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RECOGNITION OF TWO SPECIES IN *EREMOCARYA* (BORAGINACEAE): EVIDENCE FROM FORNIX BODIES, NUTLETS, COROLLA SIZE, AND BIOGEOGRAPHY

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ABSTRACT

Eremocarya (Boraginaceae), a recently resurrected segregate of the genus *Cryptantha*, has generally been recognized as containing a single species, *E. micrantha*, with two varieties. Here we present evidence that these two varieties are distinct in a number of features and that they should be treated as separate species: *Eremocarya lepida* and *E. micrantha*. *Eremocarya lepida* differs from *E. micrantha* in having a significantly greater corolla limb width, nutlet length, maximum nutlet width, and maximum nutlet width: apical nutlet width. *Eremocarya lepida* also has prominent yellow fornices near the apex of the corolla throat, whereas fornices are absent and the fornix region lacks pigmentation in *E. micrantha*. In addition, we report the discovery of clusters of minute (ca. 0.1 mm long), transparent, stalked, ellipsoid structures born near the apex of the inner corolla tube that are associated with the five corolla fornices, these being unique to *E. lepida*. These structures, which we term ''fornix bodies,'' are of unknown chemistry and function, but they may possibly have a role in the pollination of the showier, larger-flowered *E. lepida*. In addition to these morphological characters, the two species differ in distribution, elevation, and plant community/vegetation. *Eremocarya lepida* occurs at higher elevation in chaparral, coniferous woodland, and high desert scrub of southern California and northern Baja California, México. *Eremocarya micrantha* occurs at lower elevations in desert habitats of Arizona, California, New Mexico, Texas, Oregon, and Utah in the United States, and Baja California and Sonora in México. All of these data strongly support recognition of two species in *Eremocarya*.

Key Words: Biogeography, Boraginaceae, *Cryptantha micrantha*, *Cryptantha micrantha* var. *lepida*, *Eremocarya lepida*, *Eremocarya micrantha*, fornix/fornices, fornix bodies.

In 1859 Torrey named the flowering plant *Eritrichium micranthum* Torrey (family Boraginaceae), as part of the Report on the United States and Mexican Boundary Survey (Holotype *G. Thurber 181*, Apr 1851; NY 00335240). Torrey diagnosed this new species as a small, canescent-hispid annual with slender, much-branched stems (Fig. 1A), linear, obtuse leaves, bracteate and crowded flowers (Fig. 1B), and minute corollas, less than ''a line'' long [i.e., less than ca. 2.1 mm] (Fig. 1B, D), the corollas lacking appendages (Fig. 1E). Nutlets are described as ''about one-third of a line long [i.e., ca. 0.7 mm], narrowly oblong, shining,'' glabrous, with a prominent inner sulcus [ventral groove] (Fig. 1G; however, note both glabrous and papillate nutlets here), the nutlets adhering to the whole length of the column [gynobase] (Fig. 1F). (Note: a ''line'' is assumed to be 1/12 in., or approximately 2.1 mm)

Subsequent to Torrey's publication, Gray (1878) named *Eritrichium micranthum* var. *lepidum* A. Gray (Holotype: *D. Cleveland s.n.*, GH 00097023). Compared to *E. micranthum* [var. *micranthum*], Gray described var. *lepidum* as ''less slender and more hirsute,'' with a corolla that is ''larger, its expanded limb 2 or 3 lines [ca. 4–6 mm] in diam. (Fig. 2A, B), the appendages or folds in the throat very manifest (Fig. 3B–E); nutlets nearly a line [i.e., a little less than 2 mm] long, puncticulate-scabrous'' (Fig. 2E). Gray contrasts *Eritrichium micranthum* Torrey var. *micrantha* as having corolla lobes ''one to two-thirds of a line long,'' [i.e., ca. 1.4–2.1 mm broad] (Fig. 1D), stating that the corolla is ''obscurely appendaged at the throat'' (Fig. 1E). Gray described the nutlets of var. *micrantha* as ''half to two-thirds of a line long'' [ca. 1–1.4 mm], and ''smooth and shining or dull and puncticulate-scabrous'' (conforming to the variation seen in Fig. 1G).

In 1885 Gray classified the two varieties of *Eritrichium* in the genus *Krynitzkia*, as *K. micrantha* (Torrey) A. Gray [var. *micrantha*] and *K. micrantha* var. *lepida* A. Gray, commenting

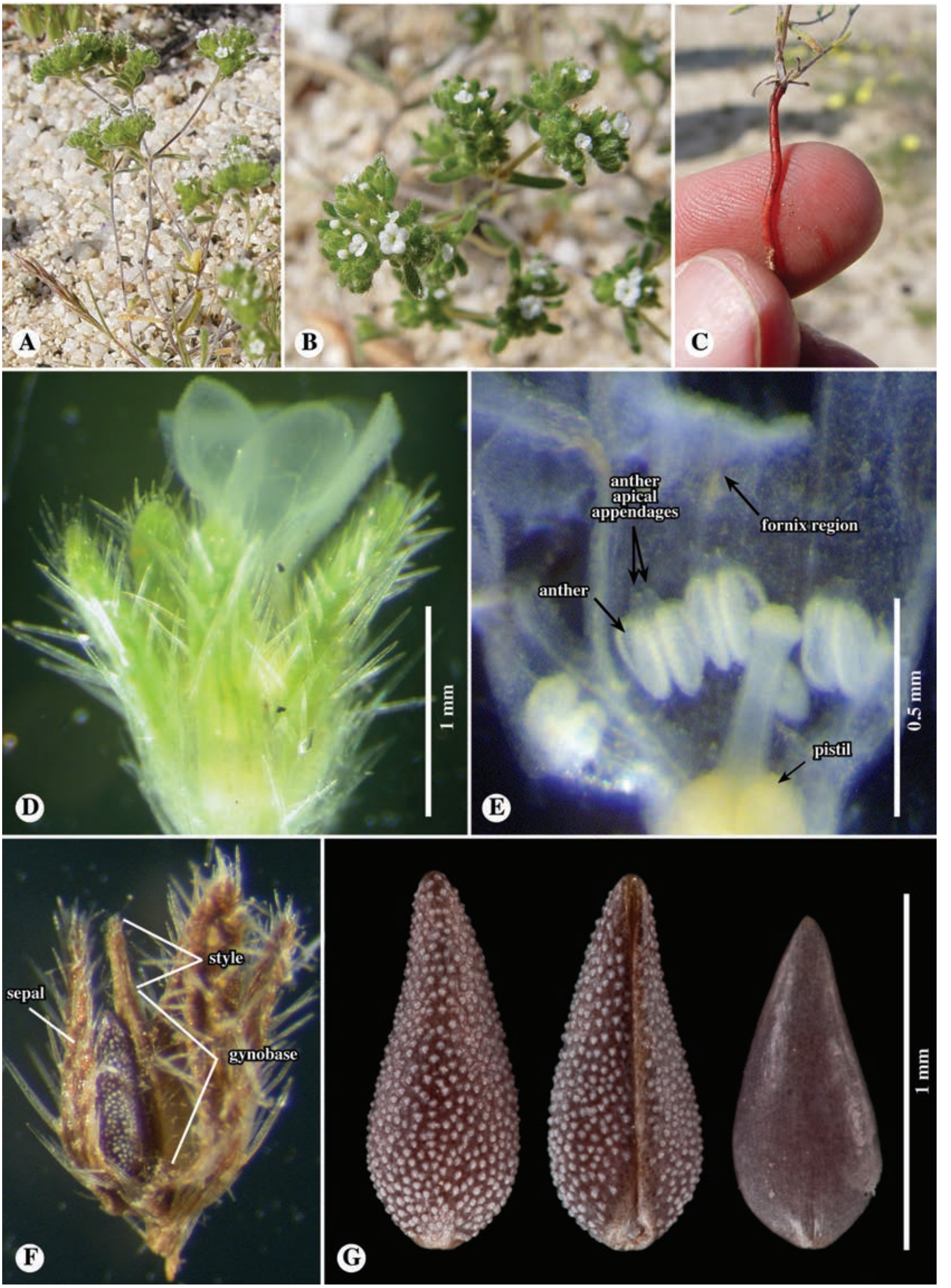

FIG. 1. *Eremocarya micrantha*. A–C. Field photographs (*Simpson 3126*, SDSU 19604). A. Whole plant, a small annual. B. Inflorescence. Note small flowers. C. Root, with red pigmentation. D–E. Flowers, rehydrated from dried herbarium material of same collection (*Simpson 3126*, SDSU 19604). D. Flower, side view, showing calyx and funnelform corolla. E. Open corolla, showing pistil, anthers (note two apical appendages and different levels of attachment), and absence of fornices. F. Fruiting calyx, with persistent nutlet attached to gynobase. G. Nutlets of heteromorphic individual (*Purer 4943*, SD 39169): ''rough'' (densely papillate) large/solitary nutlet at left (far left, dorsal view; middle, ventral view) and one of three smooth small/consimilar nutlets at right (dorsal view only).

