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Research in Boraginaceae: A new variety of *Cryptantha maritima*, *Cryptantha pondii* resurrected, and *Johnstonella echinosepala* transferred back to *Cryptantha*

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Abstract

A review of the species *Cryptantha maritima* (Boraginaceae) supports the continued recognition of the three varieties, these differing in corolla size, ovule and nutlet number, and calyx vestiture. Mapping of these taxa from verified specimens demonstrates some geographic trends, but also some overlap in ranges. In the process of our study, we discovered a new taxonomic entity. *Cryptantha maritima* var. *vizcainensis* is described as new. This variety is restricted to the Vizcaíno Desert of Baja California Sur, Mexico and should be considered rare, as it is known to date from only eleven collections. It differs from the other three varieties of the species in having a canescent, appressed-strigose stem vestiture lacking spreading trichomes, in having a relatively large corolla, and in having a fruit derived from two 1-ovuled ovary lobes, developing into two heteromorphic nutlets. We also discovered that the species *Cryptantha pondii*, previously treated as a synonym of *C. patula*, should be resurrected as a distinct taxon. *Cryptantha pondii* is restricted to the western Vizcaíno Desert and to Natividad Island of Baja California Sur. It is morphologically distinctive in having bracteate flowers, relatively large corollas, and four smooth nutlets heteromorphic by size. It is to date known from only three collections and should be considered extremely rare. We also reviewed the morphological and phylogenetic status of *Johnstonella echinosepala*. This taxon shows similarities to *Cryptantha maritima* and also exhibits some morphological discontinuity between Pacific and Gulf populations in Baja California Sur. Evidence from both morphological and phylogenetic studies supports the transfer of this species from the genus *Johnstonella* back to the genus *Cryptantha*. Finally, we propose that both *C. pondii* and *C. echinosepala* are likely close relatives of *C. maritima*, all of the “*Maritimae* clade,” a group distantly related to the main core of the genus *Cryptantha*. This study confirms the great importance of studying herbarium specimens in taxonomic research.

Keywords: Baja California, Baja California Sur, Mexico, taxonomy, Vizcaíno Desert

Introduction

The genus *Cryptantha* (Boraginaceae, subtribe Amsinckiinae; see Chacón *et al.* 2016) is among the largest in the family. Based on molecular phylogenetic studies (Hasenstab-Lehman & Simpson 2012; Simpson *et al.* 2017a; Mabry & Simpson 2018), *Cryptantha* is currently recognized with about 104 species and 118 total taxa (species plus infraspecies), having been split from the genera *Eremocarya*, *Greeneocharis*, *Johnstonella*, and *Oreocarya* (see Hasenstab-Lehman and Simpson 2012 for a key to genera and Amsinckiinae Working Group 2021 for updated taxonomy). In addition to phylogenetic studies, taxonomic work has also been fruitful in discovering or clarifying species delimitations in the complex (Simpson *et al.* 2013, 2014, 2016, 2019; Simpson & Kelley 2017; Simpson & Rebman 2013, 2021; Rebman and Simpson 2021).

As part of a survey of *Cryptantha* of the Baja California peninsula, Mexico (the states Baja California and Baja California Sur), we investigated the species *Cryptantha maritima* (Greene 1885: 204) Greene (1887: 117). We wished to determine both the taxonomic distinctiveness and the biogeographic distribution of its three, generally accepted varieties. We also studied specimens of a species of the genus *Johnstonella* in order to evaluate its taxonomic affinities, both with regard to recent phylogenetic studies and perceived similarities to *C. maritima*.

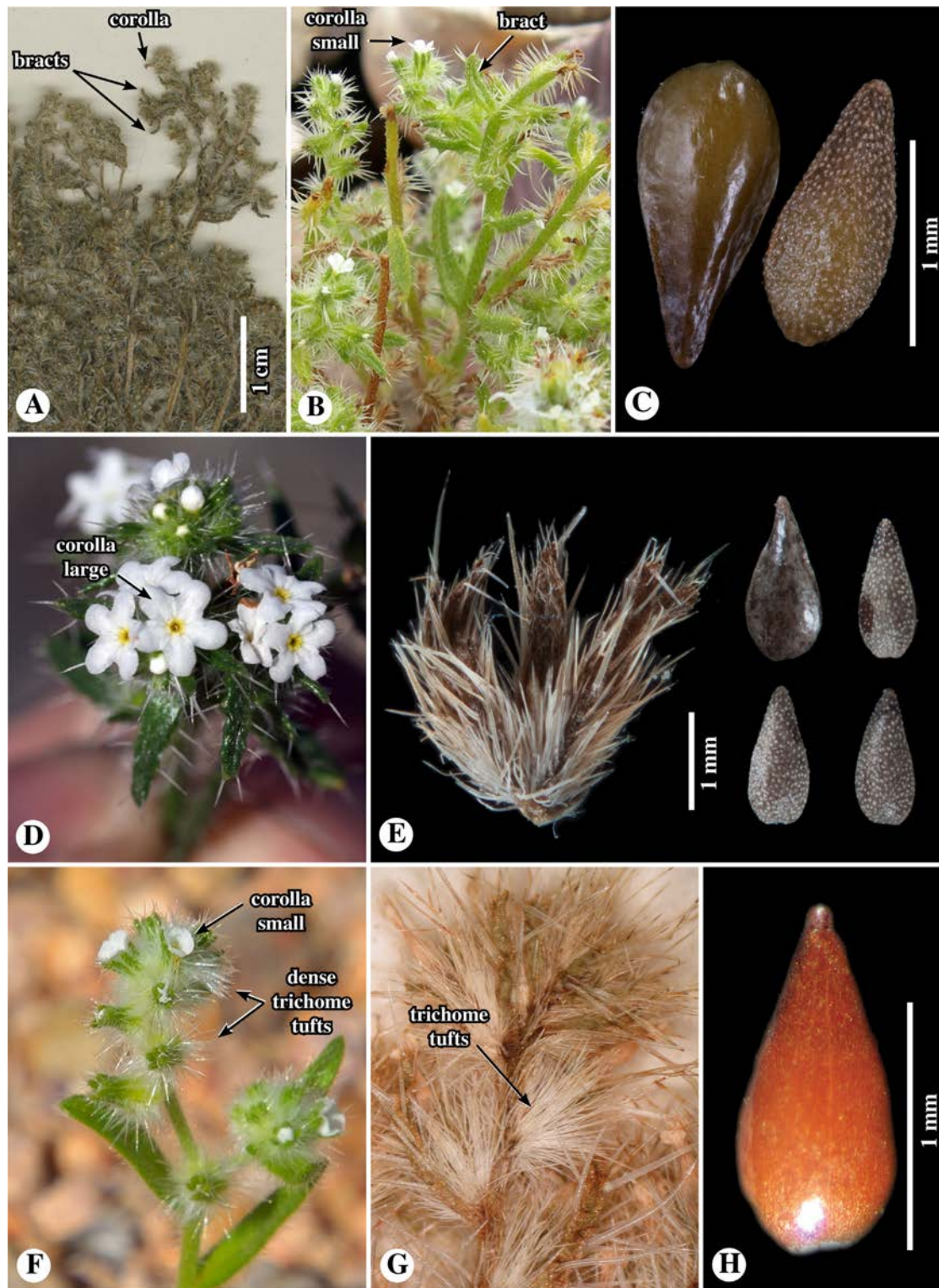


FIGURE 1. Exemplars of three varieties of *Cryptantha maritima*. A–C. *Cryptantha m. var. maritima*. A. Image of original material: *Greene s.n.*, 26 Apr 1885, Mexico, Baja California, Guadalupe Island (UC193934). Note bracts and hispid vestiture. B. Field image, showing bracts and small corollas; photograph by Jon Rebman, 2 April 2008, Mexico, Baja California Sur, Laguna San Ignacio. C. Nutlets of fruit, one larger smooth (left) and one smaller tuberculate (right), from *Simpson 2933* (SDSU19298). D, E. *Cryptantha m. var. cedrosensis*. D. Field image, showing larger corolla of this variety; photograph by Jon Rebman, 31 March 2015, Mexico, Baja California, Cedros Island. E. Fruiting calyx with four nutlets dissected out, these heteromorphic with one larger smooth and three smaller tuberculate; from *Rebman 2446*, 17 March 1994 (HCIB6234). F–H. *Cryptantha m. var. pilosa*. F. Field image, showing bracts, dense tufts of hairs, and small corollas; photograph courtesy of Pablo Ruiz, United States, Pima County, Arizona, Saguaro National Park, iNaturalist observation 39812503. G, H. Images from *C.V. Morton 2061*, 19 March 1949 (SD113111). G. Close-up of flowers and fruits, showing calyces with dense tufts of whitish, ascending hairs, characteristic of this variety. H. Solitary nutlet of fruit, this smooth.

Materials and methods

We reviewed the nomenclatural history and treatments of *Cryptantha maritima* and *Johnstonella echinosepala* (Macbride 1918: 57) Hasenstab & Simpson (2012: 754), including their protologues. We evaluated type specimens based on those protologues and online images, but for specimens for which type status was not certain, we referred to vouchers as “original material.” Herbarium specimens from ARIZ, ASU, BSCA, HCIB, RSA, SBBG, SD, SDSU, SJSU, and UCR (herbarium acronyms after Thiers 2021) of what were identified as *Cryptantha maritima* and *Johnstonella echinosepala* were examined and annotated using standard dissecting microscopy for diagnostic morphological features. Although we were unable to examine specimens from MEXU, we do cite from online data those specimens that are duplicates of those that we did physically examine. Additional online specimen images, including those of type specimens from GH, NDG, and US were also studied. In addition to qualitative observations, 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. A spreadsheet was prepared of specimen data from Baja Flora (2021), CCH2 (2021), and SEINet (2021) (see Appendix 1). Maps were prepared from georeferenced specimen data, using the mapping function of Baja Flora or the CCH1 (2021) multi-mapper tool (https://ucjeps.berkeley.edu/consortium/load_mapper_multi.html).

Results

We found the three generally accepted varieties of *Cryptantha maritima* to be taxonomically coherent, although we noted some previously unrecognized features. The distributions of these three varieties show some geographic discontinuities, but also sympatry in certain regions. In the progress of our study, we made three interesting discoveries. First, we discovered a new taxon, which we describe below as a fourth variety of *Cryptantha maritima*. Second, we discovered that the species *Cryptantha pondii* Greene (1889a: 291), a taxon of the peninsula generally treated as a synonym of the rather widespread *Cryptantha patula* Greene (1889b: 265), is actually a quite different and distinct species and is extremely rare. Third, we discovered that *Johnstonella echinosepala* shows morphological resemblances to *Cryptantha maritima* which, along with recent phylogenetic data, justifies its transfer back to the genus *Cryptantha*. We infer that all of these taxa are likely closely related components of the “*Maritimae* clade” (Simpson *et al.* 2017a; Mabry & Simpson 2018), which is phylogenetically distinct from the “core” genus *Cryptantha* s.s. We present the details of these findings below.

CRYPTANTHA MARITIMA

Nomenclatural History

Cryptantha maritima was named by Greene (1887: 117), in a generic transfer from *Krynitzkia maritima* Greene (1885: 204), the basionym. In Greene’s publication of the basionym, no type was designated, but he cites two specimens: “First collected by Dr. Palmer, in 1875, and again by the present writer [Greene], April 26, 1885.” Johnston (1925: 48) cites “Greene in 1885 (G [=GH], UC)” as “isotypes of *K. maritima*,” which could be interpreted as isolectotypes, given Johnston designated them. Specimens we have located and observed images of include UC78555, UC78557, and UC193934, all collected by Greene on 26 April 1885 from Guadalupe Island, Baja California, Mexico (see Fig. 1A, 2A,B), corresponding to Johnston’s citation. Comparable specimens from GH or from NDG (the latter where many of Greene’s collections were transferred) have not been located, but one from US (US1320711), also labeled “*E. L. Greene*, April 26, 1885, Guadalupe Island” is another likely isolectotype. However, given the uncertainty of type status, we here refer to these specimens as “original material.”

In the protologue of the basionym, Greene (1885: 204) described the species as: “Erect, a span to a foot high, intricately and compactly branching: leaves linear, an inch long, setose with short bristles: spikes elongated, with only here and there a leafy bract: calyx a line [ca. 2.2 mm] long, short-bristly, not villous: nutlet solitary, hardly a half line [ca. 1.1 mm] long, dark brown and shining, ovate-lanceolate in outline, ventral face flat, the closed groove terminating in a triangular or roundish scar.”

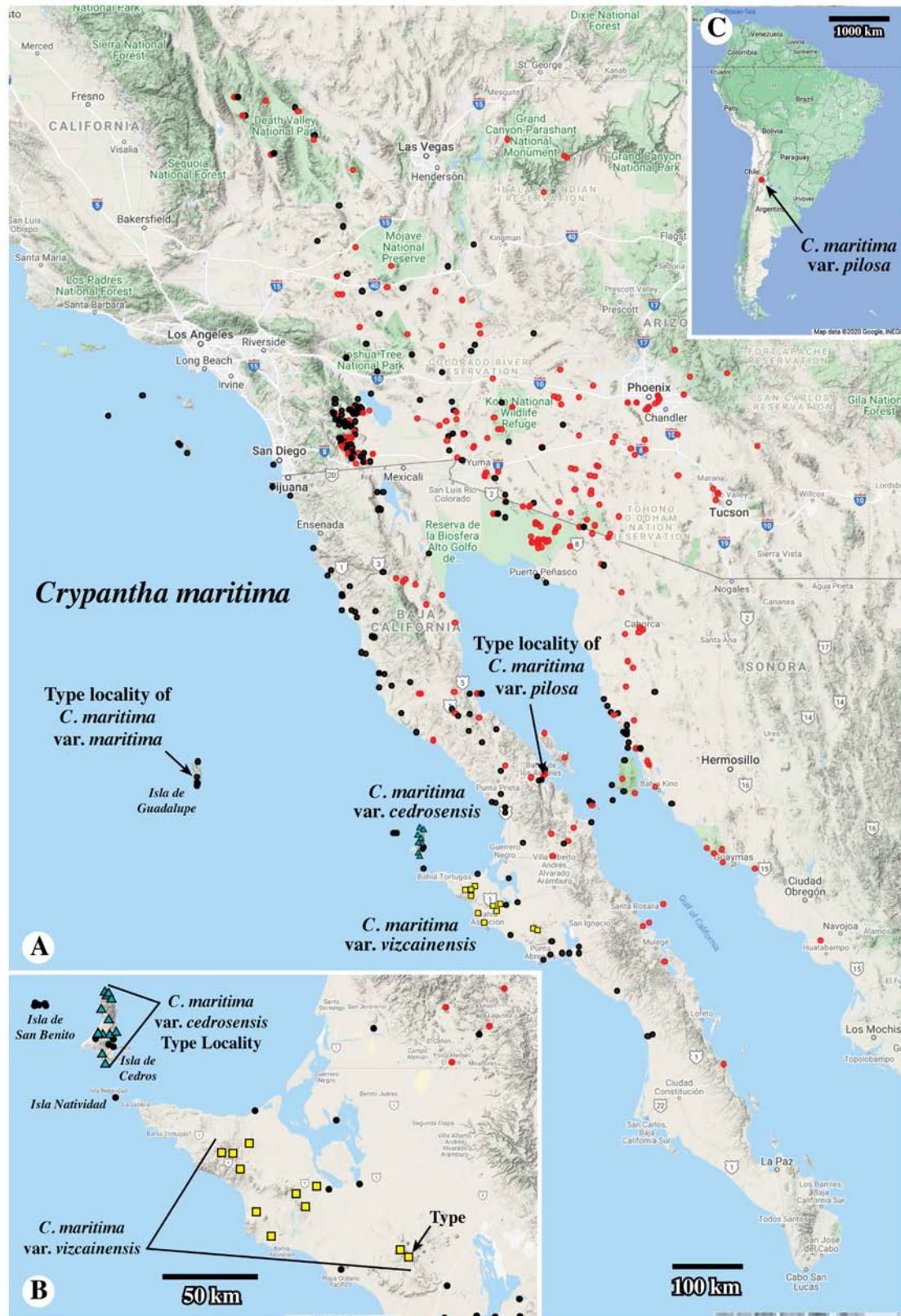


FIGURE 2. Distribution maps of varieties of *Cryptantha maritima*. Data from Baja Flora (2021), CCH2 (2021), GBIF (2020), and SEINet (2021), all specimens annotated by the authors (Appendix 1). A, B. Distribution in North America. A. Full distribution map. B. Close-up of Vizcaino Peninsula and adjacent islands. Note location of type populations and restriction of *C. maritima* var. *cedrosensis* to Cedros Island and of *C. maritima* var. *vizcainensis* to the western Vizcaino region. Black dots=*C. maritima* var. *maritima*; red dots=*C. maritima* var. *pilosa*; green triangles=*C. maritima* var. *cedrosensis*; yellow squares=*C. maritima* var. *vizcainensis*. C. Distribution of *C. maritima* var. *pilosa* in Argentina, South America, data from GBIF (2020). All maps from ©Google 2021, INEGI Data.

