



## Taxonomy of the winged popcorn flower: *Cryptantha pterocarya* (Boraginaceae)

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### Abstract

*Cryptantha pterocarya* (Boraginaceae), the winged nut popcorn flower, is distinguished in part by nutlets with marginal, typically lobed wings. Four varieties of this species have been accepted in recent treatments: vars. *cycloptera*, *pterocarya*, *purpusii*, and *stenoloba*. We tested the taxonomic discreteness, degree of variation, and geographic range of these varieties of *C. pterocarya* by examining material from numerous voucher specimens. We quantified differences among specimens by measuring or calculating twenty features of the corolla and fruit, the latter focusing on mature (fruiting) calyx and nutlet characteristics. Type specimens of all four varieties were examined and quantified, and all specimens were georeferenced and mapped. From our observations and measurements, we recognize two new morphological forms in the complex, termed the “pseudocycloptera” form and the “truncata” form. The “pseudocycloptera” form is similar to var. *pterocarya* but is homomorphic, with all four nutlets winged. The “truncata” form is similar to var. *cycloptera*, but is heteromorphic, with the odd nutlet having a reduced basal wing (somewhat truncate in shape) and having a slightly reduced gynobase stipe. We conclude that *C. p.* var. *pterocarya*, var. *purpusii*, and var. *stenoloba* should continue to be recognized as taxa at that rank. The “pseudocycloptera” form, although generally morphologically discrete in nutlet heteromorphism, shows some intergradation, even within a specimen, of the typical form of *C. p.* var. *pterocarya* and exhibits no clear geographic discontinuity; it should thus be recognized as a homomorphic form of that taxon, which we formally name forma *pseudocycloptera*. Variety *purpusii* should continue to be recognized at that rank given its variation in nutlet wing morphology but with continuity in geographic range. Variety *stenoloba* should also continue to be recognized at this rank given its distinctive calyx and nutlet body size and shape, but having a quite limited geographic range. We conclude that what has been most commonly recognized as *C. pterocarya* var. *cycloptera* should be resurrected to the rank of species, as *C. cycloptera*, because of the distinctiveness of this taxon in three, discrete morphological characters, one of which (gynobase stipe) was previously undescribed. The “truncata” form, which shows some intergradation with *C. cycloptera* and lacks geographic discontinuity, should be recognized as a heteromorphic form of *C. cycloptera*, which we formally name forma *truncata*. A revised key is proposed to better accommodate the identity of these taxa and forms. We hope that future molecular studies will elucidate the phylogenetic relationships, character evolution, and geographic history of this interesting taxonomic complex.

**Key words:** Boraginaceae, *Cryptantha*, *Cryptantha cycloptera*, *Cryptantha pterocarya*, nutlet, taxonomy

### Introduction

*Cryptantha pterocarya* (Torrey) Greene (1887: 120), often commonly known as the “winged popcorn flower,” is a species of the family Boraginaceae, tribe Cynoglosseae (Långström & Chase 2002, Cohen 2014, Weigend et al. 2013), subtribe Amsinckiinae Brand (1931: 204, =Cryptanthinae of Hasenstab-Lehman & Simpson 2012). This species occurs in Arizona, California, Colorado, Idaho, Nevada, New Mexico, Oregon, Texas, Utah, Washington in the U.S. (Kartesz 2014, Kelley and Simpson, in prep), and in Baja California (BajaFlora 2014), Sonora, and Chihuahua in Mexico (SEINet 2014). The species is distinctive within the genus in having four nutlets per fruit (reduced in number in some specimens) with a tuberculate-papillate nutlet body and at least some nutlets having a marginal wing that is typically lobed, but reduced to a ridge in certain specimens. Nutlets are either homomorphic, with all nutlets similar in form, or heteromorphic, with three (consimilar) nutlets alike and one (odd) nutlet more persistently attached to the gynobase, with a reduced or absent wing in some taxa or forms. Heteromorphic fruits are found in many members of the family

Boraginaceae and may serve as an adaptive dispersal device with the larger nutlet remaining attached to the calyx and the similar nutlets dispersing separately (Grau 1983).

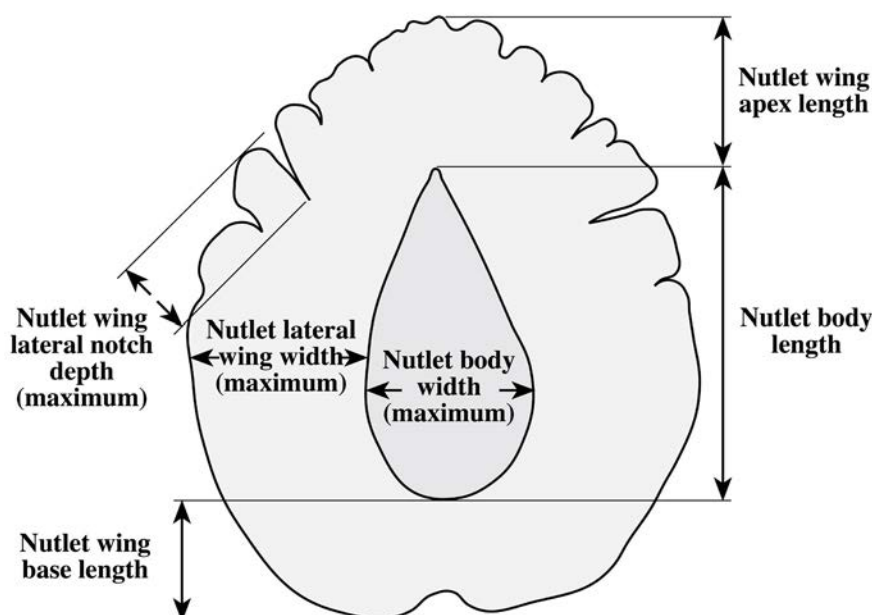
*Cryptantha pterocarya* is divided into as many as four varieties in recent treatments (e.g., Abrams 1951, Cronquist 1984, Kearney & Peebles 1960, Kelley & Wilken 1993, Kelley *et al.* 2012): var. *pterocarya*, var. *cycloptera* (Greene) J. F. MacBride (1916: 44), var. *purpusii* Jepson (1925: 849), and var. *stenoloba* I. M. Johnston (1939: 391), the last sometimes not recognized. Variety *pterocarya* has heteromorphic nutlets, the odd nutlet unwinged and the three consimilar nutlets winged laterally and apically but not at the nutlet base. Variety *cycloptera* has homomorphic nutlets, all of which are winged, the wing completely encircling the nutlet body, including the base (although the latter feature is usually not mentioned in taxonomic treatments or keys). Variety *purpusii* has either heteromorphic or homomorphic nutlets with the wing reduced, sometimes to a narrow rim. Finally, variety *stenoloba* is identical to var. *pterocarya* in nutlet morphology, but is distinguished in having a markedly longer calyx.

Of these four varieties, var. *cycloptera* was originally treated as a separate species, *C. cycloptera* Greene (1887: 120), but was reduced in rank to variety by Macbride (1916) and has been treated as a variety in most taxonomic treatments to date (e.g., in all of the treatments cited earlier). In addition, one taxonomic synonym of *C. pterocarya* has been described: *C. pterocarya* (Torrey) Greene var. *pectinata* (A. Gray) Brand (1931: 55). The basionym of this variety, *Eritrichium pterocaryum* Torrey var. *pectinatum* A. Gray (1874: 61) was originally diagnosed as “forma alis fructus pectinato-multifidis” (form with fruit wing pectinate, i.e. with comb-like divisions) and a subsequent new combination, *Krynitzkia pterocaryum* (Torrey) A. Gray var. *pectinata* (A. Gray) A. Gray (1885: 276) as “forma ala nucularum pectinato-laciniata” (form with wing of the nutlet pectinate-lacinate, i.e., having comb-like to irregular divisions). However, this taxon has not been accepted in any subsequent taxonomic treatments of which we are aware, and Johnston (1925: 54), based in part on the doubtful identify of the type specimen (listed by him as *Parry 168–169*, which we recently located as NY 01111827), stated “it seems best to drop the varietal name *pectinatum* as a *nomen confusum*, particularly since the lobing of the nutlet-wing seems to be too hopelessly variable and unimportant to justify nomenclatural recognition.” These morphological characters and taxonomic issues likely led Johnston (1925: 53) to state that *C. pterocarya* was “one of the most interesting species in the genus.”

The objective of this study is to evaluate the distinctiveness of the varieties and forms of *Cryptantha pterocarya* using morphometric analyses and to note correlations of these forms with geographic range. The closely related species, *C. oxygona* (A. Gray) Greene (1887: 120), which differs from *C. pterocarya* in having a large corolla, but otherwise resembles forms of *C. pterocarya* var. *purpusii* with reduced nutlet wings, was included in some analyses for comparison.

## Materials and Methods

Herbarium specimens were obtained from eleven herbaria: Arizona State University (ASU), California Academy of Sciences (CAS, DS), Harvard University Herbarium (GH, HUH), New York Botanical Garden (NY, this a scan of the type of *C. pterocarya*), Rancho Santa Ana Botanical Garden (POM, RSA), San Diego Natural History Museum (SD), San Diego State University (SDSU), Santa Barbara Botanic Garden (SBBG), University of Arizona (ARIZ), University of California, Berkeley (JEPS, UC), and University of California, Riverside (UCR). A total of 199 specimens were sampled, annotated, georeferenced, and measured: 27 *Cryptantha pterocarya* var. *pterocarya*, 51 *C. p.* var. *cycloptera*, 50 *C. p.* var. *purpusii*, 12 *C. p.* var. *stenoloba*, 25 *C. p.* “pseudocycloptera”, 23 *C. pterocarya* “truncata”, and 11 *C. oxygona* (Appendix 3). For each specimen, the mature fruit calyx body length, calyx body width, sepal width, sepal length:width ratio (from the same sepals), and corolla limb diameter (at anthesis) were measured or calculated and averaged from 5–10 measurements. Two to three mature fruits per plant were removed and the fruits then placed on a microscope slide with double stick tape and dissected open. If nutlets were not easily removed, whole fruits were submerged in boiling deionized water for about 30 seconds and then dissected apart and air-dried. Nutlet features measured were length and maximum width of the nutlet body (not including any marginal wings), nutlet lateral wing maximum width (on one side measured perpendicular to nutlet axis, both sides measured and averaged), nutlet wing length at apex, nutlet wing length at base, and maximum wing notch depth (Fig. 1). For heteromorphic fruits, the odd nutlet was calculated separately from the consimilar nutlets. If fruits were homomorphic, all consimilar nutlets were averaged together. Lastly, the stalk (“stipe”) of the gynobase, below the attachment of the nutlets, was measured after the nutlets had been removed. Measurements were made with a video-interfaced dissecting microscope using ImageJ software (Rasband 1997–2007, see Abramoff *et al.* 2004). All measurements were averaged per herbarium specimen and used for analyses (Table 1).



**FIGURE 1.** Diagram showing nutlet features measured for statistical study.

To visualize character distributions by taxon, box plots showing the median and the four quartiles of distribution were prepared for twelve characters (listed in Table 1). These were evaluated for statistically significant differences by taxon using analysis of variance (ANOVA), with multiple comparisons made between the taxa or forms for each character using the Tukey post hoc test. All statistical analyses were performed in SYSTAT, Version 11 (Systat Software, Inc., San Jose CA; <http://www.systat.com>).

A principal components analysis (PCA) was performed on all 199 samples (Appendix 3) for 16 characters (indicated in Table 1). Variables were standardized by subtracting the total mean for each character from each sample measurement, then dividing by the total standard deviation. This guaranteed that each variable had a mean of zero and a standard deviation of 1. The factors of the PCA were plotted for the 1st versus the 2nd components, 2nd versus the 3rd components, and 1st versus 3rd components. Loadings were tabulated for each component (Table 2).

To evaluate geographic ranges, 1,955 herbarium specimens of *C. pterocarya* taxa and forms were georeferenced and mapped. Of these 1,756 specimens (including those measured) from the eleven herbaria mentioned earlier—ASU, ARIZ, GH, CAS-DS, NY, RSA-POM, SBBG, SD, SDSU, UC-JEPS, and UCR—were identified and annotated by us. An additional 199 specimen records from thirteen herbaria—BCMEX, CS, ID, NMCR, NMC, OSC, ORE, UNM, USUUB, UVSC, WILLU, WS, and WTU—were georeferenced and included but not verified by us to taxon (Appendix 3). If a variety was listed from these latter herbaria, that identification was used. For any specimen not identified to variety but located in a state where only *Cryptantha pterocarya* var. *pterocarya* was reported to occur, we felt confident to use that as the identity; otherwise that specimen was not considered. Finally, in order to assess possible correlation of wing size with geographic region in *C. pterocarya* var. *purpusii*, a graphic was prepared that portrays the relative wing width (on one side of the nutlet) as a function of a circle diameter, these overlaid on a terrain map.

**TABLE 1.** Characters used in *Cryptantha pterocarya*/*C. oxygona* analyses, all measured in mm. Note that all characters except sepal width, sepal length:width ratio in fruit, and consimilar and odd nutlet body length:width ratio were used in the PCA analysis; those with an asterisk were included in boxplots and ANOVA analyses.

Calyx Body Length in Fruit*	Consimilar Nutlet Wing Base Length*
Calyx Body Width in Fruit	Consimilar Nutlet Wing Maximum Notch Depth*
Sepal Width in Fruit*	Odd Nutlet Body Length
Sepal Length:Width Ratio in Fruit*	Odd Nutlet Body Maximum Width
Corolla Limb Diameter*	Odd Nutlet Body Length:Width Ratio
Consimilar Nutlet Body Length*	Odd Nutlet Lateral Wing Width*
Consimilar Nutlet Body Maximum Width	Odd Nutlet Wing Apex Length
Consimilar Nutlet Body Length:Width Ratio*	Odd Nutlet Wing Base Length*
Consimilar Nutlet Lateral Wing Width*	Odd Nutlet Wing Maximum Notch Depth
Consimilar Nutlet Wing Apex Length	Gynobase Stalk Length*

**TABLE 2.** Principal Components Analysis Loadings for Characters Used in Analysis. Percent of total variance explained as: axis 1 = 41%, axis 2 = 24%, and axis 3 = 9%.

Component Loadings			
Character	1	2	3
Calyx Body Length in Fruit	0.78	0.24	-0.19
Calyx Body Width in Fruit	0.73	0.32	-0.38
Corolla Limb Diameter	-0.37	0.18	0.25
Consimilar Nutlet Body Length	0.59	0.74	0.09
Consimilar Nutlet Body Max. Width	0.48	0.50	0.59
Consimilar Nutlet Lateral Wing Width	0.84	0.18	-0.23
Consimilar Nutlet Wing Apex Length	0.82	0.01	-0.24
Consimilar Nutlet Wing Base Length	0.62	-0.67	-0.05
Consimilar Nutlet Wing Max. Notch Length	0.78	0.18	-0.41
Odd Nutlet Body Length	0.53	0.77	0.10
Odd Nutlet Body Max. Width	0.43	0.55	0.55
Odd Nutlet Lateral Wing Width	0.67	-0.45	0.33
Odd Nutlet Wing Apex Length	0.68	-0.52	0.26
Odd Nutlet Wing Base Length	0.64	-0.65	0.16
Odd Nutlet Wing Max Notch Depth	0.51	-0.28	0.10
Gynobase Stalk Length	0.54	-0.67	0.18

## Results

Our observations of the holotype material of *Cryptantha pterocarya* confirm it to have heteromorphic nutlets (Fig. 2A–C). The nutlet surface is covered with numerous, minute papillae and fewer, larger, scattered tubercles. The three consimilar nutlets have prominent, usually laterally lobed wings that do not, however, extend along the nutlet base (Fig. 2B,E). The single odd nutlet lacks a wing, having a sharp nutlet margin (Fig. 2D). Tubercles of the odd nutlet are often slightly spinulose, particularly toward the nutlet apex (Fig. 2D).

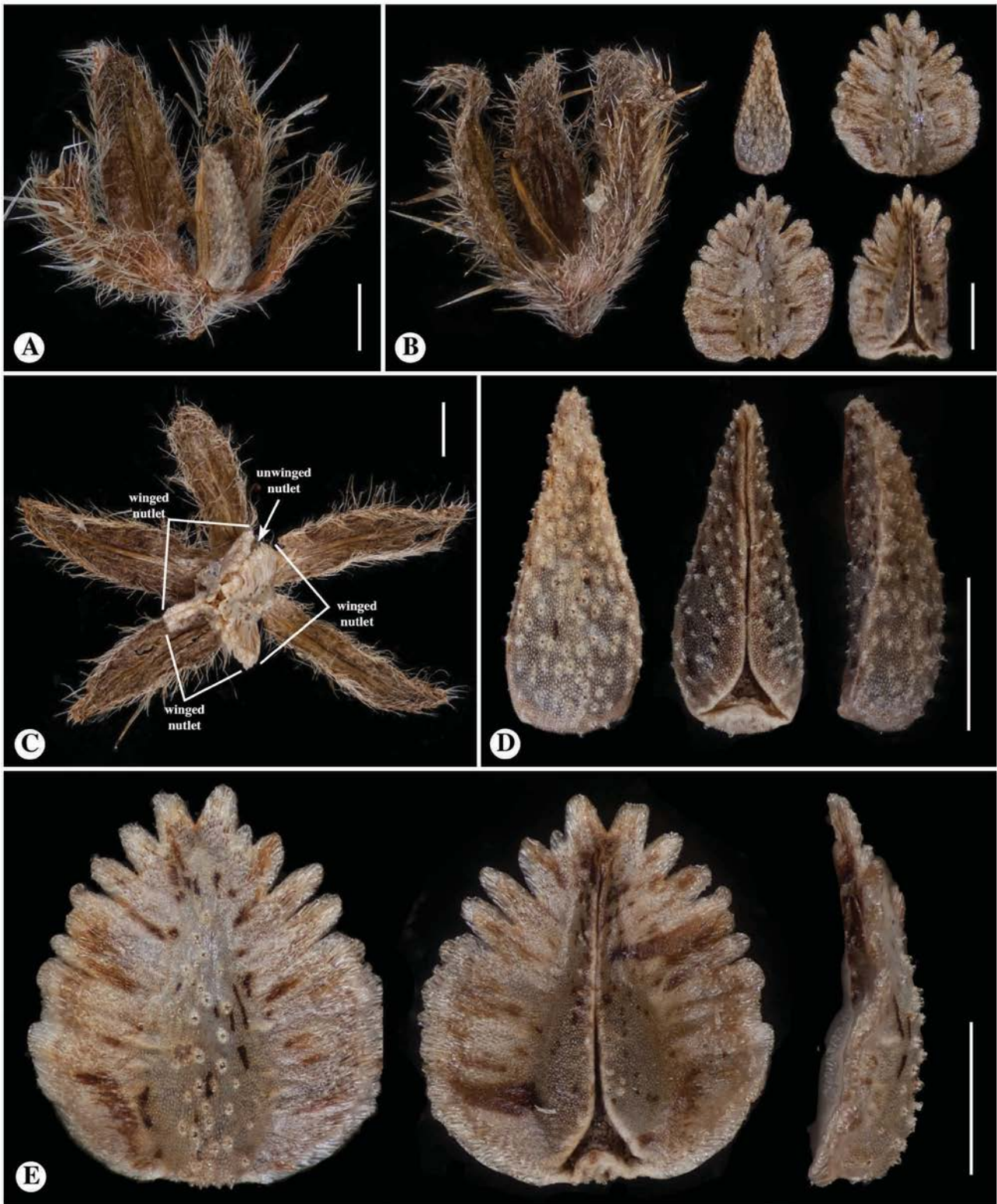
The holotype material of what is typically classified as *C. pterocarya* var. *cycloptera* confirms the nutlets to be homomorphic, all four with prominent wings that completely encircle the nutlet body, including the base (Fig. 3A–D). Variety *cycloptera* also possesses what we term a “gynobase stipe,” a stalk-like region below the gynobase (Fig. 3C). The gynobase stipe appears to spatially accommodate the basal wing of the nutlets. Variety *pterocarya* lacks any appreciable gynobase stipe, as do varieties *purpusii* and *stenoloba* (see discussion below).

Our study of numerous specimens revealed two previously undescribed “forms” of *C. pterocarya*. What we term the “pseudocycloptera” form is otherwise similar to var. *pterocarya* but is homomorphic, with all four nutlets winged, although with the wings *not* extending along the base of the nutlet body (Fig. 4A). What we term the “truncata” form is otherwise similar to var. *cycloptera*, but is heteromorphic, with the odd nutlet having a variably reduced wing along the sides and base, the basal region roughly truncate in shape (Fig. 4B, C).

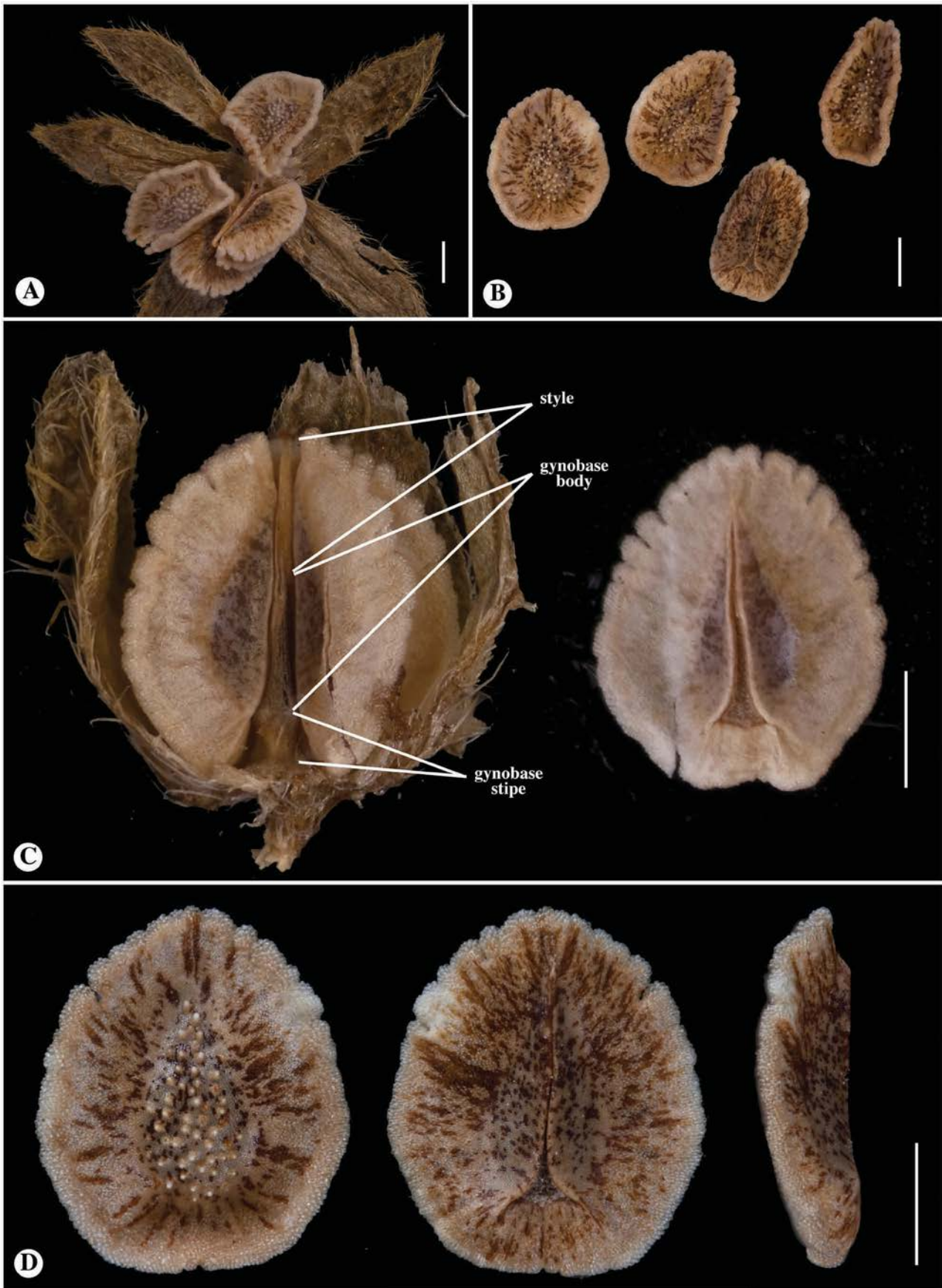
Observations of the holotype material of *C. p.* var. *purpusii* shows it to have heteromorphic nutlets (Fig. 5), the consimilar nutlets with reduced, shallowly lobed (fringed) wings and the odd nutlet unwinged, resembling the odd nutlet of *C. p.* var. *pterocarya* (Fig. 2D). However, the nutlets of *C. p.* var. *purpusii* are generally smaller than those of var. *pterocarya* (compare Fig. 5 with Fig. 2; see Fig. 7). The wing size and degree of heteromorphism in *C. p.* var. *purpusii* is rather variable among specimens, being heteromorphic with the consimilar nutlets having a well-developed wing (albeit significantly smaller than that of vars. *pterocarya* or *cycloptera*; Fig. 6A, B) to homomorphic with the wing reduced to a marginal rim (Fig. 6C, D), resembling more the “knife-like” margin of the odd nutlet of *C. p.* var. *pterocarya* (Fig. 2D). A nutlet of the related *Cryptantha utahensis* (A. Gray) Greene (1887:120), which generally is solitary (occasionally two) per fruit, was imaged for comparison (Fig. 6E). Nutlets of this species resemble the odd nutlet of *Cryptantha pterocarya* var. *pterocarya* and of some specimens of *C. pterocarya* var. *purpusii* in being tuberculate-papillate with a sharp margin, but differs in generally having a more spinulose margin and apical region (the length of spinulose processes varying from prominent to barely visible). In addition, a nutlet of the related *C. oxygona*, which has four, homomorphic nutlets per fruit, was imaged for comparison (Fig. 6F). Nutlets of this species resemble the homomorphic, sharp-angled forms of *C. pterocarya* var. *purpusii* (e.g., compare with Fig. 6D).