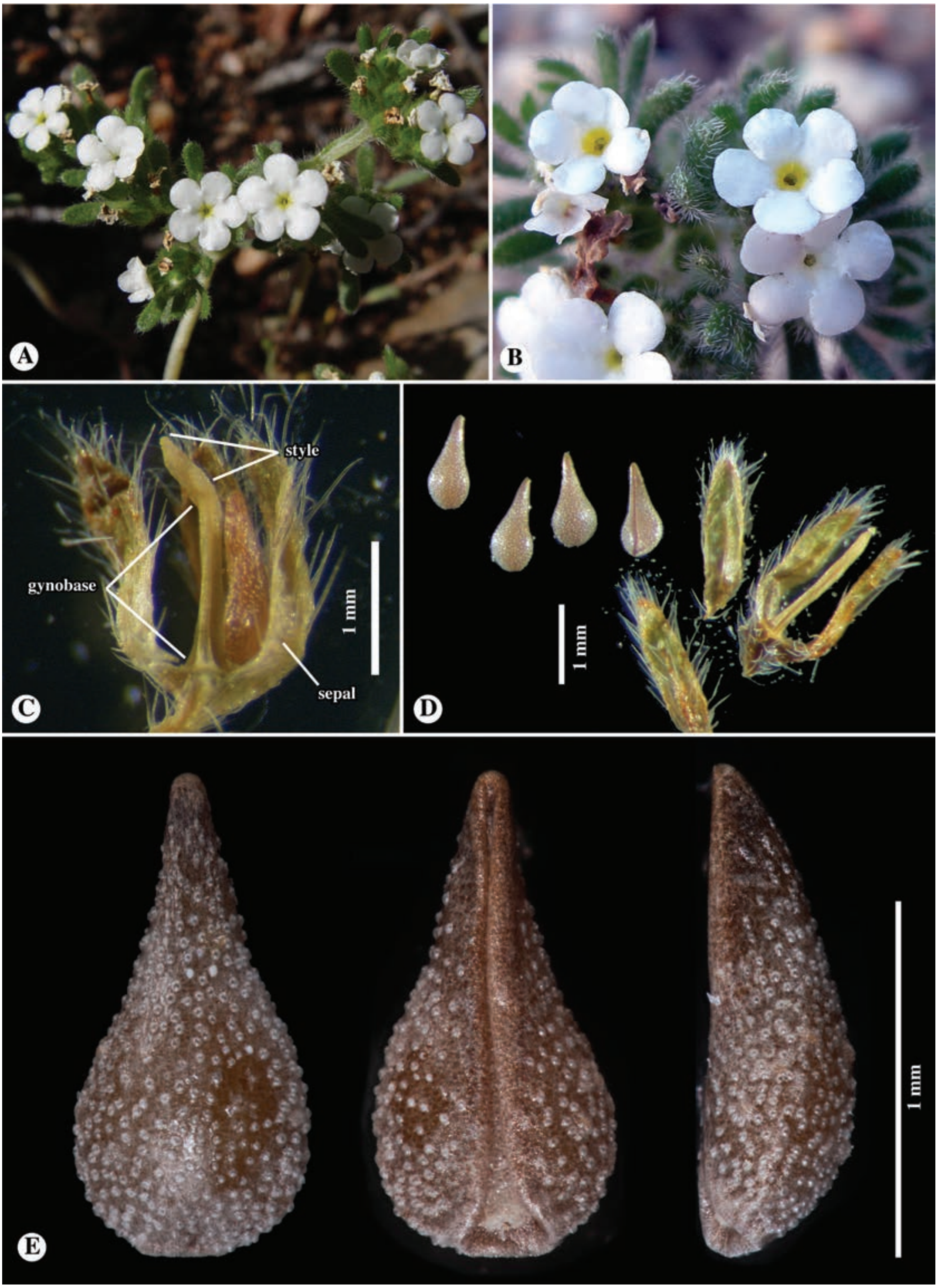

FIG. 2. *Eremocarya lepida*. A–B. Field photographs. A. Inflorescence (*Simpson 2816*, SDSU 17572). B. Flower close-ups (*Rebman*, 29 Mar 2007). C–D. Mature fruits (*Simpson 2369*, SDSU 17281). C. Fruiting calyx, with persistent nutlet attached to gynobase. D. Another fruiting calyx, showing all four, homomorphic nutlets. E. One of four homomorphic nutlets (*Simpson 2816*, SDSU 17572), in dorsal (left), ventral (middle), and side (right) views.

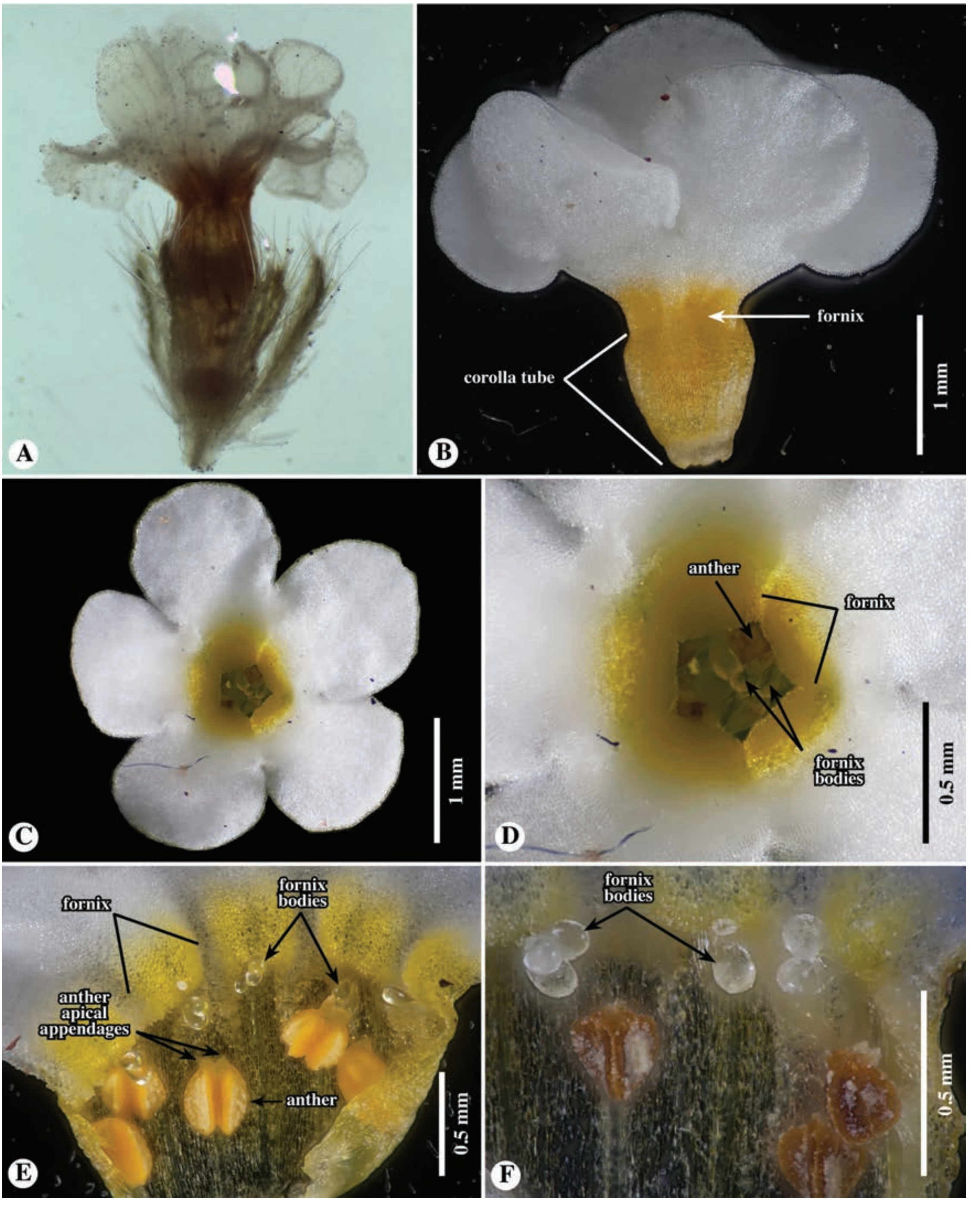

FIG. 3. *Eremocarya lepida*. A. Whole flower, rehydrated from dried herbarium material (*Simpson 8VI94J*, SDSU 5431), showing relatively large, overlapping corolla lobes. (Note: corolla has become detached from and is elevated slightly above, flower base.) B–F. Flowers, photographed from fresh material (*Simpson 3724*, SDSU 20490). B. Corolla, side view, with yellow, invaginated fornices. C. Corolla, face view, showing lobes and yellow center and fornices at upper throat. D. Close-up of C, showing fornix bodies protruding into corolla throat. E. Corolla from flower at anthesis, opened to show 1–3 transparent fornix bodies arising from each fornix. Note anthers (each with two apical appendages) arising at multiple levels, below. F. Corolla from slightly post-anthesis flower, opened to show fornix bodies, these apparently covered with pollen grains.

that "the two forms are confluent." Two years later, Greene (1887) named the new genus *Eremocarya* (Greek *eremos*, desert or solitary, and *carpos*, nut), transferring these two taxa in new combinations: *E. micrantha* (Torrey) Greene and *E. lepida* (A. Gray) Greene. Greene characterized the new genus as small, hirsute-canescent annual herbs with roots having a "deep purple stain" (Fig. 1C) [probably naphthoquinone based alkannins or shikonins; see Papageorgiou et al. 1999], "leaves all in a radical, rosulate tuft, the numerous racemose branches [actually scopioid cymes, a type of monochasium] repeatedly dichotomous and conspicuously leaf-bracted." Greene described the fruits as having short, filiform pedicels, with persistent, campanulate calyces that are 5-parted to the base (Fig. 1F), the "segments [i.e., sepals] nerveless and not hispid-bristly." The style is described as "enlarged in fruit and persistent," and the nutlets as "neither margined nor carinate" [i.e., the margin is rounded], "erect, attached for their whole length, the groove open, little dilated and not furcate at the base" (Figs. 1G, 2E). Greene gave no rationale for deviating from Gray in treating the two former varieties as separate species.

In 1909 Rydberg segregated the rough-nutlet form of *Eremocarya* as a separate species, *E. muricata* Rydberg; this was apparently named because the type material of *Eremocarya micrantha* (basionym *Eritrichium micranthum* Torrey) has smooth ("shining") nutlets, warranting description of this new, rough-nutlet form. However, Macbride (1916) rejected Rydberg's new species, citing a co-type specimen of his *Eremocarya muricata* with smooth (not rough) nutlets. Macbride agreed with the ranking of Gray's earlier classifications for the two original taxa, lowering Greene's *Eremocarya lepida* to the rank of variety, as *E. micrantha* var. *lepida* (A. Gray) J. F. Macbride. Macbride implied that this demotion in rank was related to the common variation in nutlet morphology between the two forms, pointing out that in both varieties "herbarium material seems to indicate that the smooth- and rough-fruited forms grow intermingled, even in the same population," providing "no specific value in this genus."

Johnston (1923) transferred varieties *micrantha* and *lepida* to the genus *Cryptantha*, as *C. micrantha* (Torrey) I. M. Johnston [var. *micrantha*] and *C. micrantha* var. *lepida* (A. Gray) I. M. Johnston. Johnston (1925) corroborated Macbride's observation about nutlet morphology in stating that "nutlets of *C. micrantha* are exceptionally variable." Despite this, Brand (1931) described *Eremocarya abramsiana* Brand, based on an obvious specimen of *lepida* having smooth nutlets.

Subsequent to Johnston's 1923 treatment, the classification of these two taxa as varieties of *Cryptantha micrantha* has been accepted by most botanists in almost all floras for regions where the two occur (Munz and Keck 1968; Munz 1974; Cronquist 1984; Kelley and Wilken 1993; Kelley et al. 2012). However, Mathew and Raven (1962) elevated Johnston's varieties of *Cryptantha micrantha* to the rank of subspecies, as *C. micrantha* subsp. *micrantha* and *C. m.* subsp. *lepida* (A. Gray) K. Mathew & P. H. Raven, a change that has not been widely accepted.

Based on a recent molecular phylogenetic study, Hasenstab-Lehman and Simpson (2012) resurrected the genus *Eremocarya* (and three other segregate genera of *Cryptantha*) because it comprised a clade within their subtribe Cryptanthinae separate from *Cryptantha* s.s., a classification we accept here. In fact, at least two relatively recent floristic treatments also recognized *Eremocarya* as separate from *Cryptantha*: Abrams 1951 (in his *Illustrated Flora of the Pacific States*, citing only *E. micrantha*) and Wiggins 1980 (in his *Flora of Baja California*, citing both varieties of *E. micrantha*).

