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Authors: Rebman, Jon P., and Simpson, Michael G.

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THREE NEW SPECIES OF *CRYPTANTHA* (BORAGINACEAE) FROM THE SOUTHERN CHANNEL ISLANDS OF CALIFORNIA

JON P. REBMAN

San Diego Natural History Museum, P.O. Box 121390, San Diego, CA 92112-1390

MICHAEL G. SIMPSON

Department of Biology, San Diego State University, San Diego, CA 92182 msimpson@sdsu.edu

Abstract

Three new species of Cryptantha from the Channel Islands of southern California are described. Cryptantha clementina, endemic to San Clemente Island, was formerly identified as C. traskiae I.M.Johnst. It is distinct from that species in having a low, spreading growth habit, congested inflorescence cymules, wider corolla limbs, thicker and more swollen midrib calyx trichomes, and nutlets that are tuberculate throughout the dorsal and ventral surfaces. Cryptantha kinkiensis, also endemic to San Clemente Island, was previously identified as C. intermedia (A.Gray) Greene. It differs from that species in having bifurcate cymules and nutlets with denser, smaller tubercles. Cryptantha catalinensis, endemic to Santa Catalina Island, was previously identified as either C. intermedia or C. wigginsii I.M.Johnst. It differs from C. intermedia in having bifurcate cymules and nutlets with denser, smaller nutlet tubercles. It differs from C. wigginsii in having nutlets that are tuberculate apically and low-tuberculate to glabrate basally, as opposed to densely tuberculate apically (tubercles "wart-like" and generally abutted) and glabrous and shiny basally in C. wigginsii. Cryptantha catalinensis and C. kinkiensis are somewhat similar to one another, but distinct in nutlet sculpturing and midrib calyx trichome size. We note morphological similarities and some evidence for phylogenetic relatedness among Cryptantha clementina, C. traskiae, and C. foliosa (Greene) Greene, the last endemic to Guadalupe Island, Baja California, Mexico. We also point out morphological similarities among Cryptantha catalinensis, C. kinkiensis, and C. wigginsii. Detailed molecular phylogenetic studies are needed to evaluate the evolutionary and biogeographic history of these new insular species.

Key Words: Boraginaceae, California, Channel Islands, conservation, Cryptantha catalinensis, Cryptantha clementina, Cryptantha kinkiensis, taxonomy.

Cryptantha is one of the largest genera in the family Boraginaceae, currently with over 100 species (Amsinckiinae Working Group 2021). Recent molecular phylogenetic analyses (Hasenstab-Lehman and Simpson 2012; Simpson et al. 2017; Mabry and Simpson 2018) have clarified generic circumscriptions within subtribe Amsinckiinae, to which *Cryptantha* belongs (Chacón et al. 2016). Moreover, several taxonomic studies (Mabry et al. 2016; Simpson et al. 2013, 2014, 2016, 2019; Simpson and Kelley 2017; Simpson and Rebman 2013, 2021a,b) have contributed to an understanding and recognition of species and infraspecies within *Cryptantha* and close relatives.

In the process of working on a flora of San Clemente Island (Rebman and Vanderplank unpublished data), two *Cryptantha* taxa observed and collected there were studied and determined to show differences from species to which they were previously assigned. Specimens of a *Cryptantha* taxon of questionable identity occurring on Santa Catalina Island were also studied and found to be similar to, but distinct from, one of the new taxa of San Clemente Island. Based on morphological differences in plant habit, inflorescence morphology, calyx vestiture, corolla size, and nutlet morphology, we believe that all three taxa warrant recognition at the species level, based on a taxonomic (morphologic) concept (Cronquist 1978, 1988). Here we name and describe these three species, review their distributions, habitats, and estimated population sizes, and suggest conservation listings. We also review *Cryptantha* taxa that these three new species have been previously identified as or are possible close relatives to: *C. traskiae* I.M.Johnst. endemic to San Nicolas Island, *C. wigginsii* I.M.Johnst. populations on Santa Catalina Island and mainland California, *C. intermedia* (A.Gray) Greene var. *intermedia* of mainland California and northwestern Baja California, and *C. foliosa* (Greene) Greene endemic to Guadalupe Island, Baja California.

MATERIALS AND METHODS

Samples of *Cryptantha* were collected in the field on San Clemente Island in the spring of 2019. Many of these samples were also photo-documented and the live material was processed into standard herbarium specimens. These and additional herbarium specimens of *Cryptantha* from **CATA**, **IRVC**, **RSA**, **SBBG**, **SD**, **SDSU**, **UC**, and **UCR** collected on San Clemente Island and Santa Catalina Island were studied using standard dissecting microscopy for diagnostic morphological features. Both qualitative and quantitative features were recorded in writing descriptions and summarizing features (see

CHARACTERS	TAXON			
	C. clementina	C. foliosa	C. traskiae	
Cymules	congested, not elongating; fruits touching	elongate	elongate, congested apically	
Flower bracts	generally present	absent	present	
Calyx length in fruit (mm)	ca. 5	5–7	3–4	
Calyx trichome (max.) length (mm) × width (mm)	ca. $1-2 \times 0.2-0.3$ (L:W=5.0-6.4)	ca. $1 \times 0.2-0.3$ (L:W=9.0-14.5)	ca. $1-2 \times 0.1-0.2$ (L:W=7.2-9.7)	
Corolla limb width (mm)	3-4	2-3	1-2	
Nutlet size length (mm) \times max. width (mm)	$(1.1)1.4-1.6(1.7) \times 0.6-0.9$	$1.4-1.7 \times 0.8-0.9$	$1.2-1.5 \times 0.7-0.8$	
Nutlet shape	ovate (L:W=1.8-1.9)	ovate (L:W=1.7-1.9)	ovate (L:W=1.7-1.9)	
Nutlet sculpturing	papillate, low-tuberculate throughout, ca. 16 tubercles along widest transverse line	papillate, tubercles longer, sparse, ca. 8–9 tubercles along widest transverse line	papillate, low-tuberculate apically, glabrate to glabrous basally	
Style length	extending to tip of nutlets	extending to tip of nutlets	barely exceeding nutlet tip	

TABLE 1. COMPARISON OF MORPHOLOGICAL FEATURES OF *CRYPTANTHA CLEMENTINA*, *C. FOLIOSA*, AND *C. TRASKIAE*. Abbreviations: L:W = length:width ratio; max. = maximum.

Tables 1 and 2). In addition, photographic documentation of plant components was done using a Visionary Digital Imaging System photomicroscope, a Nikon Microphot camera attached to an Olympus dissecting microscope, or a Leica Stereozoom S9i photomicroscope. Photographs with scale bars were used to measure nutlet length and maximum width and largest calyx midrib trichome (on sepals enclosing mature nutlets) length and maximum width using the software ImageJ (Rasband 1997-2007; Abramoff et al. 2004). In order to quantify differences between two of the species, maximum corolla limb width measurements were made from selected specimens (Appendix 1). Note that because of the problem of corolla shrinkage following specimen drying, maximum values rather

than averages were used to give a more accurate measure of this feature. In order to better evaluate differences among three other species, length and width measurements of largest calyx midrib trichomes were made from selected specimens of these taxa (Appendix 2). For both features boxplots were prepared for these comparisons of taxa, illustrating the median and four quartiles of distribution for the species (Fig. 12A, B). These were evaluated for statistical differences using analysis of variance (ANOVA), with multiple comparisons made between the taxon means with the Tukey post hoc test. All statistics were performed in SYSTAT, Version 11 (Systat Software, San Jose, CA). A spreadsheet was prepared of specimen data from CCH2 (2021). Formal taxonomic descriptions of three new species

TABLE 2. COMPARISON OF MORPHOLOGICAL FEATURES OF *CRYPTANTHA CATALINENSIS*, *C. KINKIENSIS*, AND *C. WIGGINSII*. Abbreviations: L:W = length:width ratio; max. = maximum.

	TAXON			
CHARACTER	C. catalinensis	C. kinkiensis	C. wigginsii	
Cymules	elongate, bifurcate (rarely solitary or trifurcate)	elongate, bifurcate (rarely solitary)	elongate, bifurcate (rarely solitary or trifurcate)	
Flower bracts	absent, occasionally present at cymule base	absent, occasionally present at cymule base	absent	
Calyx length in fruit (mm)	4–5	4–5	3-4.5(5)	
Calyx trichome (max.) length (mm) × width (mm)	$1.2-2.4 \times 0.1-0.2$ (L:W = 9.0-14.5)	1.0–1.2 ×0.2–0.3 (L:W=4.2–6.9)	ca. 1–2 ×0.1 (L:W=ca. 12–19)	
Corolla limb width (mm)	4–6	4–7(8)	3–4	
Nutlet size length (mm) \times max. width (mm)	$(1.5)1.7-2.1 \times (0.6)0.7-0.8$	$(1.5)1.6-1.9 \times 0.7-0.9$	$1.8-2.1 \times 0.7-1.0$	
Nutlet shape	lance-ovate (L:W = $2.3-2.7$)	lance-ovate (L:W = $2.1-2.3$)	lance-ovate (L:W = $2.1-2.4$)	
Nutlet sculpturing	papillate & tuberculate, tubercles dense apically, obscure to glabrate basally, ca. 16 tubercles along dorsal face at widest transverse line	papillate & tuberculate throughout, ca. 12–16 tubercles along dorsal face at widest transverse line	densely tuberculate apically, tubercles wart-like, glabrous basally	
Style length	extending 0.1–0.3 mm beyond nutlet tip	extending to or ca. 0.5 mm beyond nutlet tip	extending to tip of nutlets	

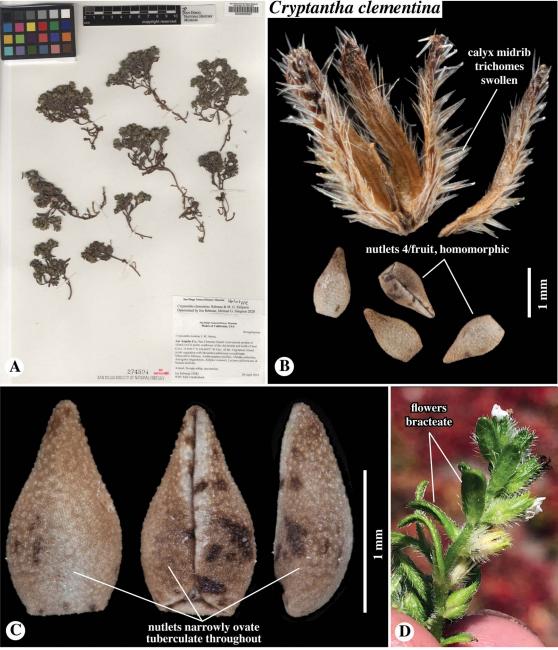


FIG. 1. *Cryptantha clementina*. A. Holotype specimen, *Rebman 35582* (SD274504), showing short plant stature and congested cymule inflorescence units. B. Calyx with swollen midrib trichomes and four homomorphic nutlets. C. Nutlet close-up, in (left to right) dorsal, ventral, and lateral views, the nutlets ovate, papillate and tuberculate throughout. D. Field image, close-up of inflorescence cymule, showing congested, bracteate flowers.

were written, with photo-documentation of field images and microscopic features. Terminology follows Simpson (2019). Maps were prepared from georeferenced specimen data, using the mapping function of the CCH1 (2021) multi-mapper tool. Comparisons were made of these three new taxa to other *Cryptantha* taxa showing morphological resemblances or having known close phylogenetic relatedness. A taxonomic key, modified from that of Kelley et al. (2012) and Kelley and Simpson (unpublished data), was written to aid workers in the identification of these taxa.