Johnston (1925: 47), in his seminal publication *The North American Species of Cryptantha*, gave a more detailed description of *Cryptantha maritima*, including that the species is “irregularly leafy-bracted throughout” with the “corolla inconspicuous” ... “0.5–1 mm. broad.” The former statement agrees with Greene (1885: 204), but Greene did not mention corolla dimensions. Johnston also stated that *C. maritima* has “... ovules 2 or 4; nutlets 1–4, heteromorphous; odd nutlet frequently alone developing, smooth, shiny, brownish, oblong-lanceolate, 1–2 mm. long, firmly affixed, next the axial calyx-lobe [i.e., nearest the inflorescence axis], groove narrow or closed throughout or opening below into a small areola; consimilar nutlets grayish, minutely tuberculate, readily deciduous, slightly smaller but otherwise like odd nutlet ...” We note that each ovule of a flower is contained within a single lobe of the ovary. Most *Cryptantha* species have a total of four ovary lobes each with one ovule (this typical of the family). All or some of the ovary lobes develop into nutlets at maturity; the remainder persist as abortive but visible ovary lobes, each containing an abortive ovule. Having only two ovules, the typical feature of *Cryptantha maritima*, is quite rare in the genus overall, only elsewhere found among North American *Cryptantha* in *Cryptantha excavata* Brandegees (1899: 452) (see Johnston 1925: 44).

Three varieties of *C. maritima* were recognized by Johnston (1925). *Cryptantha maritima* var. *genuina* [this epithet used regularly by him to refer to the autonym, in this case *C. m.* var. *maritima*] was characterized as “ovules 2; nutlets 1 or 2; calyx not conspicuously pilose” the type of the species being the aforementioned collection from Guadalupe Island. Johnston (1925: 48) lists the range of this type variety as “Nevada to Lower California [the Baja California peninsula, Mexico].”

A second variety, *Cryptantha maritima* var. *cedrosensis* (Greene 1885: 204) Johnston (1925: 48), was changed in rank by Johnston in the same publication. In the protologue for the basionym, *Krynitzkia cedrosensis* Greene (1885: 204), Greene wrote “Cedros Island, April, 1885. Dr. Gray’s cited specimens from the same locality are probably identical, although none are to be found in our collection from Dr. Veatch.” Thus, it appears that Green did not possess or allude to any specimen by Gray or Veatch in his protologue. In the protologue of *Cryptantha maritima* var. *cedrosensis*, Johnston cited the following specimens, all examined by him: “Lower California: Cedros Island. *Palmer 691* (G), *Greene in 1885* (G, UC, isotypes), *Veatch* (G), *Anthony 289* (G, UC). Thus, we consider *Greene* specimens collected in 1885 [April according to Greene 1885: 204] from Cedros Island as possible lectotypes. We have located one specimen—*E. L. Greene s.n.* (UC78461), collected 30 April 1885, Cedros Island, Baja California, Mexico (Fig. 1A)—fitting this description. We were unable to locate comparable specimens at GH [=G in Johnston]). Given the uncertainty of type status of this taxon, we refer to the UC78461 specimen as “original material.”

Johnston characterized *Cryptantha maritima* var. *cedrosensis* as “ovules 4; nutlets 1–4; otherwise as in preceding [sic] variety” [i.e., *C. m.* var. *maritima*]. Based on all of our sources and observations, *Cryptantha m.* var. *cedrosensis* is endemic to its eponym, Cedros Island, Baja California, Mexico.

Finally, a third variety was originally named and described by Johnston in the same publication: *C. maritima* var. *pilosa* Johnston (1922: 445). Johnston characterized this variety as differing from the type in having “... calyx pilis longe patentibus ...” [calyx with long, spreading hairs], designating “*Palmer 551* (UC, type; G, isotype).” Thus, we accept the holotype as the *Palmer 551* collection, collected 1887, (UC78622), but have been unable to locate his designated isotype at GH. This collection was made “on stony ridges at Los Angeles Bay [Bahia de los Angeles], Baja California.” Johnston cites this variety as “frequent in the deserts of southeastern California. From Logan Nevada, where collected by Kennedy, it ranges south to Santa Agueda (*Palmer 2142*) in Baja California [Sur].”

Some subsequent floras and checklists have recognized the varieties of Johnston (e.g., Kearney & Peebles 1960; Wiggins 1980; Rebman *et al.* 2016), whereas others have not (e.g., Kelley & Wilken 1993; Kelley *et al.* 2012). *Cryptantha maritima* var. *maritima* and *C. m.* var. *pilosa* in particular have been considered to form a grade in their diagnostic features (Simpson & Hasenstab 2009).

Morphological Study and Status of the Varieties of *Cryptantha maritima*

We studied 573 herbarium specimens of *Cryptantha maritima* throughout its range. From our observations we conclude that the three varieties cited by Johnston (1925) should be retained, differing in the features Johnston noted in ovule number and calyx vestiture. The three are distinctive, but because there appears to be some intergradation between them in a few specimens, we believe that the varietal rank is appropriate. *Cryptantha maritima* as a species is characterized in having bracts that subtend the cymules and many, but not all, flowers (bracteate flowers being a feature not common in the genus) and in having heteromorphic nutlets with one, larger smooth nutlet (axial in position; see below) and 0–3 smaller minutely tuberculate nutlets (Fig. 1C, E, H). As Johnston (1925: 47) mentioned, in some plants, or in some fruits of a plant, only a single nutlet develops, this being smooth (e.g., Fig. 1H), but this feature is

not diagnostic for a given variety. *Cryptantha m. var. maritima* is distinct in having small corollas and two ovules per ovary (i.e., two ovary lobes), with 1–2 nutlets developing (Fig. 1A–C). *Cryptantha m. var. cedrosensis* is distinct in having four ovules per ovary (thus, four ovary lobes), with 1–4 nutlets developing, each nutlet with a single seed (Fig. 1E). However, we observed that the corolla of *C. maritima* var. *cedrosensis* is most often relatively large (limb 3–5 mm wide; see Fig. 1D), only rarely small (limb ca. 1–2 mm wide). The larger corolla size appears to be a new finding, as Johnston (1925) cited the 1–2 mm dimensions for the entire species and did not mention a corolla size difference in the protologue for *C. m. var. cedrosensis*. This discrepancy may have been because the type specimen examined by Johnston appears to be well into the fruiting stage and shows no apparent evidence of having larger corollas (our personal observation of the online image). *Cryptantha m. var. pilosa*, like *C. m. var. maritima*, has small corollas and two ovules per ovary (thus, having two ovary lobes), with 1–2 nutlets developing. However, *Cryptantha m. var. pilosa* is generally easy to tell at a glance by its dense tufts of whitish, ascending trichomes arising along the sepals (see below for a more detailed description).

A map of the three varieties shows some geographic trends. We confirm that *C. m. var. cedrosensis* is found only on Cedros Island; however, specimens of *C. m. var. maritima* also rarely occur there. In the Baja California peninsular region, *Cryptantha m. var. maritima* occurs primarily on the western side, on the Pacific islands of Guadalupe, San Benitos, and Natividad, and more rarely on the central eastern side and adjacent Gulf islands. It also occurs in southwestern San Diego County and on three of the United States Channel Islands, is common in the Colorado Desert and into the Mohave Desert of southeastern California, and ranges east to Arizona and Sonora, Mexico (Figs. 2A, B). *Cryptantha m. var. pilosa* apparently does not occur on any of the Pacific Islands and is more common in the north-central and eastern (Gulf) side of the Baja California peninsula. It otherwise follows the distribution of *C. m. var. m.*, but is much more widespread in Arizona and southern Sonora, Mexico and is the most easterly variety of the species (Fig. 2A). *Cryptantha m. var. pilosa* is the only member of the genus, as currently defined, that also occurs in South America, with collections in Argentina (GBIF 2020, Zuloaga *et al.* 2008; Fig. 2C), an example of an American amphitropic disjunct (see Williams *et al.* 2017, Simpson *et al.* 2017b).

In our study of this species, we discovered specimens of a plant restricted to the western Vizcaino Desert of Baja California Sur, Mexico that is similar to *Cryptantha maritima* but also quite distinctive from the three described varieties. This form has two ovules per fruit but is unique in having relatively large (limbs 3–5 mm wide) corollas and almost entirely canescent appressed-strigose stems and inflorescence axes, with very few to no spreading, hispid trichomes. We think this plant form should be recognized as a new taxon, described as follows:

Taxonomy

Cryptantha maritima (Greene) Greene var. ***vizcainensis*** Rebman & M.G.Simpson, var. nov. (Figs. 3 & 4)

Type:—MEXICO. Baja California Sur: Picachos de Santa Clara, north slope of SE peak, occasional on north slope, 600 meters elevation, 27°07'N, 113°37'W, 3 February 1973, R. Moran & J.L. Reveal 19707 (holotype SD92511!, isotype US02908745=US2796919!) [Note: georeferenced coordinates that were estimated from label data are indicated with “*”, otherwise verbatim from label data.]

Paratypes (alphabetical by collector and number):—MEXICO. Baja California Sur: Vizcaino peninsula south of Laguna Ojo de Liebre, at the eastern base of the “Sierra de Vizcaino” in a portion of the range known as Sierra Campo Nuevo, at the end of a small track winding 6.1 miles west of the road to Bahia Asuncion, 3.6 miles south of the junction with the road to Bahia Tortugas, rocky upper bajada and steep rocky slopes with low scrub of *Ambrosia chenopodiifolia*, *Pachycormus discolor*, *Stenocereus*, *Pachycereus*, *Errazurizia* and some *Larrea*, common annual, flowers white, 300–500 meters elevation, near 27°21' N, 114°10'W, 30 April 1993, S. Boyd *et al.* 8086 (MEXU666794; RSA576907!); rocky slopes and outwash plain with *Pachycormus*, *Bursera*, *Fouquieria*, *Ambrosia* and *Jatropha*, E base of Sierra de Placeros, 40 km SE of San Jose de Castro, flowers white, 366 meters elevation, 27.44347°N, 114.116654°W, 24 March 1984, D.E. Breedlove 60891 (MEXU484431, RSA497744!); 35 km SE of Bahia Tortugas, pacific slope of Sierra de Placeros, rocky slope with *Bursera*, *Jatropha*, *Pachycormus*, *Ambrosia* and *Simmondsia*, flowers white, 460 meters elevation, 27.60463°N, 114.603°W*, 7 March 1985, D.E. Breedlove 62324 (MEXU484782, RSA497109!); eastern bajada of Sierra Calvario, Systema de Sierra Vizcaino, small perennial bush, desert of dispersed succulent trees and suffrutescent shrubs, 60–243 meters elevation, 27.4125°N, 114.220833°W*, 10–15 March 1947, H.S. Gentry 797 (ARIZ123309!); Picachos de Santa Clara, 350 meters elevation, 27°09'N, 113°40'W, 3 February 1973, R. Moran &

J.L. Reveal 19663 (SD92540!, US02908744=US2796920); 8 road miles northwest of Asunción, fairly common in bed of arroyo, 70 meters elevation, 27°13'N, 114°21'W, 4 February 1973, *R. Moran & J.L. Reveal 19758* (SD92558!, US02908741=US2796922); Arroyo Malarrimo, 11 miles south of the mouth, occasional in arroyo, 75 meters elevation, 27°29'N, 114°29'W, 6 February 1973, *R. Moran & J.L. Reveal 19878* (SD92358!); at pass at head of Arroyo Largo, occasional, 480 meters elevation, 27°36'N, 114°39'W, 8 February 1973, *R. Moran & J.L. Reveal 19949* (SD92556!, US02908742=US2796924); north slope of Cerro Azul, fairly common near base, 400 meters elevation, 27°32'N, 114°32'W, 9 February 1973, *R. Moran & J.L. Reveal 19973* (SD92328!); Arroyo Calvario 6.0 miles north of San Andrés, 130 meters elevation, 27°20'N, 114°26'W, 10 February 1973, *R. Moran & J.L. Reveal 20004* (MEXU220305, SD92509!, US02908748=US2796916).

