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# Cat's Eyes and Popcorn Flowers: Phylogenetic Systematics of the Genus *Cryptantha* s. l. (Boraginaceae)

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***Abstract***—*Cryptantha* (Boraginaceae) is a group of approximately 200 annual and perennial species, representing two-thirds of the diversity within subtribe Cryptanthinae. The genus exhibits an amphitropic distribution, occurring in temperate and desert regions of western North and South America. Fifty samples of 45 species of *Cryptantha* s. l., exemplars of the related genera *Amsinckia*, *Pectocarya*, and *Plagiobothrys*, and four outgroup taxa were sequenced for two gene regions, the nuclear ribosomal gene, ITS, and the $trnL_{\mathrm{UAA}}$ intron region of the chloroplast genome. These data were used to assess phylogenetic relationships using parsimony, maximum likelihood, and Bayesian inference methods. *Cryptantha* s. l. was found to be polyphyletic, with its members placed among several well-supported clades. Based on these analyses, we propose resurrection of the genera *Eremocarya*, *Greeneocharis*, *Johnstonella*, and *Oreocarya*, and recognition of a newly delimited *Cryptantha* s. s. The related genera *Amsinckia* and *Pectocarya* were resolved as monophyletic and most closely related to various clades within *Cryptantha* s. l. *Plagiobothrys* was resolved as polyphyletic in three clades, these clades corresponding to previously named sections or groups of sections. The Cryptanthinae is supported as monophyletic. Character trait analyses support the multiple, derived evolution of perenniality, reduction in nutlet number, nutlet heteromorphism, smooth nutlet sculpturing, heterostyly, and cleistogamy. Although sampling is incomplete, this study generally supports the hypothesis of repeated, unidirectional dispersal events, from North to South America. Genera resurrected include: *Eremocarya*, *Greeneocharis*, *Johnstonella*, and *Oreocarya*. New combinations include: ***Greeneocharis circumscissa*** var. ***rosulata***, ***Greeneocharis similis***, ***Oreocarya atwoodii***, ***Oreocarya barnebyi***, ***Oreocarya compacta***, ***Oreocarya crassipes***, ***Oreocarya creutzfeldtii***, ***Oreocarya fulvocanescens*** var. ***nitida***, ***Oreocarya grahamii***, ***Oreocarya hypsophila***, ***Oreocarya johnstonii***, ***Oreocarya ochroleuca***, ***Oreocarya roosiorum***, ***Oreocarya schoolcraftii***, ***Oreocarya semiglabra***, ***Oreocarya shackletteana***, ***Oreocarya sobolifera***, ***Oreocarya subcapitata***, ***Oreocarya suffruticosa*** var. ***arenicola***, ***Oreocarya suffruticosa*** var. ***laxa***, ***Oreocarya suffruticosa*** var. ***pustulosa***, ***Oreocarya suffruticosa*** var. ***setosa***, ***Oreocarya welshii***, ***Johnstonella angelica***, ***Johnstonella angustifolia***, ***Johnstonella costata***, ***Johnstonella diplotricha***, ***Johnstonella echinosepala***, ***Johnstonella fastigiata***, ***Johnstonella grayi*** var. ***cryptochaeta***, ***Johnstonella grayi*** var. ***grayi***, ***Johnstonella grayi*** var. ***nesiotica***, ***Johnstonella holoptera***, ***Johnstonella micromeres***, ***Johnstonella parviflora***, and ***Johnstonella pusilla***.

***Keywords***—*Amsinckia*, biogeography, *Pectocarya, Plagiobothrys,* taxonomy, trait evolution.

*Cryptantha* Lehmann ex G. Don, commonly known as "cat's eye" or "popcorn flower," is a genus of the family Boraginaceae. The circumscription of this family has changed repeatedly over the years (Engler and Prantl 1897; Ferguson 1999; Gottschling et al. 2001; Heywood et al. 2007; APG III 2009), with various authors recognizing broad or narrow family concepts with different arrangements of subgroups. Here we accept the APG III (2009) system of classification recognizing a broad Boraginaceae, which may be divided into subfamilies Boraginoideae, Cordioideae, Ehretioideae, Heliotropoideae, Hydrophylloideae, and Lennoideae (Stevens 2001 onwards). *Cryptantha* firmly belongs within subfamily Boraginoideae, a group characterized by an inflorescence that is a circinate, scorpioid cyme (Buys and Hilger 2003), a deeply 4–lobed ovary with a gynobasic style, and a fruit that is a schizocarp of nutlets (Gottschling et al. 2001).

Since the 1920s, *Cryptantha* has been circumscribed broadly, inclusive of several segregate genera; we refer to this genus concept as *Cryptantha* s. l. The genus is amphitropically distributed, with taxa in mostly temperate or desert regions of both western North America and western South America, but absent in intervening tropical regions. As currently delimited in most treatments, *Cryptantha* s. l. has about 200 species (see Simpson 2011). The greatest diversity, approximately 130 species, occurs in western North America, with distributions from Alaska to southern Mexico, and from the Pacific coast and east to Texas (Johnston 1925; Payson 1927; Higgins 1971, 1979). Approximately 70 species occur in western South America, in Peru, Chile, Bolivia, and east to Argentina (Reiche 1910; Johnston 1927; Schwarzer 2007; Teillier 2009; Zuloaga et al. 2008). Three species, *C. albida*, *C. circumscissa*, and *C. maritima*, are distributed in both North and South America.