Our observations of the type material of *Cryptantha pterocarya* var. *stenoloba* (Fig. 7A,C) confirms the presence of heteromorphic nutlets (Fig. 7C, E, F) that are otherwise similar to *C. p.* var. *pterocarya* (Fig. 7G) and *C. p.* var.

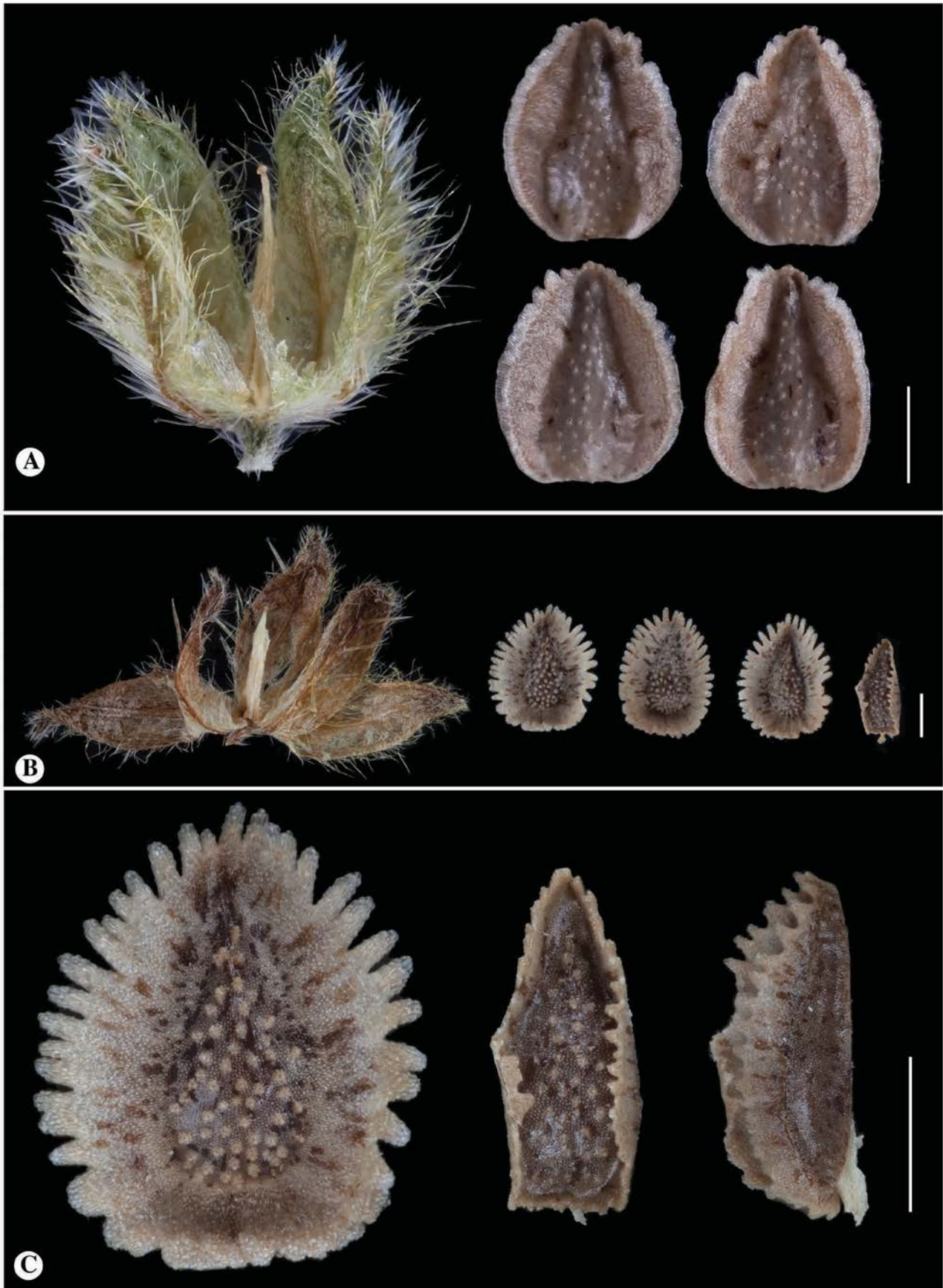
*purpusii* (Fig. 7I) in lacking a basal nutlet wing characteristic of *C. pterocarya* var. *cycloptera* (Fig. 7H). Variety *stenoloba* is also confirmed to have a considerably larger calyx (Fig. 7A–C) than *C. p.* var. *pterocarya* (Fig. 7D).



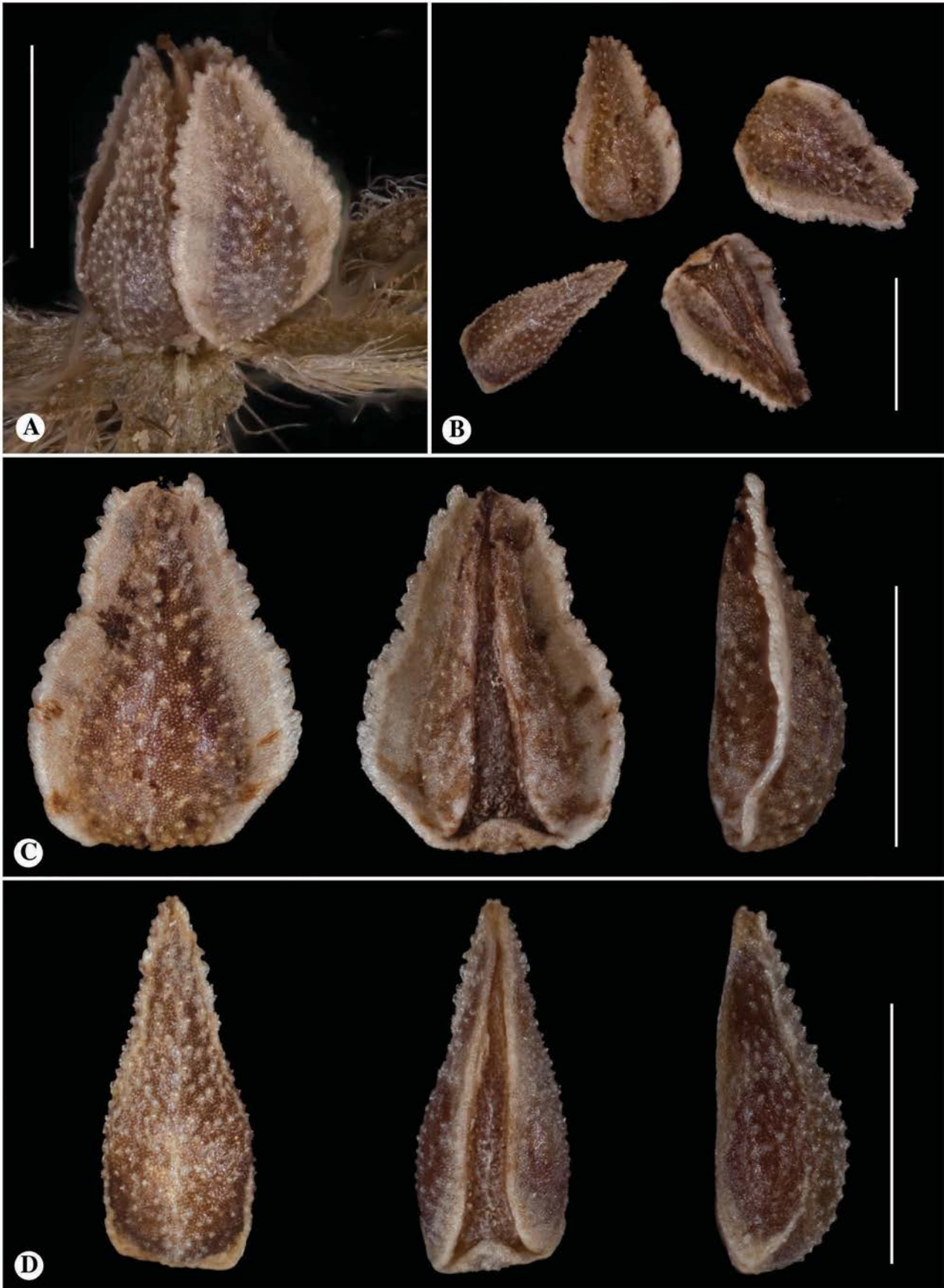
**FIGURE 2.** *Cryptantha pterocarya* var. *pterocarya*, Wilkes Expedition 1047 (Holotype). A. Fruit, with odd, unwinged, persistent nutlet attached to gynobase, winged nutlets removed or fallen off. B. Fruit, showing calyx and gynobase/style (left) and four, heteromorphic nutlets (right). C. Fruit with calyx, showing three winged and one unwinged nutlets attached to central gynobase. D. Unwinged, odd nutlet in dorsal (left), ventral (middle), and side (right) views. E. One of three winged, consimilar nutlets in dorsal (left), ventral (middle), and side (right) views. Scale bars = 1 mm.



**FIGURE 3.** *Cryptantha pterocarya* var. *cycloptera* [*C. cycloptera*], Pringle s.n. (Holotype). A. Fruit with calyx and four nutlets. B. Nutlets of fruit removed; note homomorphism. C. Fruit, side view, with one nutlet removed. Note gynobase body, style, and elongate gynobase stipe. D. Single nutlet in dorsal (left), ventral (middle), and side (right) views. Scale bars = 1 mm.

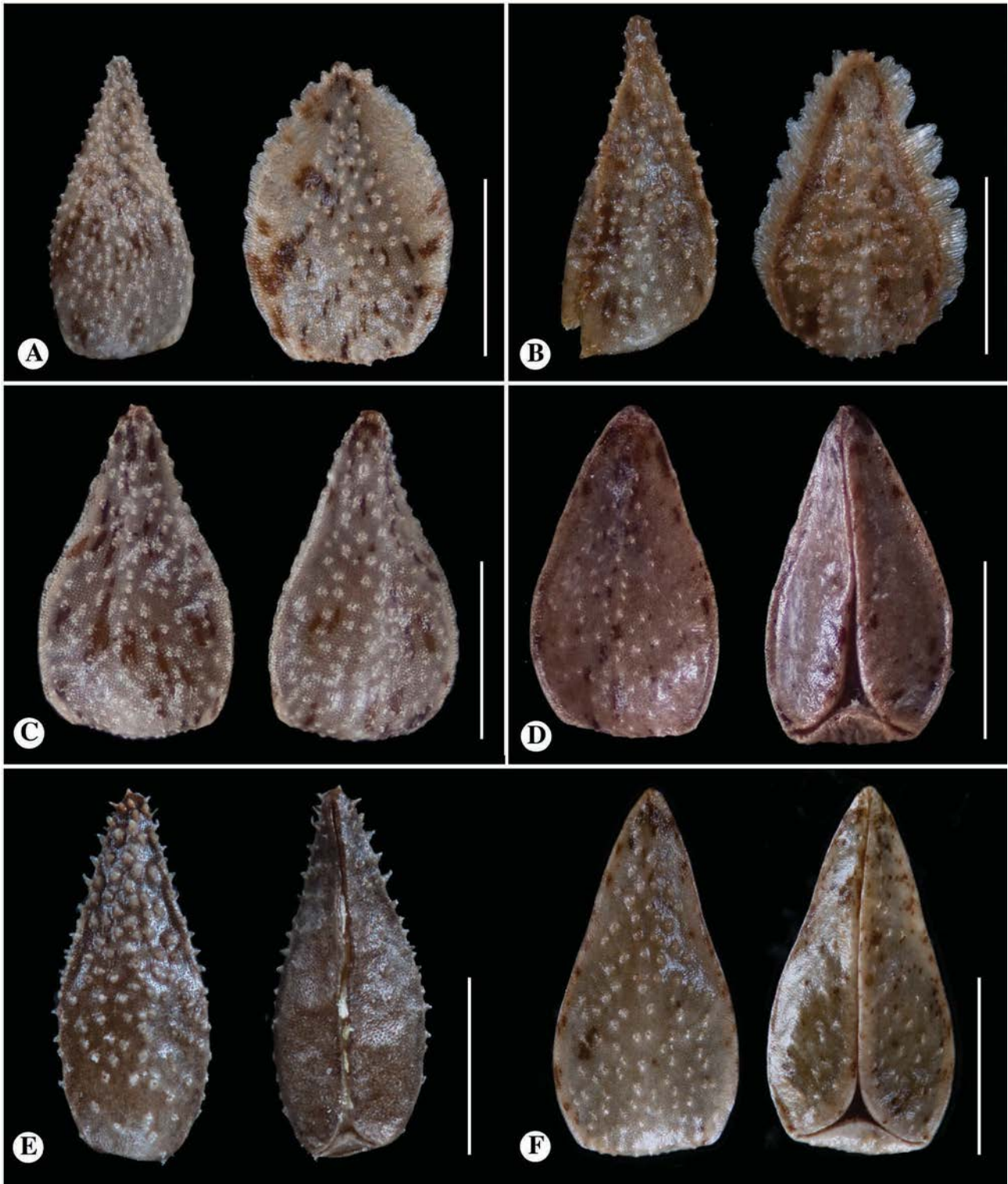


**FIGURE 4.** A. *Cryptantha pterocarya* “pseudocycloptera” form (SD 18704), with homomorphic nutlets, all similar to the consimilar nutlets of typical *C. p.* var. *pterocarya*. B–C. *Cryptantha pterocarya* var. *cycloptera* [*C. cycloptera*], “truncata” form (ASU 217654), with three consimilar, winged nutlets (wing encircling nutlet body) and one odd nutlet with reduced wing at sides and base. Scale bars = 1 mm.

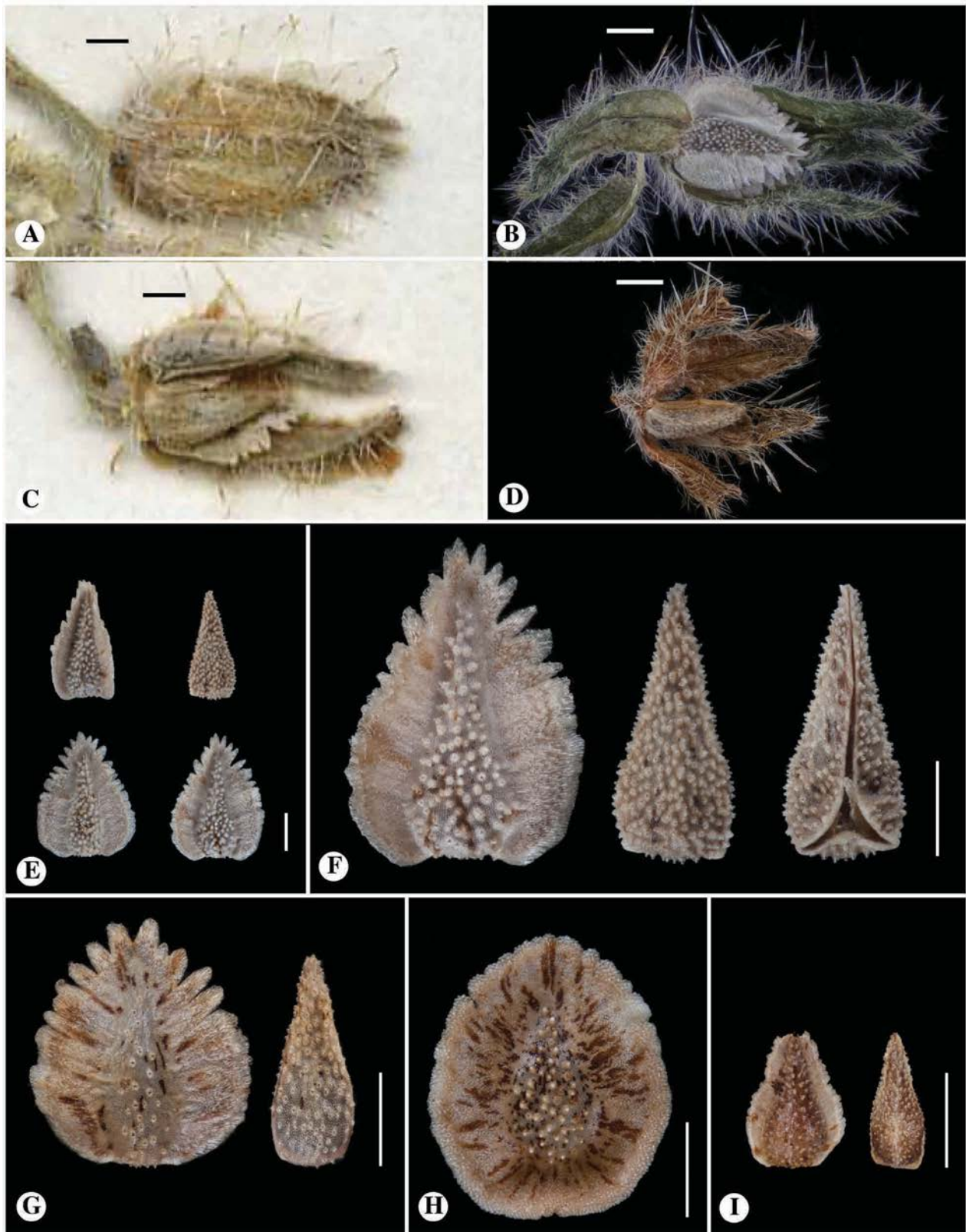


**FIGURE 5.** *Cryptantha pterocarya* var. *purpusii*, Purpus 5433 (Holotype). A. Fruit with calyx and four nutlets. B. Nutlets of fruit removed; note heteromorphism. C. One of three consimilar, winged nutlets in dorsal (left), ventral (middle), and side (right) views. D. Odd, unwinged nutlet in dorsal (left), ventral (middle), and side (right) views. Scale bars = 1 mm.





**FIGURE 6.** A–D. *Cryptantha pterocarya* var. *purpusii*, showing variation in nutlet morphology. A. Specimen with heteromorphic nutlets, odd nutlet unwinged (left) and consimilar nutlets with relatively broad wing (right) (RSA 730967). B. Specimen with heteromorphic nutlets, odd nutlet marginally ridged (left), consimilar nutlets (right) more narrowly winged, winged strongly lobed (SD 91861). C–D. Specimens with homomorphic nutlets, nutlet margin ridged. (C, SDSU 18624; D, RSA 728905). E. Nutlet of *Cryptantha utahensis* (SDSU 17286), shown for comparison with odd, unwinged nutlet of *C. pterocarya*; dorsal view (left), ventral view (right). F. Nutlet of *Cryptantha oxygona* (RSA 717219), shown for comparison with certain forms of *C. pterocarya* var. *purpusii*; dorsal view (left), ventral view (right). Scale bars = 1 mm.

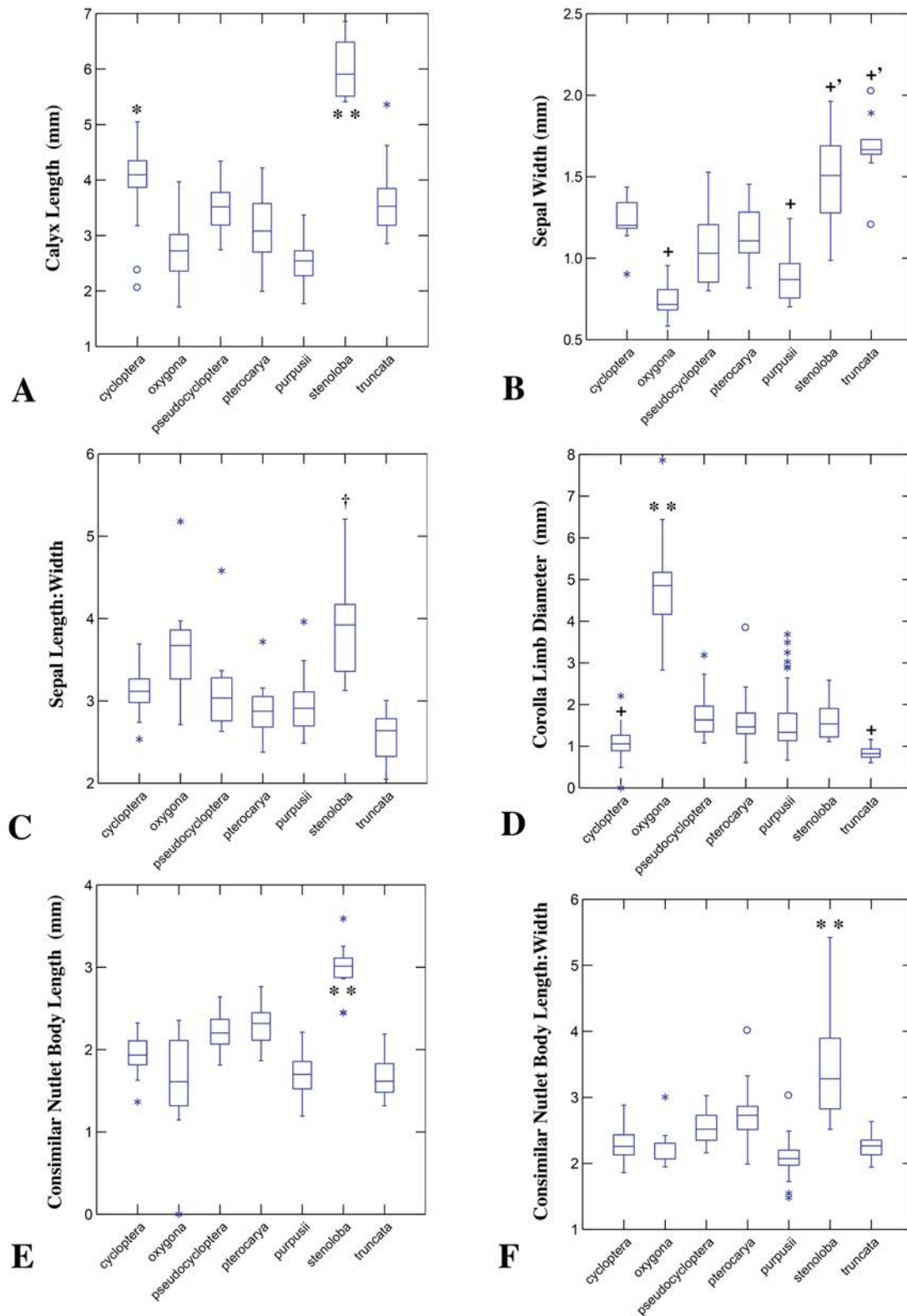


**FIGURE 7.** A–C. *Cryptantha pterocarya* var. *stenoloba*, showing elongate calyx and nutlets. A, C. *Maguire & Blood 4466* (Holotype), images from scanned herbarium sheet. B. Fruits of additional specimen of *C. p.* var. *stenoloba* (RSA 782075). D. *Cryptantha p.* var. *pterocarya* (NY 00335248, Holotype) for comparison. Note shorter nutlets and considerably shorter calyx. E, F. *Cryptantha p.* var. *stenoloba* (GH barcode 00096072, Holotype). E. Four nutlets of a single fruit, showing heteromorphism, with three consimilar nutlets winged only on sides and one odd, unwinged nutlet. F. One of consimilar nutlets, dorsal view (left) and single odd nutlet in dorsal (middle) and ventral (right) views. G–I. Comparison of nutlet form with other varieties, all to the same scale as “F.” G. *Cryptantha p.* var. *pterocarya* (NY 00335248, Holotype). H. *Cryptantha pterocarya* var. *cycloptera* [*C. cycloptera*] (CAS 202, barcode 0006884, Holotype). I. *Cryptantha p.* var. *purpusii*, (JEPS 2548, Holotype). Scale bars = 1 mm.