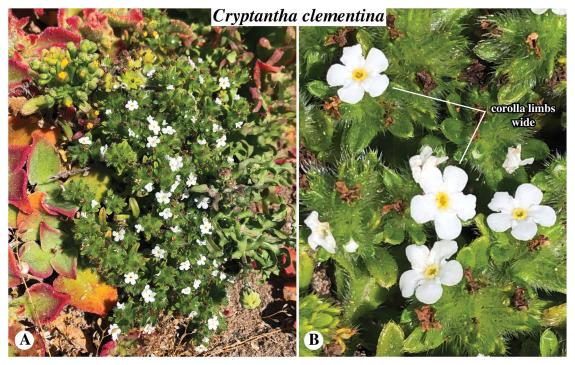


FIG. 2. *Cryptantha clementina*, field images. A. Whole plant with low, spreading, decumbent habit, growing among the non-native, naturalized *Mesembryanthemum crystallinum* and *Hornungia procumbens* and the native *Amblyopappus pusillus* and *Malacothrix foliosus*. B. Close-up of flowers, showing relatively wide corolla limbs with yellow fornices.

RESULTS AND DISCUSSION

Taxonomic Treatment 1

Cryptantha clementina Rebman & M.G.Simpson, sp. nov.—Type: USA, California, Los Angeles County, San Clemente Island, west-central portion of island on Eel Point, southwest of old airstrip and north of Seal Cove, 32.91913°N, 118.54472°W, elev. 16 m, vegetation: island scrub vegetation with Mesembryanthemum crystallinum, Malacothrix foliosa, Amblyopappus pusillus, Abronia umbellata, Astragalus miguelensis, Atriplex watsonii, Lycium californicum, and Suaeda taxifolia, annual, flowers white, uncommon, 29 April 2019, Jon Rebman 35582 with Sula Vanderplank (holotype SD274504; isotype: SBBG).

Description. (Figs. 1–2). Plant annual; roots not reddish. Stems spreading to decumbent or rarely erect, short, ca. 5–15 cm tall, densely branched, surface vestiture densely appressed and ascending hirsute, trichomes white, ca. 1 mm long. Leaves numerous, grading from basal vegetative leaves to inflorescence and floral bracts; basal and cauline leaves $15-25 \text{ mm} \times 2-3 \text{ mm}$ (maximum width), sessile, narrowly oblanceolate, apex rounded to obtuse, midrib ridged abaxially, sunken adaxially; adaxially hirsute, trichomes white, ascending to

appressed, generally minutely pustulate; abaxially hirsute to hispid, trichomes white, ascending, basally swollen, prominently pustulate, pustules of 2 concentric rows of white to transparent, slightly radially elongate cells. Inflorescence of numerous solitary or paired cymules, congested, not elongating at maturity, generally 2-5 cm long, calyces in fruit touching, bracts generally present at base of cymule, these similar and slightly smaller than vegetative leaves. Flower bracts generally present, foliaceous. Pedicel short, <0.5 mm long, not lengthening in fruit. Calyx asymmetric, ascending in fruit, lance-ovoid in overall shape, ca. 2 mm long at anthesis, 5 mm long in fruit, sepals distinct, generally erect, linear to lanceolate, apices rounded, adaxial surface glabrous basally, appressed short hirsute apically, abaxial surface with ascending to appressed, hirsute trichomes along margin and marginal region, midrib greatly thickened, whitish to yellowish, bearing, on sepals away from inflorescence axis, dense, stout, horizontal to ascending hispid trichomes in 2-4 vertical rows, trichomes narrowly conical, hollow, appearing swollen, ca. 1-2 mm long, ca. 0.2–0.3 mm wide at base, whitish to yellowish, surface smooth to minutely papillate, basally attached to thickening on calyx midrib, midrib trichomes narrower on sepals facing toward inflorescence axis. Corolla white, rotate, tube as long as calyx, limb 3-4 mm in diameter, fornices conspicuous, yellow to white. Gynobase ca. 3/4

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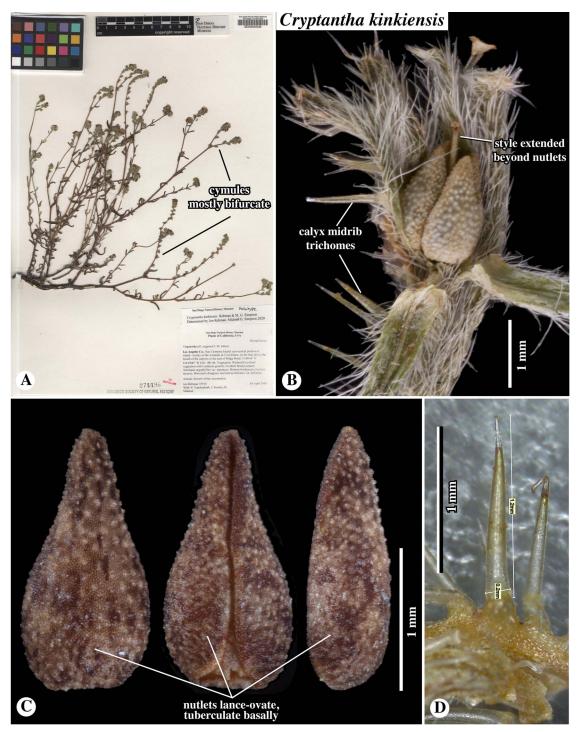


FIG. 3. *Cryptantha kinkiensis.* A–C. Holotype specimen, *Rebman 35515* (SD274496), showing numerous, erect branches, with mostly bifurcate cymules. B. Calyx showing stout midrib trichomes, opened to show four, papillate-tuberculate nutlets and style extended beyond nutlet apices. C. Nutlet close-up, in (left to right) dorsal, ventral, and lateral views, showing papillate and tuberculate sculpturing throughout. D. Close-up of swollen, hispid trichomes of calyx midrib, showing measurement of length and basal width, from *Thorne 36135* (SD90494).

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FIG. 4. *Cryptantha kinkiensis*, field images. A. Whole plants. B. Bifurcate cymules of inflorescence. C. Close-up of flowers, showing relatively large corolla limbs with yellow to white fornices. D, E. Close-up of elongate inflorescence cymules, showing appressed and spreading trichomes of stem axes, ebracteate flowers, and swollen midrib calyx trichomes.

length of nutlets. **Style** extending to height of mature nutlet apices. **Nutlets** generally 4, sometimes reduced in number by abortion, (1.1)1.4-1.6(1.7) mm long \times 0.6–0.9 mm at widest region, homomorphic, brownish, ovate (average length:width ratio=1.8–1.9), base truncate, margins rounded, apex short-acuminate, adaxially shallowly convexly 2-planed, abaxially low convex, both surfaces

densely papillate and low-tuberculate throughout, tubercles low, apically rounded, ca. 16 tubercles across dorsal face at widest transverse line, spinal ridge not evident, ventral groove mostly closed, not raised along margin, bifid at base delimiting small, triangular areole.

Diagnosis. Cryptantha clementina is similar to C. traskiae in having flowers mostly bracteate and

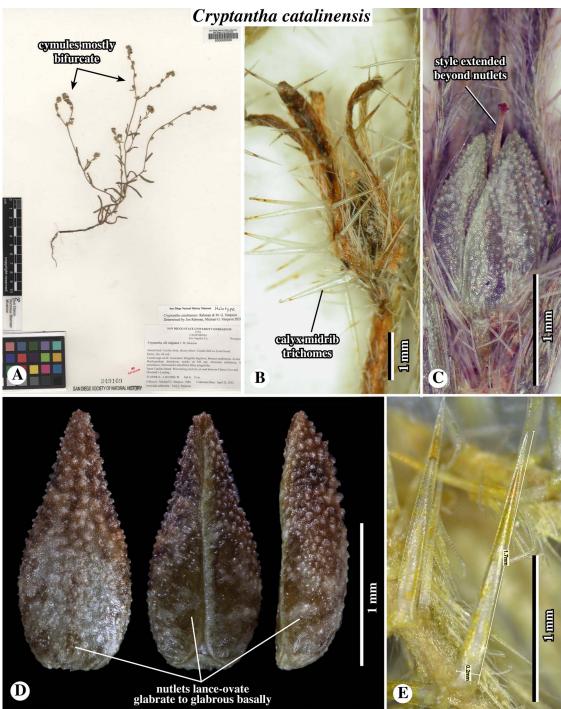


FIG. 5. Cryptantha catalinensis. A. Holotype specimen, Simpson 3682 (SD249169). B. Calyx, showing outer sepals with thickened midribs and stout, hispid trichomes, from *Hoefs* 1268 (CATA743). C,D. Fruit, from Simpson 3686 (SD249169). C. Calyx opened up, showing four, homomorphic nutlets and style extended beyond nutlet apices. D. Nutlet close-up, in (left to right) dorsal, ventral, and lateral views showing papillate and tuberculate sculpturing on apical dorsal side, becoming glabrate with reduced to absent tubercles at base dorsally, glabrous at base ventrally. E. Close-up of calyx midrib trichomes, showing measurement of length and basal width, from *Hoefs* 1194 (CATA699).

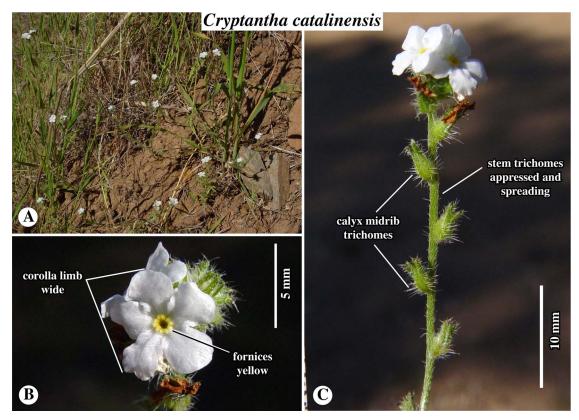


FIG. 6. *Cryptantha catalinensis*, field images. A. Whole plants. B. Flower close-up, showing relatively large corolla limb with yellow fornices. C. Close-up of apical region of flowering cymule, showing appressed and spreading trichomes of stem axis and calyx midrib trichomes.

generally four, homomorphic nutlets per fruit, the nutlets ovate, short acuminate, papillate and tuberculate, ca. 1.4–1.7 mm long. It differs in having larger corollas (limb generally 3–4 mm wide versus 1–2 mm in *C. traskiae*), a short stature and mostly spreading to decumbent habit (versus taller and mostly erect to ascending in *C. traskiae*), congested inflorescence cymules (versus elongate to apically congested cymules in *C. traskiae*), and nutlets densely papillate and tuberculate throughout (versus basally glabrate to glabrous dorsally in *C. traskiae*).