Members of the genus are strigose to hispid, annual, biennial, or perennial herbs, with simple to highly branched, generally ascending to erect stems and simple, basal to cauline, generally linear, lanceolate, or oblanceolate leaves (Johnston 1925; Payson 1927; Munz and Keck 1959, 1968; Higgins 1971; Kelley and Wilken 1993, Mabberley 2008; Simpson and Hasenstab 2009; Kelley et al. 2012). The shape, degree of fusion, vestiture, and orientation of the accrescent, fruiting calyx are often used as diagnostic features. Flowers are chasmogamous in most taxa, but may also be cleistogamous in members of subgenera *Cryptantha*, *Krynitzkia*, and *Geocarya*, plants of the last bearing fruits modified into lenticular structures (Grau 1983). The corolla limb ranges in size from less than one mm to two cm wide. Corollas are almost universally white (yellow in a few species) and are rotate to salverform, with five, often yellow fornices (invaginated, folded regions) surrounding the corolla throat.

The number of nutlets that develop to maturity can vary from one to four; these are attached to narrowly-pyramidal receptacular tissue (the gynobase) from which a style and stigma arise. Nutlets are generally ovate to lanceolate in shape and can detach from or remain attached to the gynobase within the calyx at dispersal. Several species on both continents have fruits with nutlets that are heteromorphic in size and/or sculpturing; in these, there are often three smaller, easily detached nutlets, and one larger nutlet that is strongly adnate to the gynobase. The pericarp wall is variable in sculpturing and color. The attachment scar is generally a shallow, triangular areole (generally not rimmed or elevated), which is continuous with a ventral groove that extends to or near the nutlet apex. It is the ventral groove that was deemed diagnostic for the genus as a whole (Johnston 1925, 1927; Higgins 1971). Numerous vegetative and floral features are used to distinguish among *Cryptantha* species and infraspecies, but nutlet morphology is the most important taxonomic criterion (Simpson and Hasenstab 2009).

*Cryptantha* s. l. has been classified in the tribe Eritrichieae in most taxonomic treatments, the tribe characterized by heterocolpate pollen (Hargrove and Simpson 2003), an elongate to pyrimidal gynobase, and a submedial nutlet attachment scar (Bentham and Hooker 1873; Al-Shehbaz 1991; Takhtajan 1997). Brand (1925), however, classified *Cryptantha* as a member of the tribe Cryptantheae or subtribe Cryptanthinae (Brand 1931). Långström and Chase (2002), in a study evaluating the tribes of the Boraginoideae, included one species of *Cryptantha* (*C. virgata*, of section *Oreocarya*) in their analysis. These authors concluded that the tribe Eritrichieae, in which *Cryptantha* has usually been placed, is not monophyletic and should be abandoned; in their treatment *Cryptantha* belongs to a clade corresponding to an expanded tribe Cynoglosseae and characterized by heterocolpate pollen (see Hargrove and Simpson 2003). Their taxon sample was too limited to evaluate relationships of *Cryptantha* to other genera.

Table 1 presents the various generic names applied to species within *Cryptantha* s. l., as currently circumscribed. Although some species of *Cryptantha* s. l. were originally placed in the genera *Myosotis*, *Lithospermum*, *Echinospermum,* or *Rochelia,* many were originally or subsequently placed in the heterogeneous genus *Eritrichium*. The name *Cryptantha* originated with Don (1837), who provided the first formal diagnosis for the genus in association with two South American species (*C. glomerata* and *C. microcarpa*). These species names were cited earlier by Fischer and Meyer (1836) but validly published by Don (1837) (see Johnston 1925, 1935 for nomenclatural history). Fischer and Meyer (1841) subsequently described the genus *Kryntizkia* for a single North American species, *K. leiocarpa*, later transferred to *Cryptantha* (see below).

TABLE 1. Genera within which *Cryptantha* s. l. species have been placed and place of original publication.

| | |
|---|---|
| ***Cryptantha*** Lehm. ex G. Don | A General History of the Dichlamydeous Plants 4(1): 373. 1837. |
| ***Echinosperum*** Sw. ex Lehm. | Pl. Asperif. Nucif. 1: 113. 1818. |
| ***Eremocarya*** Greene | Pittonia 1: 58. 1887. |
| ***Eritrichium*** Schrad. ex Gaudin | Flora Helvetica 2: 4, 57. 1828. |
| ***Greeneocharis*** Gürke & Harms | Natürlichen Pflanzenfamilien [Engler & Prantl] Regist. 460. 1899. |
| ***Hemisphaerocarya*** Brand | Repertorium Specierum Novarum Regni Vegetabilis 24: 59. 1927. |
| ***Johnstonella*** Brand | Repertorium Specierum Novarum Regni Vegetabilis 21: 249. 1925. |
| ***Krynitzkia*** Fisch. & C. A. Mey. | Index Seminum [St. Petersburg] 7: 52. 1841. |
| ***Lithospermum*** L. | Species Plantarum 1: 132. 1753. |
| ***Myosotis*** L. | Species Plantarum 1: 131. 1753. |
| ***Oreocarya*** Greene | Pittonia 1: 57. 1887. |
| ***Piptocalyx*** Torr., ined. | United States Exploring Expedition 17(2): 413, t. 12. 1874. |
| ***Rochelia*** Rch. | Flora 7: 243. 1824. |
| ***Wheelerella*** G. B. Grant, ined. | Bulletin of the Southern California Academy of Sciences 5: 28. 1906. |