The two varieties of *Eremocarya micrantha* [*Cryptantha m.*] have been separated based primarily on corolla limb size and color and size of the five corolla throat "fornices" (singular "fornix," also known as "appendages"), the latter constituting invaginations of the corolla tissue, infolded toward the central floral axis along a common radius with the corolla lobes and slightly protruding into the upper throat. The key to these taxa, treated as varieties of *Cryptantha micrantha*, from Kelley et al. (2012) reads:

Corolla limb 1.5–4 mm diam., appendages larger than minute, yellow .... **var. *lepida***
Corolla limb 0.5–1.2 mm diam., appendages minute, ± white .... **var. *micrantha***

Mathew and Raven (1962) found both taxa to have a common chromosome number of n = 12. Thus, they did not argue for their classification as separate species. These authors stated that the two taxa "have not been found growing together" and "appear to be largely geographic entities best recognized as subspecies."

Kelley et al. (2012) described the geographic and ecologic separation of the two entities. Variety *lepida* occurs in "mountain slopes, flats, valleys, granite-based gravelly soils, generally conifer forest, also chaparral, foothill woodland, Joshua-tree woodland, 300–2800 m," flowering "March–August." In the United States this taxon is almost entirely restricted to California, occurring in the southern Sierra Nevada, Tehachapi Mountains, Transverse Range, Peninsular Range, and the northern area and the region of the Great Basin east of the Sierra Nevada Mountains. Variety *lepida* also occurs in multiple

TABLE 1. PRINCIPAL COMPONENTS ANALYSIS LOADINGS FOR CHARACTERS USED IN TWO ANALYSES: SIX CHARACTERS/FIVE CHARACTERS. Percent of total variance explained: axis 1 = 72.467/71.487, axis 2 = 18.159/19.261, and axis 3 = 5.298/5.04.

Character	Component loadings		
	1	2	3
Corolla limb width	0.91/0.897	0.132/0.084	0.336/−0.425
Nutlet length	0.879/0.874	0.265/0.338	−0.304/0.235
Nutlet maximum width	0.928/0.928	0.255/0.247	−0.154/0.07
Nutlet apical width	0.703476483	0.934/0.863	0.055/−0.051
Nutlet apical width : Nutlet maximum width	0.944/0.951	−0.251/−0.187	−0.131/0.09
Fornix body length	0.936/N.A.	−0.034/N.A.	0.263/N.A.

populations in Baja California, Mexico (Wiggins 1980; Baja Flora 2013).

Variety *micrantha* occurs in "desert flats, washes, sandy to fine-gravelly soils, <1900 m" (Kelley et al. 2012). The range of var. *micrantha* overlaps with but is much more widespread than var. *lepida*, the former occurring in southeastern California, the Great Basin, and desert regions of Arizona, New Mexico, Nevada, southeastern Oregon, western Texas, Utah, and also in Baja California and Sonora, Mexico (Baja Flora 2013; Plant Resources Center 2013; SEINet 2013).

The purpose of this article is to present evidence that these two taxonomic entities (referred to below as simply "micrantha" and "lepida") should be treated at the rank of species. We present several morphological features (including one thought to be new to science) and cite more detailed biogeographic evidence for their classification as separate species.

MATERIALS AND METHODS

Herbarium specimens were obtained and studied from the following herbaria: California Academy of Sciences (CAS), San Diego Natural History Museum (SD), San Diego State University (SDSU), and the University of California, Berkeley (JEPS, UC). A total of 352 herbarium specimens were sampled, annotated, and recorded for latitude/longitude and elevation (or these estimated from label data). From a randomly chosen subset of 45 of these specimens (approximately half for each form), dried flowers of both taxa were boiled for 2–3 min 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 and the corolla throat was slit and the two edges peeled back, followed by staining with a drop of 0.5% toluidine blue. The corolla throat fornix region was observed, and the presence, size (length and width), and number per fornix of peculiar "fornix bodies" (see Results section) were measured with a video-interfaced dissecting microscope, using ImageJ software (Rasband 1997–2007, see Abramoff et al. 2004).

From the same 45 specimens, 3–4 mature fruits were detached and the nutlets removed and placed in dorsal (abaxial) view. The length, maximum width (below the middle), and width at 1/4 relative distance from the apex were measured using ImageJ. Nutlet data were segregated based on fruit heteromorphism. If selected fruits contained heteromorphic nutlets, the single ("odd") large nutlet was tabulated separately from the generally 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.

Bivariate plots were prepared for nutlet length (mm) versus corolla limb width (mm) and for nutlet length (mm) versus the ratio of maximum nutlet width to width at 1/4 relative distance from the apex (this width to width ratio an estimate of the degree of attenuation of the apical portion of the nutlet). In addition, bivariate plots were prepared for elevation (m) versus corolla limb width (mm) and for elevation (m) versus nutlet length (mm).

A principal components analysis (PCA) was conducted on samples having complete data for six characters: 1) corolla limb width; 2) length of "fornix bodies" (see below; if bodies absent, a zero was assigned); 3) nutlet length; 4) nutlet maximum width; 5) nutlet width 1/4 relative distance from the apex; and 6) ratio of maximum nutlet width to width at 1/4 relative distance from the apex. A second PCA was conducted using these characters except for fornix body length; this was done to compare the effect of this novel feature on the distinctiveness of the two taxa. 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 and 2nd versus 3rd components (only the former illustrated and discussed), and component loadings were tabulated (Table 1). All statistical analyses were performed in SYSTAT, Version 11 (Systat Software, Inc., San Jose, CA USA, http://www. systat.com).

To visualize character distributions by taxon, box plots showing the median and the four quartiles of distribution were prepared for 1) corolla limb width (mm); 2) nutlet length (mm); 3) nutlet maximum width (mm); 4) nutlet apical width (1/4 from apex, mm); 5) the ratio of nutlet maximum width: width 1/4 from apex; and 6) elevation (m). Each of these features was evaluated for statistically significant differences by taxon with a t-test. Statistical differences between the two taxa for a particular character were tabulated and the variation in these features illustrated in box plot diagrams, using Systat.

A map was prepared showing the distributions of all specimens examined and annotated to variety (indicated with an exclamation mark in Appendix 1) plus specimens not examined by us but identified to variety in databases (data from the CCH 2013, SEINet 2013, and BajaFlora 2013), a total of 554 specimen collections. Specimen records identified only to species (as *Cryptantha micrantha*, with no variety indicated) were not mapped, with the exception of 14 records: 11 records from northern Nevada and southeastern Oregon from the CPNH (2013) and three Texas records from the Plant Resources Center (2013). However, based on ranges cited in the literature, we feel confident that these represent what has generally been recognized as *Cryptantha micrantha* var. *micrantha*, what we are indicating as "micrantha." Our total mapping records include specimens from ARIZ, ASC, BCMEX, CAS, CIC, DES, DH, HCIB, IRVC, JEPS, JOTR, LL, MWI, OSC, POM, RSA, SD, SDSU, TEX, UC, UCD, UCR, UNM, VVC, and WILLU (acronyms of herbaria after Holmgren and Holmgren 1998 onwards). In addition, maps were prepared of San Diego County from the San Diego County Plant Atlas (2013) and Baja Flora (2013) databases, but using only specimens verified by us; these maps show more detailed representations of plant community and vegetation types.

Results

We observed that the corolla of "lepida" is generally rotate, i.e., with horizontal, orbicular lobes (Fig. 3A), whereas the corolla of "micrantha" tends to be more infundibular, with generally ascending, oblong lobes (Fig. 1D). We confirmed, as originally described by Gray (1878), that the fornices of "lepida" are prominent and have a yellowish pigmentation (Figs. 2B, 3C). We also note that the corolla tube is also yellow, a feature probably missed in earlier descriptions given the tube is not normally visible because it is covered by the calyx. However, in "micrantha" we detected no evident fornices and no yellow pigmentation in the fornix region (Fig. 1B, E). We also report the observation of anthers at different levels and the presence of anther apical appendages for both "micrantha" (Fig. 1E) and "lepida" (Fig. 3E), which to our knowledge has not been previously described. We do not yet know if any of these androecial features are unique to these taxa within the Cryptanthinae; a detailed study of the corolla and androecium morphology of the complex will be the topic of another study.

An interesting discovery is the presence of unusual and distinctive structures attached to the fornices of "lepida", but absent in all "micrantha" specimens observed. These structures, which we term "fornix bodies," are ellipsoid, transparent (in fresh material), and stalked (Fig. 3D–F); they occur in groups of about three (ranging from 1–4, rarely 5), arising from the middle-lower portion of each of the five fornices of a corolla and positioned well above the anthers (Fig. 3E, F). The fornix bodies have a mean length of 0.11 mm (not including the stalk) and an average width of 0.08 mm. Viewed from a face-view of the corolla throat opening and from corolla longitudinal sections, these bodies appear pendant, with a horizontal to reclined orientation (Fig. 3D–F). We point out that the fornix bodies of "lepida" are evident in live material under high magnification (even with a strong hand lens), but are more difficult to see in dried material.

A bivariate plot of nutlet length versus corolla limb width shows morphological separation between the two taxa (Fig. 4A). A bivariate plot of nutlet length versus the ratio of nutlet maximum to width 1/4 from the apex also shows separation between the two taxa, but with more of a continuum (Fig. 4B). In either plot, no appreciable difference is noted between samples of "micrantha" having homomorphic versus heteromorphic nutlets. A bivariate plot of elevation versus corolla limb width shows moderate separation between the two taxa (Fig. 4C), but one of elevation versus nutlet length shows more of a continuous grade (Fig. 4D).

The PCA shows a discrete separation between "lepida" and "micrantha" utilizing six characters (Fig. 4E). The first principal component, explaining 72% of the overall variance, corresponds to size, with five characters (corolla limb width, fornix body length, nutlet length, nutlet maximum width, and ratio of nutlet maximum width: nutlet apical width) loading heavily, at 0.879–0.944 (Table 1). This separation between taxa persists in the PCA analysis that excludes fornix body length (Fig. 4F), with very similar variance and component loading values (Table 1).