Paratypes. USA, CALIFORNIA, Los Angeles County, San Clemente Island. R. M. Beauchamp 3222 (SD86340!), 24 Mar 1972, slope south of Eel Point., 32.91835°N, 118.54384°W, 25 m elev.; R. M. Beauchamp 4144 (SD278627!), 22 May 1976, dune south of Eel Point Canyon, 23 m elev.; V. Englert SERG 10-28 (SD278628!), 18 Mar 2010, south dunes, big dunes, 32.99359°N, 118.57734°W, 49 m elev.; M. Elvin 121 (RSA678434!), 24 March 1996, on dunes, 32.99361°N, 118.58000°W, 24 m elev.; H. Ferguson 31 (SD278626!), 16 Apr 1980, Eel Pt. Rd. near Red Rock, 32.94444°N, 118.54861°W, 15 m elev.; S. Junak SCI-259 (SBBG131887, SD274027!), 27 Mar 1996, just S of Eel Cove Canyon, in opening between shrubs, 32.91590°N, 118.5376°W, 24 m elev.; S. Junak SCI-265 (SD274029!), 27 Mar 1996, just NE of Eel Point, on Eel Point peninsula, 32.92350°N, 118.5394°W, 50 m elev.; S. Junak SCI-361 (RSA878906!, SBBG136989), 22 Apr 1996, sandy flats at unnamed point at NE end of island, 33.03032°N, 118.57503°W, 9 m elev.; S. Junak SCI-409 (RSA879010!, SBBG137075, SD271453!), 26 Apr 1996, just NE of rd. 0.47 mi. from China Point light at 152 degree bearing, 32.81050°N, 118.42724°W, 40 m elev.; S. Junak SCI-440 (RSA878698!, SBBG136980, SD271451!, UCR285471), 8 May 1996, 0.28 mi. from "darter" at 320° bearing, NW of NW dunes., 33.00116°N, 118.58159°W, 30 m elev.; S. Junak SCI-444 (RSA878766!, SD271452!), 8 May 1996, NE end of NW dunes, 0.55 mi from triangulation point "Darter" at 305 deg bearing, 0.60 mi from triangulation "Flasher" at 169 deg bearing, 32.99690°N, 118.5774°W, 61 m elev.; A. liston 801-3 (RSA515103!, SBBG95684), 29 Apr 1989, main dune area at Darter Rd, NW part of island, 32.9923°N, 118.57640°W; P. Morrell 124 (RSA549913!), 4 Apr 1992, 2 km SSW of Wilson Cove on W side of island; J. Powell 1416 (IRVC19873!), 15 April 1980, West Cove, sand dunes; R. Thorne 35992 (RSA232822!, SD90374!),

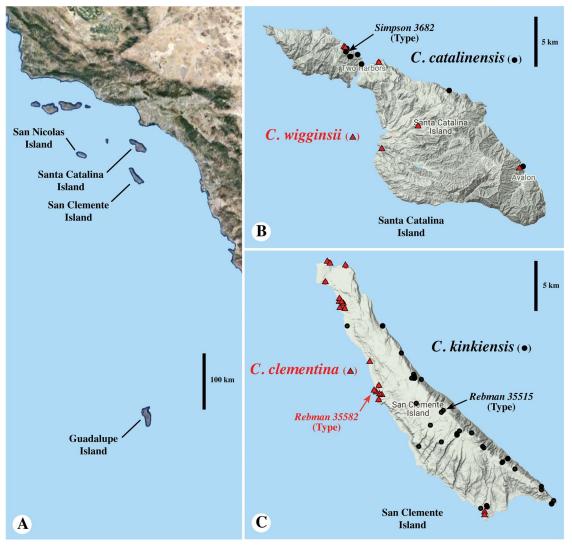


FIG. 7. A. Map showing geographic positions of San Nicolas, Santa Catalina, and San Clemente islands, California, USA, and of Guadalupe Island, Baja California, Mexico. B. Map of Santa Catalina Island, showing herbarium collection distributions of *C. catalinensis* (black dots) and *C. wigginsii* (red triangles) Note type locality of the former. C. Map of San Clemente Island, showing herbarium collection distributions of *C. clementina* (red triangles) and *C. kinkiensis* (black dots). Note type localities for each.

15 Apr 1966, sand of old raised beach, 2/3 mile SSE of Eel Point and N of Seal Cove, 30 m elev.

Endemism, Habitat, Distribution, and Associates. Cryptantha clementina is endemic to San Clemente Island, occurring on dunes or coastal flats with sandy substrates at lower (9–60m) elevations near the immediate coast and mostly on the western and northern side of the island (Fig. 7C). Observed associates (with updated nomenclature) include: Abronia umbellata Lam., Amblyopappus pusillus Hook. & Arn., Ambrosia chamissonis (Less.) Greene, Astragalus miguelensis Greene, Astragalus nevinii A.Gray, Atriplex semibaccata R.Br, Atriplex watsonii A.Nelson ex Abrams, Bergerocactus emoryi (Engelm.) Britton & Rose, Bromus diandrus Roth, Cylindropuntia prolifera (Engelm.) F.M.Knuth, Dipterostemon capitatus (Benth.) Rydb., Erodium cicutarium (L.) L'Hér., Extriplex californica (Moq.) E.H.Zacharias, Herniaria hirsuta L. var. cinerea (DC.) Loret & Barrandon, Hordeum murinum L., Hornungia procumbens (L.) Hayek, Lycium californicum Nutt., Malacothrix foliosa A.Gray subsp. foliosa, Mesembryanthemum crystallinum L., Mesembryanthemum nodiflorum L., Perityle emoryi Torr., Phacelia distans Benth., Spergularia macrotheca (Cham. & Schltdl.) Heynh., and Suaeda taxifolia (Standl.) Standl.

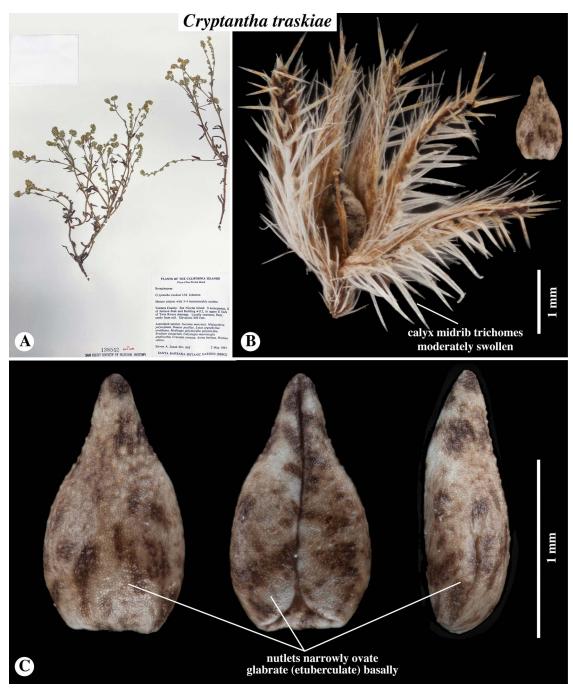


FIG. 8. *Cryptantha traskiae*. A. Exemplar specimen, *Junak SN-645* (SD138542). A. Herbarium specimen, showing erect habit of plants. B. Open calyx, showing sepals with swollen, hispid trichomes and two (of generally four) nutlets, the style extending to or just beyond the nutlet apex. C. Nutlet close-up, in (left to right) dorsal, ventral, and lateral views, the surface papillate and tuberculate apically, grading into glabrate (etuberculate) to glabrous basally on dorsal and ventral surfaces.

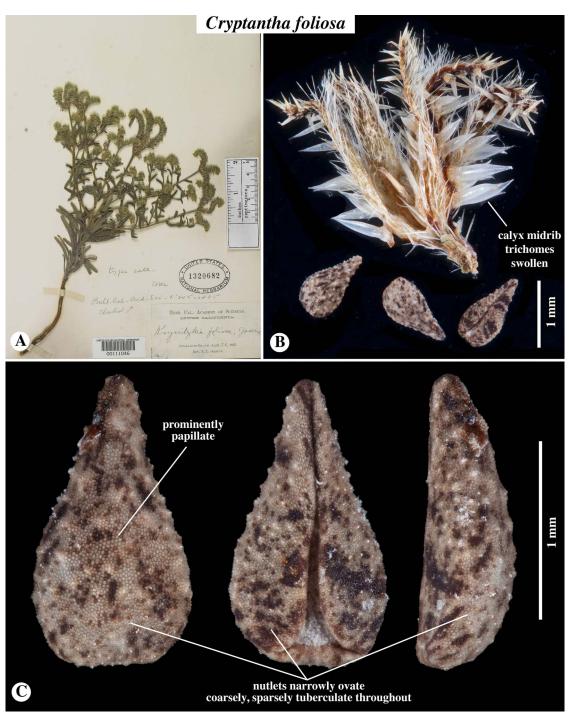


FIG. 9. *Cryptantha foliosa*. A. Holotype specimen *Greene s.n.*, 26 Apr 1885 (US1320682). B, C. Exemplar, *Rebman 6837* (SD155047). B. Open calyx, showing sepals with stout, hispid, very swollen trichomes and three (of generally four) nutlets of fruit. C. Nutlet close-up, in (left to right) dorsal, ventral, and lateral views, densely and prominently papillate and coarsely and sparsely tuberculate.

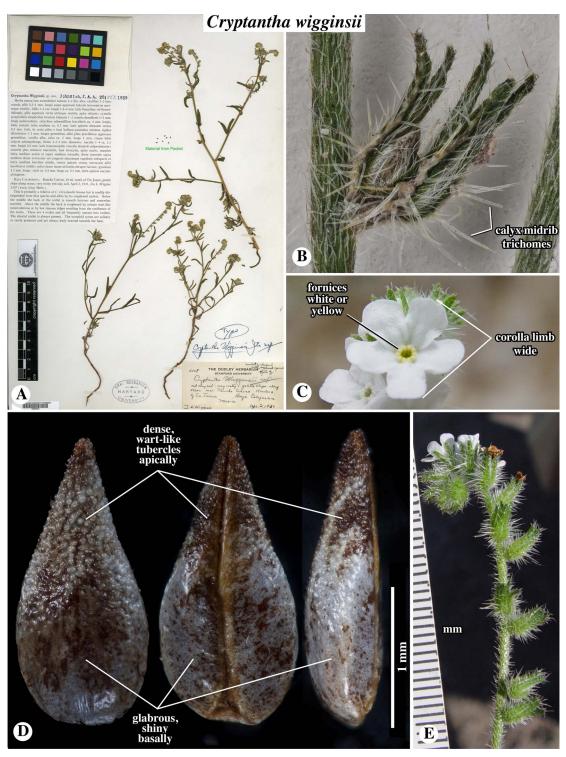


FIG. 10. Cryptantha wigginsii. A,B,D. Holotype, Wiggins 5107 (GH00096301). A. Herbarium specimen, showing erect to ascending branches. B. Partially open calyx, showing sepal midrib trichomes. C. Field image of relatively wide corolla showing yellow and white fornices, from Simpson 3684 (SDSU20033) D. Nutlet close-up, in (left to right) dorsal, ventral, and lateral views, the surface densely tuberculate apically (tubercles "wart-like"), glabrous and shiny basally. E. Close up of cymule, showing appressed and spreading trichomes of axis and hispid trichomes of calyx midrib, from Simpson 3673 (SDSU20062).

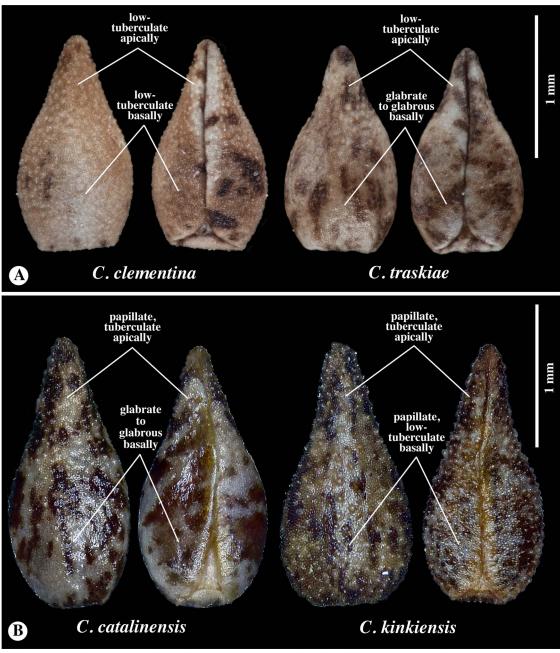


FIG. 11. Comparison of nutlet morphology of species pairs, nutlets in dorsal (left) and ventral (right) views, all at same scale. A. Left: *Cryptantha clementina*, from holotype, *Rebman 35582* (SD274504). Right: *Cryptantha traskiae*, from *Philbrick B69-187* (SBBG33798). B. Left: *Cryptantha catalinensis*, from *Crockett 621* (CATA479). Right: *Cryptantha kinkiensis*, from holotype, *Rebman 35515* (SD274496).