Dismantling of the genus *Eritrichium* was initiated by Gray (1885), who placed North American species that would later become *Cryptantha* and *Plagiobothrys* Fisch. & C. A. Meyer into *Krynitzkia*. Greene (1887a) further refined the treatment of American representatives of *Eritrichium*, noting the ventral keel as a distinguishing character of the genus *Plagiobothrys* (including *Allocarya* Greene) from *Krynitzkia.* Greene (1887b) recognized the genus *Piptocalyx* Torr. (an illegitimate later homonym of *Piptocalyx* Oliv. ex Benth. [= *Greeneocharis* Gürke & Harms; see below]; Table 1), segregating *Piptocalyx* from *Cryptantha* based on the presence in the former of persistent pedicels and dichotomous cymes. Additionally, Greene (1887b) created two new genera from the species of *Krynitzkia*: *Oreocarya*, consisting of biennial or perennial herbs with radical leaves, and *Eremocarya*, distinguished by dense, bracteate, and dichotomous inflorescences, persistent calyces, and enlarged, persistent styles (Table 1). Subsequently, Greene (1887c) greatly expanded the genus *Cryptantha* to include numerous North American species that had been previously placed in the genus *Krynitzkia*, essentially disbanding the latter. Gürke and Harms (1899) described yet another genus, *Greeneocharis* [*Wheelerella*, ined.], consisting of one species, *G. circumscissa* (transferred from *Lithospermum* L.), which was later recognized as a *Cryptantha*. These taxonomic issues will be discussed further below in the context of our phylogenetic results.

Brand (1925) recognized the genus *Johnstonella* to segregate the perennial *C. racemosa* and *C. inequata* (the latter described by Brand as perennial, but as annual by subsequent authors) from the perennial *Oreocarya* and the remaining members of *Cryptantha* (Table 1). In a monographic treatment of the North American species of *Cryptantha*, Johnston (1925) circumscribed this genus to include *Eremocarya, Johnstonella,* and *Piptocalyx* [= *Greeneocharis*], with his 57 recognized species placed into 15 series. Subsequently, Johnston (1927) published treatments of South American Boraginaceae, recognizing *Cryptantha* as having three sections in South America: *Krynitzkia, Geocarya,* and *Eucryptantha* [= *Cryptantha*]. From these studies, Johnston concluded that the perennial, North American *Oreocarya* species should also be included in *Cryptantha* to form one large, homogenous genus. Payson (1927), in a monograph of the taxa of section *Oreocarya* (in which he recognized six series), agreed with Johnston that *Oreocarya* should be combined with *Cryptantha.* In this monograph Payson recognized four sections in *Cryptantha*: *Eucryptantha* [= *Cryptantha*], *Geocarya, Krynitzkia* (inclusive of *Eremocarya, Greeneocharis*, and *Johnstonella*), and *Oreocarya.* Table 2 provides diagnostic features and biogeographic ranges of these sections. Also, Brand (1927) proposed recognition of the genus *Hemisphaerocarya* to encompass *Cryptantha cinerea* [*C. jamesii*, ined.; see Cronquist et al. 1984] and four closely associated species because of the distinct, globular nutlets present in these taxa. However, this taxon was treated by all subsequent authors as either a *Cryptantha*, section or subgenus *Oreocarya*, or a member of the genus *Oreocarya* (see below).

Since the 1920s, taxonomists have described several new species of *Cryptantha* s. l., but the sections of Payson (1927) have remained largely unchanged. Higgins (1971), another expert on the perennial taxa, published a revised monograph of *Oreocarya,* and agreed with Johnston and Payson on the inclusion of *Oreocarya* within *Cryptantha*, elevating the four sections of Johnston (1927) and Payson (1927) to subgenera.

Table 2. Sections of *Cryptantha* s. l. recognized by Johnston (1927) and Payson (1927), and their diagnostic features and biogeographic range.

| | |
|---|---|
| ***Eucryptantha* [= *Cryptantha*]** | Plants with cleistogamous flowers. Cleistogamous flowers similar to chasmogamic flowers, except for closed corolla. Cleistogamous flowers located in axils of leaves and often throughout the inflorescence. Restricted to South America. |
| ***Geocarya*** | Plants with cleistogamous flowers. Basal cleistogamous flowers with fruits highly specialized into lenticular structures. Restricted to South America. |
| ***Krynitzkia* (including *Eremocarya*, *Greeneocharis*, and *Johnstonella*)** | Annual plants having only chasmogamous flowers. Distributed in North and South America. |
| ***Oreocarya*** | Perennial or biennial herbs, producing only chasmogamous flowers. Restricted to North America. |

Most recent classifications follow the treatments of Johnston, Payson, and Higgins in circumscribing *Cryptantha* in the broad sense (*Cryptantha* s. l.), as encompassing all four sections or subgenera. However, two relatively recent floras (Abrams 1951; Weber 1987) recognized *Oreocarya* as a genus separate from *Cryptantha.*

Few phylogenetic studies have been published on this complex. Payson (1927) and Higgins (1971) both speculated that the perennial species of *Oreocarya* constituted the earliest diverging lineage of the *Cryptantha* s. l. complex, but these suggestions were not based on phylogenetic analyses.