Based on our sampling of dried herbarium material, the corolla limb width of "lepida", with a mean of 2.4 mm, is significantly larger ($P < 0.01$) than that of "micrantha", mean = 1.0 mm

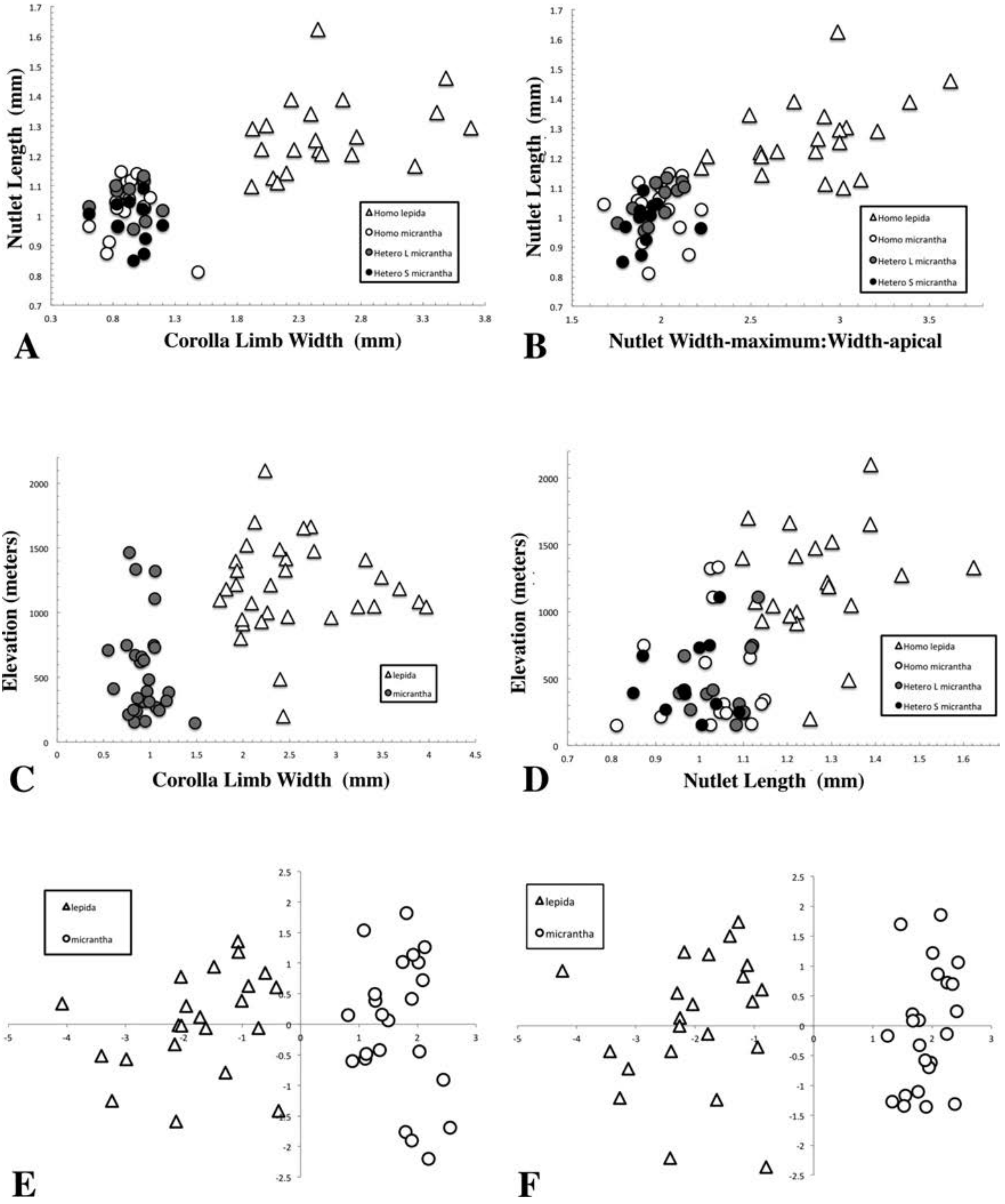

FIG. 4. A–D. Bivariate plots of measurements from examined specimens. A. Nutlet length (mm) versus corolla limb width (mm). B. Nutlet length (mm) versus ratio of nutlet maximum width:width at apex (ca. 1/4 distance from tip). C. Elevation (meters) versus corolla limb width (mm). D. Elevation (meters) versus nutlet length (mm). E–F. Principal Components Analsyis (PCA) plots of first and second factors, showing clear separation of *lepida* and *micrantha*. E. Analysis of six characters, including fornix body length. F. Analysis of five characters, excluding fornix body length. Symbols: Homo = homomorphic nutlet form; Hetero L = large nutlet of heteromorphic form; Hetero S = small nutlet of heteromorphic form.

(Fig. 5A). This is not surprising, given that corolla size is the most cited feature distinguishing between the two taxa since their inception (even though corolla dimensions can shrink considerably upon drying). The nutlet length of "lepida" (mean = 1.26 mm) is also significantly greater ($P < 0.01$) than that of "micrantha" (mean = 1.02 mm; Fig. 5B). The maximum nutlet width is significantly greater ($P < 0.01$) in "lepida" (mean = 0.54 mm) than in "micrantha" (mean = 0.41 mm; Fig. 5C). Although the width at 1/4 down from the apex in "lepida" (mean = 0.20 mm) is significantly less ($P < 0.01$) than that of "micrantha" (mean = 0.23 mm), there is a fair amount of overlap (Fig. 5D). Moreover, the ratio of maximum nutlet width to nutlet width 1/4 from the apex is significantly greater ($P < 0.01$) in "lepida" (mean = 2.84) than in "micrantha" (mean = 1.92), with virtually no overlap (Fig. 5E). This metric roughly quantifies the observed difference in nutlet shape, that of "lepida" being apically acuminate, and that of "micrantha" being narrowly acute with relatively straight sides. Finally, the elevation of "lepida" (mean = 1200 m) and "micrantha" (mean = 500 m) are also significantly different ($P < 0.01$), but with some overlap (Fig. 5F).

A map of the two taxa (Figs. 6, 7) shows discrete geographic (elevation and vegetation) boundaries between the two taxa. Generally, "lepida" occurs in higher elevation, mountainous regions and is restricted to mostly southern California (some populations also occur in the southern Sierra Nevada) and northern Baja California, México (Fig. 6). In contrast, "micrantha" is generally much more widespread, occurring in Arizona, California, New Mexico, Oregon, Texas, and Utah in the United States; in Mexico, populations are known in Sonora, and northern to southern Baja California. In San Diego County and the Baja California peninsula specifically (for which we have maps of plant community/vegetation types), "lepida" occurs in mostly chaparral, coniferous forest, and high desert regions, whereas "micrantha" occurs in lower elevation, generally creosote bush scrub of the Lower Colorado Desert (Fig. 7A, B), with sympatry of populations rare.

Discussion

It is clear that the two taxonomic entities, "lepida" and "micrantha", differ in several features, the former with corollas significantly broader and nutlets significantly longer, wider at maximum width, and smaller at apical width, with the maximum width: apical width ratio significantly greater. These metrics quantify the qualitative differences in nutlet shape observed between the two taxa. From our observations, "micrantha" nutlets may be homomorphic (in which case nutlets are all smooth or all papillate) or heteromorphic, the latter by size only or usually by sculpturing and size, with one large/odd, finely papillate large nutlet and generally three smooth smaller nutlets; see Fig. 1E. We did not observe any samples of "lepida" with heteromorphic nutlets, and all nutlets of this taxon were finely papillate. However, descriptions from the literature (e.g., Macbride 1916; Johnston 1925) indicate that there is considerable variation in sculpturing in both taxa.

Of additional importance, "lepida" has prominent, yellow fornices that are invariably associated with the unique "fornix bodies" described here, whereas "micrantha" lacks any obvious fornices, these regions being white and without exception lacking fornix bodies. The statistical analyses presented here justify these distinctions. In fact, the PCA analyses show the two taxa well separated, even when the average length (zero in "micrantha") of fornix bodies was not included.

Based on these numerous differences, we feel that these two taxa should be treated as separate species, using a taxonomic species concept (Cronquist 1978, 1988). Utilizing the resurrected genus name *Eremocarya* (Hasenstab-Lehman and Simpson 2012), we recommend that these taxa be recognized as *Eremocarya micrantha* and *Eremocarya lepida* (see Taxonomic section for complete synonomy). In fact, Cronquist (1984, p. 286) hinted at supporting our conclusion, stating "The var. *lepida* (A. Gray) I. M. Johnston, with larger corolla-limb, is confined to southern California and adjacent Baja California; it may prove to be a distinct species."

Even with the suite of features reviewed here, *Eremocarya micrantha* and *E. lepida* can be difficult to distinguish. The two taxa resemble one another in having red-pigmented roots and a similar branching pattern, inflorescence and bract morphology, and floral structure. In the field, *E. lepida* is generally more robust (at maturity often a little taller than wide) and has obvious, relatively showy corollas, but the latter can shrink significantly on a dried herbarium sheet. The fornix bodies of *E. lepida* also readily distinguish the two taxa, but these are very tiny and difficult to see in live material, even with a hand lens; they are even more difficult to see from dried, herbarium material, sometimes requiring re-hydration (e.g., by boiling) and staining (for better visualization). Nutlet morphology, both length and shape, is one of the better criteria to separate the two taxa. In addition, *Eremocarya micrantha* can be difficult to distinguish in the field from the phylogenetically distant *Greeneocharis circumscissa* (Hook. & Arn.) Rydberg (*Cryptantha circumscissa* [Hook. & Arn.] I. M. Johnston), which has similar red-pigmented roots, inflorescence branching, and floral bracts, but differs in calyx, nutlet, and gynobase