Phenology. Based on observations and data from available specimens, *Cryptantha clementina* flowers and fruits from March to April, fruiting plants likely persisting into May.

Common Name. We suggest "San Clemente Island Dune Cryptantha" or the shortened "Clemente Dune Cryptantha" as potential common names.

Etymology. The specific epithet means "of San *Clemente* Island," where the species is endemic.

Taxonomic Treatment 2

Cryptantha kinkiensis Rebman & M.G.Simpson, sp. nov.—Type: USA, California, Los Angeles

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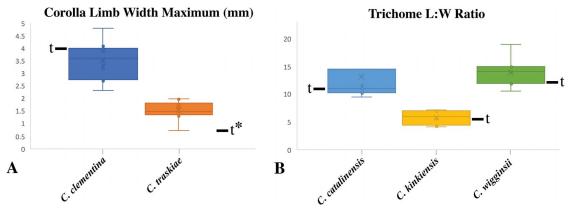


FIG. 12. A. Boxplot of maximum corolla limb width (mm) of *Cryptantha clementina* and *C. traskiae*, the former statistically larger than the latter (at P<0.01), with no overlap. Values of type specimens indicated by "t". Note that measurement of the type specimen of *Cryptantha traskiae* (t*) is likely an underestimate due to its advanced phenological state. B. Boxplot of calyx midrib trichome length:width ratio of samples of *Cryptantha catalinensis*, *C. wigginsii*, and *C. kinkiensis*, the last statistically smaller in this feature than the other two (at P < 0.01), with no overlap. Values of type specimens indicated by "t".

County, San Clemente Island, east-central portion of island, vicinity of the wetlands at Twin Dams, on the flats above the mouth of the canyon, to the east of Ridge Road, 32.90164°N, 118.47087°W, 481 m elev., vegetation: wetland/grassland vegetation with *Lasthenia gracilis, Erodium brachycarpum, Acmispon argophyllus* var. *argenteus, Bromus hordeaceus, Festuca myuros, Microseris douglasii,* and *Juncus bufonius* var. *bufonius,* annual, flowers white, uncommon, 16 April 2019, Jon Rebman 35515 with S. Vanderplank, J. Koontz, and B. Munson (holotype SD274496; isotypes: CAS, RSA,SBBG, SDSU, UC).

Description. (Figs. 3-4). Plant annual; roots not reddish. Stems erect, rarely decumbent, up to 35 cm tall, with many branches from base, surface with only appressed-strigose (trichomes ca. 1 mm long) in upper stems, or with both appressed-strigose and spreading-hirsute (the latter ca. 1.5 mm long) throughout but especially below, all trichomes white. Leaves, grading from basal vegetative leaves to inflorescence bracts; basal and cauline leaves ca. 15–20 mm \times 3–4 mm (maximum width), sessile, narrowly lanceolate to linear, apex rounded, midrib ridged abaxially, sunken adaxially, trichomes white, adaxially hirsute, ascending to appressed, generally minutely pustulate, abaxially with coarser, hirsute to hispid (straight to incurved), horizontal to ascending, basally swollen and prominently pustulate trichomes, pustules of 2 concentric rows of white to transparent, slightly radially elongate cells. **Inflorescence** of mostly paired cymules arising from elongate stems, cymules elongating at maturity, up to 15 cm long, typically with a flower at junction of cymules, fruits spread apart basally, touching apically, one or more inflorescence bracts often present at cymule base, these generally linear, much smaller than vegetative

leaves. Flower bracts generally absent, occasionally present near cymule base. Pedicel stout, 0.5-1 mm long, not lengthening in fruit. Calyx asymmetric, mostly ascending in fruit, lance-ovoid in overall shape, ca. 2 mm long at anthesis, 4-5 mm long in fruit, sepals distinct, lanceolate, apices rounded, tip often recurved, adaxial surface glabrous basally, appressed short hirsute apically, abaxial surface with ascending to appressed, hirsute trichomes along margin and marginal region, midrib greatly thickened, whitish to yellowish to occasionally darkened, bearing, on sepals away from inflorescence axis, dense, stout, horizontal to reflexed hispid trichomes in 1-2 vertical rows, trichomes narrowly conical, hollow, appearing swollen, ca. 1.0-1.2 mm long, ca. 0.2–0.3 mm wide at base (average length: width ratio = 4.2-6.9), whitish to yellowish, surface smooth to minutely papillate, with tissue thickening at point of attachment, midrib trichomes thinner on sepals facing toward inflorescence axis. Corolla white, rotate, tube as long as calyx, limb 4-7(-8) mm in diameter, fornices conspicuous, yellow to white. Gynobase ca. 2/3 length of nutlet. Style extending to 0.5 mm beyond height of mature nutlet apices. Nutlets generally 4, $(1.5)1.6-1.9 \text{ mm long} \times 0.7-0.9$ mm at widest region, homomorphic, brownish, lance-ovate (average length:width ratio=2.1-2.3), base truncate, margins rounded, apex slightly acuminate, adaxially shallowly convexly 2-planed, abaxially low convex, both surfaces densely papillate and tuberculate throughout, tubercles small, generally with raised base and translucent, slightly pointed, slightly incurved at tips, tubercles larger apically, ca. 12-16 tubercles across dorsal face at widest transverse line, spinal ridge not evident, ventral groove closed to slightly open, one edge sometimes overlapping the other, bifid at base delimiting small, triangular areole.

Diagnosis. Cryptantha kinkiensis is similar to *C. intermedia* var. *intermedia* in having appressedstrigose and spreading stem trichomes, mostly ebracteate flowers, relatively large, showy corollas, and generally four, homomorphic nutlets per fruit, the nutlets papillate and tuberculate. It differs in having bifurcate cymules (versus trifurcate in *C. intermedia* var. *intermedia*), and nutlets with relatively small, dense tubercles (versus coarsely tuberculate in *C. intermedia* var. *intermedia*).

Paratypes. USA. CALIFORNIA, Los Angeles County, San Clemente Island. R. M. Beauchamp 148 (SDSU05426!), 28 Jan 1967, 32.815022°N, 118.42411°W, 103 m elev.; R. M. Beauchamp 280 (SD66886!), 18 Mar 1967, Canyon below Lemon Tank, 32.9320°N, 118.5022°W, 277 m elev.; R. M. Beauchamp 303 (SDSU05420!), 18 Mar 1967, on exposed ledges in canyon below Lemon Tank, 32.9302°N, 118.5047°W, 336 m elev.; R. M. Beauchamp 554 (SDSU05402!), 3 Jun 1967, on south hillside above Horse Canyon, 32.880576°N, 118.45645°W, 427 m elev.; R. M. Beauchamp 3242 (SD86346!), 24 Mar 1972, on grassy slope, Thirst, 32.88333°N, 118.45417°W, 600 m elev.; R. M. Beauchamp 4125 (SD278630!), 22 May 1976, south side of canyon below Lemon Tank, 314 m elev.; E. R. Blakley 6339 (SD85025!), 7 Dec 1963, shallow canyon sloping to ocean, 200 feet north of Lighthouse, north of Pyramid Head., 32.82080°N, 118.3539°W, 53 m elev.; S. Boyd 4152 (RSA526158!), 6 Apr 1990, Lemon Tank Canyon, E side of island; S. Boyd 4180 (RSA526596!), 7 Apr 1990, upper reaches of China Canyon, S end of island, W side; S. Boyd 4253B (RSA526514!), 7 Apr 1990, lower half of China Canyon, S end of island, W side, 32.81397°N, 118.43150°W; S. Boyd 4290 (RSA527670!), 8 Apr 1990, E side of island, Bryce Canyon near Malo Point; S. Boyd 4339 (RSA527776!), 8 Apr 1990, east side of island, near Malo Point, second canyon south of Bryce Canyon; S. Boyd 4363 (RSA527642!, SBBG97038, SD217244!, UC1595601!, UCR71242), 8 Apr 1990, east side of island, near Malo Point, third canyon south of Bryce Canyon., 32.85560°N, 118.408°W, 318 m elev.; S. Boyd 4382 (RSA527663!, SD217245!), 8 Apr 1990, east side of island, near Malo Point, third canyon south of Bryce Canyon., 32.85560°N, 118.408°W, 318 m elev.; M. Dunkle 7260 (POM368264!, POM668263!), 4 Apr 1939, grassy slope, Chenetti Canyon; H. Ferguson 42 (SD275427!), 30 Apr 1980, vista N. of building at head of canyon, 32.88110°N, 118.4408°W, 502 m elev.; H. Ferguson 127 (SD278634!), 24 Mar 1980, E. side just south of Nots Canyon, 32.97778°N, 118.53667°W, 61 m elev.; H. Ferguson 213 (SD278633!), 11 Mar 1980, SW end of island near Pyramid foot, 32.81667°N, 118.355°W, 12 m elev.; H. Ferguson 226 (SD278632!), 24 Mar 1980, Mosquito Cove grassland, 32.85694°N, 118.40028°W, 15 m elev.; E. Havstad 19 (SD275428!), 23 Apr 2013, Top of Canchalagua

Canyon, 32.8490°N, 118.395°W, 315 m elev.; S. Junak SC1-355 (RSA878673!, SD271450!), 16 Apr 1996, along S side of Eagle Cyn., 32.86807°N, 118.42766°W, 476 m elev.; A. Liston 794-1 (RSA515104!), 28 Apr 1989, Deadman's Curve above Eagle Canyon., 32.86944°N, 118.42917°W, 473 m elev.; P. A. Munz 6661 (POM19016!, UC1601672!), 9 April 1923, dry slope, east coast; P. A. Munz 6674 (POM19136!), 9 Apr 1923, grassy slope on east coast, 32.90785°N, 118.49997°W; P. A. Munz 6678 (POM19108!), 9 Apr 1923, grassy slope halfway between "Casa Blanca" and Lemon Tank; P. A. Munz 6712 (POM18215!), 10 Apr 1923, grassy slope in middle of island; P. A. Munz 6712 (POM18215!), 10 Apr 1923, middle of island; N. Murbarger 13 (UC557782!), March 1936, east side on a mesa summit; F. W. Peirson 3423 (RSA79600!), 9 Apr 1923, north slope about 3 miles SE of Wilson's Cove; P. Raven 17196 (RSA159352!), 10 Apr 1962, Nfacing clayey slopes, summit of Thirst, 579 m elev.; P. Raven 17201 (RSA159350!), 10 Apr 1962, N-facing clayey slopes, summit of Thirst, 579 m elev.; P. Raven 17271 (RSA159351!), 11 Apr 1962, dunes on coast north of a point due west of Wall 2, 32.97694°N, 118.57361°W, 9 m elev.; P. Raven 17316 (RSA159357!), 12 Apr 1962, Near foot of canyon south of canyon below the Tomb, west side of island, 32.86917°N, 118.49694°W, 107 m elev.; P. Raven 17681 (RSA159342!), 9 May 1962, clayey grassland near head of canyon above Mosquito Cove, 335 m elev.; J. Rebman 3099 (SD139320!), 26 Apr 1996, Knob Canyon on southeast side of island, 32.83333°N, 118.36667°W, 200 m elev.; J. Rebman 35459 (SD274497!), 15 Apr 2019, SE portion of island, SHOBA (Shore Bombardment Area), north side of Guds Mountain to the east of Ridge Road, 32.83062°N, 118.36684°W, 223 m elev.; T. Ross 5132 (RSA534002!, SBBG98090, UC1587729!), 17 May 1991, 1400 ft SSE of Jack (not Jack Pt), 1350 ft NW of mouth of Larkspur Cyn, 32.95295°N, 118.51575°W, 145 m elev.; T. Ross 5164 (RSA533890!), 18 May 1991, grassy flats 950 ft WNW of Stone at top of Stone Canyon drainage; T. Ross 5172 (RSA533979!, SBBG98683), 18 May 1991, 1100 ft SSW of Twin Dams, 1450 ft NNW of Boulder marker (1859), 32.8996°N, 118.4731°W, 491 m elev.; T. Ross 5175 (RSA533908!, SBBG98661), 18 May 1991, 1100 ft SSW of Twin Dams, 1450 ft NNW of Boulder marker (1859), 32.8996°N, 118.4731°W, 491 m elev.; T. Ross 5294 (RSA534032!, SBBG98414), 19 May 1991, W fork of Near-Death Cyn, draining to Mosquito Cove (drainage beginning 800 ft N of Rest, 1800 ft SE of Malo Knoll, 32.85540°N, 118.4076°W, 274 m elev.; T. Ross 5432 (RSA536085!, SBBG98530), 21 May 1991, upper Box Cyn above area where cyn bottom is 1175 ft, 32.87310°N, 118.47280°W, 396 m elev.; *T. Ross 5490* (RSA535741!, SBBG98518, UC1587206!), 22 May 1991, lower Tota Cyn, 32.92890°N, 118.49460°W, 67 m elev.; R. Thorne 35999 (RSA251437!), 15 Apr 1966, rocky SW-facing bluff 2/3 mile SSE of Eel Point and