The dissertation of Schwarzer (2007) focused on the Peruvian members of the genera *Amsinckia* Lehm., *Cryptantha*, *Pectocarya* DC. ex Meisn., and *Plagiobothrys*. This work includes a cladogram (cited as H. H. Hilger, unpublished) based on $trnL_{UAA}$ intron cpDNA data, in which members of the genera *Allocarya* (usually treated as a section of *Plagiobothrys*), *Amsinckia*, *Cryptantha* s. s., *Eremocarya*, *Harpagonella* A. Gray, *Oreocarya*, *Pectocarya*, and *Plagiobothrys* s. s. form a well-supported monophyletic group, referred to as tribe Cryptantheae (Brand 1925). Schwarzer (2007), from his own analysis using *trnS-G* cpDNA data, presents a cladogram of 34 species of tribe Cryptantheae and two outgroup species. This tree shows a monophyletic *Pectocarya* (five species, with *P. setosa* of section *Gruvelia* sister to the other four species of section *Pectocarya*) sister to the remaining taxa, whose interrelationships are largely unresolved, but including a monophyletic *Amsinckia* (four species), a mostly monophyletic but partly unresolved *Plagiobothrys* (15 species), and an unresolved *Cryptantha* (10 species). Section *Allocarya* of *Plagiobothrys* is monophyletic and nested within the larger, unresolved *Plagiobothrys*. Within *Cryptantha* s. l., section *Cryptantha* (two species) is sister to section *Geocarya* (two species), the two forming a well-supported clade. Section *Krynitzkia* (five species) forms an unresolved polytomy, and section *Oreocarya* is unresolved, as it is represented by only one species (Schwarzer 2007).

Finally, Weigend et al. (2010), in a study of tribal relationships in the Boraginoideae using *trnL-F* cpDNA sequences, obtained results similar to Långström and Chase (2002). Weigend et al. included two species of *Cryptantha*, two of *Plagiobothrys*, and one of *Amsinckia*. These three genera are each monophyletic and together form a well-supported clade (corresponding to tribe Cryptantheae of Schwarzer 2007) nested within a larger Cynoglosseae s. l. Far too few taxa of *Cryptantha* were used to evaluate phylogenetic relationships in the complex.

Given that the recent studies of Långström and Chase (2002) and Weigend et al. (2010) recognize an expanded tribe Cynoglosseae (inclusive of the tribe Cryptantheae of Schwarzer 2007), we recognize *Cryptantha* s. l. as belonging to subtribe Cryptanthinae (Brand 1931). We test whether this group corresponds to a clade comprised of *Cryptantha* s. l. and the genera *Amsinckia, Pectocarya,* and *Plagiobothrys.*

The primary objective of this study is to assess phylogenetic relationships of members of the genus *Cryptantha* and morphologically similar genera *Amsinckia, Pectocarya,* and *Plagiobothrys* of the Cryptanthinae using molecular sequence data from the $trnL_{UAA}$ chloroplast intron part of the *trnL-F* locus, and nuclear ribosomal ITS regions. The monophyly of the Cryptanthinae, of *Cryptantha* s. l., and of previously recognized genera, subgenera, and sections in the complex are tested. Relationships among the clades encompassing these taxa are also evaluated. The best estimate of phylogeny is used to revise the classification of this complex. Additionally, this phylogeny is used to assess evolution of features that have traditionally been used in past taxonomic studies and to assess biogeographic history with respect to the amphitropic distribution of *Cryptantha* s. l.

## Materials and Methods

***Plant Samples***—Specimens were obtained from dried herbarium material on loan from herbaria at the University of Colorado Museum (COLO), Universidad de Concepción (CONC), Missouri Botanical Garden (MO), Rancho Santa Ana Botanic Garden (RSA), San Diego Natural History Museum (SD), San Diego State University (SDSU), Museo Botánico (SI), and the University of California-Berkeley (UC-JEPS) (Appendix 1). Vouchered field collections were used to supplement herbarium specimens for species that had not been recently collected. At least one representative of each currently recognized section, *Oreocarya*, *Krinitzkia*, *Cryptantha* and *Geocarya*, were sampled. Additional members of Cryptanthinae (as defined here) were sampled: *Amsinckia* (four species), *Pectocarya* (three species), and *Plagiobothrys* (seven species total, in four of five recognized sections). We were unable to sequence the monospecific *Harpagonella*, which is usually included in this complex. In addition, one species each of *Cynoglossum* and *Hackelia* and two species of *Myosotis* were included to test monophyly of the Cryptanthinae. Two species of *Phacelia*, well outside subfamily Boraginoideae, were used to root the tree. All sequences are original to this study, except for the sequences of *Myosotis* and *Phacelia,* which were obtained from GenBank (Appendix 1).