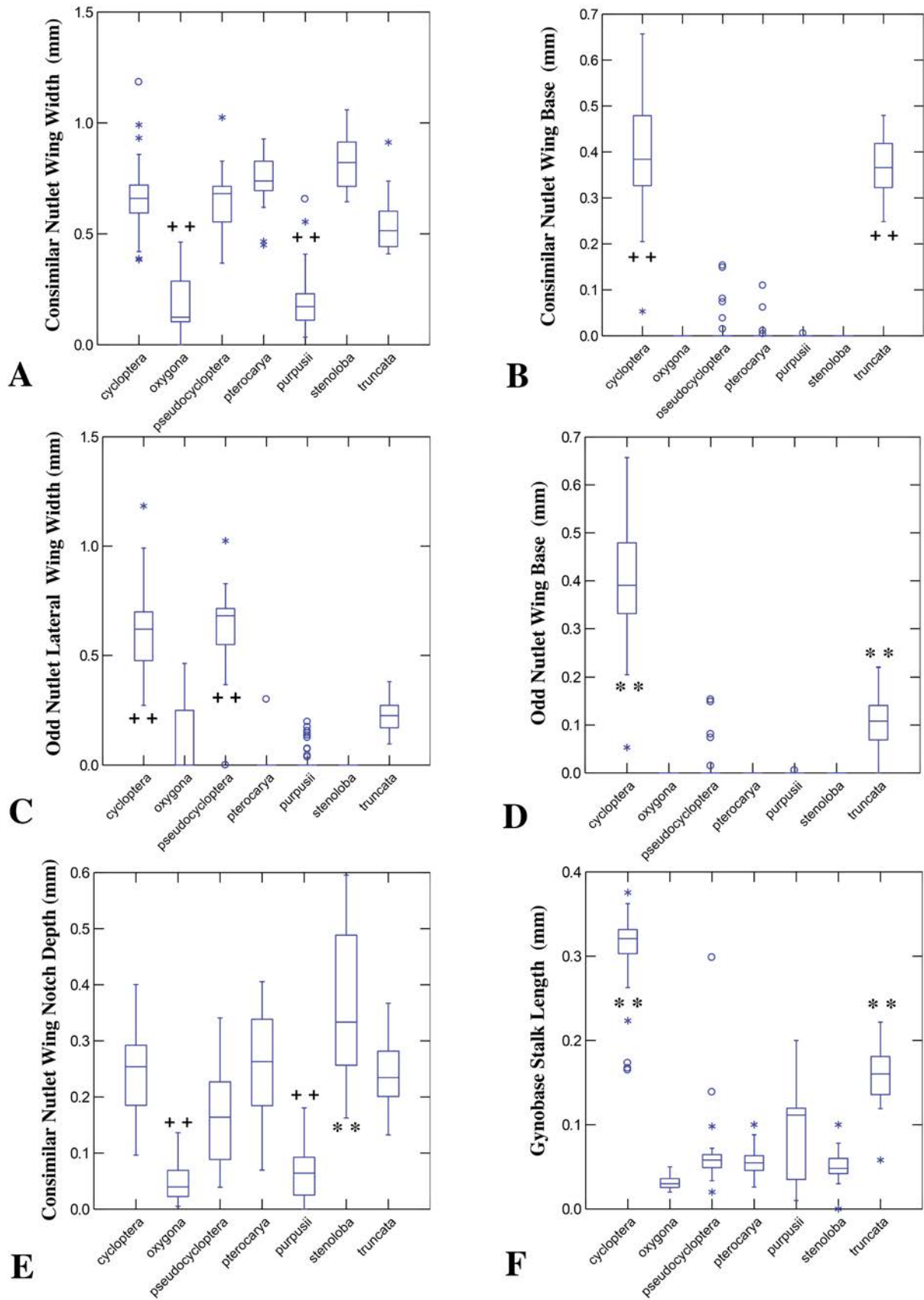
Boxplots and ANOVAs of selected characters indicate that, if the above taxa/forms are set as discrete: 1) *Cryptantha pterocarya* var. *stenoloba* has a significantly longer calyx body length ( $p < 0.01$ ) relative to all other taxa with no overlap; *C. p.* var. *cycloptera* has a significantly longer calyx body length ( $p < 0.05$ ) relative to the remaining taxa, although with considerable overlap (Fig. 8A); 2) No taxon has significantly wider or narrower sepals relative to the other taxa; however, *C. p.* var. *stenoloba* and the “truncata” form have significantly wider sepals than the other five taxa/forms ( $p < 0.05$ ) with overlap, but not to one another, and *C. oxygona* and *C. p.* var. *purpusii* have significantly narrower sepals than the other five taxa/forms ( $p < 0.05$ ) but not to one another with overlap (Fig. 8B); 3) *Cryptantha pterocarya* var. *stenoloba* has a sepal length:width ratio significantly greater than all other taxa and forms of *C. pterocarya* ( $p < 0.05$ ) but not with *C. oxygona*, the latter not significantly different from the other five taxa or forms (Fig. 8C); 4) *Cryptantha oxygona* has a significantly wider corolla limb diameter ( $p < 0.01$ ) with some overlap, whereas *C. p.* var. *cycloptera* and the “truncata” form have a significantly smaller corolla limb diameter than all other taxa/forms but not to one another ( $p < 0.05$ ) with considerable overlap (Fig. 8D); 5) *Cryptantha p.* var. *stenoloba* has a significantly longer nutlet body length ( $p < 0.01$ ) than all other taxa/forms with some overlap (Fig. 8E); 6) *Cryptantha p.* var. *stenoloba* has a significantly greater nutlet body length:width ratio ( $p < 0.01$ ) than all other taxa/forms with some overlap (Fig. 8F); 7) *Cryptantha oxygona* and *C. p.* var. *purpusii* have significantly smaller lateral wing widths relative to all other taxa ( $p < 0.05$ ) with some overlap, but not to one another (Fig. 9A); 8) *Cryptantha pterocarya* var. *cycloptera* and the “truncata” form have a consimilar basal nutlet wing significantly longer than all other taxa and forms with almost no overlap ( $p < 0.01$ ), but not to one another (Fig. 9B); 9) *Cryptantha p.* var. *cycloptera* and the “pseudocycloptera” form have a significantly wider odd nutlet lateral wing width relative to all other taxa and forms ( $p < 0.01$ ) but not to one another (Fig. 9C); 10) the “truncata” form has an odd nutlet wing base that is significantly longer than all other taxa and forms except *C. pterocarya* var. *cycloptera* ( $p < 0.01$ ), and the latter has a nutlet wing base significantly longer than all taxa and forms ( $p < 0.01$ ), with some overlap (Fig. 9D; note that because *C. p.* var. *cycloptera* is homomorphic, the “odd” nutlet wing base is the same as that of the consimilar ones); 11) *Cryptantha p.* var. *stenoloba* has a significantly greater consimilar nutlet wing notch depth than all other taxa or forms ( $p < 0.01$ ) although with considerable overlap; *C. oxygona* and *C. p.* var. *purpusii* have a significantly smaller consimilar nutlet wing notch depth than all other taxa or forms ( $p < 0.01$ ) with considerable overlap, but not with one another (Fig. 9E); and 12) *Cryptantha pterocarya* var. *cycloptera* and the “truncata” form have a gynobase stalk length that is significantly longer than all other taxa and forms but not to one another, the latter intermediate (Fig. 9F). All other discrete features, including the extrinsic feature elevation, were found to lack any significant differences between taxa and forms (plots not shown).

Principal components analysis (PCA) shows general grouping of the varieties and forms of *C. pterocarya* (Fig. 10). A plot of the 1st and 2nd factors shows relatively strong separation of varieties *cycloptera*, *purpusii*, and *stenoloba*, with greater overlap of the other varieties and forms (Fig. 10A); the “truncata” form is near but overlaps with var. *cycloptera*, and var. *pterocarya* and the “pseudocycloptera” form overlaps mostly with one another (Fig. 10A). A plot of the 2nd and 3rd factors shows relatively strong separation of varieties *cycloptera* and *stenoloba* with some separation of var. *pterocarya* and the “truncata” form, but with strong overlap of var. *purpusii* and the “pseudocycloptera” form (Fig. 10B). A plot of the 1st and 3rd factors shows mostly overlap of all taxa and forms, except for strong separation of variety *purpusii* (Fig. 10C).

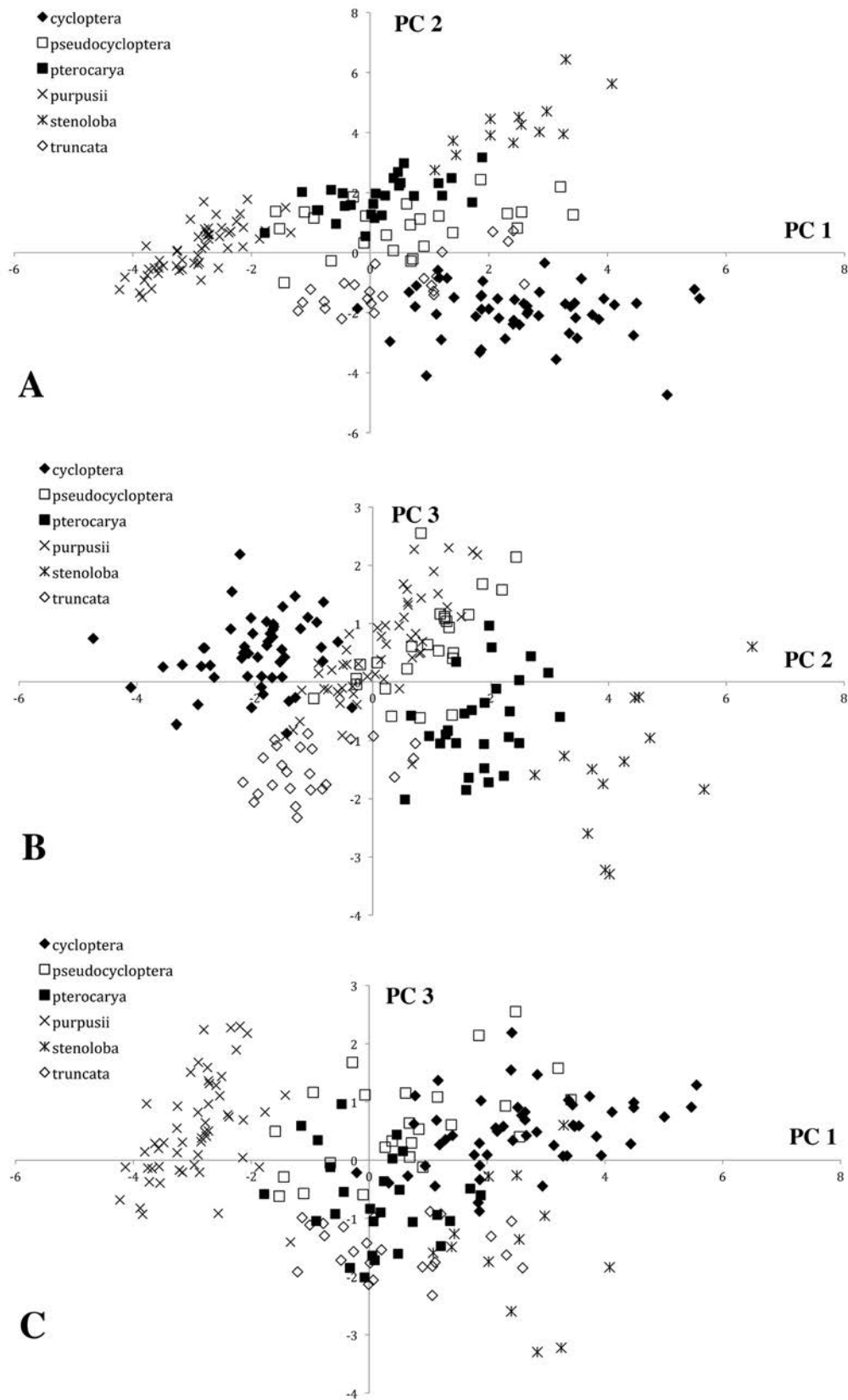
Principal components analysis loadings and percent of total variance explained by factor are listed in Table 2. Factor 1 explains 41% of the total variance with heavy loading for consimilar nutlet lateral wing width (0.84), consimilar nutlet wing apex length (0.82), consimilar nutlet maximum wing notch depth (0.78), calyx body length (0.78), and calyx body width (0.73). Factor 2 explains 24% of the total variance, with heavy loading for odd nutlet body length (0.77), consimilar nutlet body length (0.74), consimilar nutlet wing base length (-0.67), gynobase stalk length (-0.67), and odd nutlet wing base length (-0.65). Factor 3 explains only 9% of the total variance, with heaviest loading for consimilar nutlet body maximum width (0.59). These factors can be explained given that: 1) var. *stenoloba* differs in having a relatively large calyx (heavy loading in PC1 for calyx body length at 0.78); 2) var. *cycloptera* differs in having a relatively broad nutlet wing, especially at the base (heavy loading in PC1 for consimilar nutlet lateral wing width at 0.84, for consimilar nutlet wing apex length at 0.82, and in PC2 for consimilar nutlet wing base length at -0.67) and an elongated gynobase stalk (heavy loading in PC2 for gynobase stalk length at -0.67); and 3) var. *purpusii* differs in having relatively small nutlets with a reduced lateral wing width (heavy loading in PC1 for consimilar lateral nutlet wing width at 0.84, for consimilar nutlet wing apex length at 0.82, and in PC2 for consimilar nutlet wing base length at 0.67).



**FIGURE 8.** Box plots of characters analyzed for *Cryptantha pterocarya* var. *cycloptera*, *C. oxygona*, *C. p.* “*pseudocycloptera*” form, *C. p.* var. *pterocarya*, *C. p.* var. *purpusii*, *C. p.* var. *stenoloba*, and *C. p.* “*truncata*” form. A. Calyx body length in fruit (mm). B. Sepal width (mm). C. Sepal length:width ratio. D. Corolla limb diameter (mm). E. Consimilar nutlet body length (mm). F. Consimilar nutlet length:width ratio. Taxa that are significantly different from all other taxa and forms are indicated with double asterisks (\*\*) ( $p < 0.01$ ). Pairs of taxa that are significantly different from all other taxa or forms except from one another are indicated by two plus symbols (++) ( $p < 0.01$ ) or a single plus symbol (+ or +) ( $p < 0.05$ ). The “†” symbol indicated statistical difference between all other taxa and forms of *C. pterocarya* but not with *C. oxygona*. Outliers are indicated by a single small asterisk and extreme outliers, greater than 1.5 times the data are indicated by a small open circle. Statistical differences determined via ANOVA Tukey post hoc test.



**FIGURE 9.** Box plots of additional characters analyzed for the same taxa as in Figure 9. A. Consimilar nutlet maximum wing width (mm). B. Consimilar nutlet wing base (mm). C. Odd nutlet lateral wing width (mm). D. Odd nutlet wing base (mm). E. Consimilar nutlet wing (maximum) notch depth (mm). F. Gynobase stalk length (mm). Symbols and analyses as in Figure 9.



**FIGURE 10.** A. Principal Components Analysis (PCA) of factors 1 and 2, including the four varieties of *Cryptantha pterocarya*, the “pseudocycloptera” form of *C. p.* var. *pterocarya*, and the “truncata” form of *C. p.* var. *cycloptera*. B. Same as above, but comparing factors 2 and 3. C. Same as above, but comparing factors 1 and 3.

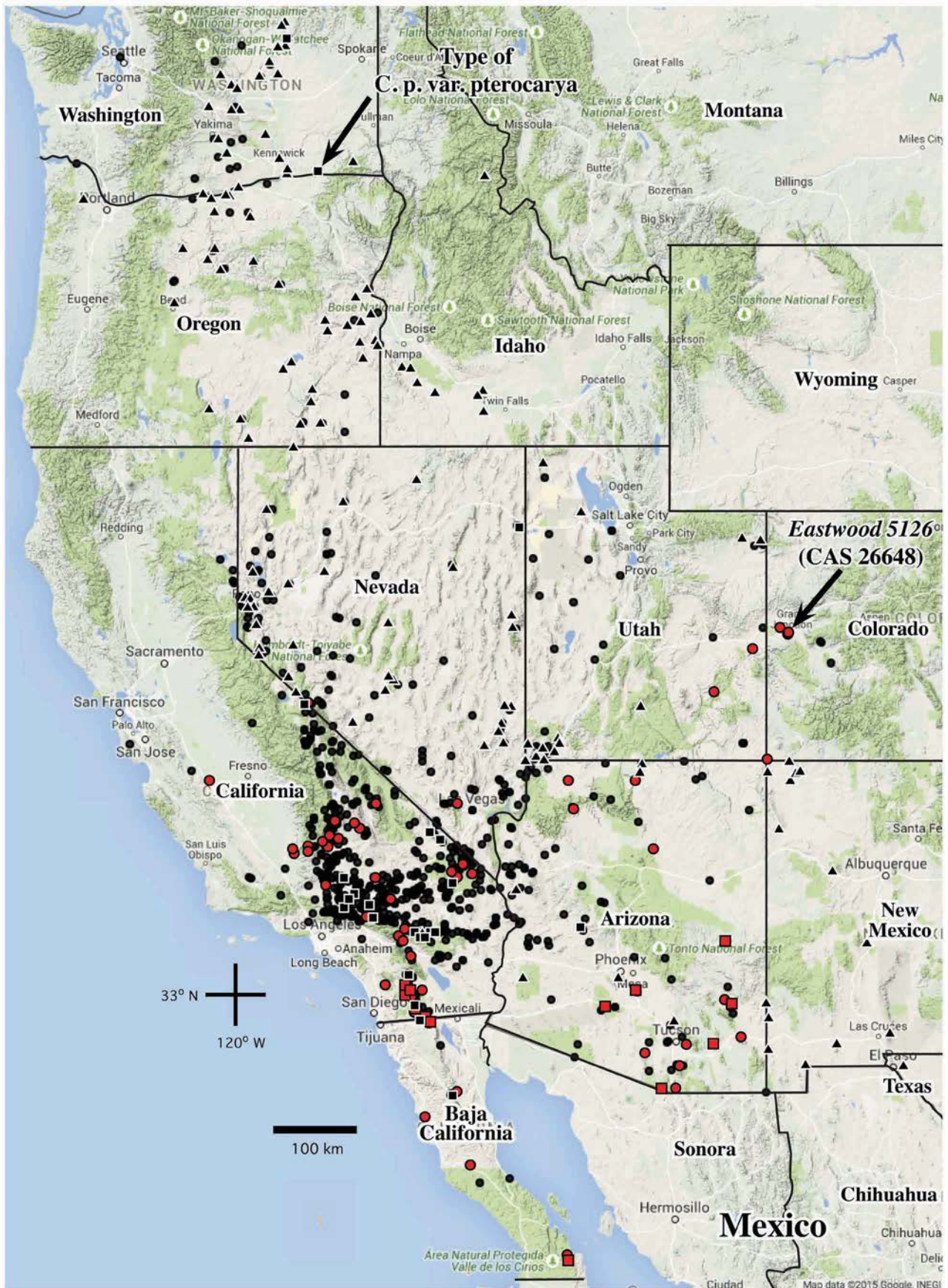
A plot of the distribution of the *C. pterocarya* taxa and forms shows some correspondence with geographic ranges (Figs. 11, 12). Variety *pterocarya* has the most extensive range of any variety or form, occurring in Arizona, California, Colorado, Idaho, Nevada, New Mexico, Oregon, Utah, Washington in the U.S. and in Baja California, and the northern border of Sonora and Chihuahua in Mexico (Fig. 11). The “pseudocycloptera” form overlaps considerably with *C. pterocarya* var. *pterocarya* but is more restricted in range, restricted to the southwestern U.S. in southern California, southern Nevada, Arizona, eastern Utah, and western Colorado (Fig. 11). Variety *purpusii* occurs in the Argus Mountains and along the escarpment of the Sierra Nevada and Peninsular Ranges of California and Baja California with a couple of verified populations in southern Nevada and northeastern California (Fig. 12A). Variety *stenoloba* has the narrowest range, occurring near the Colorado River in eastern California and western Arizona along the Virgin River in southern Nevada and northwestern Arizona (Fig. 12A). Variety *cycloptera* occurs in the southwestern U.S. from southeastern California to western Texas and in northern Baja California and northeastern Sonora, Mexico (Fig. 12B), with considerable overlap with var. *pterocarya* (Fig. 11). Finally, the “truncata” form overlaps considerably with var. *cycloptera*, but is more restricted in range, not occurring in New Mexico or Texas (Fig. 12B).

The wing size of *C. pterocarya* var. *purpusii* shows some local clustering with respect to geographic range (Fig. 13), but no clear trends are evident.