N of Seal Cove, 76 m elev.; *R. Thorne 36067* (**RSA**232792!), 16 Apr 1966, steep slope of canyon below Lemon Tank, near dump, **S** of Nanny, 198 m elev.; *R. Thorne 36135* (**SD**90494!), 17 Apr 1966, near Lemon Tank, south of Nanny, northwest side of island, 32.93360°N, 118.50240°W, 305 m elev.; *R. Thorne 42782* (**RSA**251524!, **SD**90553!), 11 Apr 1973, plateau in Middle Ranch area at head of Middle Ranch Canyon, 32.8880°N, 118.4845°W, 425 m elev.

Endemism, Habitat, Distribution, and Associates. Cryptantha kinkiensis is endemic to San Clemente Island, occurring on flats and slopes mostly at higher elevations (50-600 meters, most populations >200 meters) throughout much of the island (Fig. 7C). Very little is recorded about the substrate of collections, with that of two collections (Raven 17201, 17271) described as "clayey slopes." It is often found in island scrub and grassland vegetation. Observed associates (with updated nomenclature) include: Achillea millefolium L., Acmispon argophyllus (A.Gray) Brouillet var. argenteus (Dunkle) Brouillet, Allium praecox Brandegee, Amsinckia intermedia Fisch. & C.A.Mey., Artemisia californica Less., Avena barbata Pott ex Link, Bergerocactus emoryi, Bromus diandrus, Bromus hordeaceus L., Bromus rubens L., Calystegia macrostegia (Greene) Brummitt ssp. amplissima Brummitt, Cylindropuntia prolifera, Daucus pusillus Michx., Dipterostemon capitatus, Erodium brachycarpum (Godr.) Thell., Festuca myuros L., Lasthenia gracilis (DC.) Greene, Lepidium nitidum Nutt., Lupinus bicolor Lindl., Lupinus succulentus Douglas ex K.Koch, Malosma laurina (Nutt.) Nutt. ex Abrams, Melica imperfecta Trin., Microseris douglasii (DC.) Sch.Bip., Opuntia littoralis (Engelm.) Cockerell, and Trifolium palmeri S.Watson.

Phenology. Based on observations and data from available specimens, *Cryptantha kinkiensis* appears to flower and fruit from March to May.

Etymology. The specific epithet is from the Tongva name *Kinki* for San Clemente Island (Kroeber 1925) + *-ensis*, of or from, in reference to its distribution and endemism on this island.

Common Name. We suggest "San Clemente Island Upland Cryptantha" or the shortened "Clemente Upland Cryptantha" as potential common names.

Taxonomic Treatment 3

Cryptantha catalinensis M.G.Simpson & Rebman, sp. nov.—Type: USA, California, Los Angeles County, Santa Catalina Island, west-facing road cut, on road between Cherry Cove and Howland's Landing, 33.45508°N, 118.51696°W, 51 m elev., coastal sage scrub, associates: Selaginella bigelovii, Bromus madritensis, Avena barbata, Brachypodium distachyon, nearby on hill top: Artemisia californica, Mimulus aurantiacus, Heteromeles arbutifolia, Rhus integrifolia, annual herb, corolla white, throat yellow, corolla limb ca. 6 mm broad, rocky, tan, silt soil, 21 April 2012, *Michael G. Simpson 3682* with Lori L. Simpson (holotype: **SD**249169; isotypes: **SDSU**, **UC**).

Description. (Figs. 5-6). Plant annual; roots not reddish. Stems erect, sometimes decumbent, ca. 10-50 cm tall, with a few branches from base, surface with appressed-strigose (ca. 1 mm long) or especially below with both appressed-strigose and spreading, hirsute to hispidulous trichomes (the latter ca. 1.5-2.0 mm long), all trichomes white. Leaves grading from basal vegetative leaves to inflorescence bracts; basal leaves ca. $15-20 \text{ mm} \times \text{ca. 1 mm}$, sessile, linear, apex rounded, midrib ridged abaxially, sunken adaxially, trichomes white, adaxially hirsute, ascending to appressed, generally minutely pustulate, marginally and abaxially with coarser, hirsute to hispid (straight to incurved), horizontal to ascending, basally swollen and prominently pustulate trichomes, pustules of 2 concentric rows of slightly radially elongate, white to brownish cells. Inflorescence of mostly paired (rarely solitary or trifurcate), cymules arising from erect stems, elongating at maturity, up to 15 cm, typically with a flower at junction of cymules, fruits spread apart, not touching at maturity, one or more bracts often present at cymule base, these generally linear, much smaller than vegetative leaves. Flower bracts generally absent, occasionally present near cymule base. Pedicel stout, 0.5-1 mm long, not lengthening in fruit. Calyx slightly asymmetric, ascending in fruit, lance-ovoid in overall shape, ca. 2 mm long at anthesis, 4-5 mm long in fruit, sepals distinct, lanceolate, apices rounded, tip often recurved, adaxial surface glabrous basally, appressed short hirsute apically, abaxial surface with ascending to appressed, hirsute trichomes along margin and marginal region, midrib thickened, usually whitish, bearing, on sepals away from inflorescence axis, dense, horizontal to reflexed hispid trichomes in 1-2 vertical rows, trichomes narrowly conical, hollow, appearing slightly swollen, ca. 1.2-2.4 mm long, 0.1-0.2 mm wide at base (length:width ratio=9.0-14.5), whitish to yellowish, surface smooth to minutely papillate, with thickening at point of attachment, midrib trichomes thinner on sepals facing toward inflorescence axis. Corolla white, rotate, tube as long as calyx, limb 4–6 mm in diameter, fornices present, yellow to white. Gynobase ca. 2/3 length of nutlet. Style usually extending slightly (0.1–0.3 mm) beyond mature nutlet apices. **Nutlets** generally 4, sometimes reduced in number by abortion, homomorphic, brownish, lance-ovate, $(1.5)1.7-2.1 \text{ mm long} \times (0.6)0.7-0.8 \text{ mm at widest}$ region, length-width ratio 2.3-2.7, base truncate, margins rounded, apex narrowly acute to slightly acuminate, adaxially shallowly convexly 2-planed, abaxially low convex, dorsally papillate and tuberculate, tubercles with slightly thickened base and rounded to slightly pointed, generally translucent tip, apically densely spaced but not abutted (ca. 1

tubercle width apart), tubercles grading basally to low/obscure/glabrate, mostly glabrous on lateral and ventral sides, when visible ca. 16 tubercles across dorsal face at widest transverse line, spinal ridge absent, ventral groove closed to slightly open, one edge sometimes overlapping the other, bifid at base delimiting small, triangular areole.

Diagnosis. Cryptantha catalinensis is similar to *C. wigginsii* in having appressed-strigose and spreading stem trichomes, mostly bifurcate cymules, mostly ebracteate flowers, relatively large, showy corollas, and generally four, homomorphic nutlets per fruit, the nutlets lance-ovate, and acuminate. It differs in having nutlets with apical tubercles densely spaced but not generally abutted (versus abutted and wart-like in *C. wigginsii*), the basal dorsal surface low, obscurely tuberculate to glabrate (versus glabrous and shiny basally and dorsally in *C. wigginsii*).

Paratypes. USA. CALIFORNIA, Los Angeles County, Santa Catalina Island. A. Catalano 17-058 (CATA3352!), 21 Apr 2017, coastal sage scrub, 33.443413°N, 118.50033°W, 32 m elevation; E. Clohessy s.n. (SD222117!, SDSU20082!), 27 May 2012, west-facing road cut, on road between Cherry Cove and Howland's Landing, 33.45508°N, 118.51696°W, 51 m elev.; S. L. Crockett 621 (CATA479!), 28 Mar 1997, N side of Cherry Harbor, overlooking mud flats, 20 - 30 m upslope, 33.451805°N, 118.50447°W, 43 m elevation; M. L. Hoefs 1194 (CATA699!), 3 May 1991, steep, rocky sea bluff, 33.352367°N, 118.32891°W, 82 m elevation; M. L. Hoefs 1268 (CATA743!), 22 May 1991, grassy canyon bottom, 33.450522°N, 118.51284°W, 143 m elevation; M. L. Hoefs 1951 (CATA1030!, note: a mixed specimen with C. wigginsii; see Appendix 3), 4 May 1995, Steep, partially shaded, clay slope, 33.455831°N, 118.514729°W, 91 m elevation; D. Kraus DK-41 (CATA1861!), 1 June 2000, outside Goat Harbor burn area, on ridge just above Little Gibraltar, approximately 0.13 mile from it, 33.420021°N, 118.407086°W, 91 m elevation.

Endemism, Habitat, Distribution, and Associates. Cryptantha catalinensis is endemic to Santa Catalina Island, occurring in coastal sage scrub and grassland habitats, in populations scattered along the northern coastal regions of the island, ca. 30-140 meters in elevation (Fig. 7B). Plant associates (with updated nomenclature) recorded for all cited type specimens are: Acmispon argophyllus var. argenteus, Adenostoma fasciculatum Hook. & Arn., Antirrhinum nuttal*lianum* Benth. ex A.DC. subsp. *subsessile* (A.Gray) D.M.Thomps., Artemisia californica, Avena barbata, Brachypodium distachyon (L.) P.Beauv., Bromus rubens, Bromus madritensis L., Calystegia macrostegia, Castilleja foliolosa Hook. & Arn., Daucus pusillus, Delphinium parryi A.Gray subsp. parryi, Diplacus aurantiacus (Curtis) Jeps., Dipterostemon capitatus, Eriogonum giganteum S.Watson var. giganteum, Eriophyllum confertiflorum (DC.) A.Gray var. confertiflorum, Galium angustifolium A.Gray subsp.

angustifolium, Galium catalinense A.Gray subsp. catalinense, Genista sp., Heteromeles arbutifolia (Lindl.) M.Roem., Keckiella cordifolia (Benth.) Straw, Lysimachia arvensis (L.) U.Manns & Anderb., Marah macrocarpa (Greene) Greene, Mirabilis laevis (Benth.) Curran var. crassifolia (Choisy) Spellenb., Stipa lepida Hitchc., Opuntia littoralis, Phacelia cicutaria Greene var. hispida (A.Gray) J.T.Howell, Pseudognaphalium biolettii Anderb., Pseudognaphalium californicum (DC.) Anderb., Rhus integrifolia (Nutt.) Benth. & Hook. f. ex W.H.Brewer & S.Watson, Salvia mellifera Greene, Sanicula crassicaulis DC., Scrophularia villosa Pennell, Selaginella bigelovii Underw., Senecio lyonii A.Gray, Solanum douglasii Dunal, Thysanocarpus curvipes Hook., and Trifolium willdenovii Spreng.