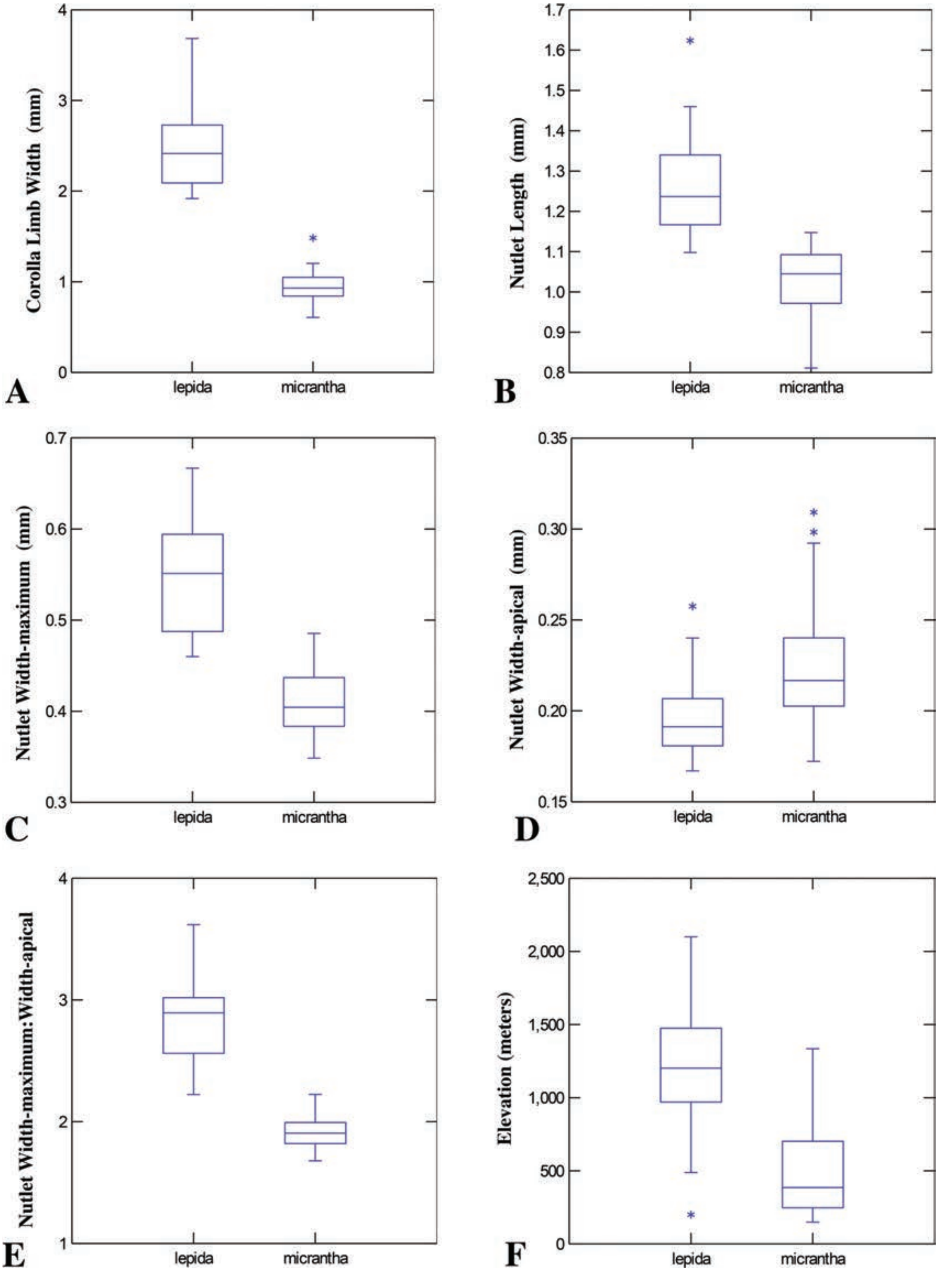

FIG. 5. Box plots of single characters analyzed for *lepida* and *micrantha*. A. Corolla limb width (mm). B. Nutlet length (mm). C. Nutlet maximum width (mm). D. Nutlet apical width, 1/4 relative distance from apex (mm). E. Ratio of nutlet maximum width: width at apex (ca. 1/4 distance from tip). F. Elevation (meters). Taxa are significantly different ($P < 0.01$, from t-test) for all characters.

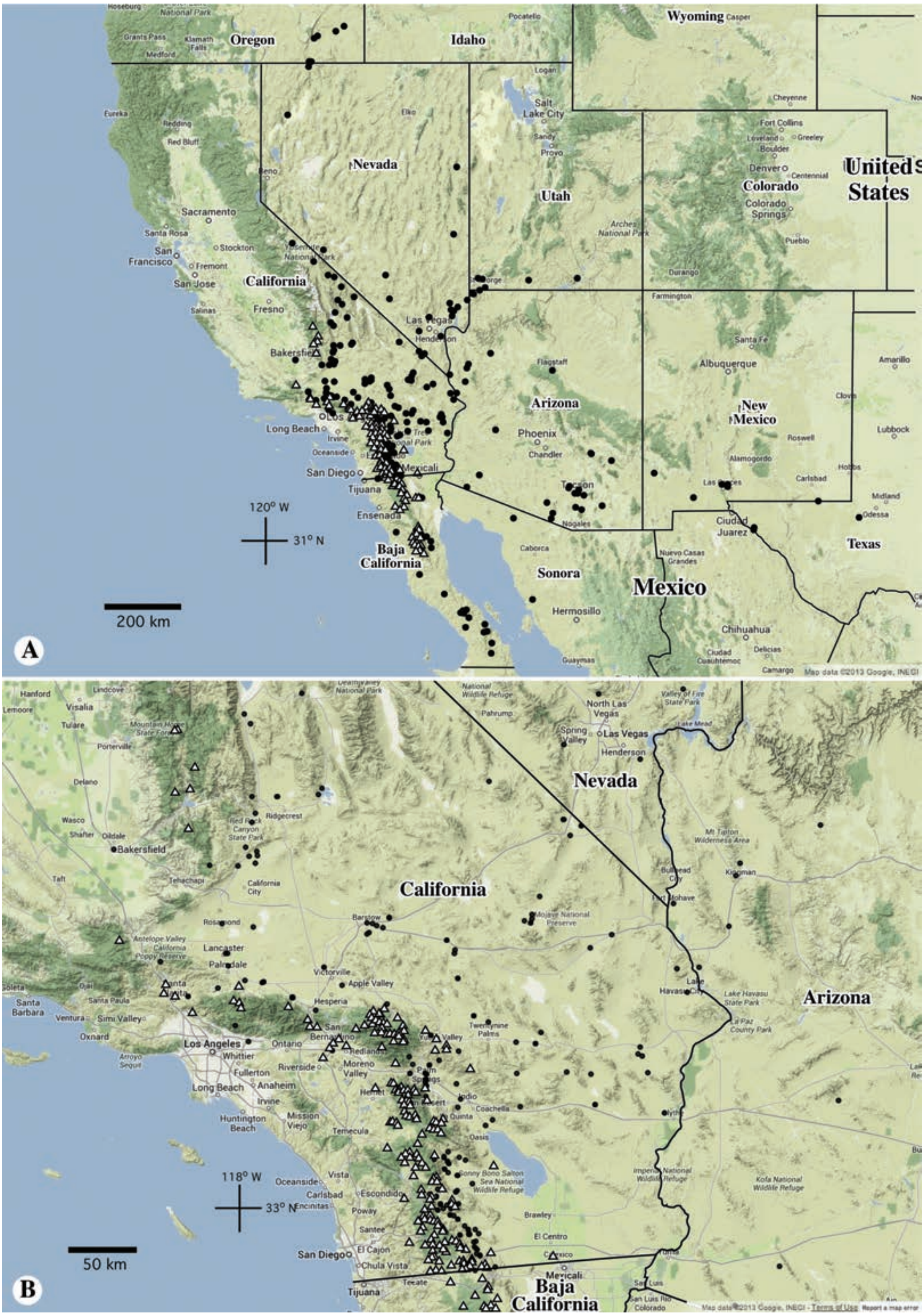

FIG. 6. Distribution map of *Eremocarya lepida* (white triangles) and *E. micrantha* (black circles), derived from georeference data of BajaFlora (2013), CCH (2013), CPNH (2013) Plant Resources Center (2013), and SEINet (2013). A. Full range of taxa, showing much wider distribution of *E. micrantha*. B. Close-up of southern California. Note differences in elevation between the two forms, with *E. lepida* found in higher elevation, mountainous regions. Map data from ©Google 2013, INEGI Data.

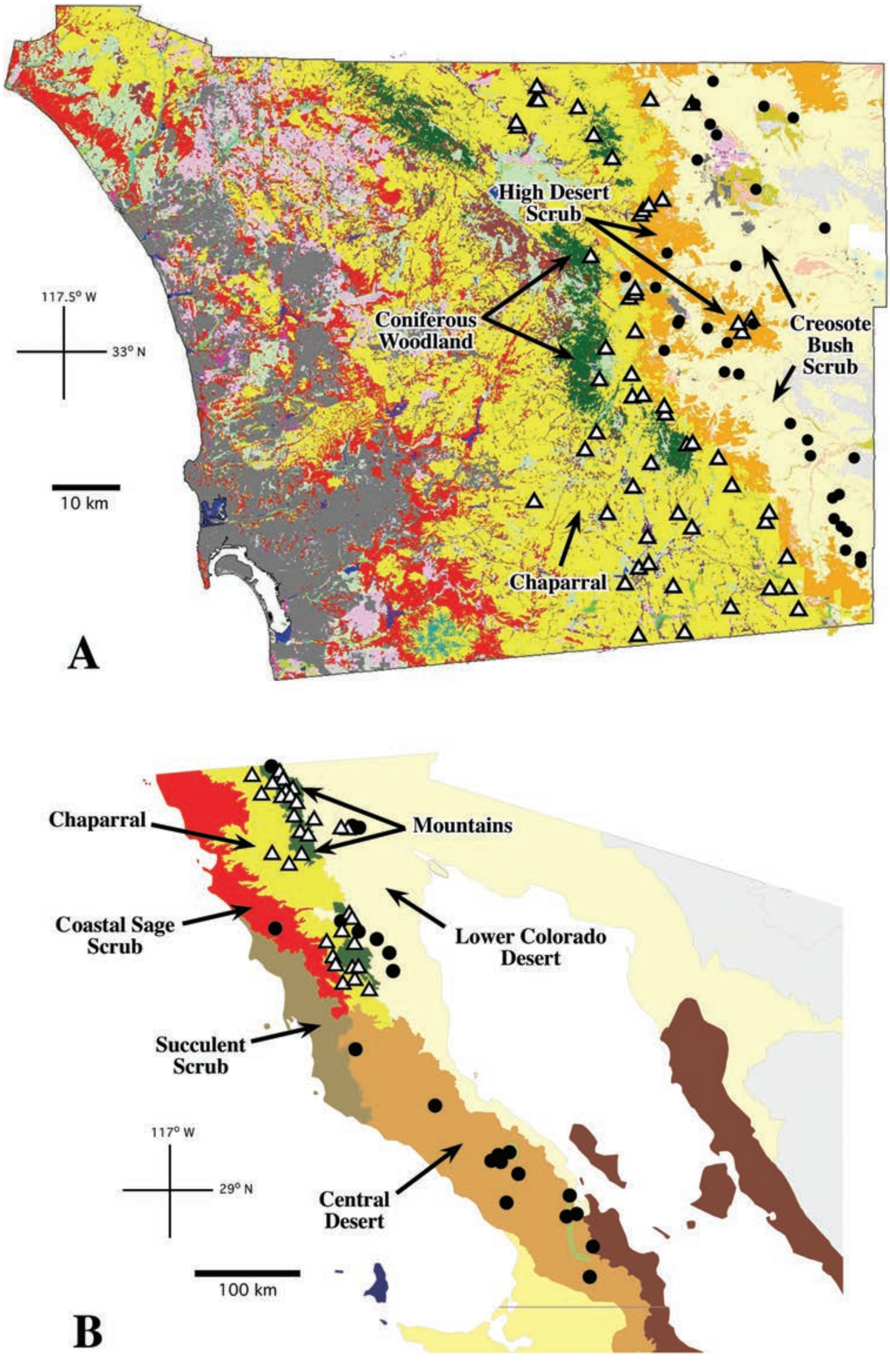

FIG. 7. Distribution map of *Eremocarya lepida* (white triangles) and *E. micrantha* (black circles). A. San Diego County, derived from georeference data of the San Diego County Plant Atlas (2013). Note distribution of *E. lepida* in chaparral, high-desert scrub, and coniferous woodland; distribution of *E. micrantha* is primarily in creosote bush scrub. B. Baja California, México, derived from verified SD specimens only. Note distribution of *E. lepida* in chaparral and mountainous areas. Distribution of *E. micrantha* is limited to the Lower Colorado Desert, Central Desert region, and a single collection in coastal sage scrub.

morphology (see Simpson and Hasenstab 2009; Hasenstab-Lehman and Simpson 2012; Kelley et al. 2012). Observation of *Eremocarya micrantha* specimens from Baja California, México 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. A study of these unusual populations will be the subject of a future study.