## Discussion

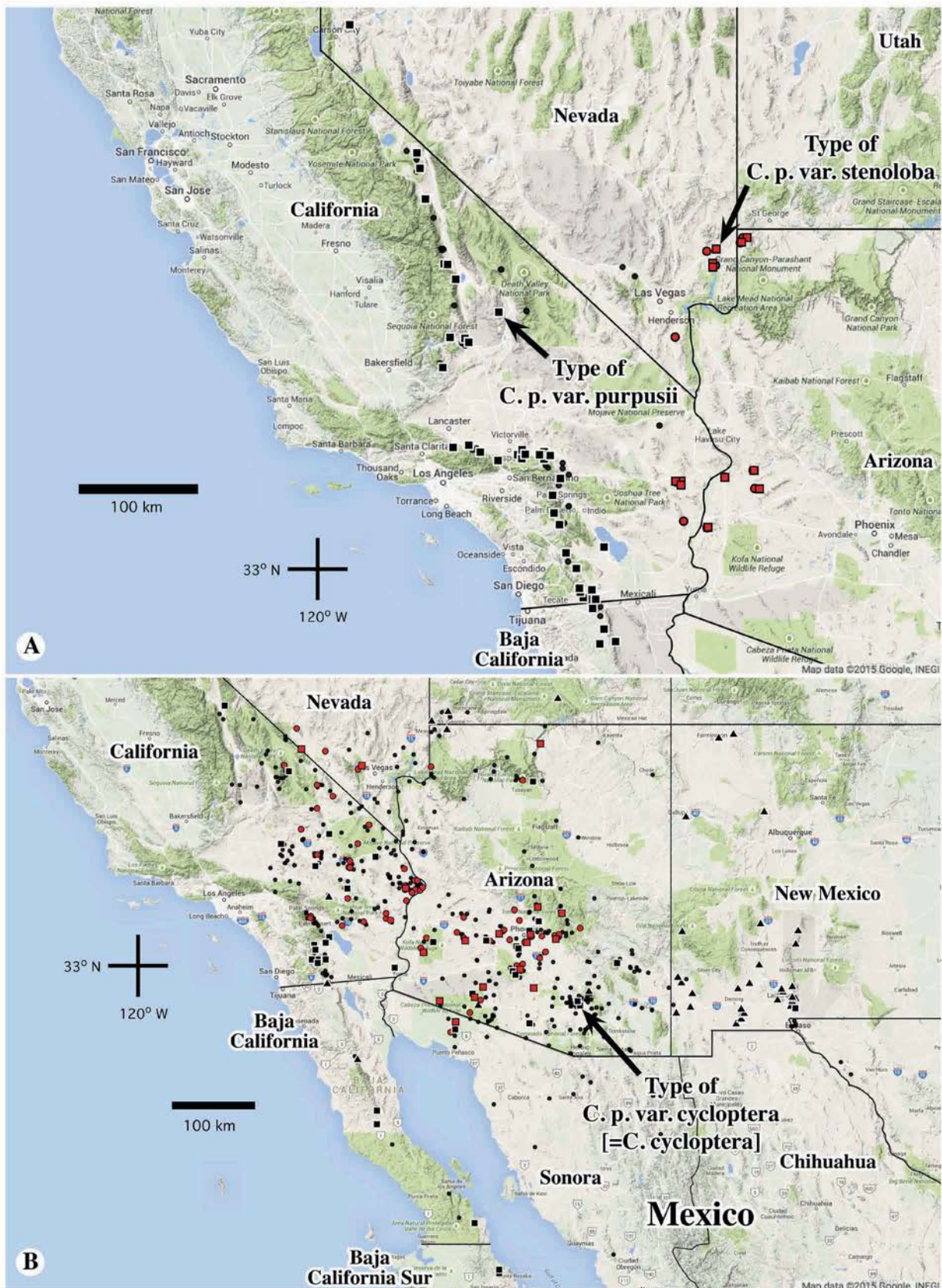
Analyses of the varieties of *Cryptantha pterocarya* suggest that three of the four generally recognized varieties, vars. *pterocarya*, *purpusii*, and *stenoloba*, should be retained as such. *Cryptantha pterocarya* var. *pterocarya* has the widest geographic range of all varieties, extending from Baja California and northern Sonora, Mexico northward to Washington state, and eastward to Idaho, Colorado, and Texas (Fig. 11); in fact, the type specimen of the species was collected in Walla Walla, Washington (Fig. 11). This type has heteromorphic nutlets with the consimilar nutlets having the characteristic lobed wings along the lateral and apical regions and the odd nutlet lacking wings, having a sharp margin and slightly spinulose tubercles (Fig. 2). In individual characters quantified here, *C. p.* var. *pterocarya* is not significantly different from any other taxa or forms (Figs. 8,9), but the combination of features listed above are diagnostic. The novel “pseudocycloptera” form described here differs from typical *C. p.* var. *pterocarya* in having homomorphic nutlets (see Fig. 9B), in which all nutlets are winged but with the wing not extending along the base (Fig. 4A). The two cannot be distinguished in any other quantitative features (Figs. 8, 9). The geographic range of the “pseudocycloptera” form is much more limited and nested within that of var. *pterocarya*, occurring primarily in deserts of southern California and northern Baja California and extending into southeastern Arizona and northeastern into the Colorado plateau of Utah and Colorado (Fig. 11). In fact, we have found populations of “typical” (i.e., based on the type specimen) var. *pterocarya* within 100 feet of the “pseudocycloptera” form. In almost all specimens studied, a given individual is invariant with respect to heteromorphism. However, we did discover a typical *C. pterocarya* var. *pterocarya* specimen in which one or more fruits had homomorphic nutlets (resembling the “pseudocycloptera” form) on the same individual (*Reveal 106*, CAS 861519!). This variation within at least one individual and the overlapping geographic range of the two forms argue that the “pseudocycloptera” form should not at this time be recognized as a taxonomic variety. The general overlap of these two forms in the PCA analysis (Fig. 10), despite the difference in heteromorphism, supports our conclusion. We argue that *C. p.* var. *pterocarya* should be recognized as having both a heteromorphic and homomorphic form with the typical heteromorphic form having an odd nutlet that lacks the wings found on the consimilar nutlets, as seen in the type material, and the homomorphic (“pseudocycloptera”) form having four winged nutlets that are identical to the consimilar nutlets of the heteromorphic form.

We believe that the recognition of a homomorphic form of *C. p.* var. *pterocarya* clarifies some past misconceptions in the group. For example, in the keys of many floristic treatments (e.g., Kearney & Peebles 1960, Kelley & Wilken 1993, Kelley *et al.* 2012), our “pseudocycloptera” form would be identified to var. *cycloptera*, the basis for our giving that name to this form, meaning “false *cycloptera*.” But, given the fact that the homomorphic “pseudocycloptera” form resembles *C. p.* var. *pterocarya* in lacking wing material at the base of the nutlet (Fig. 2; 4A; 9A), lacking any appreciable gynobase stipe (Fig. 9F), and in having appressed and spreading trichomes (see below), we believe it is clear that it is a variant of var. *pterocarya*, not a close relative to var. *cycloptera* (see below for a discussion of the last taxon). Although this variant is not always discrete within an individual, it is in almost all samples examined. We believe at this stage that it warrants recognition as a form of *C. p.* var. *pterocarya*, described as follows.

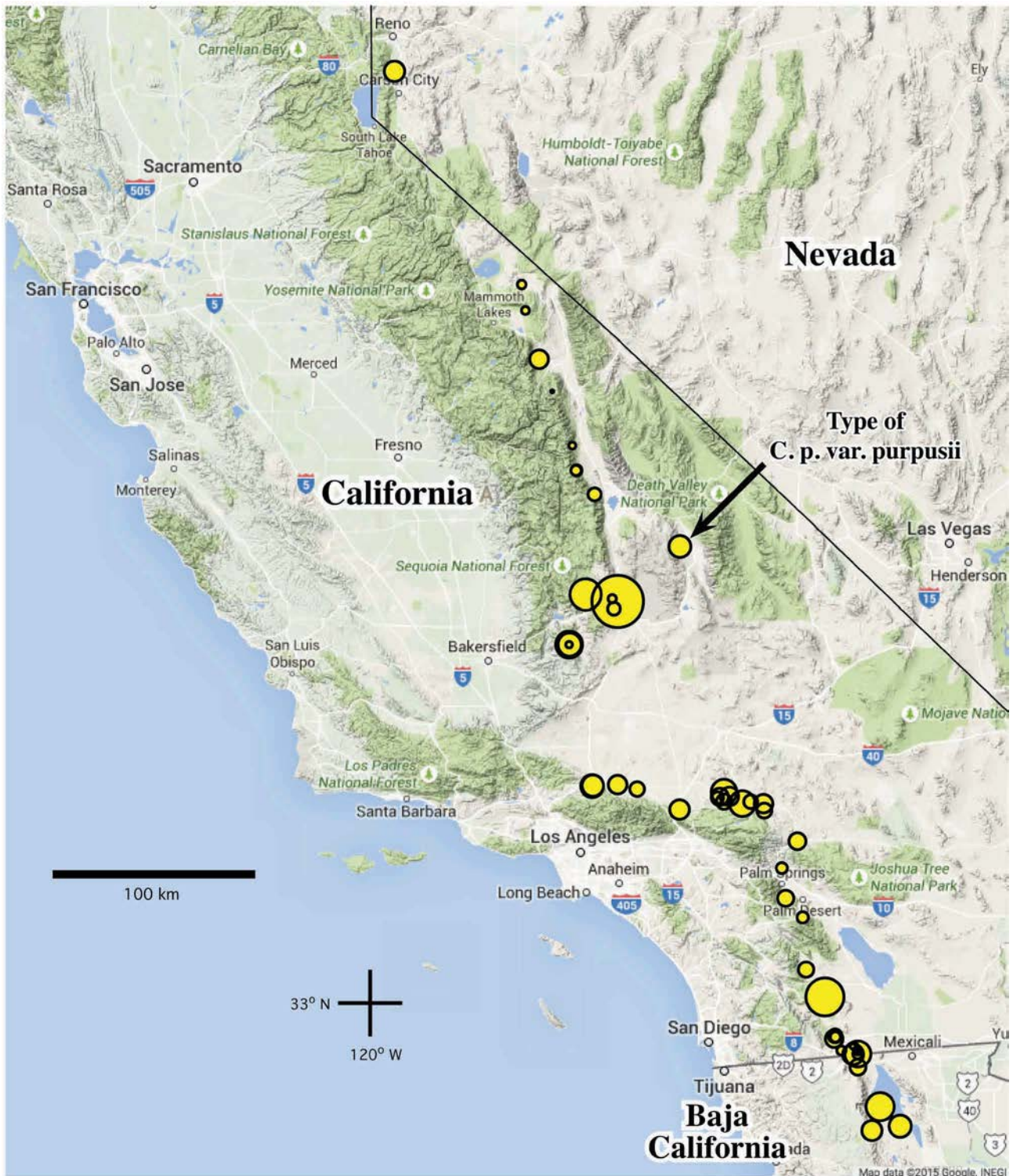


**FIGURE 11.** Distribution map of: 1) *Cryptantha pterocarya* var. *pterocarya* specimens verified to identity and measured (black squares), verified to identify but not measured (black dots), and not verified but included for geographic range mapping (black triangles); and of 2) the “pseudocycloptera” form verified to identity and measured (red squares) and verified to identity but not measured (red circles). Map data from ©Google 2015, INEGI Data.





**FIGURE 12.** A. Distribution map from specimens of: 1) *Cryptantha pterocarya* var. *purpusii* verified to identity and measured (black squares) and verified to identity but not measured (black dots); and 2) *C. pterocarya* var. *stenoloba* verified to identity and measured (red squares) and verified to identity but not measured (red circles). B. Distribution map from specimens of: 1) *Cryptantha pterocarya* var. *cycloptera* [= *C. cycloptera*] verified to identity and measured (black squares), verified to identity but not measured (black dots), and not verified but included for geographic range mapping (black triangles); and 2) the “truncata” form verified to identity and measured (red squares) and verified to identity but not measured (red circles). Map data from ©Google 2015, INEGI Data.



**FIGURE 13.** Graph showing relative size of consimilar nutlet lateral wings of *Cryptantha pterocarya* var. *purpusii*, overlain by location. Circle diameter is proportional to average wing width on one side of nutlet only. Map data from ©Google 2015, INEGI Data.

***Cryptantha pterocarya* (Torrey) Greene var. *pterocarya* forma *pseudocycloptera* M.E. Mabry & M.G. Simpson, forma nov.**

Type:—USA. California, Imperial County, In-Ko-Pah Mountains, Jacumba Natural Area, along road ascending to Valley of the Moon, granite substrate, 1000 m, 32.63944° N, -116.10111° W, 13 April 2001, *Rebman* 7221, with D. Silverman, B. Lauri, Oscar Solis (holotype SD 155821!, isotypes RSA 700474!, UC 1787754!, UCR 155804!).

**Diagnosis:**—*Cryptantha pterocarya* var. *pterocarya* forma *pseudocycloptera* is similar to the typical form of *Cryptantha pterocarya* var. *pterocarya* (forma *pterocarya*) in having prominently winged (wing generally  $\geq 0.6$  mm on one side) nutlets, the wings typically lobed and not extending to the base of the nutlet body. It differs from the typical form in having homomorphic nutlets, with all four nutlets winged.

**Etymology:**—The epithet “*pseudocycloptera*” means “false cycloptera,” in reference to its resemblance and past confusion with *Cryptantha pterocarya* var. *cycloptera* [= *C. cycloptera*].

**Paratypes:**—See Appendix 1.

Interestingly, in the typical form of *C. pterocarya* var. *pterocarya*, the odd nutlet of heteromorphic specimens shows a resemblance to *C. utahensis* in shape (both lance-ovate), sculpturing (both papillate-tuberculate with often spinulose tubercles especially toward the nutlet apex), and in having a sharp “knife-like” margin (Fig. 6E). *Cryptantha utahensis* was included in series *Pterocaryae* by Johnston (1925) along with *C. oxygona* and *C. pterocarya* (including vars. *cycloptera*, *pterocarya*, and later *stenoloba*, the last described by Johnston 1939). However, *Cryptantha utahensis* typically has only one nutlet per fruit (rarely two, and then homomorphic) and never exhibits any appreciable marginal wing. It is because of these clear differences in morphology that we did not include *C. utahensis* in our comparative analyses.

*Cryptantha p.* var. *purpusii* warrants continued recognition at the varietal level. Variety *purpusii* is discrete among the other varieties or forms of *C. pterocarya* in having a significantly narrower nutlet wing (Fig. 5; 6; 9A). Variety *purpusii* also generally has a smaller nutlet body length, more closely approaching that of *C. oxygona* and the “*truncata*” form (Fig. 8E), but lacking any significant difference. Variety *purpusii* has a relatively narrow range, found in the Argus Mountains and along the escarpment of the Sierra Nevada and Peninsular Ranges of California and Baja California, plus a few populations in mountains of western Nevada (Fig. 12A). This geographic continuity provides additional evidence for its continued recognition as a taxon. However, variety *purpusii* represents a greater challenge to characterize, as it is quite variable in nutlet morphology. Some samples approach var. *pterocarya* in being heteromorphic with consimilar nutlets having a relatively broad wing width (e. g., Fig. 6A). Other samples are homomorphic and have a narrow nutlet wing (e. g., Fig. 6C, D), in some more of a marginal ridge, these approaching *C. oxygona* (Fig. 6F). However, *Cryptantha oxygona* is different from all *C. pterocarya* varieties and forms in its significantly larger corolla diameter (Fig. 8D), although with some overlap; this feature alone generally clearly distinguishes *C. oxygona* from the varieties and forms of *C. pterocarya*, warranting its continued recognition as a separate species. In identification of *C. p.* var. *purpusii* we used the previous designation of a wing width less than 0.5 mm (Kelley *et al.* 2012). One specimen measured 0.55 mm in wing width, but had a small nutlet body length and therefore was classified as *C. p.* var. *purpusii*. We suggest, from results of this analysis, that *C. p.* var. *pterocarya* and var. *stenoloba* (see below) be distinguished as having a wing width 0.6 mm and larger and *C. p.* var. *purpusii* as having a wing width less than 0.6 mm, a smaller nutlet body, and located in a more restricted range.

Interestingly, the distribution of *C. oxygona* (not illustrated) parallels that of *C. p.* var. *purpusii* in occurring mostly along the escarpment of the upper peninsular range (as far south as northern San Diego County) and along the escarpment of the southern Sierra Nevada (as far north as Yosemite), but is more widespread than var. *purpusii* in the Tehachapi Range, the central-northern transverse range, and along the (mostly) eastern slopes of the southern coastal ranges of California. It appears to be restricted to California, with some populations near the border with western Nevada.

*Cryptantha pterocarya* var. *stenoloba* also warrants continued recognition at the varietal level. It is discrete from other varieties and forms in having a significantly longer calyx (Fig. 7A–C; 8A), a significantly longer sepal length: width ratio (Fig. 8C), a significantly longer consimilar nutlet body (Fig. 8E), and longer consimilar nutlet body length: width ratio (Fig. 8F; see Fig. 7F), these last two features not recognized previously. This taxon has the narrowest range of any variety or form, occurring near the Colorado River basin in southeastern California, western Arizona, and southern Nevada, and near the Virgin River basin in southeastern Nevada and northwestern Arizona (Fig. 12A). Variety *stenoloba* most likely represents a diverging taxon of var. *pterocarya* as it shares many morphological similarities in nutlet morphology, the nutlets heteromorphic, the consimilar nutlets with a broad wing (Fig. 9A), and an essentially absent wing at the base (Fig. 9B, D; see Fig. 7E, F). Given its discreteness, it is possible that *C. p.* var. *stenoloba* could be recognized at the species level in the future. But, because of the overlap it shows in some features, we elect to treat it at the rank of variety at this time. It should definitely be included in local floristic treatments, where it is often missing (e. g., Kelley & Wilken 1993; Kelley *et al.* 2012). We cite four specimens (RSA 774935, RSA 782075, SDSU 20929, UCR 214870, all from San Bernardino County), which constitute new state records for California.

We noticed no significant differences in consimilar nutlet wing notch depth, except for *C. p.* var. *stenoloba*, which has a significantly deeper, but highly overlapping, notch depth relative to all other taxa or forms (Fig. 9E). We have

no basis for believing that *C. p.* var. *stenoloba* represents the elusive *C. p.* var. *pectinata*. Although we were unable to physically examine the presumed (although confused; see earlier quote by Johnston 1925) type specimen of *C. p.* var. *pectinata*, our measurements of the digital scan of this specimen (Parry 168-169, NY 01111827) shows it to have relatively wide and short sepals, the length measuring 3.7–4.7 mm, well below that of variety *stenoloba*. Still, it is intriguing that this type specimen of var. *pectinata*, which might show some resemblance in wing notch depth to var. *stenoloba*, was collected near St. George, Utah in the Virgin River Valley, very near known populations of var. *stenoloba* (see Fig. 12A). However, based on variation of this feature observed in this study, we reject *C. p.* var. *pectinata* as a valid taxon, as other taxonomists have in recent treatments. Lastly with regard to this feature, *Cryptantha oxygona* and *C. pterocarya* var. *purpusii* have significantly smaller notch depths relative to other taxa or forms, but not to one another (Fig. 9E). This is not unexpected given the relatively smaller wing width of these two taxa (Fig. 5, 6A–D, F).

*Cryptantha pterocarya* var. *cycloptera* and the “truncata” form are similar to one another in together having a significantly longer consimilar nutlet wing base (Fig. 9B), a longer odd nutlet wing base (Fig. 9D), and a longer gynobase stalk length (Fig. 9F), although note that in the last two features, var. *cycloptera* and the “truncata” form are statistically different from one another, with the “truncata” form intermediate to var. *cycloptera* and the other taxa/forms. We emphasize the clarification that only *C. p.* var. *cycloptera* and the “truncata” form have any appreciable nutlet basal wing and any appreciable gynobase stalk. In addition, we note that from our qualitative observations only *C. p.* var. *cycloptera* and the “truncata” form have an upper stem vestiture composed of only appressed trichomes; the other forms have appressed and spreading trichomes. From these data, we propose that *C. pterocarya* var. *cycloptera* be re-elevated to species level (as *C. cycloptera* (Greene) Greene), using a taxonomic species concept (Cronquist 1978, 1988). Interestingly, Cronquist (1984) also implied the distinctiveness of var. *cycloptera* by suggesting that varieties *pterocarya*, *purpusii*, and *stenoloba* be classified together within a subspecies (not described), separate from var. *cycloptera* (Cronquist 1984, p. 257). The geographic range of *Cryptantha cycloptera* overlaps considerably with *C. pterocarya*, but is more restricted, occurring only in the southern half of California, southern Nevada, most of Arizona, southern Utah, western New Mexico and Texas, and Baja California and Sonora, Mexico (Fig. 12B).

We believe we have elucidated the original basis for the transfer in rank of *C. cycloptera* to a variety of *C. pterocarya* by Macbride (1916). In that treatment, Macbride stated (with regard to this taxon): “However, a study of the ample material in the Gray Herbarium seems to prove conclusively that it is, at best, only a geographical variety of *C. pterocarya*. In the first place, the ventral face of the nutlets may or may not be smooth in either of the proposed species. Secondly, all of the nutlets may be winged and yet the wings not extend across the base, as for example in the plants collected at Grand Junction, Colorado, by Alice Eastwood. When one considers the fact that the ventral faces of these winged nutlet are rough, one is puzzled as to whether the plants are more nearly related to *C. pterocarya* or to *C. cycloptera*. However, it must be noted that it is only the southwestern material that can be referred to *C. cycloptera*. It seems advisable, therefore, to consider *C. cycloptera* as a variety of *C. pterocarya* and to include in this variety all specimens that have four winged nutlets, irrespective of whether the wing extends across the base. Although the species ranges from Washington to Utah and southern California, the variety apparently largely replaces it, in the interior of the Southwest.”

In our opinion, Macbride overemphasized nutlet heteromorphism over the presence of a basal wing (i.e., the wing completely encircling the nutlet body) in evaluating these taxa. Also, he was not aware of the gynobase stipe that is obviously correlated with a basally positioned wing. Nor did he consider stem pubescence in his evaluation. The Alice Eastwood specimen he mentions we believe to be *Eastwood 5126* (CAS 26648, collected near Grand Junction, Colorado; see Fig. 11), a specimen that we verified in this study to be a “pseudocycloptera” form, the homomorphic form of *C. pterocarya* var. *pterocarya*. As mentioned earlier, this has been an ongoing source of confusion in identification (even originally by the authors of this article), in that all homomorphic forms of *C. pterocarya* var. *pterocarya* were often identified as *C. cycloptera*, as that is the feature singled out in many keys. We do, however, agree with Macbride that the ventral surface of the nutlet of *C. pterocarya* is quite variable in sculpturing. Although we did not quantify this feature, we believe that ventral surface sculpturing is not consistent with respect to any taxon or form in the complex.

The “truncata” form is similar to *C. cycloptera* in having a consimilar nutlet wing base significantly longer than all other taxa and forms (Fig. 9B; note that in the homomorphic *C. cycloptera* all four similar nutlets were averaged for this feature). The stem pubescence of the “truncata” form is also like that of *C. cycloptera*, having solely appressed trichomes. The “truncata” form is intermediate between *C. cycloptera* and all other varieties and forms with respect to odd nutlet wing base (Fig. 9D; again, in the homomorphic *C. cycloptera* all four, similar nutlets were averaged for this feature) and gynobase stalk length (Fig. 9F). From these analyses, it is clear that the “truncata” form is much more similar to *C. cycloptera* than to any other varieties or forms. We have considered the option of treating the “truncata”

form as a variety of *C. cycloptera*, but are hesitant to do so for three reasons. First, the geographic range of the “truncata” form is more restricted than, but overlapping and nested within that, of *C. cycloptera*, with no clear discontinuity (Fig. 12B). Second, the “truncata” form of the nutlet shows a fair amount of variation in the odd nutlet basal wing width and gynobase stalk length, although the quantitative analyses do show significant differences (Fig. 9D, F). Third, we have found specimens of a typical *cycloptera* form in which one or more fruits of the “truncata” form were found on the same plant (*Damrel 1623-B*, ASU 237494) and we have found a specimen of a typical “truncata” form in which one or more fruits of the typical *cycloptera* form were found on the same plant (*Pinkava 10939*, ASU 166212); see Appendix 3. The fact that nutlets representing the two forms can be found on the same individual, suggests that the two forms of *C. cycloptera* may not be fully discrete. However, this is uncommon; almost all specimens of these forms are invariant within an individual with respect to nutlet features. Therefore, we believe at this stage that this form warrants formal recognition as a form of *C. cycloptera*.

***Cryptantha cycloptera* (Greene) Greene forma *truncata* M.E. Mabry & Rebman, forma nov.**

Type:—USA: California, San Bernardino County, Whipple Mountains, west slope just below saddle at north end of Savahia Peak, steep slopes of dark volcanic boulders and outcrops, annual, flowering, 762 m, 34.276633° N 114.5328° W, 4 May 2003, *Sarah J. De Groot 2834*, with J. Mark Porter, Naomi Fraga (holotype RSA 721252!, isotypes CAS 1123044!, ARIZ 393611)

**Diagnosis:**—*Cryptantha cycloptera* forma *truncata* is similar to the typical form of *Cryptantha cycloptera* (forma *cycloptera*) in having only appressed trichomes along the upper inflorescence stem and in having all four nutlets winged, with the wing extending along the base of the nutlet body. It differs in having heteromorphic nutlets, with one nutlet having the wing reduced on the sides and base.

**Etymology:**—The epithet “*truncata*” refers to the reduced, somewhat truncate basal wing of the odd nutlet of this form, in contrast to the rounded, well-developed basal wing of the typical form of *Cryptantha cycloptera*.

**Paratypes:**—See Appendix 2.

As with all strictly taxonomic studies, a future detailed molecular phylogenetic analysis will be extremely important in elucidating evolutionary relationships within the complex. If forma *pseudocycloptera* and forma *truncata* each are found to constitute a monophyletic clade, then their recognition at a higher taxonomic rank may be warranted. A similar study of *C. pterocarya* var. *purpusii* and var. *stenoloba* may test their monophyly and possible introgression, and may help elucidate their interrelationships to var. *pterocarya*, the type for the species. Other interesting questions are the molecular mechanism for development of heteromorphism and the other traits distinguishing the taxa and forms of this complex. Finally, the interrelationships of *C. oxygona* and *C. utahensis* to *C. pterocarya* and the evolutionary direction and possible adaptive significance of nutlet number and wing development will be an interesting avenue of future research.