***DNA Isolation and Sequencing***—DNA was isolated using a three-day, modified version of the CTAB (cetyl trimethyl ammonium bromide) protocol (Doyle and Doyle 1987; Friar 2005). Amplifications were done in 25μl volumes containing: 2.5 μl 10 × standard Mg-free buffer, 1.25 μl 1.5 μM MgCl2, 0.125 μl 5,000 U/ml *Taq* polymerase, 1.2 μl 10 μM forward and reverse primers, 1.25 μl 200 μM dNTP's, 16.375 μl $H_2O$, and 1.0 μl total of 1–10 μg/ml genomic DNA. The ITS region was amplified using ITS5a and ITS4 (Moore et al. 2006). The $trnL_{UAA}$ intron region was amplified using the following primers: trnL5′ and $trnF_{GAA}$ (Shaw et al. 2005). Amplifications were carried out on an Applied Biosystems 2720 thermal cycler. The PCR amplicons were precipitated with 20% polyethylene glycol 8000 (PEG) in 2.5 M NaCl, using equal volume of PEG to PCR product, the mixture was incubated at 37°C for 15 minutes. DNA was pelleted by centrifugation for 15 minutes at 14,000 rpm. The pellet was washed with ice-cold 80% ethanol. Sequencing was done on an ABI 3100 at the San Diego State University Microchemical Core Facility or on an ABI 3130xl at Rancho Santa Ana Botanic Garden using the same primers as for amplification.

***Sequence Editing and Alignment***—Sequences were edited using 4peaks version 1.7 (Griekspoor and Groothuis 2004) with chromatograms checked for polymorphisms, especially the ITS sequences. Sequences were aligned using ClustalW (Thompson et al. 1997); two alignments were done using gap-opening costs of 2 and 15. A final alignment was done manually in MacClade 4.08 (Maddison and Maddison 2005). Some regions within ITS were difficult to assign positional homology, and thus are considered ambiguously aligned. Analyses including and excluding these ambiguous regions revealed no change in topology, so they were included in final analyses. The final, aligned data were submitted to TreeBASE (study number 11794).

***Parsimony Analysis***—Phylogenetic analyses were done using PAUP* 4.0b6 (Swofford 2003) utilizing a parsimony optimality criterion. Parsimony analyses were conducted with the following parameters: 10,000 replicates of random taxon addition with tree bisection-reconnection (TBR) branch swapping on all the best trees at each step. All optimal trees were held at each replicate. Characters were treated as unordered and equally weighted. Gaps were treated as missing data. To test conflicts between the ITS and plastid data, incongruence length difference (ILD) test was done using a partition-homogeneity test in PAUP* (Swofford 2003). Parsimony analyses were initially done on the ITS and $trnL_{UAA}$ sequence data independently. Branch support in the parsimony analyses was assessed using 1,000 non-parametric bootstrap pseudo-replicates with 10 random-additions per replicate. All clades with a maximum parsimony bootstrap (MPBS) value of 70 or greater were considered to be strongly supported. Congruence between ITS and $trnL_{UAA}$ was assessed by comparing the strict consensus trees with mapped bootstrap values generated from the ITS and plastid data, as well as from the ILD test. The $p$ value for the ILD test was 0.974. No clades that were recovered with strong support were incongruent between the two data sets, so they were combined for a concatenated analysis. A strict consensus tree from this concatenated analysis was generated. A bootstrap analysis of the concatenated data set was calculated, using the parameters above. Maximum parsimony bootstrap values of 70 or greater are illustrated on the strict consensus tree.

***Maximum Likelihood Analysis***—Phylogenetic inference using a maximum likelihood optimality criterion (ML; Felsenstein 1981) was implemented in PAUP* 4.0b10 (Swofford 2003). The model of nucleotide evolution was selected using the Akaike information criterion (AIC; Akaike 1974; Posada and Crandall 2001) from Modeltest version 3.7 (Posada and Crandall 1998). Statistical support was assessed with a maximum likelihood bootstrap (MLBS) analysis implemented in RAxML (Stamatakis et al. 2008), with bootstrap support values estimated from 100 replicates under the GTR + I + G model of evolution. The ITS region and $trnL_{UAA}$ intron were initially analyzed separately. No strongly supported incongruences were recovered, so the final likelihood analysis was done on a combined data set.

***Bayesian Inference***—Analyses were done using MRBAYES version 3.1.2 (Huelsenbeck and Ronquist 2001), with the ITS and $trnL_{UAA}$ sequence data analyzed independently. Models for each dataset were determined using the Akaike information criterion (AIC) in Mr.Modeltest (Nylander 2004). The model of nucleotide substitution selected for each locus was TMV + I + G, which was used for all Bayesian analyses. All Bayesian analyses ran for 10,000,000 generations, with sampling every 100 generations. Consensus trees were produced from trees sampled after the standard deviation of split frequencies reached a value of 0.01, with posterior probabilities (PP) calculated. No conflicting clades with a posterior probability (PP) of 0.95 or greater were recovered in either analysis, so the data were combined for a final, concatenated analysis. In the combined analysis, the plastid locus was run as a separate process partition from the ITS data.