The two taxa also show significant differences in plant community and habitat occurrence, with *Eremocarya lepida* at higher elevation in high desert/desert transition, montane chaparral, or woodland habitats and *E. micrantha* occurring at lower elevations on the desert floor in desert scrub and arroyo vegetation. In fact, the two are significantly different in elevation, although with considerable overlap; however, we realize that an elevation parameter is a numerical-based correlate for the nonparametric concept of plant communities. The distribution map of the two taxa generally corroborates these differences in habitat, with only a few exceptions.

We know of no other flowering plant that has structures similar to the fornix bodies described here in *Eremocarya lepida*. However, they may have been missed previously because they are so small and because features of the corolla are often not described in detail among members of the Boraginaceae; fruit characters have traditionally been viewed as more important taxonomically. From our personal observations, they are absent from the related and superficially similar *Greeneocharis circumscissa*, as well as from any observed members of *Cryptantha* s.s. or of any observed members of *Amsinckia*, *Cryptantha* s.s., *Harpagonella*, *Johnstonella*, *Oreocarya*, *Pectocarya*, or *Plagiobothrys* of the subtribe Cryptanthinae (Simpson, work in progress). Interestingly, Cohen (2013) cited that "glands inside corolla" are present in most species of the Boraginaceae, including the Cynoglosseae to which *Eremocarya* belongs. However, these corolla glands are unlike those in *Eremocarya lepida* (Cohen, personal communication).

The chemical makeup and function of the observed fornix bodies in *E. lepida* are unknown. They might somehow function as part of a pollination mechanism. For example, these fornix bodies might exclude certain visiting insects from entering the corolla tube subsequently conserving pollen or nectar for true pollinators; in fact, they would appear to partially block the proboscis of a visiting pollinator (Fig. 3D). Or, they may provide some essential nutrient or resource to a pollinator, making the flowers more "attractive" for visitation and increasing pollination success. However, the fornix bodies actually appear to be rather persistent, as they appear to remain attached in older flowers (Fig. 3F) or in dried herbarium material (even though appearing deflated). We plan to study both the chemical makeup and function of these unique structures. In addition, understanding the phylogeographic relationships of these two taxa will be the goal of a future study.

Taxonomic Treatment

Eremocarya Greene, Pittonia 1(4):58–59. 1887.—TYPE *Eremocarya micrantha* (Torrey) Greene, Pittonia 1:59. 1887.

Eremocarya micrantha (Torrey) Greene, Pittonia 1(4):59. 1887. *Eritrichium micranthum* Torrey, Report on the United States and Mexican Boundary [Emory] 2(1):141. 1859. *Krynitzkia micrantha* (Torrey) A. Gray, Proceedings of the American Academy of Arts and Sciences 20:275. 1885. *Cryptantha micrantha* (Torrey) I. M. Johnston, Contributions from the Gray Herbarium of Harvard University 68:56. 1923.—TYPE: USA, Texas, El Paso, April 1851, *G. Thurber 181* (holotype, designated by Cronquist 1984: NY 335240).

Eremocarya muricata Rydberg, Bulletin of the Torrey Botanical Club 36:677. 1909.—TYPE: USA, Utah, Southern Utah, 1874, *Parry 164* (holotype LGO).

Eremocarya lepida (A. Gray) Greene, Pittonia 1(4):59. 1887. *Eritrichium micranthum* Torrey var. *lepidum* A. Gray, Synoptical Flora of North America 2(1):193. 1878. *Krynitzkia micrantha* (Torrey) A. Gray var. *lepida* (A. Gray) A. Gray, Proceedings of the American Academy of Arts and Sciences 20:275. 1885. *Eremocarya micrantha* (Torrey) Greene var. *lepida* (A. Gray) J. F. Macbride, Proceedings of the American Academy of Arts and Sciences 51(10):545. 1916. *Cryptantha micrantha* (Torrey) I. M. Johnston var. *lepida* (A. Gray) I. M. Johnston, Contributions from the Gray Herbarium of Harvard University 68:57. 1923. *Cryptantha micrantha* (Torrey) I. M. Johnston subsp. *lepida* (A. Gray) K. Mathew & P. H. Raven, Madroño 16(5):170. 1962.

Eremocarya abramsiana Brand, Pp. 77 *in* A. Engler (ed.), Das Pflanzenreich IV, 252 (Heft 97): Borraginaceae-Borraginoideae-Cryptantheae. Verlag von Wilhelm Engelmann, Leipzig. 1931.—TYPE: USA, California, San Bernardino County, near Pine Lake, Bear Valley, 5 August 1902, *L. Abrams 2904* (holotype GH97011; isotypes DS8945, POM158081, UC 153888, UC407303).

Key

The following revised key to the two species of *Eremocarya* (modified from Kelley and Simpson, in prep.) may be used to separate these taxa.

Corolla limb 0.5–1.2 mm diam., center white, fornices absent, fornix region white, lacking ellipsoid bodies; nutlets ca. 1–1.1 mm long, apex narrowly acute; plants at maturity generally wider than tall ...... ***E. micrantha***
Corolla limb 1.5–4 mm diam., center yellow, fornices conspicuous, yellow, each with a basal cluster of tiny (ca. 0.1 mm long), pendant, ellipsoid "fornix bodies;" nutlets 1.2_1.4 mm long, apex acuminate; plants at maturity generally taller than wide ... ***E. lepida***

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APPENDIX 1

VOUCHER SPECIMENS USED IN THIS STUDY, LISTED ALPHANUMERICALLY BY COLLECTOR AND COLLECTION NUMBER; DATE LISTED FOR COLLECTIONS WITHOUT A COLLECTION NUMBER (*S.N.*).

Bold Font = Collectors/vouchers for which data were measured in quantitative study. ! = Voucher verified by the authors.

***Eremocarya lepida*:** *Abrams 2089* (POM 49193); *Abrams 2904* (UC 153888!, UC 407303!); *Abrams 3594* (POM 156574); *Alderson s.n. 1893* (UC 180103!); *Almeda 6544* (CAS 831263!, SD 130518); ***Anderson 26* (SDSU 10277!);** *Andre 8145* (UCR 196107); *Angel 597* (SD 207714); 9 Jul 1895, *Anthony s.n.* (UC 1601969!); *Bacigalupi 3059* (UC 917090!); *Balls 13489* (RSA 50324); *Beauchamp 2288* (SD 85288); *Beauchamp 2336* (SD 85342); *Beauchamp 2742* (SD 85816); *Beauchamp 2861* (SD 128344); *Bell 3801* (RSA 798987); *Bourell 2980* (CAS 741818!); *Boyd 11382* (UCR 148355); *Boyd 2302* (RSA 508006, UCR 120623); 10 May 1893, *Brandegee s.n.* (UC 78818!); May 1889, *K. Brandegee s.n.* (UC 79423!); 16 Jun 1894, *T. S. Brandegee s.n.* (UC 78822!); 20 Jun 1904, *T. S. Brandegee s.n.* (UC 174930!); 30 Apr 1894, *T. S. Brandegee s.n.* (UC 79425!); 9 Jun 1951, *Brattstrom s.n.* (SD 44489!); ***Breisch 270* (SD 194947!);** *Breisch 42* (SD 172723); ***Breisch 449* (SD 201471!);** *Carter 5705* (UC 1443877!); 29 Jul 1897, *Chandler s.n.* (UC 24835!); *Charlton 1951* (RSA 483571); *Charlton 2118* (RSA 489621); *Chisaki 637* (UC 1035182!); 7 Apr 1929, *Clark s.n.* (RSA 499653); 7 Apr 2004, *Clarke s.n.* (UCR 239826); 9 Jun 1991, *Clarke s.n.* (UC 1931683!, UC 1931683); *Clemons 1041* (SD 118370); ***Clemons 1289* (SD 118945!);** *Clemons 2230* (SD 126687); *Clemons 584* (SD 115631); 1882, *Cleveland s.n.* (UC 193915!); 4 Jul 1884, *Cleveland s.n.* (UC 78823!); *Clokey 6847* (UC 857183!); 21 Jun 1910, *Condit s.n.* (UC 455977!); *Cooper 1249* (RSA 499654); ***Copp 14* (CAS 840487!, SD 134020!);** *Copp 14* (SD 134020); May 1933, *Cota s.n.* (SD 15615!); *Cowan 1255* (RSA 790339); *Cowan 1258* (RSA 790340); *Curto 285* (SD 121048); *Davidson 2819* (RSA 499651); *Davidson s.n.* (RSA 499652); 5 May 1998, *Delgadillo s.n.* (SD 154820!); *Dempster 4260* (JEPS 44382!); *Dunkle 4056* (UCR 208013); *Eastwood 2591* (UC 1601675!); *Eastwood 3173* (UC 1601674!); *Eastwood 9422* (CAS 26923!); *Eastwood 9539* (CAS 26924!); *Eggleston 19739* (POM 50736); *Elvin 2451* (IRVC 28850, UCR 127092); *Everett 23093* (UC 1080253!); *Fosberg 10680* (UC 551773!); *Fosberg 10701* (UC 551800!, UCR 47681); *Fosberg 1101* (UCR 47710); *Gander 173-44* (SD 11111); *Gander 204-28* (SD 11400); ***Gander 5123* (SD 20635, SDSU 5412!, UC 930876!);** *Gander 5603* (SD 21350); *Gander 5627* (SD 21374); *Gander 5672* (SD 21429); *Gander 5680* (SD 21437); *Gander 5881* (SD 21651); *Gander 7218* (SD 24716); *Gander 8687* (SD 27588); *Gander 9109* (SD 28534); *Gander 9356* (SD 28771); *Gander s.n. 10 Jun 1933* (SD 4195!); 11 Jun 1933, *Gander s.n.* (SD 4194!); *Griesel 718* (RSA 164774); *Grimmell 282* (CAS 26926!); *Gross 1121* (RSA 679981); *Gross 3299* (RSA 735603); *Gross 4040* (RSA 750186); *Gross 4067* (RSA 749784); *Gross 4477* (RSA 763620); *Gross 4713* (RSA 769838); *Gross 5511* (RSA 776148); *Gross 944* (RSA 679944); *Hall 1120* (UC 64426!); *Hall 2051* (UC 24832!); *Hall 2487* (UC 24831!); *Hall 3002* (UC 56860!); *Hall 5135* (UC 63333!); *Hall 6540* (UC 100875!); *Hall 7588* (UC 111522!); 24 Jun 1901, *Hall s.n.* (UC 24833!); May 1901, *Hall s.n.* (UC 24830!); 2 Mar 1987, *Hawks s.n.* (UCR 47194); *Helmkamp 4096* (UCR 110966); *Helmkamp 4113* (UCR 110994); *Hendrickson 15* (SD 137396); *Hendrickson 1953* (SD 196338!); *Hendrickson 3043* (SD 205616); *Hendrickson 3771A* (SD 214888); *Henrickson 19925* (RSA 656795); *Hirshberg 210* (SD 135173); *Honer 3419* (RSA 761037); *Honer 3594* (RSA 764252); *Howe 547* (SD 113114); *Howell s.n. 17 Jun 1971* (CAS 862225!); *Jackson 79-2* (SD 114923); 18 Jun 1922, *Jaeger s.n.* (DH 140398!); *Jepson 11796* (JEPS 67692!); *Jepson 1295* (JEPS 67968!); *Jepson 1308b* (JEPS 67969!); *Jepson 17119* (JEPS 67973!); *Jepson 4888* (JEPS 67970!); *Jepson 4896* (JEPS 67971!); *Jepson 8751* (JEPS 67972!); *Jones 3182* (UC 380868!, UC 881598!); *Jones 7065* (POM 72314); 27 Apr 1882, *Jones s.n.* (POM 72315); *Kamb 1155* (UC 1178517!); *Kamb 1908* (UC 1051659!); *Kasapligil 3228* (UC 1516007!); *Keck 21* (POM 97229); *Keck 84* (POM 97232); *La Doux 2619* (JOTR 32503); *La Doux 2813* (JOTR 33922); 18 Feb 1988, *LaPres.n.* (UCR 50418); 23 Jun 1975, *Latting s.n.* (UCR 157301); *Levin 1674* (SD 119269!); *Lint 2037* (RSA 463700); *Macias 463* (SD 165072!); *Marsden 106* (SD 163799); *Marsden 400B* (SD 207715); ***Marsden 491* (SD 205615!);** *Marsden 578* (SD 205614); *Marsden 80* (SD 163798); *Meyer 160* (UC 489041!); *Meyer 428* (JEPS 67966!); 8 Jun 2005, *Misenhelter s.n.* (UCR 202235); *Moldenke 25474* (SD 82945); *Moran 10923* (SD 53840!); *Moran 11126* (SD 54693!); *Moran 12717* (UC 1345885!); *Moran 13869* (SD 64660!); ***Moran 13898* (SD 64661!);** *Moran 14381* (SD 79677!); *Moran 14475* (SD 79678!); *Moran 14906* (SD 72336!, UC 1361697!); *Moran 15001* (SD 69225!); *Moran 21288* (SD 86898!); *Moran 22039* (SD 91906!); ***Moran 22063* (SD 91864!);** *Moran 22143* (SD 91487!); *Moran 22958* (SD 95519!); *Moran 23334* (SD 96974!); *Moran 24086* (SD 97110!); *Moran 27342* (SD 103646!); ***Moran 27427* (SD 103440!);** *Moran 27448* (SD 103457!); ***Moran 28894* (SD 105525!);** *Moran 30665* (SD 111068!); *Moran 3430* (UC 1112358!. UC 1112775!, SD 48056!); *Moran 8112* (SD 60715!, UC 1199949!, UC 1298136!); *Munz 10646* (POM 96716); *Munz 5421* (POM 13001, UC 218237!); *Munz 5475* (POM 13197, UC 1601673!); *Munz 5722* (UC 1601676!, UC 218205!);