The nomenclature we accept from our study of this complex of taxa is summarized in Table 3. A revised key is presented here of Johnston’s (1925) series *Pterocaryae* (modified in part from Kelley *et al.* 2012), clarifying the identity of the entities that we propose in this paper:

1. Nutlets 1(2), margin a ± flat narrow rim to sharp-angled, tubercles often spinulose especially toward apex ..... *C. utahensis*
- Nutlets generally 4(3), margin occasionally sharp-angled, generally narrow- to wide-winged along entirety, nutlet tubercles not or slightly spinulose ..... 2
2. Flower limb typically (3)4–8 mm in diameter ..... *C. oxygona*
- Flower limb less than 4 mm in diameter ..... 3
3. At least some nutlets with marginal wing encircling entire nutlet body, including base; nutlets homomorphic with all 4 winged (forma *cycloptera*), or heteromorphic with odd nutlet having reduced wing at sides and base (forma *truncata*) ..... *C. cycloptera*
- All nutlets lacking a marginal wing at base of nutlet body, nutlets homomorphic or heteromorphic ..... 4
4. At least some nutlets with narrow, lobed or toothed wings <0.6 mm wide, or with narrow, linear, marginal rim; nutlet body 1.2–2.2 mm long ..... *C. pterocarya* var. *purpusii*
- At least some nutlets with prominent, apically lobed or toothed wings >0.6 mm wide; nutlet body 1.8–3.2 mm long ..... 5
5. Calyx body in fruit ovoid, 3–4(6) mm long, sepals lance-ovate to lanceolate (length:width ratio 2–4); nutlets heteromorphic with one nutlet unwinged (forma *pterocarya*) or homomorphic with all four nutlets winged (forma *pseudocycloptera*), nutlet body generally 1.8–2.8 mm long, wing width of consimilar nutlets 0.6 mm and greater ..... *C. pterocarya* var. *pterocarya*
- Calyx body in fruit lance-ovoid, 5–8 mm long, sepals lanceolate (length:width ratio 3–5); nutlets heteromorphic, the odd nutlet unwinged, nutlet body generally 2.8–3.2 mm long ..... *C. pterocarya* var. *stenoloba*

**TABLE 3.** Nomenclature and synonymy of names accepted in this study.

**Cryptantha cycloptera** (Greene) Greene (1887: 120).

*Krynitzkia cycloptera* Greene (1885: 207) (**Basionym**). *Cryptantha pterocarya* (Torrey) Greene var. *cycloptera* (Greene) J. F. Macbride (1916: 44). **Type:**—USA. Arizona: Pima County, hills near Tucson, 15 April 1884, *Cyrus Guernsey Pringle s.n.* (holotype CAS 202, barcode 0006884).

**Cryptantha cycloptera** (Greene) Greene forma **truncata** M.E. Mabry & Rebman, forma nov.

**Type:**—USA. California: San Bernardino County, Whipple Mountains, west slope just below saddle at north end of Savahia Peak, 4 May 2003, *Sarah J. De Groot 2834* (holotype RSA 721252, isotypes: CAS 1123044, ARIZ 393611).

**Cryptantha pterocarya** (Torrey) Greene (1887: 120).

*Eritrichium pterocaryum* Torrey (1859: 142) (**Basionym**). *Krynitzkia pterocarya* (Torrey) A. Gray (1885: 276). **Type:**—USA: Washington, Wallah Wallah, s.d., 1859, *Wilkes Expedition 1047* (holotype NY 335248).

= *Eritrichium pterocaryum* Torrey var. *pectinatum* A. Gray (1874: 61). *Krynitzkia pterocarya* (Torrey) A. Gray var. *pectinata* (A. Gray) A. Gray (1885: 276). *Cryptantha pterocarya* (Torrey) Greene var. *pectinata* (A. Gray) Brand (1931: 55). **Type:**—USA. Utah, 1874, *C. Parry 168-49* (isotypes ISC-v-0000202, NY00335256).

**Cryptantha pterocarya** (Torrey) Greene var. **pterocarya** forma **pseudocycloptera** M.E. Mabry & M.G. Simpson, forma nov.

**Type:**—USA. California: Imperial County, In-Ko-Pah Mountains, Jacumba Natural Area, along road ascending to Valley of the Moon, 13 April 2001, *Rebman 7221* (holotype SD 155821, isotypes RSA 700474, UC 1787754, UCR 155804).

**Cryptantha pterocarya** (Torrey) Greene var. **purpusii** Jepson (1925: 849).

**Type:**—USA. California: Inyo County, Argus Mountains, June 1897, *C. A. Purpus 5433* (holotype JEPS 2548).

**Cryptantha pterocarya** (Torrey) Greene var. **stenoloba** I. M. Johnston (1939: 391).

**Type:**—USA. Nevada: Clark County, desert 15 mi E. of Glendale, 19 May 1933, *B. Maguire & H. L. Blood 4466* (holotype GH 00096072).

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**APPENDIX 1:** Paratypes for *Cryptantha pterocarya* (Torrey) Greene var. *pterocarya* forma *pseudocycloptera* M.E. Mabry & M.G. Simpson, forma *nov.* (listed alphanumerically by collector and collection number; bold font = collectors/vouchers for which data were measured in our quantitative study;! = voucher verified by the authors)

*Abrams 11963* (DS 162714!); *Abrams 3* (DS 8658!); *Andre 13072* (RSA 770194B!); *Barth 1557* (SD 233517!); *Bell 3405* (RSA 787858!); *Broder 675* (DS 500782!); *Burch IIV95B* (SDSU 14135!); ***Burch IIV95B* (SDSU 14135!)**; *Charlton 4741* (RSA 552554!); *Clemons 1423* (SD 119073!); ***Clemons 1967* (SD 120963!)**; *Clokey 6859* (UC 857243!); *Clokey 7673* (DS 365468!); *Davidson 5821* (RSA 499787!); *Dunkle s.n.* (RSA 499773!); *Eastwood 5126* (CAS 26648!); *Eastwood 8873* (CAS 294537!); *Eastwood s.n.* (CAS 26647!); *Elmer 3716* (DS 8641!); *Elvin 2799* (UCR 152957!); *Elvin 4720* (UCR 175766!); *Epling s.n.* (DS 238505!); *Evermann s.n.* (CAS 26678!); ***Feld 01-145* (ASU 236493!)**; *Fraga 1035* (UCR 195308!); *Fraga 595* (UC 1927483!); *Fraga 760* (UC 1921990!); *Guertin 149* (ARIZ 367072!); ***Guertin 149* (ARIZ 367072!)**; *Guilliams 605* (SDSU 18955!); ***Guilliams 605* (SDSU 18955!)**; *Hall 2839* (UC 56846!); ***Harbison 4438* (SD 32463!)**; ***Harbison 4445* (SD 32470!)**; *Harris s.n.* (ASU 123856!); *Hendrickson 126* (SD 161800!); ***Hendrickson 126* (SD 161800!)**; *Hendrickson 2808* (SD 205630!); ***Hendrickson 2808* (SD 205630!)**; *Hendrickson 2904* (SD 205626!); ***Hendrickson 2904* (SD 205626!)**; *Hendrickson 3771B* (SDSU 19427!, SD 214895!); ***Hendrickson 3771B* (SDSU 19427!)**; *Hendrickson 414B* (SD 172711!); ***Hendrickson 414B* (SD 172711!)**; *Hitchcock 25549* (DS 618425!); *Hoffman 533* (SBBG 063950!); ***Howe 2* (SD 63805!)**; *Howell 37244A* (CAS 604391!); *Howell 37996* (CAS 863057!); *Howell 45704* (CAS 863058!); *Howell 47763* (CAS 798236!); *Jepson 17130* (JEPS 67793!); ***Jonsson 580* (SD 115627!)**; *La Doux 483* (RSA 764899B!); ***Marsden 488* (SD 207724!)**; ***Marsden 559 B* (SD 207721!)**; *Mays s.n.* (ASU147557!); *McClinktock 52-187* (CAS 373289!); *McClinktock 52-379* (CAS 373291!); *McDougall 19* (ARIZ 16727!); *McDougall 54* (ARIZ 16836!); *McLaughlin 4368* (ARIZ 305073!); ***McManus 196* (ARIZ 19158!)**; *McManus s.n.* (ARIZ 191568!); *McNair 36* (SD 212043!); ***Moran 12643* (SD 65312!)**; ***Moran 14802* (SD 67288!)**; *Moran 22962* (SD 95532!); *Moran 26937* (SD 102503!); *Muller 3085* (SBBG 47089!); ***Mulligan 1770* (SD 200749!)**; *Osterhout 5999* (POM 114020!, UC 857246!); *Penalosa 554* (CAS 515828D!); *Philbrick s.n.* (SBBG 43331!); *Prigge 2724* (UCR 32417!); *Purpus 5825* (UC 78740B!); *Quibell 949* (DS 358037!); ***Rea 1688* (SD 132090!)**; *Rebman 23748* (SD 222108!); *Reeder 9659* (ARIZ 16833!); *Reeder s.n.* (ARIZ 345515!); *Reeves 6505* (ASU106927!); ***Rhineheart* (ARIZ 30267!)**; *Sanders 16350* (UCR 88427!); *Sanders 23936* (UCR 116806!); *Shultz 6854* (CAS 899438!); *Silverman 3971* (JEPS 103092!, SBBG 116574!); ***Simpson 2374* (SDSU 17298!, SD 180704!)**; *Smith 367* (JEPS 26297!); *Swinney 10496* (UCR 220268!); *Taylor 16754* (UC 1731344!); *Theroux 217* (UCR 89586!); *Twisselmann 2682* (CAS 515835B!); *Twisselmann 8186* (CAS 515832!, CAS 604381!, SBBG 19672!); *Van Devender s.n.* (ARIZ 16858!); *Vasek 3* (UCR 4405!); *Vasek s.n.* (ARIZ 247385!); *Vestal 50965.7* (DS 572919!); *Vickery 287* (UC 1058591!); *Weber 11240* (UC 1223928!); *White 9377* (RSA 695955!); *Wiggins 1991* (DS 365991!); *Wiggins 2270* (DS 365990!); *Wiggins 7593* (DS 265733!); *Wiggins 7797* (DS 263724!).

**APPENDIX 2:** Paratypes for *Cryptantha cycloptera* (Greene) Greene forma *truncata* M.E. Mabry & Rebman, forma *nov.* (listed alphanumerically by collector and collection number; bold font = collectors/vouchers for which data were measured in our quantitative study;! = voucher verified by the authors)

***Annable 472* (ARIZ 263687!)**; *Atwood 17590* (UC 1719462!); *Beatley 12147* (DS 635864!); *Benson 4169* (POM 287678!); *Boyd 2182* (CAS 802819!); *Boyd 7780* (SBBG 087958!); *Christy 893-c* (ASU 200473!); *Clemons 451* (SD 115578!); *Clokey 7673* (UC 900477!); ***Clokey 7673A* (ARIZ 98340, ASU 68369, DS 365469!)**; ***Crooks* (ARIZ 98328!)**; *Damrel 1174* (ASU 227064!); ***Damrel 1174* (ASU 227064!)**; *Damrel 1623-B* (ASU 237494!); *Daniel 4183* (CAS 746376!); ***Darrow 2458* (ARIZ 18221!)**; *Davidson 7723* (RSA 499771!); *De Groot 1086* (RSA 705445!); *De Groot 1442* (RSA 721023!); *De Groot 1517* (CAS 1063485!, RSA 721046!); *De Groot 1655* (RSA 721036!); *De Groot 2130* (RSA 721040!); *De Groot 2296* (RSA 721042!); *De Groot 2363* (RSA 721244!); *De Groot 2441* (RSA 721044!); *De Groot 2710* (RSA 721251!); *De Groot 6609* (RSA 779356!); *Dearing 4812* (SBBG 29800!); *Dearing 4819* (SBBG 105067!); *Denham s.n.* (ASU 66540!); *Doan 1382* (ASU 246689!); ***Doan 603* (ASU 256083!)**; *Eastwood 16900* (CAS 167872!); *Fear s.n.* (ASU 166157!); ***Felger* (ARIZ 195096!)**; *Felger 01-145* (ARIZ 63085!); *Felger 03-122* (ARIZ 366313!); *Felger 03-127* (ARIZ 364770!); ***Felger 19468* (ARIZ 196888!)**; *Felger 19542* (ARIZ 194728!); *Gillespie 5367* (DS 217483!); *Gillespie 5367* (DS 217594B!); *Gillespie 5367* (UC 499469!); *Gillespie 8845* (UC 489503!); *Gilman 1119* (DS 285954!); *Gross 1763* (RSA 705715!); *Gross 1889* (RSA 705826!); *Gross 3183* (RSA 737785!); *Gross 3284* (RSA 737742!); *Gross 3714* (RSA 749738!); *Hansen 19427* (ARIZ 195096!); *Hansen 19468* (ARIZ 196888!); *Henrickson 9290* (DS 734183!); *Higgins 21969* (ASU 238424!); *Hoffman sn* (RSA 499783!); *Holmgren*



6577 (CAS 576577!); Jones 25808 (DS 698311!); **Keil 15459 (ASU 15740!)**; Keil 2838 (ASU 24728!); **Keil 3047 (ASU 22290!)**; **Keil 3187 (ASU 23449!)**; Keil 4056 (ASU 24092!); Landrum 7639 (ASU 217654!); **Landrum 7639 (ASU 217654!)**; LaPre sn (RSA 614680!); Lehto 11685 (ASU 117434!); Lehto 11855 (ASU 38926!); Lehto 11900 (ASU 38924!); Lehto 15459 (ASU 15740!); Lehto 4767-a (ASU 38925!); Lehto L-18381 (ASU 168479!); **Lehto L23531 (ASU 105305!)**; Lott 72 (ASU 8793!); Makings 1956 (ASU 264688!); McLellan 1158 (ASU 211831!); McLellan 1159 (ASU 223417!); Minckley s.n. (ASU 208271!); Munz 15729 (DS 280386!); Nevers 79 (CAS 739346!); Newton 592 (ASU 278943!); Newton 634 (ASU 279167!); Parish 731 (DS 89277!); **Peebles 9114 (ARIZ 96258!)**; **Phillips (ARIZ 189427!)**; Pinkava 10939 (ASU 166212!); **Pinkava 4704 (ASU 117451!)**; Pinkava 5730 (ASU 68719!); Rebman 1355 (ASU 188111!); Reeves 6821 (ASU 97093!); Reeves s.n. (ASU 106990!); **Reina-G 96-105 (ARIZ 323752!)**; **Russell 11209 (ASU 10316!)**; Russo 436 (ASU 156733!); Russo 462 (ASU 156731!); **Russo 730 (ASU 156740!)**; Sakaki 19882 (ARIZ 188910!); Sanders 12128 (RSA 554021!); Sanders 36599 (RSA 755866!); Sanders 6144 (SBBG 6271!); Simpson 3671 (SDSU 20064!); **Stitt (ASU 06537!)**; **Stitt 1158 (ASU 211831!)**; Stitt s.n. (ASU 66537!); Stoughton 903 (RSA 777543!); Sundell 76 (ASU 69385!); Thornber 524 (ARIZ 16672!); Toumey 239 (ARIZ 16802!); Walters 377 (ASU 232337!); Wheeler 7036 (RSA 614809!); **Whipple 3918 (ARIZ 330758!)**; Wiggins 8730 (ARIZ 16753!); Williams 78-33-18 (CAS 805261!); Wojciechowski 1342 (CAS 1104806!); Wright 1764 (UC 24725!).

**APPENDIX 3.** Voucher specimens used in this study for each taxon and form, listed alphanumerically by collector and collection number. Bold Font = Collectors/vouchers for which data were measured in quantitative study. ! = Voucher verified by the authors. Holotype specimens indicated by “—**TYPE.**”

**Cryptantha cycloptera forma cycloptera:**—Abrams 12965 (DS 213431!); Abrams 7267 (DS 98421!); Abrams s.n. (DS 98141!); Ackerman 31118 (UC 1546732!); Alexander 945 (UC 665793!); Allred 2775 (NMC R 91118); Allred 2818 (NMC R 91126); Allred 8597 (NMC R 91724); Anderson 7488 (NMC 132842); Anderson 7501 (NMC 3166532); Anderson 841 (ARIZ 111868!); Andre 10157 (UCR 211396!); Andre 10740 (UCR 215587!); Andre 10808 (UCR 216089!); Andre 11893 (UCR 215820!); Andre 12163 (UCR 217052!); Andre 12193 (RSA 764791!); Andre 12428 (UCR 218528!); Andre 12503 (UCR 218711!); Andre 12559 (RSA 768758!); Andre 12683 (UCR 217686!); Andre 12728 (UCR 217967!); Andre 13168 (UCR 218377!); Andre 13231 (UCR 216641!); Andre 15098 (UCR 226699!); Andre 16056 (UCR 226689!); Andre 16119 (UCR 226703!); Andre 16383 (UCR 226615!); Andre 16505 (RSA 778305!); Andre 7540 (UCR 183123!); Andre 9401 (UCR 200507!); Andre 9719 (UCR 203333!); **Angel 148 (SD 167731!)**; Annable 472 (ARIZ 263687!); Aulenbrock 139 (UCR 41667!); Baker 15233 (ARIZ 365655!); Baker 15233 (ASU 267882!); Baker 16496 (ARIZ 388107!); Baker 8278 (ASU 179424!); Baker 8828 (ASU 188899!); Baker 8978 (ASU 195453!); Barnes 3197 (UVSC 2154526); Barnes 4210 (UVSC 2156537); Barnes 4266 (UVSC 2156492); Barth 1379 (SD 226399!); Barth 1402 (SD 226398!); Barth 406 (SD 169350!); Bell 21 (RSA 779589!); Bell 693 (RSA 779785!); Benson 4181 (POM 287677!); Bertelsen 2007-9 (ARIZ 387958!); Bingham 344 (ARIZ 151553!); Bolton 94-11 (ARIZ 357344!); Bowers 1124 (ARIZ 219439!); Bowers 2249-2573 (ARIZ 242139!); Bowers 2256 (ARIZ 242242!); Bowers R-963 (ARIZ 242722!); Bowers R-995 (ARIZ 242738!); Boyd 10601 (RSA 701908, UCR 148499!); Boyd 10705 (RSA 701563!); Boyd 11883 (RSA 731043!); Boyd 12229 (RSA 772000B, UCR 218306!); Boyd 1449 (RSA 516909, UCR 60820!); Boyd 2159 (RSA 480073, UCR 52020!); Boyd 2182 (RSA 480093, UCR 52021!); Boyd 7734 (RSA 565639!); **Boyd 7780 (SD 136879, CAS 906178, RSA570350, UCR89511!)**; Brandegees s.n. (UC 78607!); Breedlove 17298 (CAS 513376!); Breedlove 58557 (CAS 689354!); Brown s.n. (ARIZ 98331!); **Buegge 79 (ASU 226954!)**; Bundy 2433 (ASU 101858!); Bundy 2462-A (ASU 101857!); Burgess s.n. (ARIZ 259462!); Butterwick 2660 (ASU 129903!); Butterwick 7068 (CAS 763087, ASU 152646!); **Canfield (SD 40500!)**; Canfield 40500 (UC 1063857!); Carter 1273 (UC 1582995!); Chamberland 1848 (ARIZ 360699!); Christie 108 (SD 140876!); **Christie 108 (SD 140876!)**; Christy 1298 (ASU 200135!); Clark 11403 (UNM 4073755); Clayton 55 (ASU 8529!); Clokey 8089 (CAS 305605, UC 900470, UC 900478!); Clokey 8206 (UC 857232!); Colille 720 (DS 89305!); Columbus 829 (NMC R 90949); Columbus 940 (NMC 132855); Coombs 2433 (ARIZ 16725!); Coombs 2462-A (ARIZ 16812!); Correll 23827 (UC 1412852!); Correll 38342 (UC 1368205!); Correll 38364 (UC 1356673!); Cottam 8374 (ARIZ 119210!); Cowan 1006 (CAS 1007653!); Crooks s.n. (ARIZ 16785!); Crum 1832 (UC 61130!); **D.J. Pinkava 4762 (ASU 137232!)**; Damrel 1623-B (ASU 237494!); **Daniel 2600 (ASU 129979!)**; Daniel 3889 (ASU 154566!); Darrow 2458 (ARIZ 18221!); Darrow s.n. (ARIZ 16703!); Davidson 1818 (RSA 499772!); Davidson s.n. (RSA 499770!); De Groot 1093 (RSA 721031!); De Groot 1231 (RSA 715872!); De Groot 1290 (RSA 705449!); De Groot 1517 (ARIZ 393609!); De Groot 1553 (RSA 721033!); De Groot 1605 (RSA 721034!); De Groot 1694 (RSA 721037!); De Groot 1836 (CAS 1123048, RSA 721038!); De Groot 1988 (RSA 721045!); De Groot 2026 (CAS 1063486, RSA 721032, ARIZ 393608!);