Description:—**Plants** annual herbs, 12–40 cm tall, canescent. **Stems** stout, woody in texture, 2–5 mm in diameter, not reddish, with an erect primary shoot giving rise to several inclined to ascending or decumbent secondary shoots at base and along primary axis, secondary shoots slightly shorter than or as long as primary, stem vestiture canescent, antrorse-appressed strigose, trichomes numerous, whitish, ca. 1 mm long. **Leaves** spiral, absent at plant base (possibly deciduous) or present, these densely clustered, generally shriveled, cauline leaves larger, becoming reduced toward inflorescence, mostly flat, ca. 10–50 mm × 1–3 mm, sessile, base widely cuneate, margin entire to irregularly dentate, apex acute to rounded, midrib flat to very slightly raised, both surfaces hirsute and epustulate to hispid and basally pustulate, trichomes whitish, horizontal to ascending, wider at base, point of attachment swollen (termed a “pustule”), consisting of 1–3 concentric rows of white to transparent, radially elongate cells, especially prominent in shriveled, basal leaves. **Inflorescence** a series of ascending, racemosely arranged, circinate scorpioid cymules, these clustered in younger plants, elongating at maturity, peduncles ca. 5–20 mm long, commonly with a flower at junction with generating axis, cymules basally bracteate, bracts similar to leaves but reduced in size, ca. 20 flowers per cymule, fruits not touching at maturity, mostly 2–3 mm apart, more so near cymule base, axes canescent antrorse appressed-strigillose, trichomes ≤ ca. 0.5 mm long. **Flowers** typically bracteate near base of cymule, sporadically bracteate distally. **Calyx** ascending to inclined in fruit, lance-ovoid in shape, 1–2 mm long in flower, 2–3 mm in fruit, sepals distinct, erect, narrowly lanceolate, apically acute to rounded, apices slightly recurved, adaxial surface glabrous in lower half, sparsely appressed hirsute in upper, trichomes <0.5 mm, abaxial surface hirsute with often dense, appressed to ascending white trichomes ca. 0.5 mm long along and inside margin, midrib thickened and hispid (mostly on sepals away from cymule axis), trichomes ascending to inclined, stout, basally thickened, white, straight to sometimes curved, ca. 1.5–2 mm long. **Corolla** white, rotate, tube same length as calyx, limb 3–5 (1–1.5) mm in diameter [Note: measured from dried herbarium material of all types], appendages (fornices) present, color unknown. **Gynobase** very narrowly conical, ≥3/4 nutlet length. **Style** ca. 0.3 mm long, tip/stigma extending ca. 0.1 mm beyond large nutlet. **Ovary lobes/ovules** two. **Nutlets** two, erect, brown, symmetric, lance-ovate, adaxially shallowly 2-planed convex, abaxially broadly convex, heteromorphic, larger nutlet smooth, shiny, adjacent to cymule axis (axial), more firmly attached to gynobase, 1.5–1.7 mm × ca. 0.6 mm, ventral groove slightly open, groove sides not raised, minutely bifid at base with no to a very small areole, smaller nutlet, 1.2–1.3 mm × ca. 0.5 mm, minutely tuberculate both surfaces, with ca. 16–18 tubercles across dorsal face at greatest width, tubercles low, brown to light brown, papillae not observed, ventral groove closed, minutely bifid at base, no areole observed.

Diagnosis:—*Cryptantha maritima* var. *vizcainensis* is similar to most individuals of *C. maritima* var. *cedrosensis* in having relatively large (3–5 mm) corollas. It differs in having a canescent stem vestiture with appressed trichomes only, as opposed to a strigose and hirsute vestiture with both appressed and spreading trichomes in the latter, and in having two ovary lobes and ovules per ovary, these typically developing into two nutlets, as opposed to four ovary lobes and ovules and up to four nutlets per fruit in the latter.

Distribution, Habitat, and Endemism:—*Cryptantha maritima* var. *vizcainensis* is endemic to the western Vizcaino Desert region of Baja California Sur (Fig. 2A,B). The habitat of the *Boyd 8086*, *Breedlove 60891 & 62324*, and *Gentry 797* paratype specimens is described from specimen label information as “rocky upper bajada and steep rocky slopes with low scrub,” “rocky slopes and outwash plain,” “rocky slope,” and “bajada,” respectively. Associated plants recorded from these collections were: *Ambrosia*, *Ambrosia chenopodiifolia* (Benth.) W.W.Payne, *Bursera*, *Erazurizia*, *Fouquieria*, *Jatropha*, *Larrea*, *Pachycereus*, *Pachycormus*, *Pachycormus discolor* (Benth.) Coville ex Standl., *Simmondsia*, and *Stenocereus*. The habitat and vegetation were not described in the label information of the vouchers collected by Reid Moran, including the holotype and isotypes. However, based on Moran’s field notes (<http://bajaflores.org/MoranNotesSearch.aspx>) for the period of time of these collections (3–10 February 1973), the following dominant plants are recorded as occurring in the vegetation type where some of his specimens were collected (listed with current taxonomy): *Ambrosia magdalenae* (Brandege) W.W.Payne, *Apiastrum angustifolium* Nutt. in Torr. & A.Gray, *Bahiopsis microphylla* (Vasey & Rose) E.E.Schill. & Panero, *Bebbia juncea* (Benth.) Greene, *Condea emoryi*

(Torr.) Harley & J.F.B.Pastore, *Cylindropuntia cholla* (F.A.C.Weber) F.M.Knuth, *Ebenopsis confinis* (Standl.) Barneby & J.W.Grimes, *Encelia stenophylla* Greene, *Emmenanthe penduliflora* Benth., *Eriogonum fasciculatum* Benth. var. *emphereium* Reveal, *Gambelia juncea* (Benth.) D.A.Sutton, *Jatropha cinerea* (Ortega) Müll.Arg., *Lophocereus schottii* (Engelm.) Britton & Rose, *Prosopis glandulosa* var. *torreyana* (L.D.Benson) M.C.Johnst., *Salvia cedrosensis* Greene, *Stenocereus gummosus* (Engelm.) A.C.Gibson & K.E.Horak, and *Yucca valida* Brandegee.

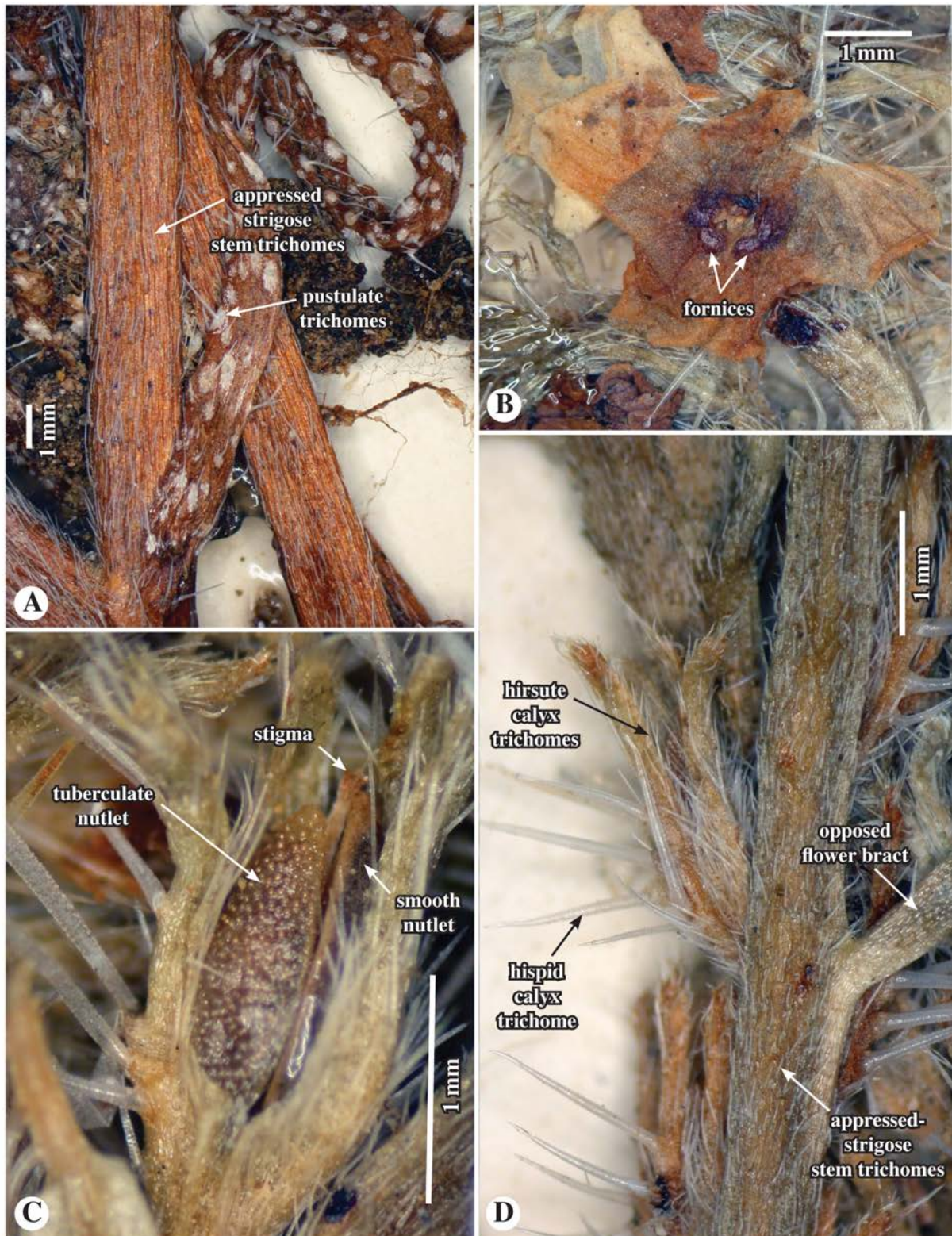


FIGURE 3. *Cryptantha maritima* var. *vizcainensis*. Images from Moran 19878 (SD92358). A. Close-up of base of primary shoot, showing strigose stem vestiture and pustulate trichomes of leaves. B. Corolla face, showing relatively large limb diameter and fornicies. C. Mature fruit, calyx opened, showing two nutlets and style, extending just beyond larger, smooth nutlet. D. Close-up of cymule, showing appressed-strigose stem vestiture, flower bract, calyces with hirsute marginal regions of ascending trichomes, and hispid midribs with stout, inclined or spreading trichomes, the latter more prominent on the side away from the inflorescence axis.

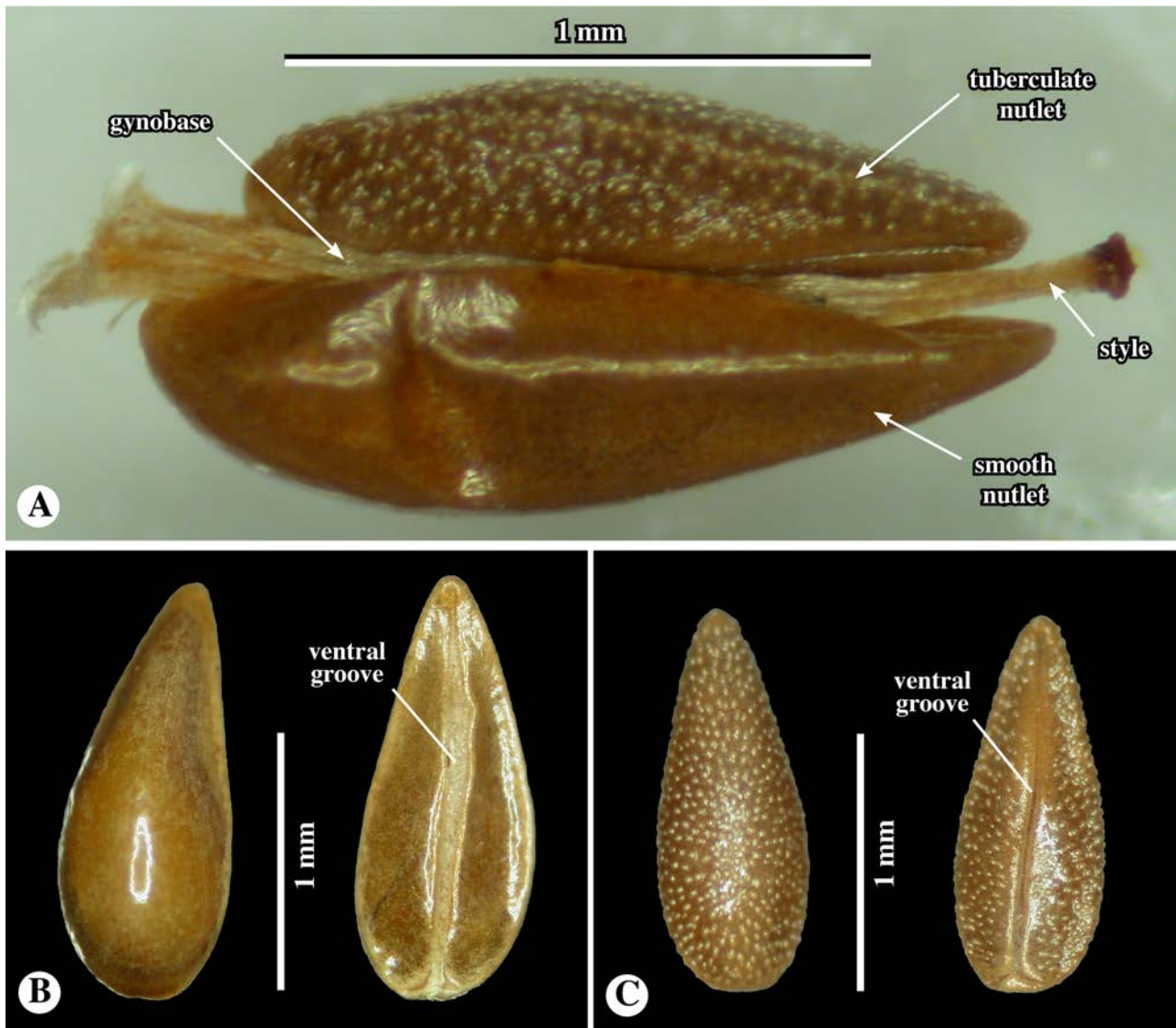


FIGURE 4. *Cryptantha maritima* var. *vizcainensis*. Images from Moran 19878 (SD92358). A. Gynobase, nutlets, and style/stigma detached from a single fruit. B. Larger, smooth nutlet, in dorsal (left) and ventral (right) views. C. Smaller, tuberculate nutlet, in dorsal (left) and ventral (right) views. Note ventral groove, short bifid at base.

Phenology:—Based on data from available specimens, *Cryptantha maritima* var. *vizcainensis* appears to flower from February to April.

Etymology:—The varietal epithet *vizcainensis* means “of the Vizcaíno Desert,” where it is endemic.

Suggested Common Name:—Vizcaíno Desert *Cryptantha*.

Rationale for rank:—This new taxon is unique in its combination of a larger corolla, two ovules and two 1-seeded nutlets per fruit, and canescent-strigose stem vestiture. One collection (Moran 19758, SD92558) was mixed with one individual typical of the new variety and one with small corollas (limb 1–1.5 mm wide), a potential intermediate to *C. maritima* var. *maritima*. Thus, we chose to retain this new taxon as a variety of *Cryptantha maritima*, as it is otherwise quite similar to the other members of that species.

Conservation status:—This new variety occurs in a limited region of the western Vizcaíno Desert of Baja California Sur and is currently known from only 11 collections (see Fig. 2B). This region has been relatively undercollected and is dependent on late monsoonal, hurricane driven, or early winter rains for annuals to grow. It should be noted that this part of the peninsula lies between the normal northern winter and southern summer rainfall regimes; as a result, rains are highly unpredictable, and the region is very dry in most years. Given the sparsity of collections and limited range, we suggest that *Cryptantha maritima* var. *vizcainensis* be listed as rare, equivalent to a CNPS ranking of 1B.1 (CNPS 2021).