Phenology. Based on observations and data from available specimens, *Cryptantha catalinensis* appears to flower and fruit from March to May.

Etymology. The epithet means "of Santa *Catalina* Island," where the species is endemic.

Common Name. We suggest "Santa Catalina Island Cryptantha" as a common name.

Comparison of *Cryptantha clementina*, *C. traskiae*, and *C. foliosa*

Past floristic surveys of San Clemente Island (e.g., Raven 1963) identified populations of Cryptantha traskiae as occurring on the island, these now treated by us as a separate species, Cryptantha *clementina*. Based on morphological similarities, we believe that C. clementing is a close relative of both the San Nicolas Island endemic C. traskiae (Fig. 8), with which it had previously been combined, and of C. foliosa (Fig. 9), endemic to Guadalupe Island, Baja California, Mexico (Ratay et al. 2014) (see map, Fig. 7A). The three species are similar to one another in nutlet shape and size and in relative style length. All have four nutlets (sometimes one or more abortive), that are homomorphic and ovate (their length:width ratio = 1.7-1.9). Nutlet size of the three species is similar, with C. clementina (1.1)1.4-1.6(1.7) mm long, C. traskiae 1.2-1.5 mm long, and C. foliosa 1.4-1.7 mm long (Table 1). All have a style extending up to or barely exceeding the nutlet tip. They can differ in cymule elongation, presence of flower bracts, calyx length (in fruit), calyx midrib trichome width, corolla limb width, and nutlet sculpturing (Table 1). Cryptantha clementina is unique in having congested cymules throughout at maturity, with flowers and fruits abutted to one another. Cryptantha traskiae has more elongate cymules (Fig. 8A), but these can be "congested at tips" (Kelley et al. 2012). Cryptantha clementina and C. traskiae have at least several flowers with bracts (see Fig. 1D), whereas flowers of C. foliosa are ebracteate. Cryptantha traskiae generally has smaller (3–4 mm long) calyces,

although the calyx lengths of C. clementina (ca. 5 mm) and C. foliosa (5-7 mm) are close in size. Cryptantha foliosa and C. clementina are similar in both having quite thick, hollow (variously described as "swollen" or "inflated") midrib calyx trichomes, with a maximum basal width of 0.2-0.3 mm; those of C. traskiae also appearing swollen but somewhat thinner, ca. 0.1-0.2 mm maximum width. Cryptantha clementina has a noticeably larger corolla (limb 3–4 mm wide); that of C. traskiae is relatively small (limb 1-2 mm wide). Our ANOVA statistical comparison of corolla limb width between these two species (specimens cited in Appendix 1) shows them to be statistically different (P < 0.01), with no overlap (Fig. 12A), although we point out the difficulty in assessing corolla size from dried herbarium specimens for some of these measurements. Based on published descriptions, the corolla limb width of C. foliosa is cited as 2–3 mm wide, intermediate to that of C. clementina and C. traskiae. Finally, all three species differ in nutlet sculpturing. Although all are papillate and tuberculate, Cryptantha clementina has low, denser tubercles, ca. 16 tubercles along a transverse line at the widest point of the dorsal face, these dispersed throughout the whole of the dorsal face (Figs. 1C, 11A). Cryptantha traskiae has tubercles similar in size and density, but is characteristically glabrate to sometimes glabrous in the dorsal, basal half (Figs. 8C, 11A). Cryptantha foliosa is distinctive in having larger (longer), but sparser tubercles throughout the dorsal face, ca. 8–9 tubercles along a transverse line at the widest point (Fig. 9C).

The close relationship of *Cryptantha foliosa*, and *C. traskiae* is corroborated by the molecular phylogenetic study of Hasenstab-Lehman and Simpson (2012), which included samples of the two taxa (their *C. traskiae* specimen was from San Nicolas Island, the type locality). In that study the two species were found to be each other's closest relative with strong support in all analyses and with these two sister to *C. decipiens* (M.E.Jones) A.Heller. We hypothesize that *Cryptantha clementina* is likely part of an exclusive clade with *C. foliosa* and *C. traskiae*.

The three Pacific islands where Cryptantha clementina, C. foliosa, and C. traskiae occur are separated by varying amounts of ocean distance. San Nicolas Island and San Clemente Island are ca. 80 km (50 miles) apart, whereas Guadalupe Island is ca. 400 and 460 km (250 and 285 miles) from San Clemente and San Nicolas Islands, respectively. A reasonable hypothesis is that bird migration (or possibly rafting) resulted in the long-distance transfer of propagules of an ancestral Cryptantha between the islands (see Moody 2000). The possibility of long-distance dispersal may be supported by the 21 examples of conspecific island plants native to Guadalupe Island and one or more of the California Channel Islands (see Ratay et al. 2014 for listing). Direct evidence for the phylogeographic history of these and these *Cryptantha* taxa must await future studies.

Comparison of *Cryptantha catalinensis*, *C. kinkiensis*, and *C. wigginsii*

Cryptantha catalinensis and C. kinkiensis resemble one another in a number of features. They are similar in their mostly erect to ascending habit and branching pattern (Figs. 3A, 4A, 5A, 6A) and in having both appressed-strigose and spreading-hirsute stem trichomes (Figs. 4D, 6C). Both have elongate, mostly bifurcate (very rarely solitary or trifurcate) inflorescence cymules (Figs. 3A, 4B, 5A). They are similar in calyx length, corolla limb diameter (Figs. 4C, 6B), and relative style length (Figs. 3B, 5C) (Table 2). The fruits of both are also similar in having generally four, homomorphic, lance-ovate [(1.5)1.6-2.1 mm long, length: width ratio 2.1–2.7), papillate and tuberculate nutlets. They differ in nutlet sculpturing, that of C. kinkiensis being tuberculate throughout the dorsal surface (although the tubercles are typically larger apically; Figs. 3C, 11B), whereas C. catalinensis has what we term glabrate to glabrous basal dorsal, lateral, and ventral surfaces, where the tubercles are obscure to absent (Figs. 5D, 11B). Second, the calyx trichomes of C. kinkiensis (Figs. 3B, D, 4E) are slightly shorter and basally wider than those of either C. catalinensis (Figs. 5B, E, 6C; Table 2) or C. wigginsii (Fig. 10B). Based on samples measured (Appendix 2), the calyx midrib trichome length: width ratio of C. kinkiensis is less than C. catalinensis and C. wigginsii, statistically different from our ANOVA analysis at P< 0.01, with no overlap; those of C. catalinensis and C. wigginsii are not statistically different from one another; see below (Fig. 12B; Table 2).

Given their similarity to one another, we considered the option of treating Cryptantha kinkiensis and C. catalinensis as varieties of one species, but rejected this for three reasons. First, they can be distinguished, based on the aforementioned nutlet sculpturing and calyx midrib trichome features, with no evident intergradation between them. Second, they are on different islands, with San Clemente and Santa Catalina being approximately 80 km (50 miles) apart (Fig. 7A). Both gene flow and propagule dispersal between these islands are probably quite rare events; thus, they are likely reproductively isolated. Third, given we have no data on the phylogenetic relationships of these taxa (see below), we do not know if they are each other's closest relative, which would be implied in using an infraspecific rank.

We have some knowledge of phylogenetic relationships of *Cryptantha catalinensis* based on a single sample (identified at that time as *Cryptantha* aff. *wigginsii*) sequenced in Simpson et al. (2017) and Mabry and Simpson (2018), with somewhat equivocal results. In the former study, *C. catalinensis* was sister to *C. decipiens* in two analyses (cpDNA and mtDNA) and sister to a clade of *C. affinis* (A.Gray) Greene, *C. clevelandii* Greene, and *C. corollata* (I.M.Johnst.) I.M.Johnst. in another analysis

(nrDNA). In the latter study, C. catalinensis was sister to C. decipiens in three analyses (cpDNA, concatenated, and Astral) and sister to a clade of C. affinis, C. clevelandii, and C. corollata in two analyses (mtDNA and nrDNA). Unfortunately, neither C. kinkiensis nor (true) C. wigginsii was included in these two studies. It is interesting, however, that in several analyses of these two studies, Cryptantha *catalinensis* shows a close relationship to *C. decipiens*, which we have stated previously is sister to C. traskiae and C. foliosa in the analyses of Hasesenstab-Lehman and Simpson (2012). This may be suggestive of at least a relatively close relationship of C. catalinensis with C. foliosa and C. traskiae (and perhaps, by implication, with C. clementina and C. kinkiensis).

Cryptantha wigginsii (see Fig. 10) is also similar to both C. catalinensis and C. kinkiensis in many of the features mentioned (see Table 2). However, C. wigginsii has a shorter style length (Table 2) and a unique nutlet sculpturing, with dense, "wart-like" tubercles found only on the apical dorsal face, being glabrous and shiny on the basal dorsal face (Fig. 10D). As mentioned, based on samples measured (Appendix 2) and our ANOVA analysis, the calyx midrib trichome length: width ratio of C. wigginsii is similar to that of *C*. *catalinensis* (P > 0.05) with both of these statistically different from C. kinkiensis (P <0.01; Fig. 12B; Table 2). Santa Catalina Island is the only island where C. wigginsii is documented to occur (see Simpson et al. 2013), to date known from only six collections (Appendix 3; see Figure 7B); three of these occur near or among known populations of C. catalinensis [one of these three, Hoefs 1951 (CATA1030), is a mixed collection of C. catalinensis and C. wigginsii] and three occur more disjunctly, two in central and western regions of the island (Fig. 7B). We have observed that the nutlets of some island collections are slightly different from that of the type specimen, with lower, slightly sparser tubercles on the apical portion (see examples from Amsinckiinae Working Group 2021). We also point out the similarity of C. wigginsii nutlets, which are shiny and glabrous basally, with those of C. catalinensis, which are what we term as "glabrate" basally on the dorsal surface and typically glabrous on the ventral surface. Evolutionary relationships between C. catalinensis and C. wigginsii (mainland and island populations) will be of great interest to evaluate (see below).

Mainland populations of *Cryptantha wigginsii* typically, but not always, occur on a clay substrate (see Simpson et al. 2013). Of the Santa Catalina Island populations of *C. wigginsii*, only three of the six known collections describe the substrate. Two of these – *Hoefs 1951* (CATA103) and *Thorne 42470* (RSA353854) describe the substrate as a "clay slope" and "bare clay openings," respectively. One collection – *Simpson 3684* (SDSU20033, UC1999564) – describes it as "rocky granite rock … brown silty-sand soil." For *Cryptantha catalinensis*, only three of the

eight known collections cite the substrate. Only one of these – *Hoefs 1951* (CATA103) describes it as a "clay slope." [Note that *Hoefs 1951* is a mixed collection of the two species.] The other two – *Crockett 621* (CATA479) and the type collection *Simpson 3682* (SD249169, SDSU20032, UC1999565) – describe it as "rocky slope, metamorphics" and "rocky, tan, silt soil," respectively. Thus, there appears to be a tendency for both species to occur on clay soils, but not obligately. Future population surveys with more detailed ecological information will aid in evaluating abiotic conditions for the two taxa.

Comparison with Cryptantha intermedia

Most of the paratypes that we cite for both *Cryptantha catalinensis* and *C. kinkiensis* were originally identified as *Cryptantha intermedia*. In addition, it is very likely that what was identified as *C. intermedia* in past floristic treatments of Santa Catalina Island (e.g., Millspaugh and Nuttall 1923) and of San Clemente Island (Raven 1963) correspond to *C. catalinensis* and *C. kinkiensis*, respectively. Although we have not been able to locate and examine all specimens from the two islands cited in past works as *C. intermedia*, those that we have seen were clearly identified as one of the two new species. Based on our studies, there is no evidence that *C. intermedia* occurs on either San Clemente Island or Santa Catalina Island.