*De Groot 2182* (CAS 1063487!); *De Groot 2250* (RSA 721041!); *De Groot 2363* (CAS 1123046!); *De Groot 2503* (RSA 721249!); *De Groot 2522* (RSA 721247!); *De Groot 2599* (RSA 721248!); *De Groot 2617* (CAS 1123047, RSA 721250!); *De Groot 2766* (RSA 721035!); *De Groot 3833* (RSA 721245B!); *De Groot 3994* (RSA 721246!); *De Groot 4586* (RSA 709862!); *De Groot 4669* (CAS 1125267, RSA 709976!); *De Groot 4683* (RSA 709965!); *De Groot 6324* (RSA 772082!); *De Groot 6489* (RSA 779524!); *De Groot 6489* (SD 219001!); *De Groot 6683* (RSA 778990!); *Dearing s.n.* (SBBG 118916!); *Demaree 42055-A* (ARIZ 157212!); *Dennis s.n.* (ARIZ 16831!); **Doan 1382 (SD 196804, ARIZ396819!); Doan 1446 (SD 166022, ASU251181!); Doan 449** (ASU 236245!); *Douglas 58* (ARIZ 16818!); *Douglas 58* (ARIZ 170694!); *Drees 20827* (ARIZ 194735!); *Duek s.n.* (RSA 314980!); *Dunn 7459* (UNM 4073746); *Duran 2666* (UC 402784!); **Duran s.n. (SD 4204!); Eastwood 17143** (CAS 167874!); *Eastwood 18063* (CAS 188884!); *Eastwood 5987* (CAS 26643!); *Eastwood 7656* (CAS 275521!); *Eastwood 8131* (CAS 26645!); *Eastwood 8864* (CAS 294536, DS 296384!); *Eastwood 8994* (CAS 294538!); *Eastwood 9090* (CAS 294539!); *Eastwood s.n.* (CAS 26641!); *Elias 9266* (RSA 361861!); **Everitt s.n. (ARIZ 196735!); Faulkner 385** (UCR 33817!); *Felger 01-329-C* (ARIZ 358267!); *Felger 01-356* (ARIZ 358907!); *Felger 03-233* (ARIZ 369835!); *Felger 03-333* (ARIZ 365314, ASU 267022!); *Felger 18987* (ARIZ 263965!); *Felger 7255* (ARIZ 365207!); *Felger 7647* (ASU 266924!); *Felger 88-122* (ARIZ 305572!); *Felger 88-304* (ARIZ 305519!); *Felger 93-123* (ARIZ 314654!); *Felger s.n.* (ARIZ 188147!); *Felger s.n.* (ARIZ 194963!); *Ferris 13302* (DS 391804, JEPS 20705B!); *Ferris 7225* (DS 181387!); *Ferris 7280* (DS 181271!); *Ferris 9712* (DS 268330!); *Fink 515* (NMC R 91947); *Fink 521* (NMC R 91948); *Fischer 5982* (ASU 124772!); **Fischer 6011 (ARIZ 233611, ASU133538!); Fletcher 3741** (UNM 4073753); *Fletcher 5941* (UNM 4073736); *Fosberg 10604* (UC 533179!); *Fosberg 10607* (CAS 252117!); *Fosberg 10649* (UC 551855!); *Fosberg 404* (UCR 47832!); *Fraga 317* (RSA 720531!); *Freeman 2143* (CAS 781080!); *Freeman s.n.* (ASU 166219!); **Gander 3159 (SD 16704!); Gander 8953 (SD 28374!); Garton 16915** (ARIZ 228953!); *Gentry 5972* (POM 369245!); *Gierisch 4103* (ASU 96384!); *Gillespie 5476* (DS 217511!); *Gillespie 5476* (UC 489464!); *Gillespie 8819* (DS 219606, UC 467497!); *Gillespie 8845* (DS 220865!); *Gillespie 8853.5* (DS 217594A!); *Glenn 8* (UCR 72188!); *Glenn s.n.* (RSA 554249!); *Goodding 23-52* (ARIZ 120515, ARIZ 16756!); *Goodding 48-52* (ARIZ 120492, ARIZ 16639!); *Goodding 4897* (ARIZ 329095!); *Goodding 66-58* (ARIZ 151370!); *Goodding s.n.* (DS 311370!); *Goodman 35* (RSA 652501!); *Gould 1480* (CAS 320253, DS 324875, POM 298806, UC 857105, ARIZ 20121!); *Gould 2920* (ARIZ 20517!); *Gregory 1377* (SD 183753!); **Gregory 1377 (SD 183753!); Gregory 2654** (SD 205628!); **Gregory 2654 (SD 205628!); Gross 1428** (RSA 703379!); *Gross 1451* (RSA 703399!); *Gross 1468* (RSA 707098!); *Gross 2878* (RSA 732670!); *Gross 2944* (RSA 732542!); *Gross 2981* (RSA 732498B!); *Gross 3002* (RSA 732578, UC 1745591!); *Gross 3121* (RSA 735537B!); *Gross 3183* (UCR 211870!); **Guilliams 619 (SDSU 18949!); Guilliams 621 (SDSU 18950!); Gullion 160** (UC 985047!); *Gullion 469* (UC 100843!); *Gustafson 2484* (RSA 499774!); *Hall 6807* (UC 1007241!); *Halverson 380* (ASU 28761!); *Hansen s.n.* (ARIZ 188996!); *Hansen s.n.* (ARIZ 189120!); *Hansen s.n.* (ARIZ 195453!); *Hansen s.n.* (ARIZ 195607!); *Hansen s.n.* (ARIZ 219524!); **Harbison 41.8 (SD 28896!); Harbison 41.99A (SD 29151!); Harbison s.n. (SD 16842!); Harbison s.n. (SD 16899!); Harlan 295-d** (ARIZ 311214!); *Harrison 8658* (ARIZ 96262!); *Harrison 9114* (UC 499488!); *Harrison s.n.* (ARIZ 96281!); *Hastings 9025* (ARIZ 405279!); *Heil 32173* (UNM 4119878); *Helmkamp 3045* (UCR 104875!); *Helmkamp 6367* (UCR 122801!); *Helmkamp sn* (UCR 90205!); **Hendrickson 16491 (SD 100055!); Hendrickson 3507** (SD 214191!); *Hendrickson 4470* (SD 208485!); *Hendrickson 4555* (SD 210832!); *Hendrickson 4578* (SD 210833!); **Hendrickson 476 (SD 172710!); Hendrickson 9260** (CAS 734185!); *Herbar 104* (ARIZ 16846!); *Herbar 104* (ARIZ 98327!); *Hess 1841* (NMC 132853); *Hess s.n.* (ARIZ 170553!); *Higgins 6282* (ASU 167829!); *Hitchcock 25549* (UC 1345886!); *Hodgson 16151* (ASU 280353!); *Hoffmann s.n.* (SBBG 53391!); *Holmgren 2064* (ID 108322); *Holmgren 6723* (ASU 86578!); *Holmgren 7583* (ID 108324, ASU93383); *Honer 2840* (RSA 758102!); *Hoover 10912* (UC 1368206!); *Hoover 10912* (UC 1392728!); **Howe s.n. (SD 63843!); Howell 22386** (CAS 359740!); *Howell 24535* (ARIZ 16752!); *Howell 3558* (CAS 177001!); *Howell 49117* (CAS 56525!); *Howell 52352* (CAS 593328!); *Howell s.n.* (CAS 359578!); *Jenke 264* (ASU 275618!); *Jenke 611* (ASU 279595!); *Jenkins 1513* (CAS 982239!); *Jenkins 82-425a* (ARIZ 311390!); *Jepson 11785* (JEPS 67796!); *Jepson 12564* (JEPS 67795!); *Jepson 5874* (JEPS 67798!); *Jepson 6985* (JEPS 67797!); *Johnson s.n.* (ARIZ 176783!); **Jones 1477 (ASU 282253!); Jones 25633** (POM 178071!); *Jones 3753* (UC 1178542!); **Jonsson 451 (SD 115578!); Joyal 2160** (ASU 192868!); *Kamb 819* (UC 1178394!); *Kearney 10893* (ARIZ 96287!); *Kearney 13151* (ARIZ 96263!); *Kearney 9231* (ARIZ 96257!); *Keck 3004* (DS 718381!); *Keck 3918* (DS 252785, DS 718384!); *Keck 4135* (DS 287979!); *Keil 1478* (ASU 10794!); *Keil 3236* (ASU 24713!); *Keil K-11258* (ASU 83440!); *La Doux 604* (RSA 777946!); *La Doux 79* (UCR 183261!); *Lane 670* (ASU 86998!); *Lane 831* (ASU 86997!); *Lehto 10649* (ASU 166160!); *Lehto 10721* (ASU 166178!); *Lehto 11097* (ASU 162886!); *Lehto 11448* (ASU 59092!); *Lehto 15417-a* (ASU 15784!); *Lehto 1631* (ASU 67714!); *Lehto 251* (ASU 6542!); *Lehto 4583* (ASU 38927!); *Lehto L-19731* (ASU 83970!); *Lehto L-20012* (ASU 86157!); *Lehto L-20067* (ASU 86472!); *Lehto L-21036* (ASU 91309!); *Lehto L-22589*

(ASU 252523!); *Lehto L-23426* (ASU 105306!); *Lehto L-23531* (ASU 105305!); *Lester 72* (ASU 268235!); *Lindley 415* (SDSU20825!); *Lowler 523* (DS 3000051!); *Maguire 10124* (ARIZ 111864, UC 553397!); *Maguire 10124* (UC 551860!); *Maguire 10553* (ARIZ 111865!); *Maguire 10804* (UC 553404!); *Maguire 11026* (ARIZ 111866!); *Maguire 1535* (UC 521464!); *Maguire 4970* (UC 528720!); *Makings 1904* (ASU 265753!); ***Makings 1956* (SD 166021, ASU264688!); *Marsden 31V92A* (SDSU 17729!); *Marsen 381* (SD 207725!); *Marsh* (SDSU 05416!); *Marsh 1252* (SDSU20049!); *Martin 54* (ASU 66539!); *Mason 314* (ASU 56074!); *Mason 936* (ARIZ 252096!); *Mauz 24-28* (ARIZ 368061!); *Mays s.n.* (ASU 147557!); *Mays s.n.* (ASU 147619!); *Mays s.n.* (ASU 170229!); *Mays s.n.* (ASU 170314!); *Mays s.n.* (ASU 170315!); *Mays s.n.* (ASU 170316!); *Mays s.n.* (ASU 170547!); *McClinktock 52-467* (CAS 373290!); *McClinktock 52-48* (CAS 433673!); *McGill 1994* (ARIZ 294661, ASU 168700!); *McGill 6113* (ASU 272019!); *McGill LAM-1124* (ASU 102692!); *McGill LAM-1214* (ASU 102693!); *McGill LAM-1252* (ASU 94248!); *McGinnies s.n.* (ASU 10213!); *McGinnies s.n.* (ASU 10379!); *McLaughlin 10110* (ARIZ 376555!); *McLaughlin 10265* (ARIZ 385051!); ***McLaughlin 2962* (SD 121531, ARIZ257307!); *McLaughlin 3179* (ARIZ 16717!); *McLaughlin 6277* (ARIZ 305155!); *McLaughlin 8887* (ARIZ 373618!); *McLaughlin 9119* (ARIZ 372582!); *McLaughlin 9934* (ARIZ 372535!); *McVaugh 8028* (DS 351461!); *Metcalf 1573* (NMC 132848); *Minckley s.n.* (ASU 208271!); *Minnis s.n.* (ASU 150670!); ***Moran 12495* (SD 65314, ARIZ165414, UC125926!); *Moran 12594* (SD 65313, DS 598785!); *Moran 13075* (SD 63019, UC1353371!); *Moran 20456* (SD 87278, ASU85661!); *Moran 20486* (SD 87245!); *Moran 20678* (SD 88929!); *Moran 20782* (SD 88928!); *Moran 26926* (SD 102510!); *Mullins 252* (POM 369244B!); *Munz 14876* (DS 290422, POM 229859!); *Munz 14876* (UC 638750B!); *Munz 15729* (SBBG 63948!); *Nelson 10316* (UC 439832!); *Nelson 1247* (UC 553412!); *Nelson 3363* (UC 718047!); *Newlon 509* (JEPS 67804!); *Newton 211* (ASU 274004!); *Newton 432* (ASU 278264!); *Nichol s.n.* (ARIZ 16850!); *Nichol s.n.* (ARIZ 92711!); *Niles 557* (ARIZ 155954!); *O'Halloran 6* (ARIZ 16795!); *Orcutt 174* (CAS 715530!); *Ortiz-Barney 495* (ASU 262358!); *Parish 19208* (UC 24726!); *Parish 731* (DS 89277 A!); *Parish 9781* (DS 89281!); *Parish s.n.* (DS 134301!); *Parker 7861* (DS 358359, ARIZ 85949!); *Peebles 5196* (ARIZ 96260!); *Peebles 6528* (ARIZ 16838!); *Peebles 6528* (ARIZ 16849!); *Perrill 5037* (ARIZ 299023!); *Peterson 84* (UCR 42031!); *Phillips 1104* (UCR 69520!); *Pinkava 10047* (ASU 49435!); *Pinkava 10202* (ASU 49200!); *Pinkava 10338* (ASU 49899!); *Pinkava 10805* (ASU 50127!); *Pinkava 10847* (ASU 55557!); *Pinkava 10978* (ASU 55611!); *Pinkava 12266* (ASU 37574!); *Pinkava 12681* (ASU 42046!); *Pinkava 4642* (ASU 116986, ASU 137232!); *Pitzer 1892* (UCR 96152!); *Poindexter* (DS 288277!); *Porter 12507* (RSA 717750!); *Porter 12559* (RSA 717542!); *Porter 12586* (RSA 717552!); *Price 720-b* (ASU 269849!); *Price 735-b* (ASU 269921!); *Price 740* (ASU 269846!); *Prigge 2657* (UCR 32416!); *Prigge 2886* (UCR 32356!); *Prigge 7331* (ARIZ 314859!); *Prigge 7331* (UC 1417878!); ***Pringle s.n.* (CAS 202!—TYPE); *Pringle s.n.* (DS 243417!); *Quinn 888* (ARIZ 372949!); *Raven 12080* (UC 1084520!); *Ray K-38* (UC 1168714!); ***Rea 609* (SD 118303!); *Rebman 1355* (SD 137254!); *Rebman 18776* (SD 204181!); *Rebman 7212* (SD 155823!); *Reeves 6525* (ASU 107381!); *Reeves 6742* (ASU 106926!); *Reichenbacher 205* (ARIZ 226715!); *Reichhardt 164* (ARIZ 253055!); *Reichhardt 85-71* (ARIZ 258510!); *Reina 2003-166* (ASU 248249!); *Reina 2004-369* (ARIZ 391781!); *Reina 620* (CAS 1077115!); *Reina 96-105* (ARIZ 16702!); *Rice 110* (ASU 189935!); *Rice 1214* (ASU 190443!); *Rice 293* (ASU 191421!); *Rice 451* (ASU 191074!); *Romspert 8017* (RSA 499759!); *Rondeau 89-25* (ARIZ 16844!); *Roos sn* (UCR 19091!); *Russell 10992* (ASU 10318!); *Russell 11338* (ASU 10321!); *Russell 11349* (ASU 10317!); *Russell 62-9* (ASU 60525!); *Russo 474* (ASU 156932!); *Russo 590* (ASU 156732!); *Russo 613* (ASU 156739!); *Russo 627* (ASU 156716!); *Rutman 2003-64* (ARIZ 363548!); *Rutman 20050304-26* (ARIZ 374486!); *Rutman 20050306-8* (ARIZ 374510!); *Salvato 3971* (UCR 222886!); *Sanders 12128* (UCR 75063!); *Sanders 15450* (UCR 88265!); *Sanders 16337* (UCR 86798!); *Sanders 16450* (SD 232627!); *Sanders 23749* (CAS 1025404, UCR 116372!); *Sanders 23755* (UCR 116763!); *Sanders 23794* (UCR 116445!); *Sanders 23824* (UCR 116635!); *Sanders 34683* (UCR 192239!); *Sanders 36414* (UCR 204063!); *Sanders 36437* (UCR 203815!); *Sanders 36467* (UCR 203623!); *Sanders 36599* (UCR 211024!); *Sanders 36663* (UCR 210845!); *Sanders 36721* (UCR 210849!); *Sanders 36785* (UCR 210960!); *Sanders 37476* (UCR 214586!); *Sanders 38226* (CAS 1121078, UCR 214445!); *Sanders 39134* (UCR 225569!); *Sanders 6119* (UCR 41610!); *Sanders 9033* (UCR 132814!); *Sanders 947* (UCR 18153A!); ***Scheidlinger s.n.* (SDSU 18156 B!); *Shervanick 683* (POM 319926!); *Shervanick 701* (CAS 1022098!); *Shreve 5125-A* (ARIZ 92698!); *Shreve 7340* (ARIZ 16845!); *Shreve 7340* (ARIZ 98323!); *Shreve 8920* (ARIZ 98322!); *Shreve 8920* (UC 724388!); *Shreve 9464* (ARIZ 16746, ARIZ 98329!); ***Simpson 3050* (SDSU 18453!); *Simpson 3662* (SDSU 20022!); *Simpson 3671* (SDSU 20064!); *Simpson 3672* (SDSU 20049!); *Sivinski 1040* (UNM 4073742); *Sivinski 1666* (UNM 4073744); *Sivinski 3524* (UNM 4027876); *Sivinski 3581* (UNM 4029290); *Sivinski 4211* (UNM 4029859); *Sivinski 983* (UNM 4073741); *Sivinski 991* (UNM 4073743); *Sivinski 995* (UNM 4073750); *Sivinski 997* (UNM 4073749); *Sivinski s.n.* (UNM 4073751); *Smith 1563* (ASU 58899!); *Spaulding 75-6* (ARIZ 198271!); *Spellenberg 13354* (NMC 132724); *Spellenberg 2239* (NMC 132845); *Spellenberg 3004* (NMC 132851); *Spellenberg 3004* (NMC 132852); *Spellenberg 5064* (NMC 132843); *Spellenberg 8405* (NMC 132854);**************

*Spencer 200* (CAS 26635!); *Stevens s.n.* (ASU 216357!); *Stewart 691* (UCR 89717!); *Stewart s.n.* (UCR 38134!); *Stoughton 1035* (RSA 776649!); *Stoughton 1282* (RSA 777309!); *Stoughton 973* (RSA 777442!); *Strandberg 428* (ARIZ 166895, ARIZ 16729!); *Swanson 346* (RSA 776757!); *Swearingen 1018* (RSA 319951!); *Taylor 6882* (JEPS 90334!); *Tedford 608* (ARIZ 387986!); *Theroux 1274* (ARIZ 200447!); *Theroux 1716* (ASU 165732!); *Theroux 1737* (ARIZ 200583!); *Thornber 2486* (ARIZ 16750!); *Thornber 4714* (ARIZ 92705!); *Thornber 4787* (ARIZ 98338, ARIZ 16710!); *Thornber 4894* (ARIZ 16848!); *Thornber 525* (CAS 920764, ARIZ 188030, ASU 221026, CAS 799517!); *Thornber 5311* (ARIZ 98339, ASU 204598, ARIZ 16822!); *Thornber 659* (ARIZ 16713!); *Thornber 659* (ARIZ 92712!); *Thornber s.n.* (ARIZ 16688!); *Thornber s.n.* (ARIZ 16874!); *Thornber s.n.* (ARIZ 328248!); *Thornber s.n.* (ARIZ 92704!); *Thornber s.n.* (ARIZ 92706!); *Thornber s.n.* (ARIZ 92713!); *Thornber s.n.* (ARIZ 92714!); *Thornber s.n.* (ARIZ 98333!); *Thornber s.n.* (ARIZ 98335!); *Thornber s.n.* (ARIZ 98336!); *Thornber s.n.* (ARIZ 98337!); *Thorne 55661* (RSA 760174!); *Thorne 60131* (BCMEX 3982); *Toumey 239* (ARIZ 98330!); *Toumey s.n.* (UC 1929676!); *Toumey s.n.* (UC 306219!); *Toumey s.n.* (UC 731790!); *Train 1602* (ARIZ 129742!); *True 8256* (CAS 618182!); *Turner 68-68* (ARIZ 169020!); *Twisselmann 11967* (CAS 515790, CAS 604393!); *Twisselmann 7107* (CAS 515808, CAS 604392!); *Unknown collector 15740* (UNM 4004374); *Van Devender 74-47* (ARIZ 16821!); *Van Devender 84-49* (ARIZ 247167!); *Van Devender 88-68* (ARIZ 278379!); *Van Devender s.n.* (ARIZ 16641!); *Van Devender s.n.* (ARIZ 184340!); *Van Devender s.n.* (ARIZ 185659!); *Van Devender s.n.* (ARIZ 187424!); *Van Devender s.n.* (ARIZ 240899!); *Walden 57* (ASU 8701!); *Ward 25* (ASU 105435!); ***Warren 68-68* (SD 78487, ARIZ16642!);** *West 180* (ARIZ 368009!); *West 76* (ARIZ 368015!); *Whipple 3918* (ARIZ 330758!); ***Whipple 3918* (SD 179253!);** *White 10211* (RSA 702787, UCR 149865!); *White 3173* (UCR 88806!); *White 3252* (UCR 89240!); *White 4024* (UCR 94035!); *White 8275* (RSA 676095!); *Whitehead 101* (ARIZ 16733!); *Whitehead s.n.* (ARIZ 16765!); *Whitehead s.n.* (ARIZ 16767!); *Whitehead s.n.* (ARIZ 191128!); *Whitehead s.n.* (ARIZ 191332!); *Wiggins 6524* (DS 230109!); *Wiggins 8198* (UC 662530!); *Wiggins 8445* (UC 665786, ARIZ 16787!); *Wiggins 86* (DS 507106!); *Wiggins 8730* (DS 312252!); *Wiggins s.n.* (ARIZ 203268!); *Wilson s.n.* (UC 595708!); *Winblad sn* (CAS 252330!); *Wolf 6657* (ARIZ 142656!); *Wolf s.n.* (UC 711799!); ***Woodin 19336* (SD 92033!);** *Wooton 359* (NMC 132849); *Wooton 3824* (NMC 132844); *Wooton s.n.* (NMC 132847); *Worthington 11718* (CAS 1000519!); *Worthington 18956* (ASU 259205!); *Worthington 26269* (UNM 4020504); *Worthington 26340* (UNM 4020539, ARIZ349087); *Worthington 4247* (ARIZ 226559!); *Wright 1770* (UC 24721!); *Yates 6456* (UC 1051611!); *Zabriskie s.n.* (SBBG 14715!).

***Cryptantha pterocarya* var. *pterocarya* forma *pterocarya*:**—*Abrams 11201* (DS 180499!); *Abrams 11809* (DS 161908!); *Abrams 11881* (DS 162994!); *Abrams 11890* (DS 163024!); *Abrams 11963* (UC 857245!); *Abrams 14037* (DS 280948!); *Abrams 14169* (DS 280993!); *Ackerman 31117* (UC 1582994!); *Ackerman 77-67* (RSA 661802!); *Ahart 11982* (JEPS 107799!); *Alava 1735* (JEPS 23016!); *Alava 1739* (JEPS 23019!); *Alava 1861* (JEPS 23095!); *Alava s.n.* (ARIZ 146511!); *Alexander 1298* (UC 666394!); *Alexander 1445* (UC 666396!); *Alexander 1455* (DS 292276!); *Alexander 2090* (UC 667385!, DS 332954!); *Alexander 2137* (UC 667384!); *Alexander 321* (UC 625649!); *Almeda 4467* (CAS 877797!); *Andre 10368* (UCR 211146!); *Andre 11893* (RSA 765343!); *Andre 11981* (UCR 215849!); *Andre 12215* (UCR 216959!); *Andre 12337* (UCR 217055!); *Andre 12342* (RSA 765590!); *Andre 12387* (RSA 765996!); *Andre 12565* (RSA 768760!); *Andre 12605* (UCR 217588!); *Andre 12701* (UCR 217986!); *Andre 12759* (UCR 218568!); *Andre 12855* (UCR 218815!); *Andre 12969* (RSA 768126!); *Andre 13056* (UCR 218034!); *Andre 13072* (RSA 770194A!); *Andre 13286* (UCR 216984!); *Andre 13311* (RSA 766035!); *Andre 13321* (UCR 216706!); *Andre 13517* (UCR 216775!); *Andre 13598* (RSA 767998!); *Andre 13676* (UCR 217231!); *Andre 13785* (RSA 765638!); *Andre 13877* (UCR 222142!); *Andre 14025* (UCR 221331!); *Andre 14231* (UCR 221944!); *Andre 15114* (UCR 226739!); *Andre 15686* (UCR 226285!); *Andre 16144* (RSA 778827!, UCR 226624!); *Andre 16311* (UCR 226175!); *Andre 16318* (UCR 226183!); *Andre 16450* (UCR 225981!); *Andre 16563* (UCR 227186!); *Andre 16711* (UCR 226276!); *Andre 16768* (UCR 226956!); *Andre 16876* (RSA 783152!); *Andre 16943* (RSA 785945!); *Andre 16972* (UCR 226409!); *Andre 17067* (UCR 225854!); *Andre 17276* (RSA 780665!, UCR 234490!); *Andre 17538* (UCR 235568!); *Andre 17735* (UCR 232940!); *Andre 17923* (UCR 235713!); *Andre 17963* (RSA 782128!); *Andre 18040* (UCR 236071!); *Andre 18372* (UCR 232534!); *Andre 18387* (RSA 779429!, UCR 232540!); *Andre 19846* (RSA 781650!); *Andre 7351* (UCR 175206!); *Andre 9253* (RSA 738652!); *Andre 9480* (RSA 735762!, UCR 199082!); *Andre 9719* (UCR 203333!); *Annable 2306* (RSA 668354!); *Annable 302* (UCR 46043!); *Applegate 5617* (DS 214127!); *Applegate 5617* (WILLU 19513); *Archer s.n.* (ARIZ 92699!); *Atwood 8557* (NY 2971660, NY 2971661); *Axelrod 309* (UC 1063856!, UC 572604!); *Bacigalupi 6238* (JEPS 22611!); *Bacigalupi 6239* (JEPS 22608!); *Bacigalupi 8506* (JEPS 29753!); *Bagley 1920* (UCR 54061!); *Bair 127* (NY 2883144); *Bair 317* (CAS 1094848!, NY 2884732!); *Baird 1981* (RSA 521435!); *Baker 10103* (ID 108342); *Baker 9007* (ASU 195460!); *Baker 975* (UC 78598!); *Baker s.n.* (WS 60449); *Ballmer s.n.* (UCR 133504!); *Balls 14849* (RSA 60003!); *Barkworth 2584* (CAS 823264 A!); *Barnes 3131* (UVSC 2154292); *Barnes 3156* (UVSC 3377746); *Barnes 3200* (UVSC 2154528); *Barnes 3811* (UVSC 2155737);