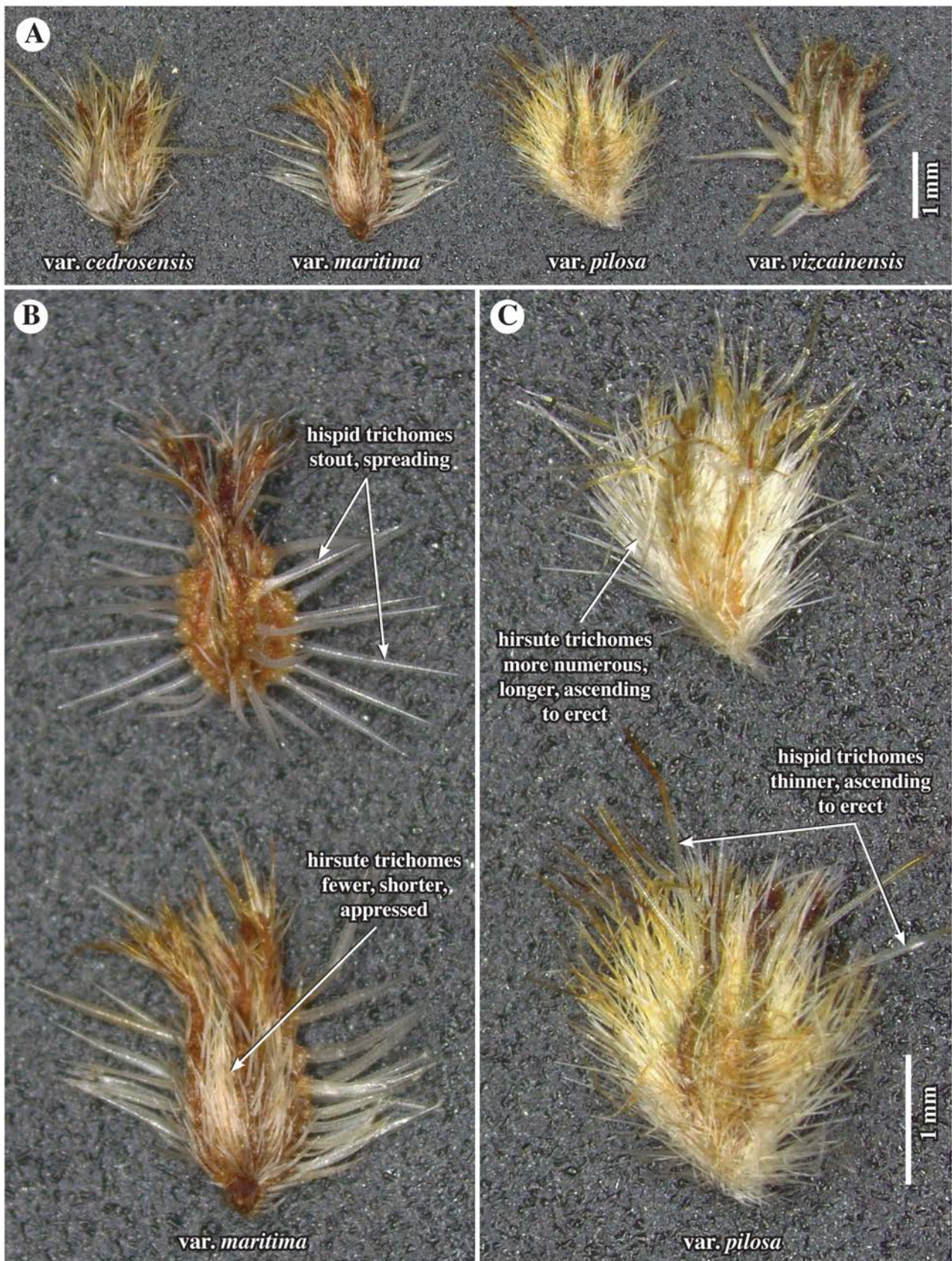


FIGURE 5. Comparisons of fruiting calyces of *Cryptantha maritima* varieties. A. *Cryptantha maritima* varieties, left-to-right: *var. cedrosensis*, *var. maritima*, *var. pilosa*, and *var. vizcainensis*. B. Two samples of *var. maritima*; note hirsute calyx margin region with few to many appressed trichomes and hispid calyx midrib with stout, mostly spreading trichomes. C. Two samples of *var. pilosa*; note densely hirsute calyx margin region with ascending to erect trichomes and hispid midribs with few, relatively thin, erect to ascending trichomes.

Identification of the varieties of *Cryptantha maritima*:—Aside from the features mentioned earlier, we present a comparison of the fruiting calyces of the four varieties of *C. maritima* in Fig. 5A. *Cryptantha maritima* vars. *maritima* and *pilosa* in particular can be difficult to distinguish because they are similar in stem vestiture, corolla size, and nutlet morphology and overlap significantly in their distribution. Note that *C. m.* var. *maritima* can be finely hirsute along and on the surface of the abaxial sepal margins, but the trichomes tend to be fewer, shorter, and appressed; the midribs are hispid with stouter trichomes more or less spreading in orientation (Fig. 5B). In contrast, *C. m.* var. *pilosa* is finely hirsute along and on the surface of the abaxial sepal margins, the trichomes more numerous, longer, and upwardly inclined to erect; the midrib is hispid, but the trichomes are fewer, thinner, and more ascending to erect in orientation (Fig. 5C).

A revised key to the four varieties of *Cryptantha maritima*, including our new taxon, is presented here:

1. Stem trichomes appressed and spreading; ovules 4, nutlets 1–4; endemic to Cedros Island, Baja California *C. maritima* var. *cedrosensis*
- Stem trichomes appressed and spreading or appressed only; ovules 2, nutlets 1–2; islands and mainland of the Baja California peninsula, southwestern United States, and/or Sonora, Mexico 2
2. Corolla limb 3–5 mm wide; stem strigose-canescens, trichomes only or predominantly appressed; endemic to the foothills and mountains of the western Vizcaíno Desert, Baja California Sur *C. maritima* var. *vizcainensis*
- Corolla limb 1–2 mm wide; stems strigose and hispid, trichomes both appressed and spreading; widespread 3
3. Calyx of mature fruits densely white-hirsute on marginal abaxial surface, trichomes inclined to erect, longest generally ≥ 1 mm long; midribs hispid, trichomes thin, ascending to erect *C. maritima* var. *pilosa*
- Calyx of mature fruits sparsely to densely white-hirsute on marginal abaxial surface, trichomes appressed, longest generally < 1 mm long; midribs hispid, trichomes stout, generally horizontal to reclined *C. maritima* var. *maritima*

CRYPTANTHA PONDII

Nomenclatural History

Cryptantha pondii was named by Greene (1889a: 291–292), with the following description: “From a few inches to nearly a foot high, rather slender, sparingly leafy and setulose, the leaves narrowly linear, an inch or two in length: spikes terminal in threes or fours on a short common peduncle, remotely bracteolate, the bracts hardly surpassing the calyces, these crowded, a line long, villous-setose but not at all hispid, persistent and open in fruit: corolla rather large: nutlets 4, smooth and shining, 1/2 line long, ovate-lanceolate, the groove closed, divaricate at the very base. Plant with the habit, aspect and persistent open calyx of the *Pterygium* section, but with the nutlets of *C. leiocarpa*.” In the protologue Greene did not designate a type nor did he cite any specimens.

Johnston (1925: 62), in his treatment of *Cryptantha patula*, treated *C. pondii* as synonymous with *C. patula*, writing: “*Cryptantha Pondii* is clearly a synonym. Although Greene described it as having ‘smooth and shiny’ nutlets and ternate or quadrinate spikes, the isotype sent Gray has granulate and tuberculate nutlets and solitary spikes as described above [for *C. patula*].”

However, Johnston (1928: 74–75) clarified the taxonomy of *Cryptantha pondii*, treating it as distinct from *C. patula*. He provided a detailed description of *C. pondii*, largely agreeing with the protologue of Greene (1889a) by characterizing the fruits as “... nutlets 4 or not infrequently fewer, subhomomorphous, with the axial (?) one obscurely surpassing the others, smooth or very obscurely and minutely tuberculate above the middle” In reviewing *C. pondii*, Johnston (1928: 75) cited “Lower California: Bay of Bartolomé, 1889, *Lieut. Pond 22*, (Greene Herb., type of *C. Pondii*; US, isotype).” We have been unable to locate specimens of this collection at NDG (B. Hellenthal, pers. comm.), to which most of Greene’s specimens were transferred, but did locate *C. F. Pond 22*, March 1889, (US41006, barcode US01050283), which we accept as the isoelectotype designated by Johnston. Johnston further listed *Cryptantha bartolomaei* Greene (1892: 232) as a synonym of *C. pondii*, citing the type of the former as: “Bay of San Bartolomé, 1889, *Lieut. Pond* (Greene Herb., type of *C. Bartolomaei*.)” Johnston (1928) believed that *C. pondii* and *C. bartolomaei* “are obviously the same species. They were collected at the same locality, on the same date and by the same collector and probably represent different portions of one collection.” Johnston further clarified his own confusion of his 1925 treatment, pointing out that the material he had examined that was received by the Gray Herbarium from Greene had been mislabeled as *C. pondii* and was actually *C. patula*, accounting for his earlier view that they were synonyms.

Johnston’s 1925 treatment of *Cryptantha* was a seminal publication for the genus and was widely accepted and referenced. Thus, this concept of *C. pondii* as a synonym of *C. patula* persisted for decades, despite his clarification in 1928. For example, in his *Flora of Baja California*, Wiggins (1980: 219–224) listed *Cryptantha pondii* in his key as a species with “nutlets, or some of them, tuberculate, papillate, rugulose, or verrucose”, not the smooth and shining nutlets described by Greene (1889a).

Resurrection of *Cryptantha pondii*

In our survey of *Cryptantha maritima*, we discovered two specimens that had been identified as that species but which had four, smooth nutlets, these slightly heteromorphic (Fig. 6). In discovering the publication of Johnston (1928), we realized that this was the true *C. pondii*. To date, we are aware of only three collections of *C. pondii*, including that of the type, all from Baja California Sur, Mexico. One collection has duplicates for a total of five herbarium specimens, but two collections consist of single known herbarium specimens (see below; recall that we were unable to locate the presumed “type” cited by Johnston, but did locate his cited “isotype,” treated here as a designated isolectotype). Two of the collections are from the extreme western portion of the Vizcaíno peninsula and one is from Natividad Island, just off the coast from that area (Fig. 7A,B). The three collections are listed here (georeferenced coordinates and elevations indicated with “*”, estimated from label data):

MEXICO. Baja California Sur: Bay of San Bartolomé [Note: Bay of San Bartolomé is now called Bahía Tortuga], ca. 5 meters elevation, 27.6907°N, 114.8935°W*, March 1889, *C. F. Pond 22*, Isolectotype: US41006=US01050283; 2–3 mile E of Punta Eugenia, Vizcaíno Desert, habitat: Maritime Desert, abundant, 100–300 feet [ca. 30–90 meters] elevation, 27.82025°N 115.0502°W* (these coordinates are the centroid of three slightly varying estimates from different herbaria records), 13 March 1949, *H.S. Gentry 8684*, ASU0014603!, DES00009392, HCIB21969!, SD86419!, UCR-80508!; Mulegé, Isla Natividad, upper south-facing talus slope of major canyon, seventh canyon northwest of lighthouse and draining from off-shore ridge to on-shore coast, associated species: *Mentzelia* and *Phacelia*, ca. 77 meters elevation*, 27.881926°N, 115.194287°W*, 25 March 1974, *R.N. Philbrick & M.R. Benedict B74-84*, SBBG49613!

We find *Cryptantha pondii* to be quite distinctive from other taxa in several features. It has linear bracts sporadically subtending peduncle bases of the cymules as well as flowers (Fig. 6A, C, F). The calyces are somewhat finely hirsute with ascending trichomes, described as “silky-hirsute” by Johnston (1928: 74) in addition to hispid along the midrib (Fig. 6D, F). And, we confirm the observations of Johnston (1928: 74) that the corollas are relatively large (Fig. 6C, F; described as 2–3 mm broad by him, which we confirm here) and that there are four nutlets per fruit, these smooth and shiny and heteromorphic by size, with the odd nutlet axial (closest to the inflorescence axis) slightly larger than the other three consimilar nutlets (Fig. 6B, D, E).

We note that although Johnston (1928) described the nutlets of *C. pondii* as “smooth or very obscurely and minutely tuberculate above the middle”, we did not observe the latter sculpturing; all nutlets we observed were smooth and shiny. In addition, we were unable to observe specimens of *C. bartolomaei*, which Johnston believed to be synonymous with *C. pondii*. In fact, the type of *C. bartolomaei* he believed was derived from the very same collection as that of *C. pondii*. Online images of *C. bartolomaei* (holotype: NDG40169; isotypes: GH00096299 and GH00096293, the last apparently a fragment from the holotype) do fit our concept of *C. pondii*. However, the type specimens of *C. bartolomaei* need to be examined and verified as equivalent to *C. pondii*, something we plan to do in the future. Note that *C. pondii* has priority of publication over *C. bartolomaei*.

Affinities of *Cryptantha pondii*

The relationships of *Cryptantha pondii* within the genus are not clear, especially because the species was not correctly recognized by most botanists. Johnston (1928: 75) stated that “The species is a very distinct one of uncertain affinities. It is probably best placed in a special Series between *Graciles* and *Ramulossimae*.” Series *Graciles* of Johnston (1925) solely included the species *Cryptantha gracilis* Osterhout (1903: 236). However, this species differs from *C. pondii* in lacking bracts, having a distinctive calyx with a conical base and numerous, fine, whitish hirsute trichomes, and in having one nutlet per fruit, the nutlet smooth but characteristically trigonous in cross-section. *Cryptantha gracilis* is centered in the Great Basin region of the United States and east into the Rocky Mountains (Kartesz 2015). Johnston’s series *Ramulossimae* solely included the species *Cryptantha fendleri* (A.Gray 1885: 268) Greene (1887: 120), distinctive in having virgate lateral branches and a fruit with four smooth nutlets, thus more like *C. pondii*. However, the calyces of *C. fendleri* are more like a typical *Cryptantha*, hispid along the midrib and appressed hirsute along the margin. Also, *C. fendleri* either lacks bracts or they are sparse on the plant, unlike *C. pondii*. *Cryptantha fendleri*, like *C. gracilis*, occurs mainly in the Great Basin and east into the Rocky Mountains of the United States. Neither *C. gracilis* nor *C. fendleri* occur in Mexico (Rebman *et al.* 2016, Villaseñor 2016).