Munz 5839 (POM 12804, UC 218109!); *Munz 8843* (POM 48717); 23 Apr 2003, *Myers s.n.* (UCR 177832); 7 Apr 2003, *Myers s.n.* (UCR 162407); *Nenow 1103* (SD 221038!); *Nenow 1301* (SD 220259); *Olmsted 3503* (RSA 171377); ***Otis 7* (SD 201473!);** *Parish 3245* (UC 78819!); *Parish 6943* (UC 166699!); 1 May 1888, *Parish s.n.* (UC 24828!); May 1887, *Parish s.n.* (JEPS 67960!); *Peirson 370* (JEPS 67967!); *Peirson 4483* (RSA 79959); *Pigniolo 1053* (SD 158770); *Pitzer 662* (RSA 511347); *Powell 63* (UC 1181847!); *Provance 1693* (UCR 111545); *Purer 6443* (SD 39201); *Purer 6651* (SD 12594, SD 39200); *Purpus s.n. May–Oct 1898* (UC 24829!); *Raven 11122* (UC 1279966!); *Raven 12580* (UC 1112443!); *Raven 14241* (UC 1241172!); 18 May 1959, *Raven s.n.* (RSA 145650); *Ray K-33* (UC 1178401!); *Rebman 11407* (SD 171650, UCR 157576); *Rebman 12152* (SD 174759); ***Rebman 17601* (SD 197223!);** *Rebman 17646* (SD 197222); *Rebman 19601* (SD 210102); *Rebman 21146* (SD 213030!); *Rebman 23390* (SD 221601); *Rebman 23610* (SD 223361); *Rebman 23658* (SD 225483); *Rebman 3902* (SD 144398); *Rebman 7210* (SD 155824!); *Rebman 7228* (SD 155825, UC 1787749!, UCR 155754); *Rebman 9019* (SD 160678, UCR 155757); Jun 1897, *Reinhardt s.n.* (UC 24836!); *Roos 3648* (UCR 25966); *Roos 3705* (UCR 23585); *Roos 6194* (RSA 659687); 18 Jul 1965, *Roos s.n.* (RSA 662062); 26 Jun 1965, *Roos s.n.* (CAS 905666!, RSA 450247); *Ross 2598* (RSA 524630, UC 1584224!, UCR 162554); *Sanders 16811* (UCR 86673); *Sanders 16841* (UCR 86811); *Sanders 204* (UCR 18398); *Sanders 26195* (IRVC 29584, RSA 712187, UCR 126911); *Sanders 31384* (UCR 163844); *Sanders 35608* (UCR 193489); *Sanders 35640* (UCR 193421); *Shevock 1074* (CAS 713389!); ***Simpson 2369* (SD 180702!, SDSU 17281!);** *Simpson 2369* (SDSU 17281); ***Simpson 2816* (SDSU 17572!); *Simpson 3109* (SD 208180, SDSU 18628!); *Simpson 3184* (SDSU 19533!); *Simpson 3320* (SDSU 19612!); *Simpson 6VI91AB* (SDSU 5418!); *Simpson 6VI91AC* (SDSU 5388!);** *Simpson 8VI94J* (SDSU 5431); *Soza 1695* (UC 1929625!); *Spencer 1301* (POM 46993); *Spencer 1347* (POM 46994); *Spencer 1864* (POM 12212); 30 Apr 1918, *Spencer s.n.* (UC 472928!); *Sullivan 453* (SD 201472); ***Sweet 266* (SD 178709!);** *Thomas 2953* (VVC 2007); *Thomas 4533* (VVC 2728); *Thorne 38080* (RSA 633317); *Thorne 49838* (RSA 281171); *Thorne 55789* (SD 124127!); *Thorne 55937* (SD 124128!); *Thorne 60451* (SD 124983!); *Thorne 61669* (SD 124981!); *Thorne 63025* (RSA 792627); *Twisselmann 8587* (UCR 79440); *van der Werff 3743* (SD 106838); *van der Werff 3824* (SD 106780); *van der Werff 3825* (SD 106773); *Vestal s.n. 21 May 1963* (MW I00013450, SEINET 3449082); *Vinton s.n. 15 Mar 2003* (SD 182665!); *Vinton s.n. 16 May 2003* (SD 182666!); *Wallace 4028* (RSA 788859); *Weatherby 665* (RSA125536); ***Wedberg 909* (SDSU 5046!);** *White 11980* (RSA 741225); *White 12204* (RSA 741175); *White 12501* (RSA 737129); *White 13209* (RSA 752009); *White 13309* (RSA 751051); *White 1833* (UCR 83423); *White 2046* (UCR 100037); *White 2129* (UCR 157678); *White 5180* (UCR 139929); *White 5375* (UCR 144099); *White 7379* (RSA 653544); *White 7489* (RSA 653505); *Wiggins 10043* (UC 718753!); *Wiggins 11809* (SD 47301!, UC 1060536!); *Wiggins 13053* (UC 1009298!); *Wiggins 15799* (UC 1303271!); *Wiggins 1843* (UC 1019586!, UC 1019609!); *Wiggins 1993* (UC 1019611!); *Wiggins 2250* (UC 1019588!, UC 1019612!); *Wiggins 2350* (UC 1019613!); *Wiggins 5289* (UC 857181!); *Wiggins 5311* (UC 660809!); *Wiggins 7813* (UC 651114!); *Wiggins 9808* (UC 718873!); *Wilder 4319* (POM 318740); *Williams-Anderson 26* (SDSU 10277); *Woglum 3055* (RSA 608561); *Wolfinger 133* (SD 217612!); *Wood 1739* (RSA 764200); *Woodcock 35* (UC 486367!); *Yates 6623* (UC 578663!, UC 1063821!).