***Trait Evolution***—Character states for each taxon were obtained from the taxonomic literature and personal observation. Characters reconstructed were diagnostic features that have previously been used to circumscribe species or infrageneric groups. All characters were binary, except nutlet number per fruit, which had four states. Characters analyzed were: 1) plant duration: annual, perennial; 2) nutlet number per fruit: one, two, three, four; 3) nutlet heteromorphism: homomorphic, with all nutlets approximately equal in size and sculpturing; heteromorphic, one nutlet differing in size and/or shape; and 4) nutlet sculpturing: smooth, with no sculpturing elements; rough, having papillae, turbercles, and/or ridges. We also examined the parsimony optimization for two additional characters, heterostyly and cleistogamy (both presence/absence), and for biogeographic distribution (North versus South America). Parsimony optimizations were implemented in Mesquite (Maddison and Maddison 2010), using the unordered states assumption. The topology of the Bayesian consensus tree and maximum likelihood tree showed no conflict in topology, and both have more clades with significant statistical support than the MP consensus tree; thus, the topology from the maximum likelihood inference was used for reconstruction of trait evolution.

## Results

***Sequence Matrices***—The concatenated matrix contained a total of 1,475 nucleotides, with 354 parimony informative characters. The cpDNA matrix was composed of 859 nucleotides with 134 parsimony informative characters, and the ITS matrix contained a total of 616 nucleotides with 220 parsimony informative characters.

***Parsimony Inference***—The parsimony analysis yielded 1,827 trees with a tree length of 1,435. The strict consensus tree of the parsimony analysis (Fig. 1) shows a monophyletic Cryptanthinae (MPBS = 78). *Cryptantha* s. l. and *Plagiobothrys*, as currently circumscribed, are polyphyletic whereas *Pectocarya* and *Amsinckia* are strongly supported as monophyletic (MPBS = 100 for each). *Cryptantha* s. l. species are placed in six major clades, all with strong bootstrap support, corresponding to four previously named genera, *Eremocarya* (MPBS = 100), *Greeneocharis* (MPBS = 100), *Johnstonella* (MPBS = 97), *Oreocarya* (MPBS = 91), plus two remaining clades, which we designate as *Cryptantha* s. s. 1 (MPBS = 71) and *Cryptantha* s. s. 2 (MPBS = 100). Relationships among these six groups are not strongly supported.

*Johnstonella*, containing eight sampled species, is the earliest diverging clade within Cyptanthineae. *Greeneocharis*, with four samples of two species, is placed sister to a clade of four *Plagiobothrys* species but without strong bootstrap support; these two together are sister to *P. jonesii*, also without robust support. *Eremocarya*, with three samples of one species and two varieties, is sister (MPBS = 70) to *Oreocarya*, with eight species sampled. The *Cryptantha* s. s. 2 group, with four samples of three species, is sister to the *Cryptantha* s. s. 1 group of 23 sampled species, but without strong bootstrap support for this relationship (Fig. 1).

***Maximum Likelihood and Bayesian Inference***—The two model based analyses converged on virtually the same topology, with no incompatibility between them. The maximum likelihood tree is presented here with both likelihood bootstrap values and Bayesian posterior probabilities shown (Fig. 2). Cryptanthinae is recovered as monophyletic (MLBS = 84, PP = 1.0). *Cryptantha* s. l. and *Plagiobothrys*, as currently circumscribed, are polyphyletic. *Amsinckia* and *Pectocarya* are again inferred to be monophyletic with strong support (MLBS = 100, PP = 1.0 for each). Six strongly supported clades of *Cryptantha* s. l. taxa are inferred, four corresponding to previously named genera, *Johnstonella* (MLBS = 95, PP = 1.0), *Greeneocharis* (MLBS = 100, PP = 1.0), *Eremocarya* (MLBS = 100, PP = 1.0), and *Oreocarya* (MLBS = 86, PP = 1.0), plus two others corresponding to a robustly supported *Cryptantha* s. s. 1 clade (MLBS = 96, PP = 1.0) and *Cryptantha* s. s. 2 clade (MLBS = 98, PP = 1.0). *Pectocarya* is the earliest diverging clade. As in the parsimony analysis, *Oreocarya* and *Eremocarya* are sister taxa (MLBS = 73); these two together are sister to *Plagiobothrys hispidus* (PP = 0.97), and all three together are sister to a clade composed of the other Cryptanthinae, minus *Pectocarya* (PP = 0.99). Within the last group, *Cryptantha* s. s. 2 is sister to all remaining Cryptanthinae, but without strong support. *Johnstonella* is sister to a clade consisting of *Greeneocharis*, *Amsinckia*, and all *Plagiobothrys* species (minus *P. hispidus*), and this clade is sister to *Cryptantha* s. s. 1 (Fig. 2).