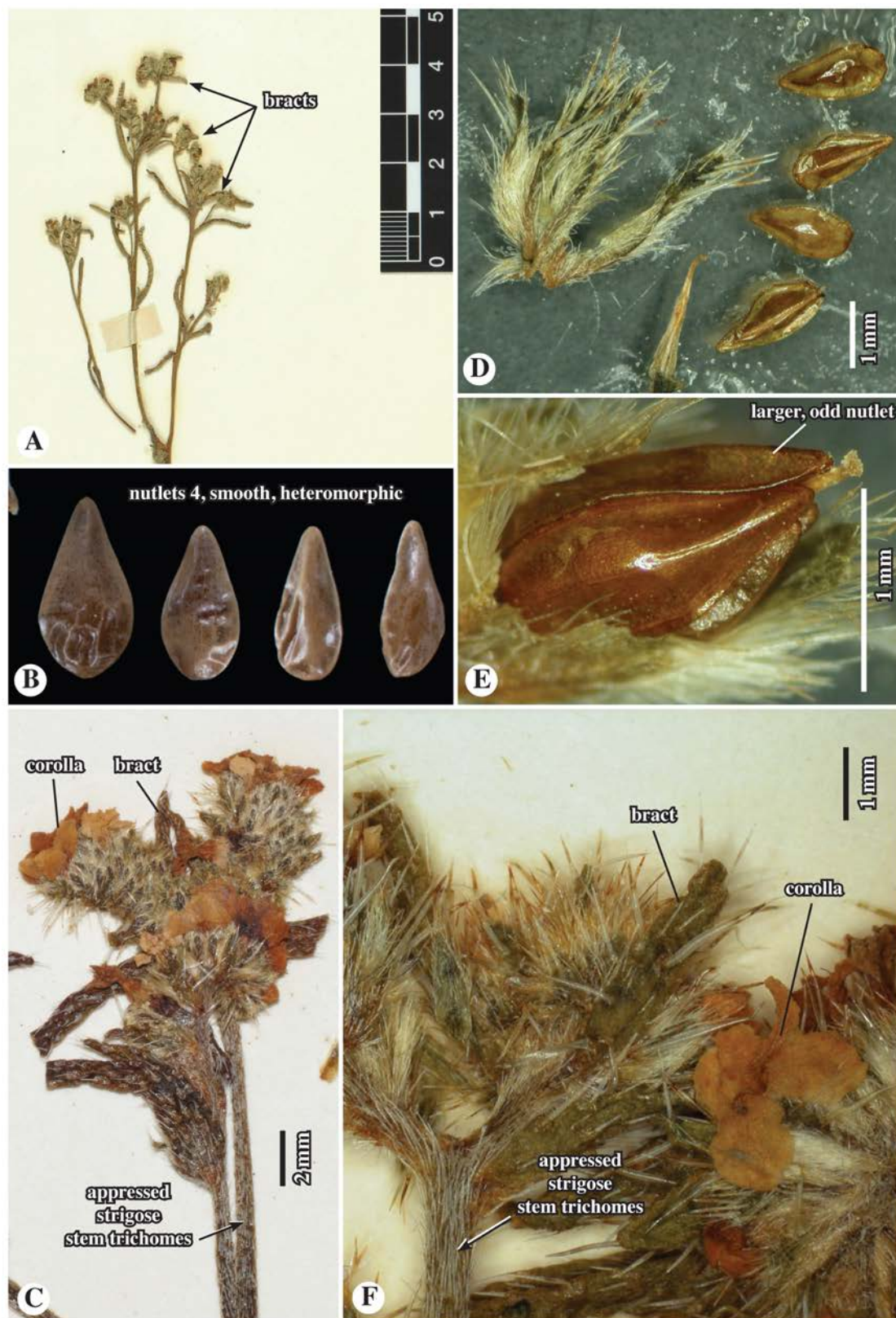


FIGURE 6. *Cryptantha pondii*. A. Close-up of single plant of presumed lectotype specimen (US41006), confirmed by Johnston (1928) as being correctly identified. Note linear, pustulate leaves and bracts at base of cymules. B, C. Images from *Gentry 8684*, 13 March 1949 (HCIB21969). B. Four nutlets removed from fruit, showing smooth surface and slight size heteromorphism. C. Close-up of cymules, showing linear bracts and relatively large corollas. D–F. Images from *Philbrick B74-84*, 25 March 1974 (SBBG49613). D. Fruit with four, smooth nutlets removed. Note finely hirsute calyx marginal region with ascending trichomes, as well as hispid calyx midrib of stouter trichomes. E. Close-up of four nutlets attached to gynobase. Note slight heteromorphism in size and slight extension of style tip/stigma from nutlet apices. F. Cymules, showing appressed-strigose vestiture of axes, scattered linear flower bracts, and relatively large corolla.

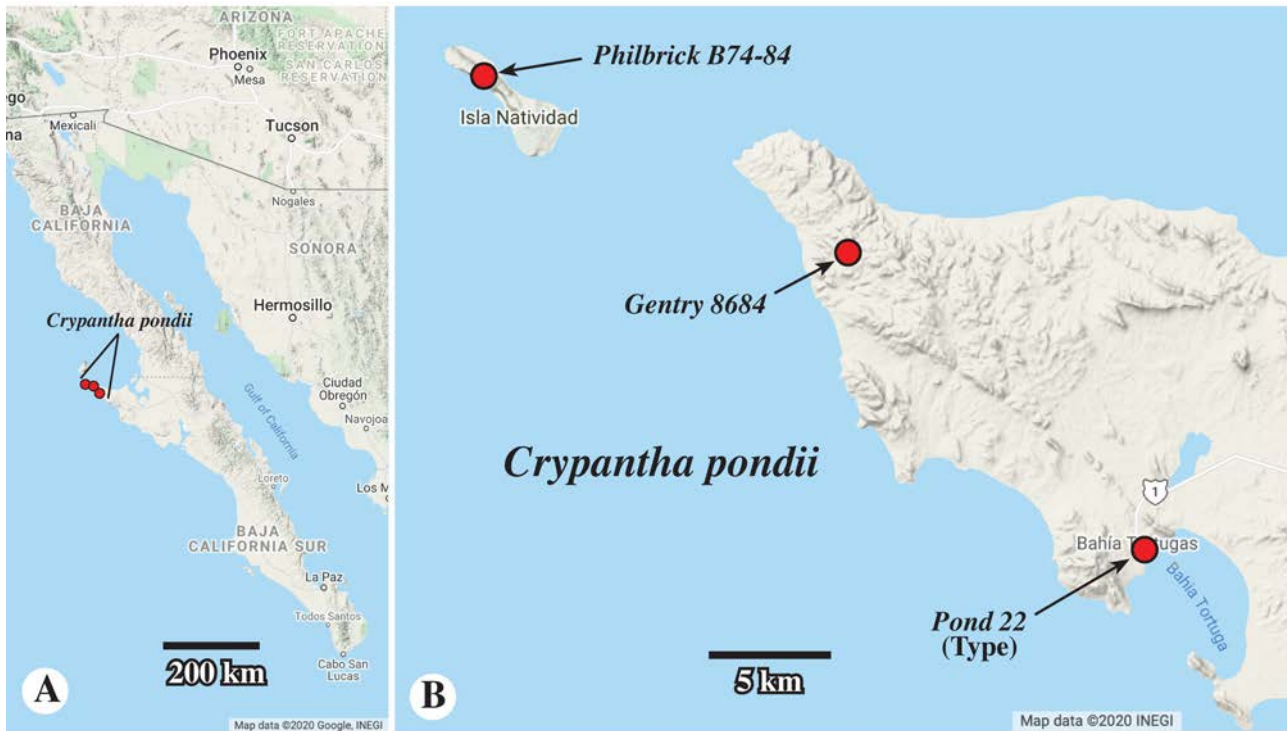


FIGURE 7. A,B. *Crypantha pondii*, distribution map of three known collections. Georeference point for the type, *Pond 22*, approximate; that of *Gentry 8684* placed as a centroid of three different georeferenced estimates. Maps from ©Google 2020, INEGI Data.

We think that *Crypantha pondii* is likely a close relative of *C. maritima*. In general habit, the two species are quite similar. Aside from the type, all vouchers (if determined beyond genus) were originally identified as either *Crypantha maritima* or as *C. maritima* var. *cedrosensis*. *Crypantha pondii* resembles *C. maritima* in having linear, pustulate bracts at the base of the cymules and scattered among the flowers. It is especially similar to *C. m.* var. *vizcainensis* in having a solely strigose stem vestiture, is similar to *C. m.* var. *cedrosensis* in having four ovules and four nutlets that are heteromorphic (by size alone in *C. pondii*) with the odd nutlet axial (nearest the inflorescence axis, as opposed to away from it), and is similar to both varieties in having relatively large corollas. It differs from all *C. maritima* varieties in lacking “rough” (minutely tuberculate) nutlets, but we note that *C. maritima* specimens will sometimes have a single nutlet; when so, it is smooth. In addition, the similar geographic range of *Crypantha pondii* (Fig. 7) and *C. maritima* var. *vizcainensis* (Fig. 2) may be indicative of a common evolutionary origin. We considered, but rejected, the taxonomic treatment of *C. pondii* as a variety of *C. maritima* because we have no clear evidence of relationships between the two species. Future molecular phylogenetic studies should clarify the interrelationships among these taxa.

Conservation status of *Crypantha pondii*

Given the fact that there are only three known collections of *Crypantha pondii*, including the type specimen, this species appears to be extremely restricted in range. As pointed out earlier, this region of the Vizcaino Desert in Baja California Sur has not been visited frequently by botanists and is dependent on largely unpredictable precipitation for growth of annuals. We will continue to look for specimens of this species and hope to visit the region ourselves in the future. However, given the extreme paucity of collections and limited range, we suggest that *Crypantha pondii* be listed as rare, equivalent to a CNPS ranking of 1B.1 (CNPS 2021).

CRYPTANTHA ECHINOSEPALA

Nomenclatural History

Crypantha echinosepala Macbride (1918: 57) was described from the type specimen *C.R. Orcutt 15*, holotype: GH00096294, isotypes MO826399, NY00335198, and US842661, collected March 1917 on Magdalena Island, Baja

California Sur, Mexico (Fig. 10). Johnston (1925: 45) described the species as having “nutlets heteromorphous, usually 4, pallid, groove narrow and scarcely dilated below; odd nutlet minutely muriculate-tuberculate, ovate, acute, 1.2–1.5 mm. long, subpersistent, next the axial calyx-lobe, margin angulate; consimilar nutlets ca. 1 mm. long, minutely tuberculate, lance-ovate” (Figs. 8, 9). Although perhaps only a difference in terminology, we would describe the odd nutlet as tuberculate-spinulose, having tubercles that end in a short, sharp point (Fig. 9B), a feature distinctive for this species.

Johnston (1925: 44) placed *Cryptantha echinosepala* in his series *Maritimae*, along with *C. dumetorum* (Gray 1885: 272) Greene (1887: 112), *C. recurvata* Coville (1895: 165), *C. micromeres* (Gray 1883: 90) Greene (1887: 113), and *C. maritima* itself. He characterized the series as [italics ours for emphasis] “Nutlets 1–4, tuberculate or muricate, usually dark with pale roughenings, lanceolate to triangular-ovate, with rounded or obtuse sides, decidedly *heteromorphous* with *odd nutlet* (sometimes alone developing) *axial and larger* as well as *occasionally less roughened* than others; style surpassed by the nutlets or reaching their tips or rarely surpassing them.” We point out the similarity of *C. echinosepala* to *C. maritima* of series *Maritimae*. Both have heteromorphic nutlets, the odd nutlet larger and axial. The odd nutlet of *C. maritima* is smooth. That of *C. echinosepala* certainly cannot be described as “less roughened,” but it is very different in sculpturing than the consimilar nutlets, the latter quite similar in the two species. Both species also have bracts at the bases of the cymules and intermittent flower bracts (Fig. 8A), although those of *C. echinosepala* are much sparser.

Transfer of *Johnstonella echinosepala* back to *Cryptantha*

The genus *Johnstonella* was resurrected by Hasenstab-Lehman & Simpson (2012), who added to the two originally described species of the genus—*J. inaequata* Brand (1925: 249) and *J. racemosa* Brand (1925: 249)—by making 11 new combinations, one of these *Johnstonella echinosepala*. However, of these 13 species in the genus, only eight had been sequenced and verified from molecular phylogenetic evidence to be part of the same clade, *Johnstonella echinosepala* not among these. The basis for transferring this species to *Johnstonella* was morphology of the nutlets, those of *J. echinosepala* being heteromorphic with whitish tubercles (in the consimilar nutlets), similar to many other members of *Johnstonella*.

The subsequent molecular phylogenetic study of Simpson *et al.* (2017a) expanded the study of *Johnstonella* by sequencing 11 of the 13 species, verifying that *Johnstonella* constitutes a well-supported clade separate from the genus *Cryptantha*. These authors also noted additional species of *Cryptantha* grouping with *Johnstonella*, four of these later transferred to the latter genus (Simpson *et al.* 2019). However, two species that had been placed in *Johnstonella* originally by Hasenstab-Lehman & Simpson (2012) based on morphology, but not sequenced by them, did not fall into the *Johnstonella* clade in the later study, these being *J. echinosepala*, which grouped with *Cryptantha maritima* of their *Maritimae* clade (see below) and *J. micromeres* (Gray 1883: 90) Hasenstab & Simpson (2012: 754), which grouped within *Cryptantha* s.s.

Morphologically, *Johnstonella echinosepala* does resemble other members of that genus in having nutlets that are heteromorphic (a condition found in a total of eight species of the genus, including *J. echinosepala*) and in having a white-minutely tuberculate nutlet sculpturing, although the latter feature is restricted to the three smaller, consimilar nutlets. However, we point out that the consimilar nutlets of *J. echinosepala* are also rather similar in shape and sculpturing to the “rough” nutlets (when present) of *Cryptantha maritima*; e.g., compare Fig. 1C or 4C with Fig. 9C. Additionally, *J. echinosepala* and all varieties of *C. maritima*, including our newly named *C. m.* var. *vizcainensis*, as well as *C. pondii* have the odd nutlet in the “axial” position, i.e., closest to the inflorescence axis (Johnston 1925, 1928, current study). In contrast, all of the other heteromorphic species of *Johnstonella*—*J. angelica* (Johnston 1924: 1143) Hasenstab & Simpson (2012: 754), *J. angustifolia* (Torrey 1857: 363) Hasenstab & M.G.Simpson (2012: 754), *J. diplotricha* (Philippi 1891: 57) Hasenstab & Simpson (2012: 754), *J. fastigiata* (Johnston 1939: 388) Hasenstab & Simpson (2012: 754), *J. inaequata*, *J. parviflora* (Philippi 1860: 39) Hasenstab & Simpson (2012: 754), and *J. racemosa*—have the odd nutlet positioned in the abaxial position, i.e. away from the inflorescence axis (Johnston 1925, 1927, 1939).