***Eremocarya micrantha*: *Anonymous 2625* (SDSU 5400!);** *Atwood 17557* (UC 1719441!); *Axelrod 307* (UC 1063824!); *Bacigalupi 6236* (JEPS 22614!); *Barth 1298* (SD 226395); *Barth 1477* (SD 226396); ***Barth 407* (SD 169356!);** *Beal 739* (JEPS 18395!); *Beatley 3715* (DH 595377!); *Beauchamp 1799* (SD 85465); *Beauchamp 1990* (SD 141844); *Beauchamp 2192* (SD 85416!); *Bell 657* (RSA 779621); 27 April 1950, *Benioff s.n.* (UC 1084521!); *Boyd 1429* (UC 1563096!); *Brainerd 1090* (CIC36366); 18 Apr 1889, *T. S. Brandegee s.n.* (UC 79306!); 14 Apr 1891, *T. S. Brandegee s.n.* (UC 79426!); 18 Apr 1895, *T. S. Brandegee s.n.* (UC 79424!); Palmetto Spring [Palm Springs], *T. S. Brandegee s.n.* (UC 79427!); *Bright 12847* (UC 598540!); *Burch 1IV95C* (SDSU 14056); *Charlton 1547* (UC 1552169!); *Clemons 1634* (SD 120961!); *Clemons 1951* (SD 122433); *Clemons 2020* (SD 122612!); 20 May 1880, *Cleveland s.n.* (UC 78821!); *Clokey 4709* (UC 857182!); *Clokey 5821* (SD 34115, UC 857180!); *Clokey 5926* (CAS 380904!, UC 900463!); *Clokey 8729* (UC 900462!); *Clokey 8730* (UC 900460!); *Clokey 8731* (CAS 380903!, UC 900461!); *Cole 905* (UC 1329936!); 21 Apr 2008, *Cooper s.n.* (UCR 193452); *Correll 38534* (LL 00034693, UC 1368220!); *Cowan 2266* (SD 127080!); *Crampton 2599* (UC 1278105!); *Cronquist 10103* (UC 1329620!); *Cronquist 10192* (DH 592832!); *Crum 1863* (UC 638805!); *Cusick 2020* (ORE76325); *Davy 2287* (UC 61135!); *De Groot 6587* (SD 219000!); 14 Mar 1995, *Delgadillo s.n.* (SD 165073!); *Dole 13* (UC 1578795!); *Duran 2743* (UC 1297585!); 17 Apr 1931, *Eastwood s.n.* (CAS 190280!); *Elmer 3682* (POM 49420); *Elvin 4661* (UCR 175753); *Elvin 514* (IRVC 29314, UCR 175753); *Ertter 6891* (UC 1562525!); ***Felger 17377* (SD 96180!);** *Felger 96-164* (ARIZ 371716); *Ferguson 4579* (UC 1554338!); *Ferris 9523* (UC 604897!); *Fosberg 10625* (UC 551812!); *Fosberg 10651* (UC 551859!); *Fosberg 3055* (UC 705061!); *Fraga 347* (UC 1927405!, UCR 200056); ***Gallup 193* (SDSU 5425!); *Gander 134* (SD 10507!);** *Gander 21* (SD 11172); *Gander 7087* (SD 24511); *Gander 7182* (SD 24606); *Gander 9* (SD 10507); *Gentry 8897* (SD 86410!); *Goodding 128-52* (UC 1025314!); *Goodding 2144* (UC 133654!); *Goodding 2203* (UC 133653!); *Gould 1594* (UC 857176!); *Gould 1657* (UC 857177!); *Gowen 551* (JEPS 116719!); *Grant 445a-6796* (UC 166838!); *Grant 445a-6796* (UC 174931!); 15 Mar 2006, *Green s.n.* (RSA 725855, UCR 170399); *Gregory 1333* (SD 172724); ***Gregory 667* (SD 158771!);** *Gross 514A* (RSA 757924); *Guilliams 566* (SDSU 18702); ***Guilliams 602* (SDSU 18956!);** *Hall 5938* (UC 100866!); *Halse 5950* (UC 1779137!); *Harbison s.n. 4 May 1939* (SD 25137!); 5 May 1939, *Harbison s.n.* (SD 25138!); *Harrison 7719* (CAS 193407!); *Heckard 4553* (JEPS 76497!); ***Hendrickson 2640* (SD 203297!);** *Hendrickson 2715* (SD 203298); ***Hendrickson 2784* (SD 205617!);** *Hendrickson 3530* (SD 214185); *Hendrickson 408* (SD 172725); ***Hendrickson 4588* (SD 210829!);** *Hendrickson 4695* (SD 210828); *Hendrickson 494* (SD 172721); *Hendrickson 514B* (SD 172722); *Hill 84* (ASC 77993); *Hitchcock 24241* (UC 1287107!); *Holmgren 7008* (UNM 54121); *Holmgren 8229* (UC 1018620!); *Hoover 3136* (UC 762462!); *Howe 2625* (SD 50962); ***Howe 2903* (SDSU 5419!);** *Howe 453* (SD 113115); *Hughes 208* (UCD 84936); *Jepson 15465* (JEPS 67949!); *Jepson 17103* (JEPS 67948!); *Jepson*

17120 (JEPS 67947!); *Jepson 17180f* (JEPS 67946!); *Jepson 18163* (JEPS 67945!); *Jepson 19504* (JEPS 67944!); *Jepson 19550* (JEPS 67943!); *Jepson 20295* (JEPS 67964!); *Jepson 20406* (JEPS 67942!); *Jepson 20539* (JEPS 67965!); *Jepson 5428* (JEPS 67956!); *Jepson 5954* (JEPS 67955!); *Jepson 7147* (JEPS 67954!); *Jepson 8603* (JEPS 67953!); *Jepson 8733* (JEPS 67952!); *Jepson 8831* (JEPS 67951!); *Jepson 8952* (JEPS 67950!); *Johnston 27R* (UC 306233!); *Jones 5023* (UC 133627!); 15 May 1920, *Jones s.n.* (UC 407942!); 2 Apr 1921, *Jones s.n.* (UC 407941!); 21 May 1884, *Jones s.n.* (UC 380863!); ***Jonsson 1634* (SD 120961!); *Jonsson 2020* (SD 122612!);** *Junak 1653* (SD 125584, UCR 58705); *Keck 4141* (UC 604178!); *Kennedy 1832* (UC 174706!); 15 Apr 1935, *Krames s.n.* (JEPS 67957!); 24 Feb 1935, *Krames s.n.* (JEPS 67958!); *La Doux 1034* (JOTR 28753); *La Doux 3052* (JOTR 33840); Apr 1881, *Lemmon s.n.* (UC 907598!); Apr 1886, *Lemmon s.n.* (UC 907601!); *Maguire 10423* (RM 147998, UC 553403!); *Maguire 16263* (UC 604223!); *Maguire 4959* (UC 533114!); *Maguire 4961* (UC 533113!); *Maguire 4963* (UC 533181!); 18 Jun 2008, *Mancuso s.n.* (NY1109936); *Mansfield 533* (CIC33195); *Mansfield 7084* (CIC34501); *Marisa Sripracha 514* (UCR 134590); *Marsden 538* (SD 205618!); *Marsden 7* (SD 159786); *Mason 2555* (UC 1393323!); *Mason 6867* (UC 573134!); *McVaugh 8193* (TEX 00034694); *Mistretta 4629* (RSA 771752); *Moran 10317.5* (SD 54531!); *Moran 10859* (SD 53783!); *Moran 12311* (SD 65317!); *Moran 12496* (SD 65316!); *Moran 12717* (SD 65315!); *Moran 19624* (SD 92326!); *Moran 20886* (SD 88930!); *Moran 22958* (SD 95519!); *Moran 30352* (SD 110836!); *Moran 30772* (SD 111259!); *Moran 6529* (SD 47530); *Moran 8112* (SD 60715!); *Morefield 3262* (UC 1534942!); *Morefield 3264* (UC 1534944!); *Morefield 3304* (UC 1535144!); *Morefield 3596* (UC 1545605!); ***Morgan K83* (SDSU 5421!);** *Munz 15644* (UC 1022816!); *Nelson 1284* (UC 595642!); *Nenow 149* (SD 174381); *Nielsen 2004011* (CIC32531); *Otting 1589* (CIC36340); *Palmer 371* (UC 79304!, UC 79305!); *Parish 2815* (POM 3709); *Parish 6943* (UCR 208136); *Parish 8464* (JEPS 67961!); *Parish s.n. May 1887* (UC 193914!); *Parish s.n. May 1895* (JEPS 67959!); *Peck 25598* (OSC79575, UC 801189!, WILLU27441); *Peebles 6975* (CAS 252113!); *Peirson s.n. 16 Feb 1920* (RSA 79960); *Pitzer 2041* (UCR 106267); ***Purer 4943* (SD 39196!);** 9 Apr 2008, *Rado s.n.* (UCR 196042); *Raven 11621* (UC 1114560!); *Rebman 11304* (SD 168432); *Rebman 11358* (SD 168431); *Rebman 1484* (SD 137251!); ***Rebman 21541A* (SD 213031!);** *Rickard 1853* (DH 562256!); *Robbins 3306b* (UC 981781!); *Rose 37152* (UC 857178!); *Rose 40319* (UC 857179!); 10 Mar 1940, *Rose s.n.* (CAS 275467!); *Ross 4964* (UC 1871251!); *Rue 91-14* (SD 133159); *Salvato 3221* (UCR 203176); *Salywon 1050* (SD 188428!); *Sanders 23840* (UCR 116613); *Sanders 23845* (UCR 116628); *Sanders 23943* (UCR 116813); *Sanders 24021* (UCR 116727); *Sanders 34502* (UCR 192610); *Sanders 34881* (UCR 194156); *Sanders 36698* (UCR 210808); *Sanders 37504* (UCR 214414); *Sanders 38262* (UCR 215039); *Sanders 7702* (UCD 119901); **13 Mar 1982, *Scheidlinger s.n.* (SDSU 18155!);** *Schreiber 990* (UC 608476!); *Schweich 762* (UC 1980484!); *Shreve 10089* (UC 664989!); ***Simpson 3126* (SDSU 19604!); *Simpson 3670* (SDSU 20043!); *Simpson 5IV97C* (SDSU 12434!);** *Smith 149* (JEPS 67963!); *Smith 64* (JEPS 67962!); *Spencer 1918* (UC 857184!); *Spencer 514* (POM 47458); *Sripracha 6* (UCR 134590); 12 Mar 1927, *Stason s.n.* (UC 573124!); *Stoughton 970* (RSA 777445); *Strother 1261* (UC 1434007!); ***Sweet 509* (SD 200747!);** *Sweet 514* (SD 200747); *Swinney 3449* (UCR 180969); *Swinney 3652* (RSA 719189, UCR 180763); *Tavares 478d* (UC 1250315!); *Taylor 16546* (UC 1731360!); *Thorne 60111* (SD 124982!); *Thorne 62954* (RSA 760357); *Thoruber 443* (UC 128172!); *Tiehm 11059* (OSC168584); *Tiehm 16118* (ID162176-bc141194); *Toumey 93* (UC 78825!); *Toumey s.n. 15 Apr 1894* (UC 24837!, UC 78824!); 3 Apr 1894, *Toumey s.n.* (UC 220606!); *True Jr. 304* (UC 1537677!); *Turner 21-237* (TEX 00300342); ***Turner 68-94* (SD 78609!);** *Vasek 600320–01* (UCR 1373B); *Vinton s.n. 18 Mar 2003* (SD 182664!); *Webster 18216* (SD 95971!); *Wiggins 11544* (UC 754314!); *Wiggins 2013* (SD 48710, UC 1019590!); *Wiggins 262* (SD 94536!); *Wiggins 9566* (UC 665774!); *Wilder 10-116* (SD 218101!); *Wilder 10-248* (SD 218100!); *Wilson 98* (UC 61134!); *Wilson s.n. May 1893* (UC 61136!); *Witham 706* (SD 80848); ***Wojtan 4IV92C* (SDSU 5394!);** *Wolf3202* (RSA 4003); *Wooten s.n. 19 Apr 1905* (DH 137011!, SD 67704!, UC 112658!, UC 480465!); *Wotjan 4IV92C* (SDSU 5394); *Wright 1772* (UC 24834!); *Yates 5394* (UC 573635!); *Yates 6400* (UC 573262!, UC 1063825!).