Cryptantha intermedia, as currently recognized (see Amsinckiinae Working Group 2021), is one of the most common and widely collected species in the genus (CCH2 2021). The typical form of C. intermedia (C. intermedia var. intermedia), which is distributed widely in cismontane habitats of mainland California and northwestern Baja California, Mexico, is indeed similar to C. catalinensis and C. kinkiensis in having branched, erect to ascending stems with both appressed-strigose and spreading hirsute to hispid trichomes (Fig. 13B, C). Cryptantha *intermedia* var. *intermedia* also has a relatively large corolla (limb 3-6 mm in diameter; Fig. 13B), and fruits with four, homomorphic, lance-ovate (to ovate), slightly apically acuminate, papillate and tuberculate nutlets. It differs from the two new species in having mostly (or at least some on an individual) trifurcate inflorescence cymules (Fig. 13A) and nutlets with much larger and less dense tubercles (Fig. 13D). Cryptantha intermedia does not have obviously swollen trichomes on the sepal midribs (Fig. 13C).

Interestingly, in his floristic treatment of San Clemente Island, Raven (1963) commented on the morphology of what he called *Cryptantha intermedia* (undoubtedly our *C. kinkiensis*) on the island, noting (p. 336) that "all of the specimens from San Clemente Island have relatively small flowers and coarse, subinflated hairs on the calyx, thus approaching *C. foliosa* Greene, an endemic to Guadalupe Island." We agree with his assessment that the San Clemente

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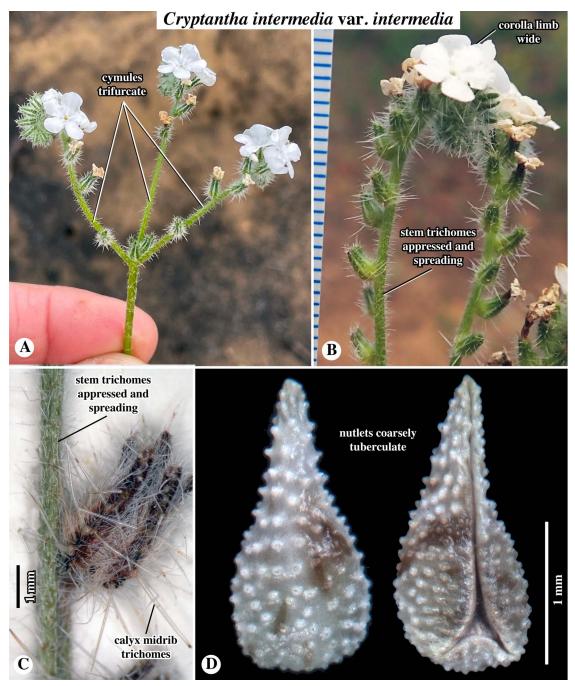


FIG. 13. Cryptantha intermedia var. intermedia. A. Field image of inflorescence, showing trifurcate cymules, typical of this taxon. Image taken by J. Rebman, San Diego County, CA, west of Fallbrook, 25 March 2021. B. Field image of cymules, showing appressed and spreading stem trichomes and relatively large corollas (*Simpson 4191*, **SDSU**22567). C. Mature calyx showing sepal midrib trichomes that are not obviously swollen (*Rebman 9362*, **SDSU**16074). D. Nutlet, in dorsal and ventral views, showing characteristic papillate and tuberculate sculpturing, the tubercles large and coarse (*Simpson 3723*, **SDSU**20790)

Island plants of the new C. *kinkiensis* have "swollen" trichomes on the calyx midribs, much like (but somewhat smaller than) those of C. *foliosa* of Guadalupe Island, and to a degree like those of C.

clementina of San Clemente Island. This trichome feature may possibly be a shared evolutionary novelty among these Pacific island species, perhaps indicative of a common ancestry.

Rarity, Endemism, and Conservation Needs

Cryptantha clementina is currently known from only 16 specimen collections on San Clemente Island. It is often surrounded by non-native, invasive species such as Atriplex semibaccata, Bromus diandrus, Erodium cicutarium, Herniaria hirsuta var. cinerea, Hordeum murinum, Hornungia procumbens, Mesembryanthemum crystallinum, and Mesembryanthemum nodiflorum; these associates are likely impeding its reproductive output. With the recognition of this new species, C. traskiae is now restricted to San Nicolas Island and in respect to distribution becomes an even rarer species. That species has already been given a California Rare Plant Rank (CNPS Inventory 2021) ranking of 1B.1 (locally rare, threatened, or endangered in California and elsewhere; seriously endangered in California, over 80% of occurrences threatened / high degree and immediacy of threat). For C. clementina, we also recommend a similar 1B.1 ranking. Additionally, we urge a management program involving careful removal of the non-native plants that often surround Cryptantha clementina in its microhabitat.

Cryptantha kinkiensis is currently known from 48 specimen collections mainly in the upper elevations of San Clemente Island. Naturalized grasses and forbs, including *Avena barbata*, *Bromus diandrus*, *Bromus hordeaceus*, *Bromus rubens*, *Erodium brachy-carpum*, and *Festuca myuros*, may compete detrimentally with this new species. Given its endemism and potential threats, we recommend a California Rare Plant Ranking (CNPS Inventory 2021) of 1B.2 (locally rare, threatened, or endangered in California, 20–80% occurrences threatened).

Cryptantha catalinensis is currently known from only eight specimen collections. Approximately 88% of Santa Catalina Island is protected by the Catalina Island Conservancy (2021). Naturalized non-native plants listed as occurring in these populations are grasses (*Avena barbata, Brachypodium distachyon, Bromus rubens, Bromus madritensis*), one forb (*Lysimachia arvensis*), and one shrub (*Genista* sp.); the last species seriously impacts native plants in areas of the island. Feral deer and pigs continue to be a threat to native plants on the island. Although more surveys are needed to evaluate the conservation needs of *C. catalinensis*, given the limited number of known populations and these potential herbivores and plant competitors, we recommend a California Rare Plant Ranking (CNPS Inventory 2021) of 1B.1 (see above). We note that *Cryptantha wigginsii*, which has several mainland populations, has a current California Rare Plant Ranking of 1B.2.

Formal listings of these three new species would join the current 64 taxa with a California Rare Plant Ranking on Santa Catalina Island (7 taxa listed as 1B.1, 18 taxa as 1B.2, 1 taxon as 1A = presumedextinct), plus 62 taxa with a California Rare Plant Ranking on San Clemente Island (8 taxa listed as 1B.1, 20 taxa as 1B.2) (from CNPS Inventory 2021). These new island endemic Cryptantha species add to the amazing and unique plant endemism that occurs on the California Channel Islands. Both San Clemente and Santa Catalina islands have the highest number of single island endemic plants in the archipelago. The addition of Cryptantha clementina and *C. kinkiensis* would increase the number of single island endemic plants on San Clemente Island from 17 to 19; the addition of C. catalinensis would increase that number on Santa Catalina Island from 9 to 10 (Junak et al. 1995; Moody 2000). These examples of rare and endemic plants highlight the need for continued conservation efforts on the California Channel Islands.

Future Taxonomic Work

This system of island endemic taxa will be ideal for population and species-level genetic studies utilizing rapidly evolving genes or gene regions. Phylogenetic analyses can test the monophyly of and evaluate relationships between the three endemic island species newly described here, the San Nicolas Island endemic Cryptantha traskiae, the Guadalupe Island endemic C. foliosa, and both Santa Catalina Island and mainland populations of Cryptantha wigginsii. Given our recognition of sympatric populations, possible introgression between C. catalinensis and C. *wigginsii* may be evaluated. Ascertaining the direction and timing of dispersal of these species between the islands will be quite interesting in analyzing biogeographic history among the Pacific islands of the Californias. Finally, quantifying genetic diversity among and between populations of these island species may help to guide their conservation and maintenance into the future.

KEY TO CRYPTANTHA, INCLUDING C. CATALINENSIS, C. CLEMENTINA, AND C. KINKIENSIS

The following key, excerpted from the recently updated treatment of *Cryptantha* in the Jepson eFlora [Jepson Flora Project (eds.) 2022] can be used to identify these three new species in the state of California, plus three other species discussed in this paper. Pertinent leads are in bold, non-applicable leads and taxa are removed. 1. Nutlet(s) all smooth or obscurely roughened

- 1' Nutlets, or at least 1, variously papillate and/or tubercled, occasionally obscurely so
- 26. At least one nutlet with margins winged or narrow, knife-like linear-rimmed
- 26' All nutlets with margins rounded or angled, not winged or linear-rimmed
 - 32. Nutlets of 1 fruit dissimilar in size and/or sculpturing
 - 32' Nutlets of 1 fruit similar in size and sculpturing

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- 37. Pedicels 2–3 mm in fruit, long-soft-hairy; calyx with 1 hair type, densely white, long-soft-hairy, without coarse bristly hairs
- 37' Pedicels 0–1.5(–2) mm in fruit, not long-soft-hairy; calyx with \geq 2 hair types, at least some coarse, bristly hairs present
 - 38. Nutlets 1(2 or 3)
 - 38' Nutlets generally (3)4
 - 47. Corolla generally inconspicuous, limb (<)1-2 mm diam
 - 48. Nutlets lance-ovate to lanceolate, length: width ratio > 2
 - 48' Nutlets ovate to wide-ovate or deltate, length: width ratio < 2
 - 51. Calyx midrib hairs recurved, short-scabrous-bristly
 - 51' Calyx midribs hairs spreading long-bristly
 - 52. Nutlet tubercles narrowly elongate, appearing spiny
 - 52' Nutlet tubercles broadly elongate, rounded, not appearing spiny
 - 53. Flower bracts present, scattered throughout length of cymes
 - Bracts thread-like; inflorescence tightly clustered; calyx 4–6 mm in fruit; nutlets wide-ovate to deltate, coarsely tubercled throughout; SnJV (presumed extinct)
 - 54' Bracts leaf-like; inflorescence elongate, at least below; calyx 3–4 mm in fruit; nutlets narrowly ovate, glabrous or becoming so basally, finely tubercled distally; s ChI (San Nicolas Island).....C. traskiae
 - 53' Flower bracts generally 0 within cymes, occasionally at base of cymes
 - 47' Corolla generally conspicuous, limb 2-8 mm diam
 - 59. Nutlets ovate to wide-ovate, length:width ratio <2
 - 60. Plants mostly spreading to decumbent; inflorescence cymes congested, flower bracts near base; s ChI (San Clemente Island) C. clementina
 - 60' Plants erect to ascending; inflorescence cymes elongate, flower bracts 0 or only at base; mainland
 - 59' Nutlets lance-ovate, length: width ratio >2
 - 63. Nutlet abaxial and adaxial surfaces glabrous or becoming so in proximal half on all sides, densely tubercled to warty in distal abaxial half
 - 64. Nutlet abaxial distal half with rounded to pointed, not wart-like tubercles, mostly not abutted, basal region becoming glabrous (tubercles low to 0) or glabrous on all sides; s ChI (Santa Catalina Island) C. catalinensis
 - 64' Nutlet abaxial distal half with dense, wart-like, abutted tubercles, basal region glabrous and shiny all sides; mainland and Santa Catalina Island