***Ancestral State Reconstructions***—Parsimony optimization of four morphological characters on the ML topology is seen in Fig. 3. Figure 3A shows that an annual plant duration is ancestral for Cryptanthinae and that perenniality arose independently as many as five times. Perennial plant duration is apomorphic for the *Oreocarya* clade; this feature has long been diagnostic for this group. Perenniality also evolved within the *Johnstonella* clade, occurring in *C. racemosa* and

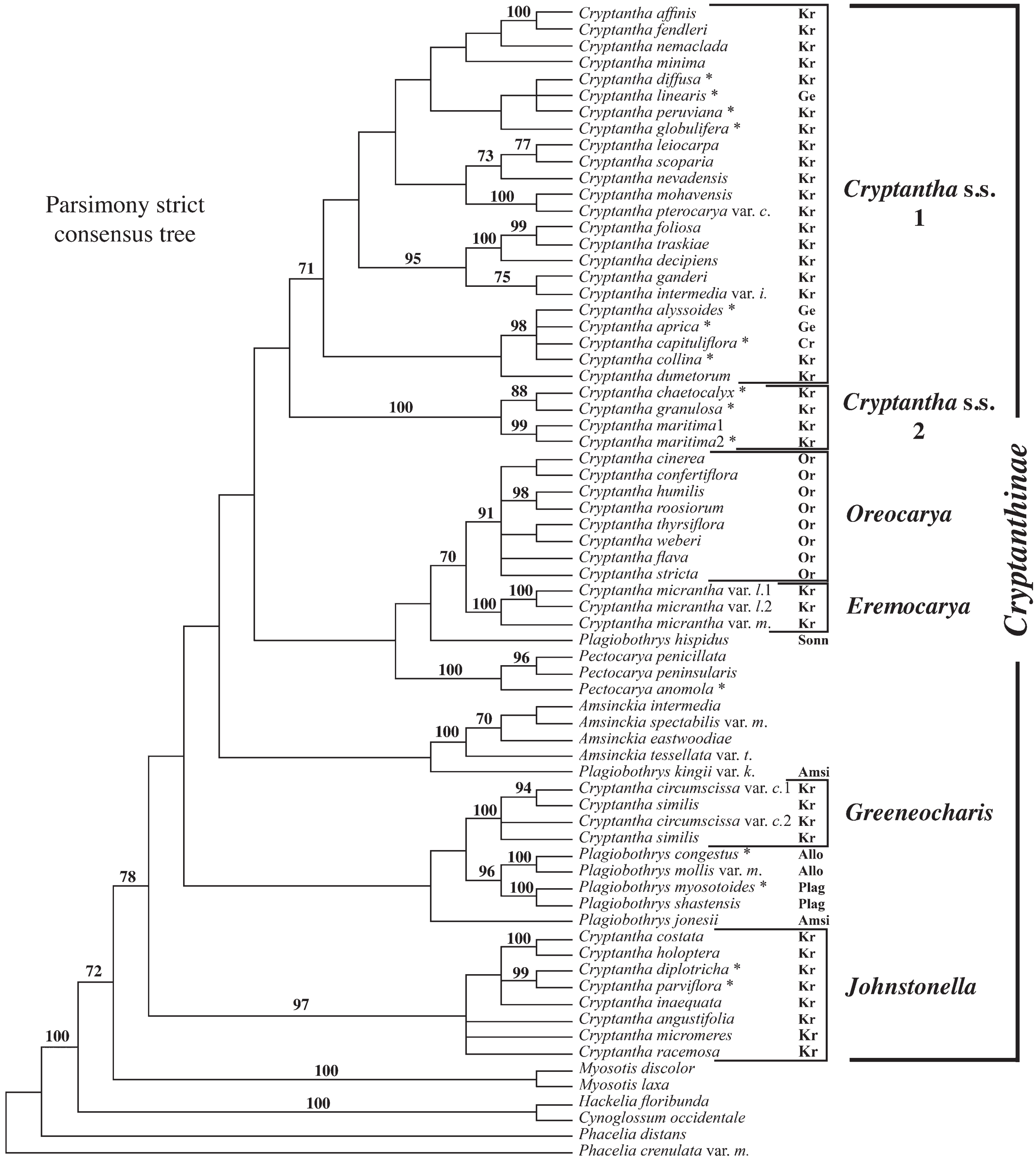

FIG. 1. Strict consensus tree from parsimony analysis with bootstrap values at well supported (≥ 70%) internodes. * = South American taxa; all others North American. *Cryptantha* section abbreviations: **Cr** = *Cryptantha*; **Ge** = *Geocarya*; **Kr** = *Krynitzkia*; **Or** = *Oreocarya*. *Plagiobothrys* section abbreviations: **Allo** = *Allocarya*; **Amsi** = *Amsinckiopsis*; **Plag** = *Plagiobothrys*; **Sonn** = *Sonnea*.

occasionally present in *C. holoptera*; however, the ancestral state for the *Johnstonella* clade is annual. Within *Cryptantha* s. s. 1, perennial duration evolved at most twice, once in each clade corresponding to the South American sections *Cryptantha* and *Geocarya* (Fig. 3A).