*Barnes 3848* (UVSC 2156034); *Barnes 4894* (UVSC 2157505); *Barnes 4942* (UVSC 2157715); *Barnes 4992* (UVSC 2157877); *Beach s.n.* (UC 1733889!); *Beal 124* (JEPS 18400!); *Beatley 12722* (RSA 230416!); *Beatley 2768* (DS 561518!); *Beatley 3349* (DS 601107!); *Beauchamp 1744* (SD 83522!); *Beauchamp 1752* (SD 86165!); *Beley 739* (CAS 781077!); *Beley 740* (CAS 781078!); *Bell 2183* (RSA 774299!); *Bell 2230* (RSA 775635!); *Bell 2242* (RSA 775388!); *Bell 2254* (RSA 775397!); *Bell 2265* (RSA 775490!); *Bell 2643* (RSA 779441!); *Bell 2681* (RSA 779184!); *Bell 2703* (RSA 779668!); *Bell 3321* (RSA 788655A!); *Bell 3347* (RSA 785250!); *Bell 703* (RSA 779692!); *Bell 705* (RSA 779694!); *Benson 5980* (POM 287679!); *Benson 8156* (RSA 430492!); *Berg 1379* (SD SU5493!); *Bowers 1636* (RSA 764451!); *Bowers s.n.* (ARIZ 238409!); *Boyd 10217* (RSA 612091!); *Boyd 10515* (RSA 689724!); *Boyd 10656* (RSA 701916!); *Boyd 10656* (UCR 148504!); *Boyd 10761* (RSA 726211!); *Boyd 11618* (RSA 776744!, RSA 777194!, UCR 225698!, SD 220044!); *Boyd 11916* (UC 1928558!); *Boyd 12229* (RSA 772000A!, UCR 218306!); *Boyd 1499* (RSA 515208!); *Boyd 1520* (RSA 517996!, UCR 138550!); *Boyd 1526* (RSA 518001!); *Boyd 1609* (RSA 491636!); *Boyd 1777* (RSA 572915!); *Boyd 6922* (RSA 562061!); *Boyd 7846* (CAS 908252!, RSA 570258!, UCR 89401!); *Brandegee* (UC 178156!); *Brandegee* (UC 178176!); *Brandegee* (UC 178178!); *Brandegee* (UC 178179!); *Brandegee* (UC 178182!); *Brandegee s.n.* (UC 78602A!); *Brandegee s.n.* (UC 78603!); *Brandegee s.n.* (UC 79358!); *Brenckle 51250* (UC 925875!); *Briggs 2* (WS 334265); *Brown 235* (ASU 100797!); *Brown 409* (ASU 100617!); *Bruff s.n.* (RSA 699867!); *Buck 872* (JEPS 86534!); *Buegge 311* (ASU 228900!); *Burge 315* (RSA 518421!); *Butterwick 6789* (ASU 159480!); *Butterwick 8970* (ASU 149390!); *Cantrell 21* (UCR 45341!); *Cantrell 32* (UCR 157715!); *Carlson s.n.* (OSC 186265); *Carlson s.n.* (UCR 46264!); *Chambers 6055* (OSC 192057); *Chambers 6064* (OSC 192051); *Charlton 5234* (RSA 555484!); *Charlton 5932* (UCR 82122!); *Chisaki 1032* (SD 51692!); *Chisaki 792* (UC 1094787!); *Chisaki 835* (UC 1094806!); *Christie 108* (UCR 99747!); *Clark s.n.* (UC 79357!); *Clemons 1018* (SD 118145!); *Clemons 1300* (SD 118946!); *Clifford 01-114* (UNM 4051244); *Clifford 03-196* (UNM 4101245); *Clifford 03-261* (RSA 731384!); *Clifford 95-417* (UNM 4062544); *Clokey 5816* (UC 857242!); *Cole 566* (UC 1329935!); *Cooper 3334* (RSA 499780!); *Cooper 3386* (RSA 499752!); *Cooper 3641* (RSA 499751!); *Cooper s.n.* (UVSC 2148267); *Cooper s.n.* (WILLU 1017); *Copeland s.n.* (DS 308869!); *Crampton 2542* (UC 1278104!); *Cronquist 6223* (WS 203540); *Cronquist 6269* (DS 350029!); *Cronquist 6269* (ORE 76199, WS 203541); *Cronquist 6901* (CAS 392082!, DS 366393!); *Cronquist 6901* (OSC 86162, WS 210309); *Cronquist 6945* (UC 1000175!); *Cronquist 6945* (WS 210301); *Cronquist 8159* (WS 248978, WTU208429); *Cronquist 9981* (UC 1279010!); *Crosswhite 636* (ASU 10320!); *Crum 1832* (UC 638750A!); *Crum 1853* (UC 638810!); *Curran s.n.* (UC 193953!); *Cutler 2229* (CAS 271433!); *Darrow s.n.* (ARIZ 83206!); *Darrow s.n.* (ARIZ 98325!); *Daubenmire 5510* (WS 216296); *Daubenmire 5833* (WS 231911); *Davidson 1760* (RSA 499762!); *Davidson 1769* (RSA 499763!); *Davidson 2698* (RSA 499753, RSA 499756!); *De Groot 1157* (RSA 705446!); *De Groot 2182* (ARIZ 393610!); *De Groot 2182* (RSA 721039!); *De Groot 3576* (RSA 711342!); *De Groot 3833* (RSA 721245A!); *Dearing 3077* (SBBG 6268!); *Dearing 4859* (SBBG 14712!); *Dearing s.n.* (SBBG 14697!); *Dearing s.n.* (SBBG 14710!); *Dearing s.n.* (SBBG 14711!); *Dearing s.n.* (SBBG 14713!); *Dearing s.n.* (SBBG 14714!); *DeDecker 1338* (SBBG 42630!); *DeDecker 1723* (RSA 622042!); *DeDecker 1726* (RSA 622045!); *DeDecker 1739* (RSA 622272!); *DeDecker 2459* (RSA 627731!); *DeDecker 3103* (RSA 616817!); *DeDecker 3164* (RSA 619650!); *DeDecker 3213* (RSA 624675!); *DeDecker 3508* (RSA 617750!); *DeDecker 5978* (RSA 626034!); *DeDecker 636* (SBBG 42686!); *DeDecker 817* (RSA 621793!); ***Dellavalle 10IV95E* (SDSU 12030!); *Dellavalle 10IV95J-I* (SDSU 12025!);** *Demaree 38926* (RSA 186148!); *Dennis s.n.* (ARIZ 187632!); *Doan 1635* (RSA 779274!); *Donahue s.n.* (RSA 499736!); *Dunkle s.n.* (RSA 499773!); ***Dunn 17666* (ASU 135163!);** *Duran 2866* (UC 1297580!); *Duran M18* (UC 1297252!); *Eastwood 1369* (CAS 206479!); *Eastwood 14748* (CAS 146323!); *Eastwood 14837* (CAS 146193!); *Eastwood 17029* (CAS 167871!); *Eastwood 17996* (CAS 188869!); *Eastwood 18120* (CAS 188878!); *Eastwood 18730* (CAS 196024!); *Eastwood 19677* (CAS 167873!); *Eastwood 3197* (CAS 26649!); *Eastwood 3954* (CAS 252317!); *Eastwood 826* (CAS 206445!); *Eastwood 8950* (CAS 294534!, UC 703051!); *Eastwood 9122* (CAS 294528!); *Eastwood 9536* (CAS 294535!); *Elvin 4723* (UCR 175762!); *Epling s.n.* (UC 563993!); *Ertter 3685* (NY 2967734); *Ertter 6023* (RSA 517326!, UC 1561303!); *Ertter 6035* (UC 1561977!); *Ertter 6039* (UC 1561290!); *Ertter 7069* (UC 1561883!); *Everett 23092* (UC 1080283!); *Eyerdam 603* (UC 581582!); *Eyerdam 644* (UC 581580!, UC 857241!); *Ferris 13202* (DS 391646!, JEPS 20705A!); *Ferris 891* (DS 91517!); *Ferris 9536* (DS 256417!); *Fiker 1632* (WS 75605); *Fiker 1637* (WS 75609); *Fischer 6053* (ASU 118011!); *Fishbein 4568* (ID 108297); *Forbes 471* (RSA 786768!); *Fosberg 10617* (CAS 252118!, RSA 499784!, UC 551837!); *Fosberg 2309* (UCR 47836!); *Fosberg 2515* (UCR 50376!); *Fraga 1035* (RSA 730534!); *Fraga 187* (RSA 720585!); *Fraga 281* (RSA 720757!, UCR 196725!, UC 1927539!); *Fraga 317* (UC 1927364!); *Fraga 433* (RSA 720856!, UC 1927392!, UCR 185163!); *Fraga 496* (RSA 721257!); *Fraga 605* (RSA 720420!); *Fraga 666* (RSA 729046!); *Freece 46* (CAS 456162!); ***Gallup 190* (SDSU 05500!);** *Gander 134* (SD 10444!); *Gander 22* (SD 11183!); *Gentry 1519-a* (NY 2893203); *Gentry Jr 1519a* (DS 629156!); *Gierisch 4656* (ARIZ 215496!); *Gifford 643* (UC 1063858!, UC 572220!); *Goodding 2202* (UC 133679!);

*Goodding 974* (NY 2893205); *Goodding 974* (POM 64241!); *Goodrich 27201* (USUUB 3405209); *Goodrich 27504* (USUUB 3405207); *Gorman s.n.* (ORE 115008); *Gould 1595* (UC 857230!); *Gould 1705* (DS324984!, UC 857233!); *Gould s.n.* (ARIZ 20098!); *Gould s.n.* (ARIZ 20118!); *Gowen 975* (JEPS 116909!); *Grable 4530* (WS 340587); *Grable 4552* (WS 340602); *Grable 4561* (WS 340669); *Green s.n.* (RSA 518329!); *Green s.n.* (UCR 170394!); *Gross 1464* (RSA 703414!); *Gross 1548* (RSA 704313!); *Gross 1619* (RSA 704181!); *Gross 1693* (RSA 705749!); *Gross 1938* (RSA 707399!, SBBG 118833!); *Gross 2018* (RSA 707152!); *Gross 2069* (RSA 710549!); *Gross 2147* (RSA 713721!); *Gross 2210* (RSA 710833!); *Gross 2320* (UCR 177446!); *Gross 2510* (UCR 197137!); *Gross 2981* (RSA 732498A!); *Gross 3076* (RSA 732684!); *Gross 3121* (RSA 735537A!); *Gross 3781* (RSA 749570!); *Gross 863* (RSA 679958!, UCR 151232!); *Gross 891* (RSA 679858!, UCR 151341!); *Gullion 449* (UC 1052047!); *Gustafson 2553* (RSA 499765!); *Hall 6803* (UC 100873!); *Hall 7245* (UC 100874!); *Halse 1321* (DS 717378!); *Halse 1321* (OSC 148661!); *Halse 133* (ARIZ 184135!); *Halse 1936* (OSC 215676); *Halse 5962* (UC 1779121!); *Hammond 11980* (UNM 4079028); *Harris 3732* (UVSC 2157284); *Hart 8* (CAS 139350!); ***Hasenstab 55* (SDSU 18692!); *Hasenstab 60* (SDSU 18699!); *Hasenstab 62* (SDSU 18703!); *Hasenstab 65* (SDSU 18706!); *Hasenstab 67* (SDSU 18709!);** *Heckard 1780* (UC 57243!); *Heil 23630* (NMC 3838615, NMC 4339508); *Heller 10971* (DS 8653!); *Heller 15972* (UC 703094!, UC 727087!); *Heller 7668* (DS 134827!, DS 8657, UC 133576!); *Heller 8275* (UC 154091!); *Heller 8365* (CAS 26640!, DS 8690!, DS 89111!); *Helmkamp 2804* (UCR 101631!); *Helmkamp 2838* (SD 224879!); *Helmkamp 2838* (UCR 104864!); *Helmkamp 3045* (UCR 104875!); *Helmkamp 3149* (UCR 103304!); *Helmkamp 3353* (UCR 118302!); *Helmkamp 6307* (UCR 121858!); *Helmkamp 6387* (UCR 123980!); *Helmkamp s.n.* (RSA 511342!); *Helmkamp s.n.* (UCR 14499!); *Henderson 14341* (DS 256062!); *Henderson 14341* (ORE 111130); *Henderson 5014* (CAS 127411!); *Henderson 5014* (ORE 76211); *Henderson 5015* (CAS 127412!, DS 144151!); *Henderson 5015* (ORE 76209); *Henderson 5211* (CAS 127581!, DS 144296!); *Henderson 5211* (ORE 76210); *Henderson 8277* (ORE 76207); *Henderson s.n.* (ORE 76200); *Henderson s.n.* (ORE 76204); *Henderson s.n.* (ORE 76205); *Henderson s.n.* (ORE 76206); *Hendrickson 9156* (DS 734184!); *Hendrickson 10483* (DS 734186!); *Hendrickson 2* (DS 734146!); *Hendrickson 2943* (SD 205629!); *Hendrickson 388* (SD 173647!); *Hendrickson 414* (SD 172712!); *Henrickson 16844* (UCR 33270!); *Henrickson 2* (DS 734182!); *Hevron 1472* (UNM 4004373); *Higgins 13049* (ASU 130866!); *Higgins 18645* (RSA 564548!); *Higgins 6575* (ASU 99613!); *Hill 33572* (UCR 123726!); *Hillman s.n.* (UC 78601!); *Hillman s.n.* (UC 78612!); *Hillmann s.n.* (DS 689896!); *Hillmann s.n.* (DS 89109!); *Hillmann s.n.* (DS 89770!); *Hindshaw s.n.* (WS 22256); *Hindshaw s.n.* (WS 22258); *Hirshberg s.n.* (RSA 489157!); *Hitchcock 8208* (UC 969872!); *Hitchcock 17342* (DS 345750!, POM 300383!, RSA 46338!, UC 776627!); *Hitchcock 20456* (WS 230327); *Hitchcock 25549* (ID 108320); *Hitchcock 25634* (DS 592435!, UC 1353230!); *Hitchcock 3404* (DS 269506!, RSA 21978!, UC 603488!, CAS 305606!); *Hitchcock 3404* (WS 89946); *Hitchcock 8208* (WS 155221); *Hitchcock 8208* (DS 312528!); *Hitchin 97-12* (WS 353241); *Hoffman s.n.* (RSA 499754!); *Hoffman s.n.* (RSA 499755!); *Hoffman s.n.* (RSA 499757!); *Hoffman s.n.* (RSA 499758!); *Hoffman s.n.* (RSA 499767!); *Hoffmann 564* (SBBG 44401!); *Hoffmann s.n.* (CAS 168346!); *Hoffmann s.n.* (CAS 178642!); *Hoffmann s.n.* (CAS 178668!); *Hoffmann s.n.* (SBBG 063951!); *Hoffmann s.n.* (SBBG 63939!); *Hoffmann s.n.* (SBBG 63940!); *Hoffmann s.n.* (SBBG 63941!); *Hoffmann s.n.* (SBBG 63942!); *Hoffmann s.n.* (SBBG 63943!); *Hoffmann s.n.* (SBBG 63944!); *Hoffmann s.n.* (SBBG 63945!); *Hoffmann s.n.* (SBBG 63946!); *Hoffmann s.n.* (SBBG 63947!); *Hogan 121* (UCR 42487!); *Holmgren 10320* (ID 108302); *Holmgren 10320* (RSA 524003!); *Holmgren 1069* (NY 2901052); *Holmgren 12320* (UC 1874817!); *Holmgren 5658* (NY 2893220); *Holmgren 5658* (RSA 253663!, ASU 88510!); *Holmgren 6577* (ID 108325); *Holmgren 7601* (CAS 637355!, ASU 93385!); *Holmgren 7601* (ID 108327); *Holmgren 7672* (ASU 93504!); *Holmgren 7788* (ASU 93384!); *Holmgren 7788* (ID 108326, NY 2893214); *Holmgren 7825* (NY 2897818); *Holmgren 7825* (RSA 264028!); *Holmgren 8165* (NY 2893215); *Holway 32* (ORE 76462); *Honer 147* (RSA 685439!); *Honer 2050* (RSA 719050!); *Honer 2121* (RSA 718678!); *Honer 2300* (RSA 718591!); *Hoover 10685* (CAS 515792!); *Hoover 10905* (CAS 536108!); *Hoover 10946* (CAS 536542!); *Hoover 3133* (UC 763260!); *Hoover 5657* (CAS 444684!); *Hoover 5683* (CAS 515833!); *Hoover 7815* (CAS 465148!); *Hoover 8054* (CAS 456149!); *Hovatter 557* (ASU 143922!); *Hovatter 641* (ASU 143887!); *Howe 2557* (SD 113081!); ***Howe 2868* (SDSU 05499!); *Howe 3189* (SDSU 05487!);** *Howell 11851* (CAS 217386!, UC 526165!); *Howell 24256* (CAS 344678!); *Howell 24535* (ARIZ 16640!); *Howell 24535* (CAS 342833!); *Howell 37210* (CAS 798203!); *Howell 37244* (CAS 861524!); *Howell 37291* (CAS 861523!); *Howell 42320* (CAS 861920!); *Howell 42431* (CAS 861919!); *Howell 43067* (CAS 798204!); *Howell 43087* (CAS 861915!); *Howell 43115* (CAS 861916!); *Howell 43181* (CAS 861917!); *Howell 47934* (CAS 798235!); *Howell 48055* (CAS 798234!); *Howell 48165* (CAS 556623!); *Howell 48243* (CAS 798233!); *Howell 4922* (CAS 181037!); *Howell s.n.* (ARIZ 65617!); *Howell s.n.* (CAS 464684!); *Howell s.n.* (CAS 861525!); *Howell s.n.* (ORE 76202); *Howell s.n.* (ORE 76203); *Howell s.n.* (WS 109164); *Jaeger s.n.* (DS 265461!); *Jaegr s.n.* (POM 98013!); *Jepson 15487* (JEPS 67794!); *Jepson 17305* (JEPS 67792!); *Jepson 18158* (JEPS 67791!); *Jepson 536* (JEPS 67803!); *Jepson 5472* (JEPS 67800!); *Jepson 5518* (JEPS

67799!); *Jercinovic 1002* (UNM 4123038); *Johnston 11489* (WS 73766); *Jones 12* (ARIZ 98326!); *Jones 1401* (ASU 282252!); *Jones 2034* (DS 698362!); *Jones 3753* (NMC 3152310); *Jones 3906* (NMC 3152311); *Jones 3906* (POM 71500!, UC 125927!, ARIZ 16743!); *Jones 6951* (POM 71904!); *Jones s.n.* (ARIZ 92700!); *Jones s.n.* (DS 698310!); *Jones s.n.* (DS 698312!); *Jones s.n.* (DS 699005!); *Jones s.n.* (POM 117587!); *Jones s.n.* (POM 118477!); *Jones s.n.* (POM 71495!); *Jones s.n.* (POM 71517!); *Jones s.n.* (POM 71562!); *Jones s.n.* (POM 71866!); *Jones s.n.* (POM 71874!); *Jones s.n.* (POM 71875!); *Jones s.n.* (POM 71900!); *Jones s.n.* (POM 71903!); *Jones s.n.* (POM 71906!); *Jones s.n.* (POM 71908!); *Jones s.n.* (POM 71911!); *Jones s.n.* (POM 71912!); *Jones s.n.* (POM 71913!); *Jones s.n.* (UC 125915!); *Joyal 2141* (ASU 192908!); *Joyal 500* (OSC 163593); *Junak 1168* (SBBG 081180!); *Junak 1274* (SBBG 081374!); *Kamb 933* (UC 1178543!); *Kanegae 53* (RSA 649143!); *Kearney 13106* (CAS 263287!, ARIZ 96285!); *Keck 3813* (DS 718383!); *Keck 4347* (DS 278109!); *Kennedy 5394* (UCR 118644!); *Kennedy 998* (DS 89110!, UC 123666!); *Kennedy 998* (NMC 3152313, NY 2893218); *Kennedy s.n.* (ARIZ 98342!); *Kirby 1044* (CAS 507129!); *Kirtland s.n.* (RSA 489199!); *Knight 2468* (UNM 4073739); *Krames 100* (JEPS 67807!); *Krantz s.n.* (RSA 509452!); *Krueger 113* (RSA 654699!); *Kurzius 1419* (RSA 320060!); *La Doux 420* (RSA 765346!); *La Doux 483* (RSA 764899A!, UCR 217815!); *La Doux 497* (RSA 780064!, UCR 217569!); *La Doux 68* (UCR 175521!); *LaPre 91* (SD 133157!); ***LaPre 91-17* (ARIZ 294066!)**; *Lapre s.n.* (ARIZ 271616!); *LaPre s.n.* (RSA 527893!); *LaPre s.n.* (RSA 528072!); *LaPre s.n.* (UCR 122330!); *LaPre s.n.* (UCR 43077!); *LaRue s.n.* (RSA 553933!); *LaRue s.n.* (UCR 90577!); *Latting s.n.* (UCR 121218!); *Latting s.n.* (UCR 133893!); *Latting s.n.* (UCR 136710!); *Latting s.n.* (UCR 141159!); *Lawlor 134* (UCR 51733!); *Lehto 10462* (ASU 166218!); *Lehto 11010-b* (ASU 166172!); *Lehto 11051* (ASU 166204!); *Lehto 11122* (ASU 58898!); *Lehto 11211* (ASU 162892!); *Lehto 11229* (ASU 166146!); *Lehto 11320* (ASU 59094!); ***Lehto 11485* (ASU 59093!)**; *Lehto L-21049* (ASU 91966!); *Lehto L-21081* (ASU 91744!); *Lehto L-21118* (ASU 91430!); *Lehto L-23767* (ASU 106312!); *Leiberg 2041* (UC 179242!); *Leiberg 41* (DS 8665, UC 154405!); *Leiberg 41* (ORE 76212); *Lindley 431* (SD SU20827!); *Linsdale 859* (CAS 365324!); *Mabry 22* (SD SU20360!); *Mabry 33* (SD SU20355!); *Macdonald 3* (RSA 678408!); *Maguire 16258* (UC 604220!); *Maguire 18040* (UC 900471!); *Maguire 18052* (UC 900472!); *Maguire 25075* (DS 312850!, UC 739223!); *Maguire 25109* (DS 312851!, UC 739298!); *Maguire 25149* (NY 2901181, NY 2971712); *Maguire 25149* (UC 739174!); *Maguire 25415* (NY 2971711); *Maguire 25415* (UC 739227!); *Maguire 2777* (POM 192098!, UC 520814!); *Maguire 4968* (UC 533180!); *Maguire s.n.* (ARIZ 28430!); *Mancuso 2068* (ID 108338); *Marsden 58* (SD 163790!); *Martin 5056* (UNM 4049913); *Maser 13-13* (OSC 144714); *Mason 6866* (UC 573070!); *McClinktock 52-271* (CAS 373318!, ARIZ 90855!); *McClinktock s.n.* (CAS 433519!); *McGhee 53* (WS 321512); *McLaughlin s.n.* (ARIZ 376448!); *McNeal 1624* (NY 2900981); *Mills C-46* (UC 1035657!); *Mistretta 2418* (RSA 755974!); *Mistretta 244* (RSA 587964!); *Mistretta 335* (RSA 659930!); *Mooney s.n.* (UC 1389250!); *Moran 10858* (SD 53784!); *Moran 23040* (SD 95546!); ***Moran 26937* (SD 102503!)**; *Morefield 1975* (RSA 463759!); *Morefield 2622* (RSA 463651!); *Morefield 3241* (RSA 370272!, UC 1534960!, UCR 47718!); *Morefield 3447* (RSA 387701!, UC 1534873!, UCR 47598!); ***Morefield 3499* (ARIZ 279486!, RSA387601!, UC1535058!, UCR48252!)**; *Morefield 4404* (RSA 437298!); *Morefield s.n.* (ARIZ 279342!); *Morefield s.n.* (ARIZ 279486!); *Morefield s.n.* (ARIZ 282524!); *Mullins 252* (POM 369244A!); *Munz 15173* (DS 290421!, UC 662531!); *Munz 2551* (DS 108408!); *Myers s.n.* (UCR 139172!); *Myrick 535* (SBBG 16437!); *Neese 16541* (UC 1579786!); *Neese 16596* (UC 1579726!); *Nelson 1739* (WS 299280); *Ness 21* (WS 331148); *Newell 74* (WS 321511); *Olmsted 89* (RSA 783419!); *Olmsted s.n.* (RSA 783421!); *Orcutt s.n.* (UC 78604A!); *Oswald 9112* (JEPS 94701!, JEPS 94832!); *Otting 767* (OSC 211208); *Packard 78-202* (OSC 154337); *Painter 15416* (SBBG 110082!); *Parfitt 2813* (ASU 125534!); *Parish 10135* (DS 89283!); *Parish 11837* (CAS 26646!, UC 306220!); *Parish 731* (DS 89277 B!); *Parish 9720* (DS 89282!, UC 185106!); *Peck 15631* (WILLU 14967); *Peck 19497* (UC 857234!); *Peck 19497* (WILLU 20819); *Peck 19837* (UC 857235!); *Peck 19842* (WILLU 21397); *Peck 20650* (UC 857228!); *Peck 20650* (WILLU 23086); *Peck 21288* (WILLU 24100); *Peck 25639* (UC 801230!); *Peck 25639* (WILLU 27326); *Peck 26144* (CAS 364065!); *Peck 3994* (WILLU 1022); *Peebles 5184* (ARIZ 96261!); *Peebles 9114* (ARIZ 16681!); *Peirson 477* (JEPS 67802!); *Peirson 5812* (UC 573115!); *Peirson 7436* (RSA 80754!); *Penalosa 2432* (CAS 515791!); *Peterson 84* (UCR 42031!); *Peterson s.n.* (ARIZ 263767!); *Philbrick s.n.* (SBBG 43330!); *Pinkava 10282* (ASU 49543!); *Pinkava 10293* (ASU 49900!); *Pinkava 11211* (ARIZ 318456!); *Piper 2961* (POM 64227!); *Piper 2961* (WS 22257); *Piper 3881* (WS 22102); *Pitzer 2036* (RSA 613765!, UCR 106291!); *Pitzer 2250* (UCR 102641!); *Pitzer s.n.* (ARIZ 345031!); *Popovich 4679* (ID 108336, OSC 220564); *Popovich 4750* (ID 108337, OSC 220667); *Porter 11715* (RSA 620122!); *Porter 11731* (RSA 620141!); *Porter 12332* (RSA 657235!); *Porter 12486* (RSA 717748!); *Prigge 2668* (UCR 32357!); *Prigge 2859* (UCR 32355!); *Prigge 3414* (UCR 32371!); *Provance 1989* (UCR 120387!); *Purer 6317* (SD 39207!); *Purpus 5825* (UC 78740A!); *Purpus 5825a* (UC 402788!); *Purpus 5986* (CAS 26636!); *Purpus 5987A* (CAS 26637!); *Rado s.n.* (UCR 196022!); *Raven 11560A* (CAS 515825!); *Raven 11854* (UC 1168705!); *Raven 11962* (CAS 515803!); *Raven 14301* (UC 1212049!); *Raven 14304* (DS 461999!); *Raven 1754* (CAS 515830!); *Raven 18894* (DS 502598!);

