender 91-19 (ARIZ291266); Douglas 933 (DES00045237); 17 April 1931, Eastwood s.n. (CAS190280); Eggleston 19869 (ARIZ38372); Engard 445 (DES00011367); Felger 1973 (ARIZ189161); Felger 7552 (ARIZ365678); Felger 17377 (SD96180); Felger 17801 (ARIZ200634); Felger 19026 (ARIZ188812); Felger 19571 (ARIZ368315); Felger 20363 (ARIZ189177); Felger 20793 (ARIZ189187); Felger 92-163A (ARIZ300111); Felger 93-252 (ARIZ303542); Felger 93-388 (ARIZ342450); Felger 96-164 (ARIZ371716); Fischer 6039 (ARIZ350332); Fishbein 10 (ARIZ300476); Fishbein 2013 (ARIZ315946); Fishbein 2256 (ARIZ319065); 29 April 1967, Forster s.n. (DES00006733); Gallup 193 (SDSU5425); Gander 134 (SD10507); Gentry 49 (ARIZ274030); Goodding 21-54 (ARIZ120707); Gould 3055 (ARIZ20751); Gould 3672 (ARIZ73131); Gregory 667 (SD158771); Groot 6587 (SD219000); Guertin 448 (ARIZ366079); Guilliams 602 (SDSU18956); Hammond 11795 (ARIZ379156); Harrison 7719 (CAS193407); Hendrickson 2640 (SD203297); Hendrickson 2784 (SD205617); Hendrickson 4588 (SD210829); Hevron 1622 (ARIZ304531); Higgins 13050 (DES00028221); Hodgson 3508 (DES00029290); Hodgson 5673 (DES00034517); Hodgson 7087 (DES00037500); Hodgson 16928 (DES00052687); Hodgson 17188 (DES00053987); Hodgson 17584 (DES00003630); Hodgson 17604 (DES00061111); Hodgson 21821 (DES00065422); Hodgson 24816 (DES00067821); Hodgson 24850 (DES00068009); Holland 1025 (DES00042570); Hoover 753 (DES00030752); Howe 2903 (SDSU5419); Jenkins 91-9 (ARIZ291265); May 21, 1884, Jones s.n. (ARIZ417393); Jordan 99 (ARIZ201923); Leon 3465 (ARIZ417780); Licher 2293 (DES00070122); Marsden 538 (SD205618); Mason 1810 (ARIZ143493); Mason 2555 (ARIZ159388); Mason 3114 (ARIZ199882); McGill 6405B (DES00003630); McLaughlin 3152 (ARIZ261818); McLaughlin 4366 (ARIZ305675); McLaughlin 9133 (ARIZ372369); Moran 30772 (SD111259); Morefield 3262 (ARIZ282195); Morefield 3596 (ARIZ284151); Morgan K83 (SDSU5421); Parker 7427 (ARIZ85736); Peebles 6975 (CAS252113); Phillips III-1973 (ARIZ187426); Purer 4943 (SD39196); Rea 657 (ARIZ262507); Rebman 21541A (SD213031); Rickard 1853 (DH562256); 10 March 1940, Rose s.n. (CAS275467); Salywon 1050 (DES00059734, SD188428); 13 March 1982, Scheidlinger s.n. (SDSU18155); Shreve 6217 (ARIZ98294); Shreve 6217 (ARIZ98294); Shreve 7891 (ARIZ98293); Simpson 3126 (SDSU19604); Simpson 3670 (SDSU20043); Simpson 5IV97C (SDSU12434); Smith 998 (ARIZ216616); 21 March 1906, Spalding s.n. (ARIZ98295); Sweet 509 (SD200747); Tedford 630 (ARIZ388080); Thornber 2171 (ARIZ417362); Thornber 2473 (ARIZ417392); Thornber 4632 (ARIZ417370); Thornber 4711 (ARIZ417364); Thornber 4892 (ARIZ417361); Thornber 5300 (ARIZ417396); Thornber 5780 (ARIZ417394); April, 1908, Thornber s.n. (ARIZ417369); 19 April 1913, Thornber s.n. (ARIZ417373); 12 April 1903, Thornber s.n. (ARIZ417363); 12 May 1905, Thornber s.n. (ARIZ417368); Tiehm 10504 (DES00031364); Tiehm 11084 (DES00032535); Tiehm 16118 (DES00067729);

*Turner 68-94* (ARIZ169031, SD78609); *White 2721* (SDSU5394); *19 April 1905, Wooton s.n.* (DH137011, DES00016498); *Whitehead 404* (DES00014812); *Wiggins 8408* (ARIZ20120); *Wiggins 14053* (ARIZ144634); *Worthington 24333* (DES00039956); *Worthington 24534* (DES00039908); *Yatskievych 85-20* (ARIZ259773); *Wojtan 4IV92C* (ARIZ187144); *Wiggins 21595* (ARIZ187144).