C. wigginsii

- 63' Nutlet dorsal surfaces tubercled throughout
 - 65. Stem hairs mostly appressed, sometimes sparsely spreading soft-bristly
 - 65' Stem hairs both appressed and spreading rough-hairy or only spreading rough-hairy to bristly
 - 67. Calyx 4.5–9 mm in fruit, lobe margins tufted-spreading hairy below middle; leaves oblong, tip obtuse
 - 67' Calyx 4-5.5 mm in fruit, lobe margins appressed fine-hairy below middle; leaves linear to lanceolate, tip acute
 - 68. Distal stem hairs spreading only, few to none appressed; fruiting calyx perpendicular to slightly angled upward relative to axis
 - 68^\prime Distal stem hairs appressed and spreading; fruiting calyx \pm ascending relative to axis
 - 69. Inflorescence cymes mostly in 1s; leaves oblong, tips obtuse to rounded; plant low, branches erect to decumbent
 - 69' Inflorescence cymes mostly in 2s or 3s; leaves generally linear, tips acute; plant erect, branches erect to ascending
 - 70. Inflorescence cymes mostly in 2s; nutlets densely and more finely tubercled; s ChI (San Clemente Island) C. kinkiensis
 - 70. Inflorescence cymes mostly in 2s or 3s; nutlets coarsely tubercled; mainland

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LITERATURE CITED

- ABRAMOFF, M. D., P. J. MAGELHAES, AND S. J. RAM. 2004. Image Processing with ImageJ. Biophotonics International 11:36–42.
- AMSINCKIINAE WORKING GROUP. 2021. Systematics of Amsinckiinae (Boraginaceae): The popcorn flowers. Website https://plants.sdsu.edu/amsinckiinae [accessed 15 January 2021].
- CATALINA ISLAND CONSERVANCY. 2021. Avalon, California. Website http://www.catalinaconservancy.org [accessed 15 January 2021].
- CCH1. 2021. Data provided by the Consortium of California Herbaria. Website http://ucjeps.berkeley. edu/consortium [accessed 15 January 2021].
- CCH2. 2021. Consortium of California Herbaria CCH2 Portal. Website http://cch2.org/portal/index.php [accessed 15 January 2021].
- CHACÓN, J., F. LUEBERT, H. H. HILGER, S. OVCINNIKOVA, F. SELVI, L. CECCHI, C. M. GUILLIAMS, K. HASEN-STAB-LEHMAN, K. SUTORÝ, M. G. SIMPSON, AND M. WEIGEND. 2016. The borage family (Boraginaceae s.str.): A revised infrafamilial classification based on new phylogenetic evidence, with emphasis on the placement of some enigmatic genera. Taxon 65:523–546.
- CNPS INVENTORY. 2021. California Native Plant Society Rare Plant Program inventory of rare and endangered plants of California (online edition, v8-03 0.39). Website http://www.rareplants.cnps.org [accessed 15 January 2021].
- CRONQUIST, A. 1978. Once again, what is a species? Pp. 3– 20 in J. A. Ramberger (ed.), Biosystematics in agriculture. Allanheld & Osmun, Montclair, NJ.
- CRONQUIST, A. 1988. The evolution and classification of flowering plants. 2nd ed. New York Botanic Garden, New York, NY.
- HASENSTAB-LEHMAN, K. E. AND M. G. SIMPSON. 2012. Cat's eyes and popcorn flowers: Phylogenetic systematics of the genus *Cryptantha* s.l. (Boraginaceae). Systematic Botany 37:738–757.
- JEPSON FLORA PROJECT (eds.) 2022. Jepson eFlora Website https://ucjeps.berkeley.edu/eflora/ [accessed 15 January 2022].
- JUNAK, S., T. AYERS, R. SCOTT, D. WILKEN, AND D. YOUNG. 1995. A flora of Santa Cruz Island. Santa Barbara Botanic Garden, Santa Barbara, CA.
- KELLEY, R. B., M. G. SIMPSON, AND K. E. HASENSTAB. 2012. Cryptantha. Pp. 455–468 in B. G. Baldwin, D. H. Goldman, D. J. Keil, R. Patterson, T. J. Rosatti, and D. H. Wilken (eds.), The Jepson manual: vascular plants of California, 2nd Edition. University of California Press, Berkeley, CA.
- KROEBER, A. L. 1925. Handbook of the Indians of California. Bureau of American Ethnology, Bulletin 78. Smithsonian Institution, Washington, D.C.
- MABRY, M. E. AND M. G. SIMPSON. 2018. Evaluating the monophyly and biogeography of *Cryptantha* (Boraginaceae). Systematic Botany 43:53–76.

- MABRY, M. E., R. A. DOWDY, L. M. SIMPSON, J. P. REBMAN, AND M. G. SIMPSON. 2016. Taxonomy of the winged popcorn flower: *Cryptantha pterocarya* (Boraginaceae). Phytotaxa 253:97–130.
- MILLSPAUGH, C. F. AND L. W. NUTTALL. 1923. Flora of Santa Catalina Island (California). Field Museum of Natural History Publication 212, Botanical Series 5:1– 413.
- MOODY, A. 2000. Analysis of plant species diversity with respect to island characteristics on the Channel Islands, California. Journal of Biogeography 27:711–723.
- RASBAND, W. S. 1997–2007. ImageJ. National Institutes of Health, Bethesda, MA. Website http://rsb.info.nih.gov/ ij [Accessed 17 June 2016].
- RATAY, S. E., S. E. VANDERPLANK, AND B. T. WILDER. 2014. Island specialists: Shared flora of the Alta and Baja California Pacific islands. Monographs of the Western North American Naturalist 7:161–220.
- RAVEN, P. H. 1963. Flora of San Clemente Island. Aliso 5:1–347.
- SIMPSON, M. G. 2019. Plant Systematics. 3rd ed. Elsevier-Academic Press, New York, NY.
- SIMPSON, M. G. AND R. B. KELLEY. 2017. Cryptantha nevadensis var. rigida elevated to species with a new name, C. juniperensis. Phytotaxa 295:227–236.
- SIMPSON, M. G. AND J. P. REBMAN. 2013. A new species of *Cryptantha* (Boraginaceae) from the Sierra de San Pedro Mártir, Baja California, Mexico. Madroño 60:35–45.
- SIMPSON, M. G. AND J. P. REBMAN. 2021a. A new species of *Cryptantha* restricted to dunes in northwestern Baja California, Mexico. Madroño 68:127–137.
- SIMPSON, M. G. AND J. P. REBMAN. 2021b. Research in Boraginaceae: A new variety of *Cryptantha maritima*, *Cryptantha pondii* resurrected, and *Johnstonella echinosepala* transferred back to *Cryptantha*. Phytotaxa 509:185–210.
- SIMPSON, M. G., M. E. MABRY, AND K. HASENSTAB-LEHMAN. 2019. Transfer of four species of *Cryptantha* to the genus *Johnstonella* (Boraginaceae). Phytotaxa 425:279–289.
- SIMPSON, M. G., L. M. SIMPSON, AND J. P. REBMAN. 2016. A new, large-flowered variety of *Eremocarya micrantha* (Boraginaceae). Madroño 63:39–54.
- SIMPSON, M. G., R. DOWDY, J. P. REBMAN, R. B. KELLEY, AND L. M. SIMPSON. 2014. Recognition of two species in *Eremocarya* (Boraginaceae): Evidence from fornix bodies, nutlets, corolla size, and biogeography. Madroño 61:259–275.
- SIMPSON, M. G., C. M. GUILLIAMS, K. E. HASENSTAB-LEHMAN, M. E. MABRY, AND L. RIPMA. 2017. Phylogeny of the popcorn flowers: Use of genome skimming to evaluate monophyly and interrelationships in subtribe Amsinckiinae (Boraginaceae). Taxon 66:1406–1420.
- SIMPSON, M. G., J. P. REBMAN, K. E. HASENSTAB-LEHMAN, C. M. GUILLIAMS, AND P. O. MCCONNELL. 2013. Cryptantha wigginsii (Boraginaceae): A presumed extinct species rediscovered. Madroño 60:24–34.

APPENDIX 1.

DOCUMENTATION OF VOUCHERS USED FOR MEASURE-MENT OF COROLLA LIMB WIDTH.

Cryptantha clementina: Beauchamp 132 (SDSU5414; Beauchamp 3222 (SD86340; Englert SERG 10-28 (SD278628; Junak SCI-259 (SD274027; Junak *SCI-265* (**SD**274029; *Junak SCI-409* (**SD**271453; *Junak SCI-440* (**SD**271451; *Junak SCI-444* (**SD**271452; *Rebman 35582* (type) (**SD**274504; *Thorne 35992* (**SD**90374).

Cryptantha traskiae: Davidson 57 (RSA499632); Guilliams 5064 (SBBG165106); Hasenstab-Lehman 1508 (SBBG164659); Hasenstab-Lehman 1750 (SBBG167521); Hasenstab-Lehman 1752 (SBBG167530); Junak SN-1369 (RSA878868); Junak SN-591 (JEPS93529); Junak SN-597 (JEPS93458); Junak SN-730 (RSA642369); Junak SN-771 (JEPS93740); Junak SN-804 (JEPS93692); Thorne 52414 (HSC202926); Trask s.n., April 1901 (type) (GH00096285).

APPENDIX 2.

DOCUMENTATION OF VOUCHERS USED FOR MEASURE-MENT OF TRICHOME DIMENSIONS.

- *Cryptantha catalinensis*: *Catalano* 17-058 (CATA3352); *Clohessy s.n.* (SDSU20082); *Crocket* 621 (CATA870); *Hoefs* 1194 (CATA699); *Hoefs* 1268 (CATA743); *Kraus* DK41 (CATA1861); *Simpson* 3682 (type) (SDSU20031).
- *Cryptantha kinkiensis*: Beauchamp 3242 (SD86346); Boyd 4382 (SD217245); Havstad 13-19 (SD275428); Junak SC1-355 (SD271450); Rebman 3099 (SD139320); Rebman 35459 (SD274497); Rebman 35515 (type) (SD274496); Ross 5490 (UC1587206); Thorne 36135 (SD90494); Thorne 42782 (SD90553).
- Cryptantha wigginsii: Guilliams 1796 (SDSU20081); Marsden 2011192B (SDSU05460); McConnell s.n.,

10 Mar 2011 (SDSU19749); McConnell s.n., 11 Mar 2011 (SDSU19749); McConnell s.n., 18 April 2012 (SDSU20063); Simpson 3673 (SDSU20062); Simpson 3675 (SDSU20019); Wiggins 5107 (type) (GH00096301).

APPENDIX 3.

KNOWN COLLECTIONS OF *CRYPTANTHA WIGGINSII* ON SANTA CATALINA ISLAND. SEE ALSO SIMPSON ET AL. (2013).

USA: California: Los Angeles County: Santa Catalina Island: F. R. Fosberg 4934 (POM368370!), 21 May 1931, between Cherry Valley and Howland's Landing., 33.4567, -118.5157, 20 meters elev.; C. M. Guilliams 2674, (SBBG143087, SD273545!), 15 Feb 2015, south road to Little Harbor within campground., 33.36785, -118.47778, 9 meters elev.; M. L. Hoefs 1951 (CATA1030!; note a mixed specimen with C. catalinensis), 4 May 1995, Steep, partially shaded, clay slope, 33.455831, -118.514729, 91 m elev.; M. G. Simpson 3684 (SDSU20033!, UC1999564!), 22 Apr 2012, road cut on north side of St. Catherine Way Road, ca. 0.25 mile along road south of entrance to Hamilton Cove Villa., 33.35123, -118.33192, 55 meters elev.; R. Thorne 35850 (SBBG31353, SD69480!), 5 Apr 1966, above stream in Cottonwood Canyon, 33.38851, -118.44019, 105 meters elev.; R. Thorne 42470 (RSA353854!), 12 Feb 1973, north of Marine Science Station at Fisherman's Cove., 33.445408, -118.48201, 46 meters elev.