The most recent molecular phylogenetic analysis, along with our observations based on morphology (including nutlet position), argue that *Johnstonella echinosepala* should be transferred back to the genus *Cryptantha*. Thus, we accept *Cryptantha echinosepala* as the correct name for this species.

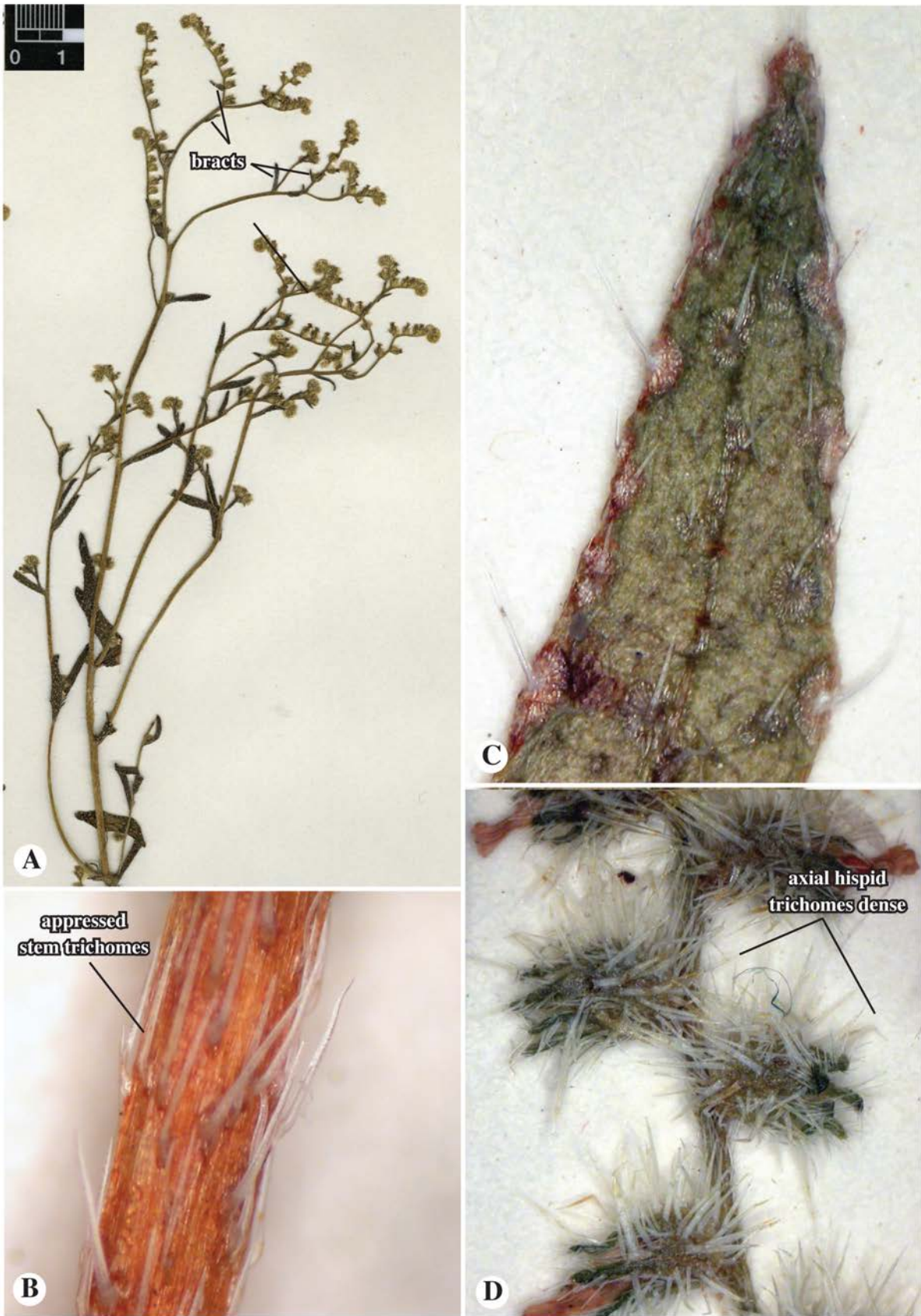


FIGURE 8. *Cryptantha echinosepala* [Johnstonella e.] A. Holotype (*Orcutt 15*, March 1917, GH00096294), close-up of one plant. Note occasional bracts at base of inflorescence cymules and scattered flower bracts. B-D. Exemplar specimen, *Carter 3894*, 20 March 1960 (SD106211). B. Stem close-up, showing in this specimen appressed-strigose trichomes. C. Basal leaf close-up, showing marginal pustulate, hispid trichomes. D. Fruit close-ups, showing characteristic hispid trichomes of calyx concentrated on the axial (upper/toward inflorescence axis) side.

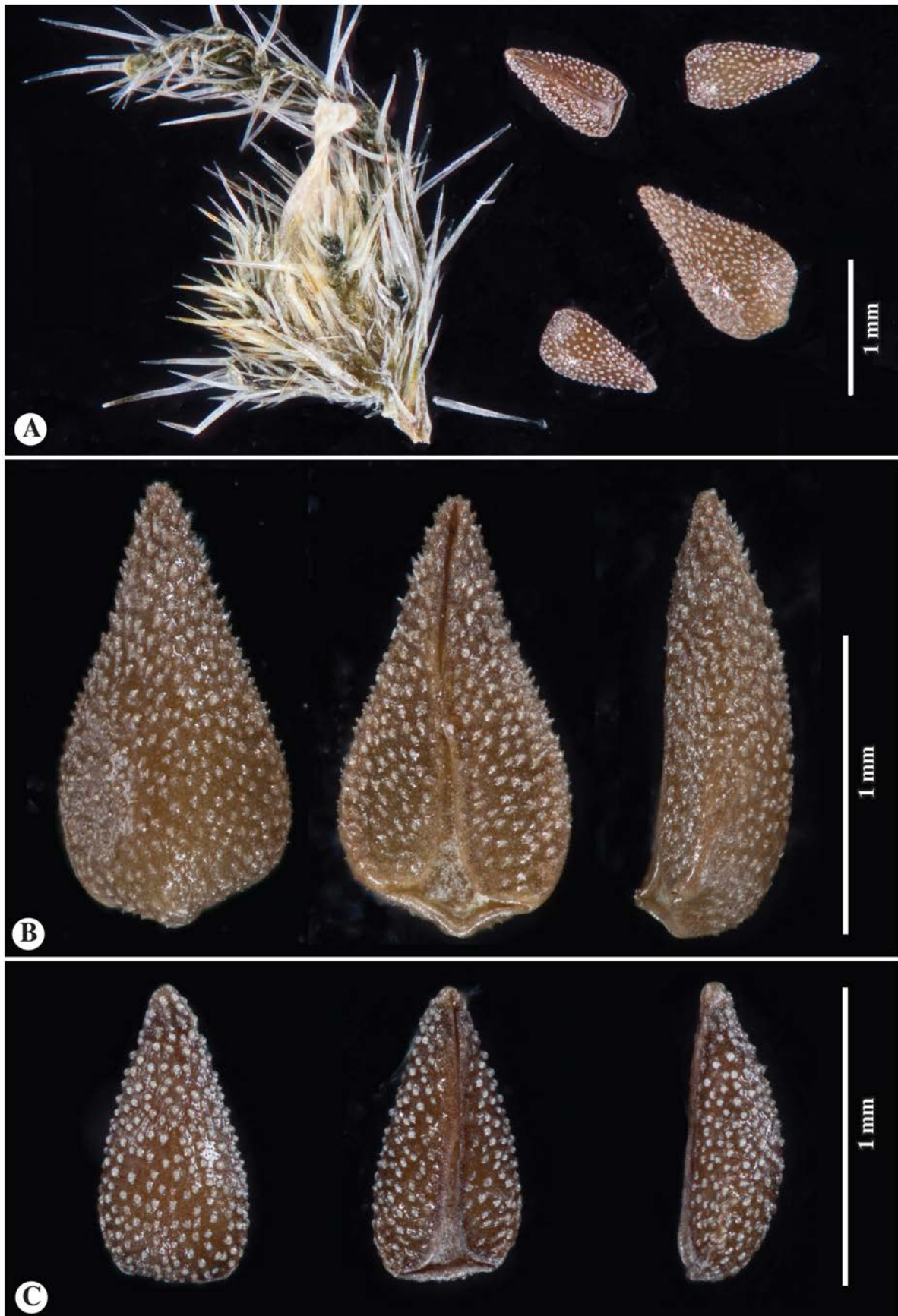


FIGURE 9. *Cryptantha echinosepala* [*Johnstonella e.*] fruit of exemplar, León 3465, 15 March 2003 (SD153719). A. Fruit with four heteromorphic nutlets removed. Note relatively small, persistent corolla. B. Close-up of large “odd” nutlet, in dorsal (left), ventral (middle), and side (right) views. Note tuberculate-spinulose sculpturing. C. Close-up of one of the small “consimilar” nutlets, in dorsal (left), ventral (middle), and side (right) views. Note tuberculate sculpturing, lacking spinules.

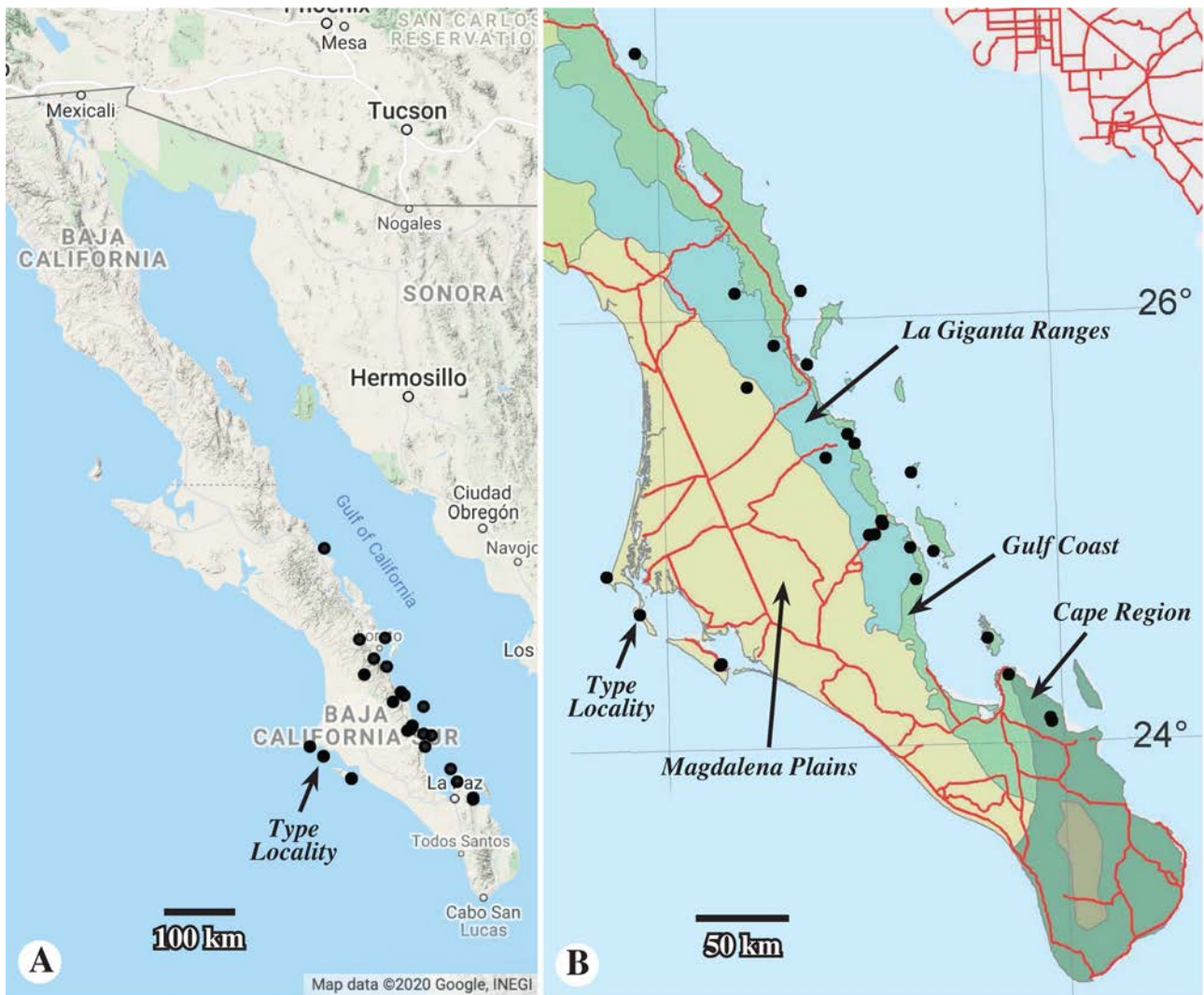


FIGURE 10. *Cryptantha echinosepala* [*Johnstonella e.*] distribution maps, coordinates from Baja Flora (2021). A. Topography map. Map from ©Google 2020, INEGI Data. B. Map from Baja Flora (2021) showing vegetation zones (after Rebman *et al.* 2016) where the species occurs.

Variation in *Cryptantha echinosepala*

In our study of *Cryptantha echinosepala*, we noted two disjunct regions of distribution, one in the islands adjacent to Magdalena Bay on the Pacific Ocean side of the Baja California peninsula, and one in the Sierra de La Giganta, Gulf of California coastal regions, and northeastern Cape region of the peninsula (Fig. 10). These two regions are separated by the extensive Magdalena Plains (Fig. 10B). A comparison of specimens from these two regions revealed some morphological differences. Plants from Magdalena Island, the type locality of *C. echinosepala*, tend to have cauline leaves lacking strong bristle-like trichomes on the margins, shorter inflorescences with the flowers more clustered, and possibly smaller calyces. Plants from the Sierra de La Giganta near the Gulf side tend to have cauline leaves with prominent marginal setose trichomes, longer inflorescence cymules with the flowers more separated, and larger calyces. We do not think that these differences are sufficient enough to give different names to the populations of these two centers of distribution at present, pending more detailed studies. If future morphometric and/or molecular analyses show strong differences between populations of these two regions, there may be justification for separating them taxonomically.