*Rea 1688* (SD 132090!); *Rebman 11334* (SD 168426!); *Rebman 1483* (ASU 208138!); *Rebman 1483* (SD 137255!); ***Rebman 16909* (SDSU 19366!, SD195789!)**; *Rebman 17608* (SD 197228!); *Rebman 17678* (SD 197227!); *Rebman 21075* (SD 213033!); *Rebman 21142* (SD 213034!); *Rebman 21580* (SD 213035!); *Renner 39* (JEPS 67805!); *Renner 60* (JEPS 67806!); *Reveal 106* (CAS 861519!); *Reveal 1125* (NY 2971710); *Rexroth s.n.* (POM 287680!); *Rider 2* (WS 339668); *Ripley 6184* (CAS 324406!); *Ripley 9380* (CAS 346831!); *Robbins 3306* (UC 993779!); *Rogers 378* (DS 292404A!); *Rogers 378* (ORE 66963, WS 112207); *Rogers 458* (ORE 66962, WS 112208); ***Rogers 458* (SD 33881!, CAS 301923!, DS 292403!, UC857238!)**; *Rondeau 88-3* (ARIZ 281004!); *Rose 48144* (CAS 349229!); *Rose s.n.* (ARIZ 126115!); *Ross 4662* (CAS 951263!, RSA 585369!); *Ross 4706* (CAS 964982!, RSA 585360!); *Ross 4797* (RSA 570148A!); *Ross 4981* (RSA 570314!); *Ross 4982* (RSA 570315!); *Ross 7601* (RSA 578657!); *Roszbach 462* (UC 1073419!); *Roszbach 463* (UC 1073335!); *Russell 11209* (UNM 4004372); *Saarni 62* (UC 1063855!); *Saarni 62* (UC 608787!); *Sandberg 260* (ORE 76213, WS 22254); *Sandberg 260* (UC 167561!); *Sandberg s.n.* (WS 22255); *Sanders 10930* (UCR 68950!); *Sanders 14524* (UCR 83170!); *Sanders 14661* (UCR 87918!); *Sanders 14716* (UCR 81619!); *Sanders 16134* (UCR 84844!); *Sanders 16309* (UCR 86263!); *Sanders 16422* (UCR 86174!); *Sanders 16621* (CAS 939284!); *Sanders 16813* (UCR 86672!); *Sanders 16988* (UCR 176732!); *Sanders 17056* (RSA 597215, UCR 86890!); *Sanders 17073* (UCR 86936!); *Sanders 17195* (UCR 127704!); *Sanders 20181* (RSA 620654!, UCR 101379!); *Sanders 20567* (UCR 112859!); *Sanders 23794* (UCR 116445!, SD 148207!); *Sanders 24010* (UCR 116736!); *Sanders 24029* (UCR 116724!); *Sanders 25885* (UCR 126120!); *Sanders 26755* (UCR 127513!); *Sanders 34435* (UCR 194524!); *Sanders 36175* (UCR 203417!); *Sanders 36212* (UCR 203401!); *Sanders 36235* (UCR 203463!); *Sanders 36290* (UCR 203455!); *Sanders 36384* (RSA 781197!, UCR 203957!); *Sanders 36425* (UCR 204074!, SD 197716!); *Sanders 36442* (UCR 203817!); *Sanders 36539* (UCR 210910!); *Sanders 36600* (UCR 211023!); *Sanders 36720* (RSA 755805!, UCR 210853!); *Sanders 36731* (UCR 210809!); *Sanders 37401* (CAS 1121092!); *Sanders 38184* (UCR 213589!); *Sanders 38237* (RSA 781252!); *Sanders 38237* (UCR 214517!); *Sanders 39* (UCR 28654!); *Sanders 39086* (UCR 224796!); *Sanders 39254* (UCR 224777!); *Sanders 39315* (UCR 225234!); *Sanders 7007* (UCR 47326!); *Sanders 7022* (UCR 47276!); *Sanders 7036* (UCR 46607!); *Sanders 7038* (UCR 47271!); *Sanders 7714* (UCR 50464!); *Sanders 9054* (UCR 57161!); *Sanders 947* (UCR 18153A!, UCR 18153B!); *Scheffer s.n.* (WS 181471); ***Scheidlinger 18150* (SDSU 18150!)**; *Scheidlinger s.n.* (SD SU18150!); *Schellenger s.n.* (JEPS 67801!); *Schmidt 13* (ARIZ 16761!); *Schoolcraft 1159* (CAS 825345!); *Secrest s.n.* (SBBG 30840!); *Sharsmith 4764* (UC 1226613!); *Sharsmith 4805* (NY 2971679); *Sharsmith 4805* (UC 1226608!); *Sharsmith 4810a* (UC 1226605!); *Sharsmith 5506* (UC 1281987!); *Sharsmith s.n.* (ARIZ 145938!); *Shevock 1602* (CAS 713390!); *Shockley 282* (UC 79359!); *Shreve 7854* (DS 252936!); *Shreve 9464* (UC 651864!, ARIZ 98329!); ***Simpson 2373* (SDSU 17304!)**; ***Simpson 2950* (SDSU 18662!)**; ***Simpson 51V97B* (SDSU 12435!)**; *Sivinski 1083* (UNM 4073729); *Sivinski 1089* (UNM 4073737); *Sivinski 7496* (UNM 4120245); *Sivinski 7571* (UNM 4120304); *Sivinski 8202* (UNM 4143432); *Smith 10516* (UCR 67935!); *Smith 10516a* (SBBG 082273!); *Smith 472* (UC 758841!); *Smith 472* (WS 84547); *Smith 5384* (ID 108332); *Smith 822* (ASU 102261!); *Snelling 5* (RSA 499769!); *Soza 1468* (RSA 679379!); *Soza 221* (RSA 618064!); *Soza 301* (RSA 619323!); *Spaulding s.n.* (ARIZ 206326!); *Spellenberg 10110* (NMC 132840); *Spellenberg 6457* (NMC 132839); *Spellenberg 6505* (NMC 132841); *Stason s.n.* (UC 573123!); *Stoughton 1043* (RSA 776129!); *Swearingen 1270* (RSA 319151!); *Swearingen 906* (RSA 319959!); ***Sweet 305* (SD 178702!)**; *Sweetsers s.n.* (UC 446800!); *Swinney 10436* (UCR 220054!); *Swinney 10489* (UCR 220277!); *Swinney 10537* (RSA 772301, UCR 221901!); *Swinney 10676* (UCR 223039!); *Swinney 10677* (RSA 771583, UCR 223041!); *Swinney 10719* (CAS 1121361, RSA 772395, UCR 222729!); *Swinney 11183* (UCR 223830!); *Swinney 3642* (RSA 717804, UCR 180988!); *Swinney 3801* (UCR 190512!); *Swinney 3954* (UCR 96067!); *Swinney 7037* (UCR 193696!); *Swinney 7190* (RSA 730076, UCR 193990!); *Swinney 7920* (UCR 190785!); *Swinney 7979* (RSA 733389!, UCR 190350!); *Swinney 8553* (RSA 747260!, UCR 205043!); *Swinney 8730* (UCR 205454!); *Swinney 8760* (UCR 205924!); *Swinney 8769* (RSA 750107!, UCR 205905!); *Taylor 10244* (JEPS 90335!); *Taylor 10275* (JEPS 90336!); *Taylor 12369* (JEPS 90333!); *Taylor 15046B* (UC 1876876!); *Taylor 16500* (UC 1731365!); *Taylor 16503* (UC 1731364!); *Taylor 3485* (UC 1731784!); *Taylor 6879* (JEPS 90331!); *Taylor 6884* (JEPS 90332!); *Templeton 5671* (RSA 499777!); *Thomas 2605* (DS 582383!); *Thomas 6567* (DS 582445!); *Thomas 6626* (DS 513134!); *Thompson 11489* (POM 224024!, DS 245068!, UC 857240!); *Thompson 6138* (DS 211379!); *Thompson 6138* (WTU17007JWT); *Thompson 8206* (CAS 215158!, DS 219708!, UC 502510!); *Thorner 525* (NMC 3152314); *Thorne 51557* (ASU 112805!); *Thorne 33805* (RSA 639277!); *Thorne 42697* (UC 1606954!, UCR 60548!, UCR 60726!); *Thorne 43075* (DS 675641!); *Thorne 45344* (UC 1606975!, UCR 60500!); *Thorne 45382* (RSA 353613!); *Thorne 49304* (CAS 909188!); *Thorne 51617* (RSA 584762!); *Thorne s.n.* (ARIZ 316579!); *Tidestrom 8638* (POM 369246!); *Tiehm 10278* (CAS 803619!, RSA 362352!); *Tiehm 10278* (ID 108311); *Tiehm 11174* (CAS 770278!, RSA 437860!); *Tiehm 11634* (CAS 811182!, RSA 486221!); *Tiehm 11634* (NY 2893206); *Tiehm 11650* (CAS 811416!, RSA 488305!); *Tiehm 11650* (NY 2968855); *Tiehm 12291* (RSA 656895!, ASU 237171!); *Tiehm 12356* (CAS



962235!); *Tiehm 12378* (CAS 962236!, RSA 656899!); *Tiehm 12405* (CAS 962237!); *Tiehm 12441* (CAS 962238!); *Tiehm 14135* (CAS 1085387!, RSA 703993A!); *Tiehm 14179* (CAS 1052487!, RSA 706059!, ASU 265070!); *Tiehm 14373* (ASU 266026!); *Tiehm 14373* (CAS 1076216!, RSA 719657!); *Tiehm 14373* (NY 2859050); *Tiehm 2065* (NY 2971669); *Tiehm 3055* (NY 2893217); *Tiehm 3151* (CAS 645617!); *Tiehm 3151* (NY 2893216); *Tiehm 4116* (CAS 754145!); *Tiehm 4116* (NY 2897362); *Tiehm 4171* (NY 2971725); *Tiehm 4844* (CAS 703435!); *Tiehm 4844* (NY 2893941); *Tiehm s.n.* (ARIZ 380360!); *Tillotson 15* (UC 1063854!); *Train 2670* (NY 2893204); *Train 2670* (UC 857236!); *Train 3503* (ID 108319, NY 2971715); *Train 3503* (UC 857237!); *True 53* (UC 857244!); *Twisselmann 10683* (CAS 515795!, CAS 604411!); *Twisselmann 10710* (SBBG 23583!); *Twisselmann 10822* (CAS 515802!, CAS 604383!); *Twisselmann 11961* (SBBG 26184!); *Twisselmann 11992* (CAS 515800!, CAS 604407!); *Twisselmann 12077* (CAS 515797!, CAS 604410!); *Twisselmann 13130* (CAS 604404!, SBBG 29219!); *Twisselmann 13149* (RSA 563310!, UCR 79433!); *Twisselmann 13482* (CAS 604406!); *Twisselmann 13491* (CAS 604405!); *Twisselmann 2682* (CAS 515835A!, CAS 604388!); *Twisselmann 2698* (CAS 515831!, CAS 604412!); *Twisselmann 3344* (CAS 493814!, CAS 515834, CAS 604387!); *Twisselmann 3500* (CAS 515827!); *Twisselmann 4281* (CAS 515809!, CAS 610245!); *Twisselmann 4289* (CAS 515810!, CAS 610246!); *Twisselmann 6824* (CAS 515807!, CAS 604386!, SBBG 15001!); *Twisselmann 6830* (CAS 515806!, CAS 604385!); *Twisselmann 6836* (CAS 515836!, CAS 604384!); *Twisselmann 6941* (CAS 493813!); *Twisselmann 7153* (CAS 604372!); *Twisselmann 8151* (CAS 515801!, CAS 604382!); *Twisselmann 8208* (CAS 515804!); *Twisselmann 9292* (CAS 515793!, CAS 609434!, SBBG 20864!); *Twisselmann 9293* (CAS 515794!); *Twisselmann s.n.* (ARIZ 306073!); *Unknown 1945* (ORE 76208); *Unknown 9600* (UNM 4073734); *Van Buren 533* (UVSC 2152200); *Van Buren 597* (UVSC 2154634); *Van Buren 711* (UVSC 2156419); *Van Buren 718* (UVSC 2156426); *Vanderplank s.n.* (RSA 725129!); *Vasek 29* (UCR 4401!); *Vasek 3* (UCR 4399!); *Vasek s.n.* (UCR 15677!); *Vreeland s.n.* (CAS 645614!); *Ward 325* (WS 179052); **Ward 70 (SD 207726!)**; *Wear s.n.* (UCR 176941!); *Weber 11356* (DS 498770!); *Weber 7405* (CAS 380908!); *Weber 7568* (CAS 380910!, DS 353339!, RSA 76442!); *Weber 7568* (UC 964675!); *Weber s.n.* (ARIZ 114960!); *Welsh 13127* (POM 324648!); *Wetherill s.n.* (ARIZ 150503!); *Wheeler s.n.* (RSA 607019!); *Wheeler s.n.* (RSA 614815!); *Wheeler s.n.* (RSA 615709!); *Wheeler s.n.* (RSA 615714!); *Wheeler s.n.* (UCR 138538!); *White 10085* (RSA 702510!); *White 10104* (RSA 702847!, UCR 149989!); *White 10932* (UCR 169903!); *White 11031* (UCR 169810!); *White 179* (UCR 80653!); *White 2853* (UCR 86326!); *White 4132* (UCR 127956!); *White 6451* (RSA 627359!); *White 6584* (RSA 627036!); *White 6687* (UCR 119876!); *White 7824* (RSA 657044!); *White 8* (RSA 627097!); *White 8299* (RSA 676032!); *White 9365* (RSA 697361!, ASU 254753!); *White 9377* (UCR 144762!); *White 9909* (RSA 702811!); *Whited 220* (WS 109166); *Whited 2611* (ORE 76198); *Whitehead 73-455* (ARIZ 191018!); *Wiggins 14102* (DS 493681!); *Wiggins 15916* (DS 506511!); *Wiggins 20611* (DS 597873!); *Wiggins 7593* (UC 665407!); *Wiggins 8450* (UC 665788!); *Wilken 16766* (SBBG 121757!); **Wilkes Exp. 1047 (NY 00335248!—TYPE)**; *Williams 75-28-13* (CAS 861526!); *Williams 78-41--2* (NY 2893207); *Williams 78-55-4* (CAS 805260!); *Williams 78-61--8* (NY 2894413); *Williams 81-16--7* (NY 2893219); *Williams 81-16-7* (CAS 739099!); *Williams 81-75--6* (NY 2893213); *Williams 81-75-6* (CAS 854894!); *Williams 82-30--12* (NY 2893212); *Williams 82-35--2* (NY 2893211); *Williams 82-35-2* (CAS 854879!); *Williams s.n.* (CAS 861521!); *Wilson s.n.* (POM 369247!); *Winbald s.n.* (CAS 252329!); *Wisura 4700* (RSA 550214!); *Witham 793* (SD 80854!); *Woglum 2350* (RSA 611556!); *Woglum 3205* (RSA 611569!); *Woglum 657* (RSA 606207!); *Wolden 521* (ASU 167027!); *Wolf 10342* (SD 42411!); **Wolf 10342 (SD 42411!)**; *Wolf 3375* (DS 280425!); *Wolf 6803* (DS 390749!, RSA 499775!, UCR 47798!); *Wolf s.n.* (ARIZ 130382!); **Wolf s.n. (ARIZ 142302!)**; *Wolf s.n.* (UC 774645!); *Wolf s.n.* (UC 774681!); *Wolfe 4656* (ASU 105728!); *Wood 1592* (RSA 763226!); *Wood 453* (RSA 768424!, UCR 224082!); *Wood 755* (RSA 763722!); *Wooton s.n.* (RSA 61640!); *York 716* (CAS 1121873!); *York 737* (CAS 1121871!); **Youngberg s.n. (SDSU 05493!)**; *Zika 9671* (OSC 168438).

**Cryptantha pterocarya var. purpusii**:—*Ackley 42* (SBBG 063937!); *Agnew sn* (DS 318901!); *Andre 13976* (UC R221871!); **Andre 13976 (UCR 221871!)**; **Andre 17858 (UCR 235174!)**; *Bell 1558* (RSA 766960!); *Bell 2378* (RSA 774911!); *Bell 2525* (RSA 774439!); *Bell 3499* (RSA 787522!); **Boyd 11916C (RSA 730967!)**; **Boyd 11916C (UCR 198375!)**; **Boyd 11916D (RSA 730966!)**; *Brandeggee sn* (UC 78602B!); *Bruff sn* (RSA 699866!); *Burnell 187* (RSA 508714!); *Chisaki 1032* (UC 211663!); *Clemons 1418* (SD 119090!); **Clemons 1631 (SD 120964!)**; *Clokey 8205* (UC 900473!); *DeDecker 1338* (RSA 617032!); *DeDecker 1887* (RSA 628687!); *DeDecker 1887* (SBBG 42798!); **DeDecker 2672 (RSA 618052!)**; *Ertter 6148* (UC 1561301!); **Fellows 144 (UCR 41228!)**; *Fosberg 10690* (CAS 252098!); **Fraga 1158 (RSA 728905!)**; *Fraga 2082* (RSA 740602!); *Fraga 595* (RSA 721264!); **Fraga 751 (RSA 729136!)**; *Fraga 760* (RSA 729145!); **Gander 149 (SD 10784!)**; *Gander 8087* (SD 26735!); **Gander 8115 (SD 26763!)**; **Gander 9119 (SD 28544!)**; **Gross 2116a (UCR 177785!)**; **Gross 2161a (RSA 709948!, UCR 177785!)**; *Hall 1161* (UC 1601965!); **Hendrickson 2873 (SD 205631!)**; *Hendrickson 94* (SD 161809!); *Hirshberg sn* (RSA 479818!); *Honer 1663* (RSA 680721!); **Honer 2121 (UCR 198161!)**; *Honer 784* (UC 1786974!); **Honer 864 (RSA 680780!)**;

*Honer 889* (UC 1787183!); *Honer 965* (RSA 680774!); *Howell 33308* (CAS 793432!); *Howell 33385* (CAS 794508!); *Howell 3943* (CAS 180264!); *Howell 47934* (RSA 595064!); *Jones sn* (DS 679124!); *Jonsson 1418* (SD 119090!); *Kelley 1657* (UCR 211406!); *Mearns 3156* (DS 8724!); *Moran 22029* (SD 91861!); *Moran 24132* (SD 97062!); *Moran 30846* (SD 111316!); *Moran 30846* (SD 111316!); *Orcutt sn* (UC 78604B!); *Provance 723* (SD 145988!); *Provance 9027* (UCR 135709!); *Purpus 5433* (JEPS 2548!—TYPE); *Raven 11962* (UC 1168710!); *Rebman 23709* (SD 226021!, SDSU 20172!); *Rebman 23746* (SD 226020!, SDSU 20174!); *Rebman 7211* (RSA 700482!, SD 155822!, UC 1787759!, UCR 155751!); *Rebman 7841* (RSA 701010!); *Rebman 8522* (SD 159505!, UC 1787864!, UCR 146010!); *Sanders 16293* (UCR 115350!); *Sanders 16621* (UCR 88732!); *Sanders 16794* (UCR 157857!); *Sanders 17015* (UCR 114777!); *Sanders 17100* (UCR 177103!); *Sanders 17251* (UCR 86220!); *Sanders 40141* (UCR 235062!); *Sanders 6536* (UCR 157741!); *Simpson 3071* (SDSU 18623!); *Simpson 3072* (SD 208265!, SDSU 18624!); *Simpson 3166* (SD 208183!, SDSU 19476!); *Soza 215* (RSA 618057!); *Swinney 11183* (RSA 774277!); *Swinney 7091* (UCR 194277!); *Taylor 10244* (RSA 530008!, UC 1584604!); *Taylor 10244* (UC 1584604!); *Thorne 39549b* (RSA 632836!); *Tiehm 4844* (RSA 323559!); *Twisselmann 10934* (CAS 604394!); *Twisselmann 13130* (SD 135633!); *Twisselmann 9502* (CAS 515796!); *Vasek s.n.* (UCR 15685!); *Vasek s.n.* (UCR 15690!); *White 3993* (UCR 91376!); *Wood 1885* (RSA 764704!).

*Cryptantha pterocarya* var. *stenoloba*:—*Andre 24800* (SDSU 20929!); *Bell 113* (RSA 782075!); *Bell 2177A* (RSA 774935!); *Butterwick 5825* (ASU 116823!); *Christian 823* (ARIZ 160366!); *Delmatier 9517* (ASU 280656!); *Hammond 11293* (ASU 224380!); *Hillyard 5825* (ARIZ 228602!); *Hillyard 5825* (ASU 116823!); *Kearney 13184* (ARIZ 96286!); *Maguire 4466* (GH 00096072!—TYPE); *Salvato 3208* (UCR 203169!); *Sanders 34585* (UCR 194543!); *Sanders 37401* (UCR 214870!); *Unknown s.n.* (UCR 235363!); *Van Devender s.n.* (ARIZ 191168!).

*Cryptantha oxygona*:—*Clokey 5825* (SD 34158!); *Ertter 5966* (SD 129727!); *Hall 2849* (UC 56847!); *Honer 251* (RSA 700137!); *Honer 667* (RSA 687466!); *Honer 703* (RSA 696182!); *Honer 732* (RSA 696676!); *Honer 811* (RSA 685321!); *Howell 45678* (CAS 794509!); *Keller 120C* (SD 26391!); *Keller 120d* (SD 26395!); *Moe 2301* (RSA 709140!); *Pringle* (HUH 00097028!); *Purer 6447* (SD 39206!); *Reiser 29?* (SD 138917!); *Jack L. Reveal 106* (UC 1338570!); *Ross 4797* (RSA 570148B!); *Sanders 6449* (SD 167190!); *Tiehm 12441* (RSA 661610!); *Twisselmann 1845* (CAS 399367!); *White 11439* (RSA 717219!).