THE *MARITIMAE* CLADE

The *Maritimae* clade (after Johnston's (1925: 44) series *Maritimae*) refers to a monophyletic group named in Simpson *et al.* (2017a) and Mabry & Simpson (2018). This clade was well-supported from molecular data and separate from the

genus *Cryptantha*, although its placement within the subtribe Amsinckiinae varied depending on the type of sequence data analyzed. Hasenstab-Lehman & Simpson 2012 first discovered that the genus *Cryptantha* s.l. was polyphyletic and best separated into six groups: the genera *Eremocarya*, *Greeneocharis*, *Johnstonella*, and *Oreocarya*, plus two other clades: a large one (termed *Cryptantha* s.s.1) containing the bulk of *Cryptantha* species and a smaller one (termed *Cryptantha* s.s.2), containing the North and South American *Cryptantha maritima* (both *C. maritima* var. *m.* of North America and a South American specimen of *C. maritima* var. *pilosa* sampled) plus two South American species: *C. granulosa* (Ruiz & Pavon 1799: 5) Johnston (1923: 54) and *C. chaetocalyx* (Philippi 1860: 39) Johnston (1927: 43). Simpson *et al.* 2017a sampled considerably more taxa in the subtribe and obtained very similar results. This later study also retrieved the same four segregate genera and a diphyletic *Cryptantha* s.s. The bulk of the species occurred in a “core” *Cryptantha* s.s. clade, this largely equivalent to *Cryptantha* s.s.1 and containing the type of the genus, *C. glomerata* Lehmann ex Don (1837: 373). A few *Cryptantha* species, however, occurred in a smaller clade, termed the *Maritimae* clade as mentioned earlier, containing taxa similar to *Cryptantha* s.s.2. The *Maritimae* clade of Simpson *et al.* (2017a) consisted of the North American *Cryptantha clokeyi* Johnston (1939: 387), *C. martirensis* M.G.Simpson & Rebman (2013: 35), and *C. muricata* (Hooker & Arnott 1840: 369) Nelson & Macbride (1916: 42) var. *muricata*, plus a sister subclade of *Cryptantha* [*Johnstonella*] *echinosepala*, *C. maritima* var. *m.*, and the South American *C. subamplexicaulis* (Philippi 1860: 39) Reiche (1907: 826). (*Cryptantha granulosa* and *C. chaetocalyx* were not sequenced in that study.) The *Maritimae* clade was well supported, but its relationship to other clades and genera of the subtribe was equivocal.

Of the five species placed by Johnston (1925: 44) in his series *Maritimae*, only two—*Cryptantha echinosepala* and *C. maritima*—occurred in the *Maritimae* clade of Simpson *et al.* (2017a). The other three species—*Cryptantha dumetorum*, *C. micromeres*, and *C. recurvata*—all group firmly within *Cryptantha* s.s. in their analyses. The similarities of *Cryptantha pondii* to *C. maritima* lead us to surmise that the former might also be best placed with the other taxa of the *Maritimae* clade, including *C. echinosepala*. Future sequencing of *C. pondii* will be needed to confirm this, although it may be difficult to obtain DNA material given its extreme rarity. However, we reiterate that this *Maritimae* clade forms a well-supported monophyletic group in the three molecular phylogenetic studies cited, a group separate from the genus *Cryptantha* s.s. The members of that clade may, in fact, best be placed in a new genus in the future, one separate from *Cryptantha*.

Conclusions

This study illustrates the great importance of accessing and studying herbarium specimens in scientific discoveries (see Bowdler 2010). From our study of herbarium specimens, originally identified as *Cryptantha maritima*, we not only annotated these to the correct variety of that species, but also discovered a variety new to science, resurrected a “lost” species, and evaluated the morphology and changed the classification of a third species. Online images are valuable as well and have been used in the recognition of new taxa (e.g., see Jiménez-Mejías, *et al.* 2017), but in our study physical dissection of tiny plant parts (e.g., trichomes and nutlets) was essential. Studies of herbarium specimens using a microscope may seem a bit of a lost art in our age of molecular biology. However, it remains an essential tool of taxonomic work, in establishing the “correct” names of specimens used in molecular phylogenetic studies. We hope that teachers will devote some time in their courses to training students in honing their “observational acuity” of plant morphology (Tomlinson 1964). Plus, we hope that the younger generation of scientists will embrace this technique as an important tool in better understanding the biodiversity of the botanical world.

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APPENDIX 1: Specimens used for distribution mapping of taxa (listed alphanumerically by collector and collection number, then herbarium accession number in parentheses; !=voucher verified by the authors).

Cryptantha echinosepala:—Carter 3894 (SD106211!); Davidson 2010 (SD90881!); Dominguez Cadena 2357 (SD259444!); Dominguez Cadena 2731 (SD261163!); Dominguez Cadena 2768 (SD153716!); Dominguez Cadena 2813 (SD153717!); Dominguez Cadena 3257 (SD222412!); Dominguez Cadena 3257 (SD222412!); Dominguez León 1863 (SD140707!); Dominguez León 1906 (SD265337!); Dominguez León 3009 (SD161959!); Dominguez León 3087 (SD153721!); Dominguez León 3409 (SD153720!); Dominguez León 3465 (SD153719!); Dominguez León 3561 (SD153718!); Dominguez León 3867 (SD190348!); Dominguez León 958 (SD161958!); Moran 18888 (SD106208!); Moran 18955 (SD106209!); Moran 3668 (SD50168!); Moran 8951.5 (SD66177!); Moran 9112.5 (SD84024!); Moran 9267 (SD84022!); Rebman 25402 (SD228804!); Rebman 29900 (SD257542!); Rebman 4775a (SD142253!); Rebman 9691 (SD153978!); Rebman 9811 (SD153977!).

Cryptantha maritima var. *cedrosensis*:—Anthony 289 (POM11642!=RSA0023562); Davidson 5500 (RSA369176!, SD107391!); Haines s.n., 4 Mar 1939 (ARIZ102660!); Moran 20342 (SD86923!); Moran 29043 (SD105632!); Oberbauer 112 (SD127739!); Philbrick 184 (SD172002!); Philbrick B73-184a (SD172002!); Rebman 2446 (ASU202716!, MEXU697141); Thorne 58562 (MEXU431027, RSA338883!, UCR43552!); Thorne 63976 (SD268577!); Vanderplank 5590 (SD251374!).

Cryptantha maritima var. *maritima*:—André 22256 (ARIZ418472!); André 23847 (SD260025!); André 24831 (SD260026!); Angel 122 (SD167737!); Angel 325 (SD194946!); Annable 256 (ARIZ263682!); Baker 13985 (ASU261158!); Baker 17086 (ASU280288!); Baker 19399 (ASU0306753!); Baker 19465 (ASU0307010!); Ballou 116 (POM97473!); Barckley 33 (SD205612!); Barth 172 (SD169359!); Barth 239 (SD169358!); Barth 284 (SD169357!); Barth 378 (SD169360!); Barth 912 (BSCA2251!); Barth 1068 (SD226393!); Barth 1124 (SD226392!); Barth 1158 (SD226394!); Barth 1190 (BSCA3281!, SD226388!); Barth 1211 (SD226385!); Barth 1274 (SD226387!); Barth 1421 (SD226389!); Barth 1467 (SD226390!); Beauchamp 1620 (SD83528!); Bezy s.n., 9 Apr 1966 (ARIZ201013!); Bigelow 357 (BSCA2253!, SD221036!); Blakley 5186 (SD85023!); Booth A-27 (ARIZ184453!); Boyd 1245 (ARIZ284150!); Boyd 1278 (UCR52478!); Boyd 3290 (UCR60852!); Boyd 3296 (RSA500932!); Boyd 3425 (RSA571364!); Boyd 5311 (RSA571580!, MEXU871516); Boyd 7815 (SD136883!); Boyd BC-123 (UCR22398!); Breedlove 60820 (RSA492326!); Breedlove 60869 (RSA497795!); Breedlove 62214 (RSA497771!); Breedlove 62298 (RSA497407!, MEXU484755); Breisch 334 (SD201470!); Burgess 4743 (ARIZ208739!); Burgess 5627 (ARIZ223259!); Burgess 6280 (ARIZ235951!, MEXU323259); Butterwick 6220 (ARIZ228458!); Cain 1581 (SD216556!); Carlquist 449 (RSA117530!); Casillas 308 (SD267038!); Charlton 1364 (UCR182275!); Chesnut s.n., 17 Apr 1982 (SDSU18137!); Chiang 1279 (MEXU547064, RSA648097!); Chisaki 1051 (MEXU99064, SD51706!); Christie 126 (SD140879!); Christy 1050a (ARIZ348209!); Clemons 427 (SD115554!); Clemons 440 (SD115567!); Clemons 1929 (SD122428!); Darrow 3767 (ARIZ73035!); Davidson 5449 (SD107359!); Dice 176 (BSCA156!); Dominguez León 2392 (ARIZ360614!); Dominguez León 2399 (ARIZ358123!); Dominguez León 4434 (SD261164!); Dunkle 7403 (SD107311!); Epling s.n., 5 Feb 1935 (RSA611385!); Felger 6871 (ARIZ200646!); Felger 12193 (ARIZ200644!); Felger 12394 (ARIZ217944!); Felger 12482 (ARIZ201004!); Felger 14041 (ARIZ200486!); Felger 14154 (ARIZ201005!); Felger 14225 (ARIZ200999!); Felger 17006 (ARIZ200641!); Felger 17042 (ARIZ200649!); Felger 17159 (ARIZ201008!); Felger 17173 (ARIZ201011!); Felger 17366 (ASU274438!); Felger 17419 (ARIZ201009!); Felger 17574 (ASU246650!); Felger 18932 (ARIZ188762!); Felger 20697 (ARIZ189126!); Felger 14085-B (ARIZ200998!); Felger 14108-A (ASU262532!); Felger 75-14 (ARIZ276360!); Felger 87-260 (ARIZ283534!); Felger 88-269 (ARIZ286727!); Garebotti s.n., 2 Apr 1966 (ARIZ201012!); Gentry 4304 (ARIZ274026!); Gentry 4316 (ARIZ274025!); Gentry 7565a (ARIZ86355!); Gregory 2693 (SD205613!); Guilliams 554 (SDSU18966!); Hasenstab 45 (SDSU18679!); Hasenstab 47 (SDSU21879!); Hasenstab 49 (SDSU18682!); Hasenstab 56 (SDSU18693!); Hendrickson 364 (BSCA5528!, SD172727!); Hendrickson 485 (SD172726!); Hendrickson 1711 (BSCA5477!, SD265575!); Hendrickson 1718 (SD173253!); Hendrickson 1740 (BSCA3532!, SD173252!); Hendrickson 2075 (SD173254!); Hendrickson 3121 (SD190619!); Hendrickson 3473 (BSCA5941!, SD269685!); Hendrickson 3641 (SD212038!); Hendrickson 4492 (SD219799!); Hendrickson 4755 (SD210826!); Hendrickson 4789 (SD210827!); Hendrickson 101718 (BSCA5493!); Howe 1228 (SD113112!); Humphrey 6815a (ARIZ170842!); Jones 3825 (ARIZ438901!); Junak 867 (SD273542!); Kearney 10905 (ARIZ96301!); Laltoo 28 (SD242755!); LaRue 91-56 (ARIZ294065!); Lewis s.n., 17 March 1968 (ASU13132!); Mabry 24 (SDSU20362!); Mabry 25 (SDSU20363!, SDSU20508!); Makings 5075 (ASU0299559!); Makings 5129 (ASU0106272!); Makings 4808b (ASU0295440!); Marsden 355 (SD207713!); McLaughlin 2016

(ARIZ215597!); *McLaughlin 2631* (ARIZ254572!); *McLaughlin 2739* (ARIZ254582!); *Meling s.n.*, 4 Apr 1982 (SD119448!); *Moorefield 3218* (ARIZ282145!); *Moorefield 3246* (ARIZ282194!); *Moran 5624* (RSA118610!); *Moran 5952* (RSA118608!); *Moran 8727* (SD84019!); *Moran 8894* (ARIZ180060!); *Moran 8907* (ASU22374!); *Moran 12302* (RSA193627!); *Moran 16994* (RSA231404!); *Moran 19729* (SD92557!); *Moran 19839* (SD92510!); *Moran 20150* (SD92329!); *Moran 20217* (SD92563!); *Moran 20312* (SD86994!); *Moran 21754* (SD91307!); *Moran 21856* (SD91170!); *Moran 23286* (SD96868!); *Moran 23546* (SD95693!); *Moran 25802* (SD100882!); *Moran 26900* (SD102634!); *Moran 30186* (SD110535!); *Mudie 774* (SD93942!); *Nenow 51* (SD165722!); *Oberbauer 19* (SD162777!); *Oberbauer 83* (SD127738!); *Oberbauer 138* (SD127741!); *Olmsted 1129* (RSA160603!); *Parker 7794* (ARIZ85933!); *Peebles 5032* (ARIZ96305!); *Peirson 11474* (SD87813!); *Philbrick 415* (SD85043!); *Philbrick s.n.*, 27 Mar 1974 (ARIZ289306!, SD121828!); *Phillips 81-9* (ARIZ435486!); *Porter 10570* (RSA751143!); *Porter 11018* (RSA656018!); *Prigge 7921* (UCR51168!); *Rebman 1515* (ASU207117!); *Rebman 6415* (SD148590!); *Rebman 6781* (SD154602!); *Rebman 6835* (SD155046!); *Rebman 14260* (BSCA3393!, SD184251!); *Rebman 14378* (SD191854!); *Rebman 14435* (BSCA5286!, SD191852!); *Rebman 14491* (BSCA3471!, SD191855!); *Rebman 14541* (BSCA3140!, SD191850!); *Rebman 14568* (SD191851!); *Rebman 16112* (SD199917!); *Rebman 16215* (BSCA3002!, SD199919!); *Rebman 16307* (SD199921!); *Rebman 16331* (SD199916!); *Rebman 16407* (BSCA2652!, SD199920!); *Rebman 16456* (SD199914!); *Rebman 16508* (SD199915!); *Rebman 16771* (BSCA5216!); *Rebman 16793* (SD200368!); *Rebman 18731* (SD204179!); *Rebman 20566* (SD213029!); *Rebman 22716* (SD222882!); *Rebman 22932* (SD222883!, UCR239739!); *Rebman 25949* (SD228808!); *Rebman 29339* (SD244988!); *Rebman 29644* (SD256902!); *Rebman 29702* (SD256905!); *Rebman 29720* (SD256904!); *Rebman 29721* (SD256903!); *Rebman 32594* (SD265937!); *Rebman 32599* (SDSU22241!, SDSU22250!); *Rebman 32662* (SD265936!); *Rebman 35527* (SD275634!); *Reeder 6810* (ARIZ207808!); *Reichardt KR2002-15* (ASU278007!); *Riggan 81* (SD212036!); *Riley 63* (SD227955!); *Riley 291* (SD253949!); *Salazar 636* (SD175887!); *Sanders 5464* (UCR38261!); *Sanders 5488* (UCR38326!); *Sanders 6412* (UCR43020!); *Sanders 7641* (UCR58063!); *Sanders 7660* (UCR58085!); *Sanders 12103* (SD140153!); *Sanders 36193* (SD237368!); *Sanders 36428* (SD197712!); *Sanders 40654* (SD250462!); *Schmidtmann 179* (SD274748!); *Shreve 6864* (ARIZ438894!); *Shreve 6937* (ARIZ438895!); *Shreve 7131* (ARIZ438897!); *Shreve 7901* (ARIZ438899!); *G. Simpson 5* (SDSU17658!); *Simpson 2933* (SDSU19298!); *Simpson 3043* (SDSU18446!); *Simpson 3134* (SDSU19610!); *Simpson 3665* (SD227428!, SDSU20050!); *Simpson 3853* (SDSU21211!); *Simpson 4050* (SDSU22034!); *Smith 2010* (UCR25905!); *Sullivan 71* (SD165263!); *Sullivan 173* (SD177257!); *Sullivan 373* (SD201469!); *Sullivan 422* (SD201468!); *Sullivan 655* (SD214889!); *Sullivan 710* (SD214890!); *Sullivan 810* (SD242556!); *Sullivan 829* (SD242555!); *Sullivan 1035* (SD247088!); *Sweet 912* (BSCA3672!, SD241296!); *Sweet 993* (SD241297!); *Sweet 1052* (SD235941!); *Sweet 1053* (SD235942!); *Sweet 1075* (SD237694!); *Sweet 1128* (SD237693!); *Swingle S.187* (ARIZ438903!); *Swingle S224* (ARIZ438904!); *Tewksbery s.n.*, 1 Aug 1992 (ARIZ300125!); *Thorne 32554b* (RSA310939!); *Thorne 32705* (RSA171201!); *Thorne 36049* (SD90638!); *Thorne 55522* (ARIZ316412!); *Thorne 58025* (RSA758760!, SD204838!); *Thorne 58461* (MEXU720505, SD124980!, UCR43501!); *Thorne 58500* (MEXU754595, UCR43581!); *Thorne 58509* (MEXU431028, UCR43551!); *Thorne 58675* (SD204834!); *Thorne 61634* (MEXU721376, RSA350111!, UCR47721!); *Thorne 61803* (RSA354072!); *Thorne 63014* (MEXU515599, MEXU1011249, RSA494597!); *Thorne 63247* (RSA864730!); *Thorne 63294* (RSA877733!); *Thorne 63304* (RSA865483!); *Thorne 63976* (RSA877722!); *Train s.n.*, 12 Apr 1937 (ARIZ438900!); *Turner 65-3* (ARIZ155926!); *Van Devender 91-81* (ARIZ291262!); *Van Devender 91-117* (ARIZ291263!); *Van Devender 91-238* (ARIZ292123!); *Van Devender s.n.*, 5 Mar 1983 (ARIZ240901!); *Van Devender s.n.*, 24 Mar 1973 (ARIZ185497!); *Vanderplank 22* (SD253948!); *Vanderplank CO-22* (RSA878194!); *Vasek s.n.*, 14 Apr 1978 (ARIZ247388!); *West 67* (SD145826!); *West 98-194* (SDSU22768!); *Wiggins 5214* (RSA261995!); *Wiggins 16877* (SD94588!); *Wiggins 16914* (SD94587!); *Wiggins 16933* (SD94533!); *Wiggins 17251* (SD94522!); *Wilder 10-407* (ARIZ415390!); *Wojciechowski 1341* (ASU281494!).

Cryptantha maritima* var. *pilosa.—*André 23984* (SD258357!); *André 24000* (SD260027!); *André 28002* (SD248145!); *Angel 181* (SD167738!); *Annable 177* (ARIZ263683!); *Atwood 26546* (ASU240168!); *Atwood 26653* (ARIZ379106!); *Atwood 26705* (ASU238864!); *Baker 15224* (ARIZ365648!, ASU267995!); *Baker 17087* (ASU280289!); *Barth 912* (BSCA2251!, SD221037!); *Barth 1156* (SD226391!); *Barth 1240* (SD226386!); *Bell 2164* (SDSU21775!); *Benson 10758* (ARIZ7660!); *Berry 9* (ASU107651!); *Bertelsen 92-46* (ARIZ296207!); *Bowers 996* (ARIZ219203!); *Bowers 1032* (ARIZ219220!); *Bowers 1074* (ARIZ219499!); *Boyd 1245* (ARIZ284150!); *Boyd 5311* (RSA571580!); *Boyd 7882* (SD136882!); *Burgess 5581* (ARIZ222706!); *Burgess 5614* (ARIZ222782!); *Burgess 6301* (ARIZ234978!); *Burgess 6517* (ARIZ248020!); *Burgess 6816* (ARIZ258508!); *Butterwick 5961* (ARIZ228533!); *Carnahan 2298* (ARIZ433567!); *Chamberland 1707* (ARIZ359797!); *Crosswhite 1725* (ASU66551!); *Darrow s.n.*, 9 Apr 1939

(ARIZ30154!); *Darrow s.n.*, 8 Apr 1939 (ARIZ32389!); *Darrow s.n.*, 20 Apr 1941 (ARIZ83203!); *De Groot 2298* (ARIZ393607!); *De Groot 8602* (SD271593!); *De Groot 8890* (SD266562!); *Doan 1462* (ASU251122!, SD166025!); *Dominguez Cadena 2767* (SD153711!); *Ducote 743* (ARIZ243778!); *Epling s.n.*, 5 Feb 1935 (ARIZ438898!, RSA611385!); *Ertter 7447* (SD208181!); *Farruggia 1765* (ASU280490!); *Felger 5965* (ARIZ362127!); *Felger 6784-B* (ARIZ200645!); *Felger 7402-B* (ARIZ201001!); *Felger 7497* (ARIZ200408!); *Felger 7625* (ARIZ201006!); *Felger 7929* (ARIZ201000!); *Felger 9703* (ARIZ201003!); *Felger 12142* (ARIZ200647!); *Felger 12659* (ARIZ217947!); *Felger 12660* (ARIZ217945!); *Felger 14041* (ARIZ200486!); *Felger 14042* (ARIZ201010!); *Felger 14243* (ARIZ365210!); *Felger 16969* (ARIZ201007!, SD96195!); *Felger 17173* (ARIZ201011!, SD96188!); *Felger 17298* (ARIZ219146!); *Felger 17716* (ARIZ219145!); *Felger 18761* (ARIZ194888!, SD92193!); *Felger 18813* (ARIZ196015!); *Felger 18878* (ARIZ195785!); *Felger 18932* (ARIZ188762!); *Felger 18981* (ARIZ188941!); *Felger 19053* (ARIZ263971!); *Felger 19098-B* (ARIZ189101!); *Felger 19175-I* (ARIZ285606!); *Felger 19184* (ARIZ188152!); *Felger 19228-G* (ARIZ194951!); *Felger 19249* (ARIZ195020!); *Felger 19261* (ARIZ195006!); *Felger 19340* (ARIZ195455!, SD92199!); *Felger 19383* (ARIZ219523!); *Felger 19428* (ARIZ195095!); *Felger 19501* (ARIZ188997!); *Felger 19616* (ARIZ188873!); *Felger 19639* (ARIZ188887!); *Felger 19742* (ARIZ188987!); *Felger 19795* (ARIZ196038!); *Felger 20647* (ASU274455!); *Felger 20666* (ARIZ189077!); *Felger 20697* (ARIZ189126!); *Felger 01-170* (ARIZ357325!); *Felger 01-727* (ARIZ360985!); *Felger 02-128* (ARIZ361630!, ASU274207!); *Felger 03-151* (ASU266951!); *Felger 03-365* (ARIZ365303!, ASU266974!); *Felger 10-134* (ARIZ415991!); *Felger 75-14* (ARIZ276360!); *Felger 86-82* (ARIZ264013!); *Felger 87-260* (ARIZ283534!); *Felger 88-51* (ARIZ286743!, MEXU490943); *Felger 88-269* (ARIZ286727!); *Felger 89-185* (ARIZ383201!); *Felger 95-204* (ARIZ316980!); *Felger s.n.*, 25 Apr 1964 (ARIZ201002!); *Fertig 28099* (ASU290476!); *Fertig 29126* (ASU293514!); *Fertig 29197* (ASU293513!); *Fertig 29266* (ASU293724!); *Fertig 29357* (ASU296255!); *Fertig 30296* (ASU293413!); *Flores 526* (ARIZ319520!, MEXU459619); *Glacy 81* (SD177258!); *Goldman DGI30b* (ASU282189!); *Gould 2952* (ARIZ20876!); *Gould 3005* (ARIZ20554!); *Gregory 1376* (SD183756!); *Gregory 2651* (SD205611!); *Harlan 244* (ARIZ311218!); *Harlan 252b* (ARIZ311358!); *Harlan 295c* (ARIZ311317!); *Harrison 8418* (ARIZ96304!); *Hazlett 6805* (SD243858!); *Helmkamp 2912* (SD144000!); *Helmkamp 2936* (SD143999!); *Hendrickson 2847* (SD205610!); *Hendrickson 3175* (ARIZ404755!, BSCA4197!, SD190620!); *Hendrickson 3620* (SD212037!); *Henry 25* (ARIZ175847!); *Ickert-Bond 509* (ASU256791!); *Jenke 357* (ASU277779!); *Jenke 366* (ASU277771!); *Jenke 391* (ASU277828!); *Jenke 393* (ASU277826!); *Jenke 654* (ASU279686!); *Jenke 784* (ASU279913!); *Jones 3825* (ARIZ438901!); *Kearney 10975* (ARIZ96303!); *Kearney 11226* (ARIZ438902!); *Landrum 9221* (ASU255102!); *Landrum 9898* (ASU240144!, MEXU1268140); *Landrum 10558* (ASU250929!); *Lehto 19827* (SD96350!); *Mahler 6068* (UCR151855!); *Makings 1905* (ASU265755!, SD166026!); *Makings 1939* (ASU264723!, SD166024!); *Makings 3619* (ASU280720!); *Makings 4802* (ASU295402!); *Makings 4855* (ASU295580!); *Makings 5075* (ASU299559!); *Makings 5129* (ASU106272!); *Marsden 622* (SD241294!); *Mauz 2005-14* (ARIZ375528!); *McLaughlin 8988* (ARIZ373779!); *McLaughlin 10071* (ARIZ376554!); *McLaughlin 10083* (ARIZ376510!); *Merello 1903* (ARIZ353597!); *Moorefield 3218* (ARIZ282145!); *Moorefield 3246* (ARIZ282194!); *Moran 4000* (SD104587!); *Moran 7910* (ARIZ158799!); *Moran 8907* (ASU22374!); *Moran 10468* (SD54150!); *Moran 12607* (ARIZ165391!); *Moran 22967* (SD95534!); *Moran 26927* (SD102502!); *Moran 28206* (SD104990!); *Newhauser s.n.*, 12 Mar 1982 (SDSU18141!); *Newton 201* (ASU273987!); *Newton 272* (ASU274045!); *Newton 635* (ASU279166!); *Peebles 15125* (ARIZ96302!); *Peterson 134* (ARIZ263684!); *Peterson 493* (ARIZ263764!); *Phillips 74-297* (ARIZ201698!); *Phillips 79-100* (ARIZ427945!); *Phillips 79-356* (ARIZ250529!); *Porter 11663* (RSA743749!); *Prigge 7921* (UCR51168!); *Provance 10080* (SD262225!, SD254558!); *Rea 946* (ARIZ262557!, SD118523!); *Rebman 1507* (ASU208328!); *Rebman 1518* (ASU207011!); *Rebman 1548* (ASU207413!); *Rebman 3982* (SD144399!, UCR105835!); *Rebman 14584* (SD191853!); *Rebman 16178* (SD199913!); *Rebman 16564* (SD199918!); *Rebman 16771* (SD200367!); *Rebman 18852* (SD211388!, SDSU19679!); *Rebman 18875* (SD211387!); *Rebman 25864* (SD228809!); *Rebman 32505* (SD265938!); *Rebman 32599* (SD265935!); *Rebman 35080* (SD274746!); *Rebman 35163* (SD274747!); *Reichenbacher 233* (ARIZ226375!); *Rondeau 89-5* (ARIZ282934!); *Rondeau 91-11* (ARIZ291264!); *Sanders 2073* (UCR26520!); *Sanders 3489* (MEXU354039, UCR30172!); *Sanders 3505* (MEXU358801, UCR30122!); *Sanders 42052* (SD260223!); *Sanders 42709* (SD262224!); *Scheidlinger s.n.*, 13 Mar 1982 (SDSU22337!); *Shreve 7074* (ARIZ438896!); *Simpson 8III98D* (SDSU13029!); *Simpson 3049* (SDSU18452!); *Simpson 3170* (SDSU19542!); *Spaulding 75-4-92* (ARIZ196853!); *Sullivan 201* (SD177256!); *Sweet 994* (SD241295!); *Sweet 1083* (SD235943!); *Thorne 57805* (MEXU720607, SD122947!, RSA330197!, UCR40460!); *Thorne 60217* (RSA346804!); *Thorne 61634* (RSA350111!); *Toolin 1745* (ARIZ236161!); *Train s.n.*, 12 Apr 1937 (ARIZ438900!); *Turner 86-22* (ARIZ258775!); *Turner 88-7* (ARIZ292695!); *Van Devender 84-46* (ARIZ247169!); *Van Devender 89-52* (ARIZ282668!); *Van Devender 91-169* (ARIZ291646!); *Van Devender 91-237* (ARIZ292124!); *Van Devender s.n.*, 31 Dec 1972 (ARIZ184278!); *Van Devender s.n.*, 14 Jan 1973 (ARIZ184289!); *Van Devender*

s.n., 10 Feb 1973 (ARIZ184359!); *Van Devender s.n.*, 4 Mar 1973 (ARIZ184505!); *Van Devender s.n.*, 18 Mar 1973 (ARIZ185030!); *Van Devender s.n.*, 24 Mar 1973 (ARIZ185497!); *Van Devender s.n.*, 25 Mar 1973 (ARIZ185677!); *Vanderplank 5075* (SD245996!); *Walters 376* (ASU231809!); *Walters 429* (ASU242062!); *West 5* (SD145823!); *West 10* (SD145822!); *West 39* (SD145824!); *Whipple 3916* (SD179254!); *Whipple 3916* (ARIZ330756!); *Wiggins 7665* (ARIZ201111!); *Wiggins 8262* (ARIZ20112!); *Wiggins 15816* (ARIZ177229!); *Wiggins 15934* (ARIZ180945!, MEXU107126); *Wiggins 16842* (SD94534!); *Wiggins 17407* (SD94585!); *Wilder 10-407* (ARIZ415390!); *Wojtan 3IV92A* (SDSU5393!).

Cryptantha maritima* var. *vizcainensis:—*Boyd 8086* (MEXU666794, RSA576907!); *Breedlove 60891* (MEXU484431, RSA497744!); *Breedlove 62324* (MEXU484782, RSA497109!); *Gentry 797* (ARIZ123309!); *Moran 19663* (SD92540!); *Moran 19707* (SD92511!); *Moran 19758* (SD92558!); *Moran 19878* (SD92358!); *Moran 19949* (SD92556!); *Moran 19973* (SD92328!); *Moran 20004* (MEXU220305, SD92509!).

Cryptantha pondii:—*Gentry 8684* (ASU0014603!, DES00009392, HCIB21969, SD86419!, UCR-80508!); *Philbrick B74-84* (SBBG49613!); *Pond 22* (US41006=US01050283!).