A fruit with four nutlets per fruit is clearly ancestral for Cryptanthinae (Fig. 3B), with reduction in nutlet number occurring up to 10 times. Within the *Cryptantha* s. s. 1 clade, three independent reductions to one nutlet per fruit occur, with several more polymorphic reductions among taxa in sections *Krynitzkia*, *Cryptantha*, and *Geocarya* (Fig. 3B). In the *Cryptantha* s. s. 2 clade, *C. maritima* (samples from both North and South America) shows a reduction from four to 1–2 nutlets. Finally, within section *Oreocarya* there are two separate

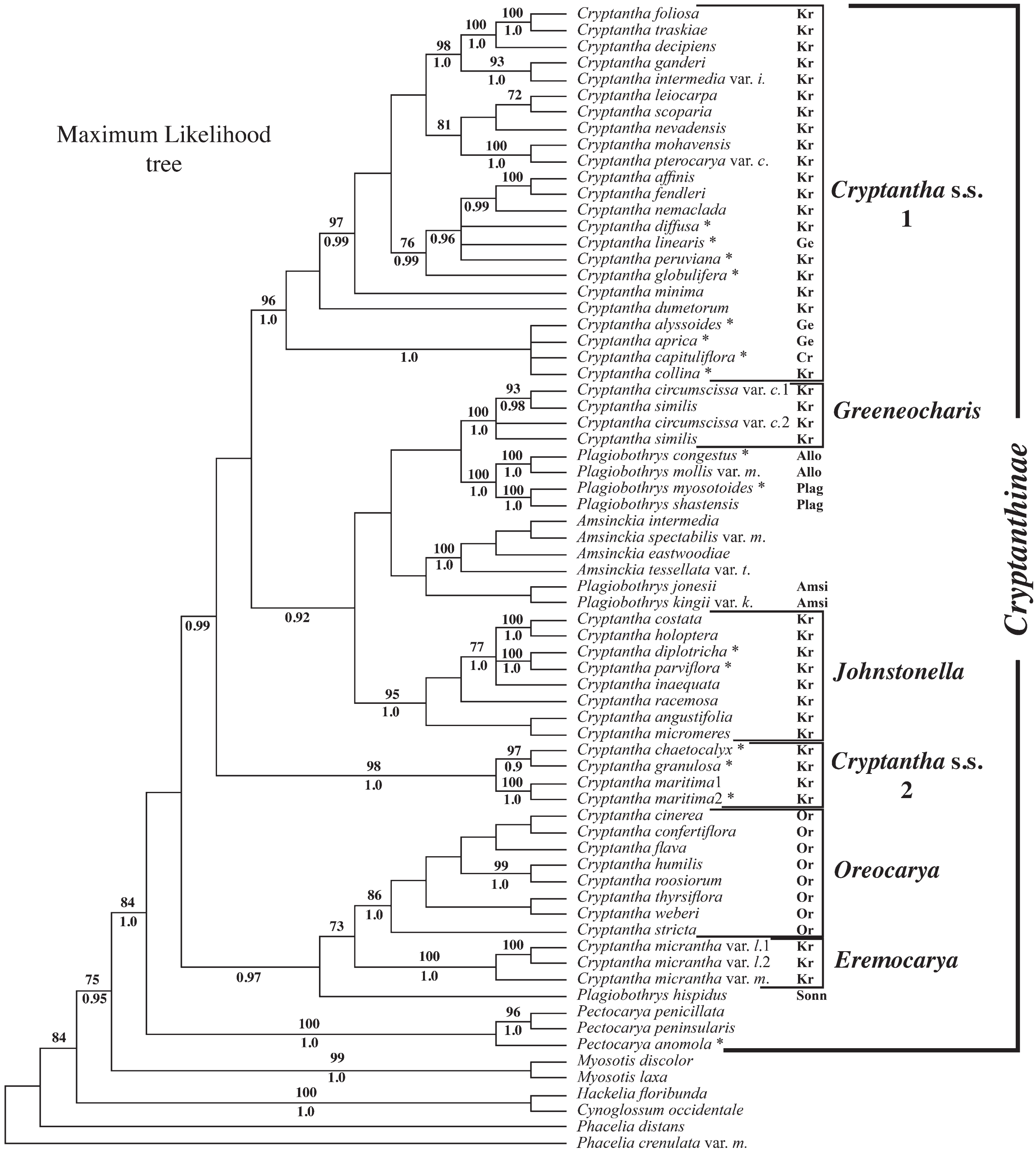

FIG. 2. Maximum likelihood phylogeny with ML bootstrap values shown above lineage and Bayesian posterior probabilities below lineage. Abbreviations as in Fig. 1.

reductions of nutlet number per fruit, from four to 1–2 or 1–3 nutlets (Fig. 3B).

Figure 3C shows reconstruction of nutlet heteromorphism, whereby nutlets develop differentially in size or in pericarp wall sculpturing within a single calyx. Homomorphic nutlets are ancestral for Cryptanthinae; heteromorphism evolved from up to seven times, depending on the optimization model. The *Johnstonella* clade unequivocally possesses a common ancestor with heteromorphic nutlets, followed by subsequent reversals to homomorphism in some lineages (Fig. 3C). Equivocal optimizations for the evolution of heteromorphism occur in the *Cryptantha* s. s. 1 and *Cryptantha* s. s. 2 clades. Finally, heteromorphism evolved independently in one lineage within *Pectocarya* (Fig. 3C).

Rough nutlets are ancestral for Cryptanthinae (Fig. 3D). Smooth nutlets have arisen independently five times in the

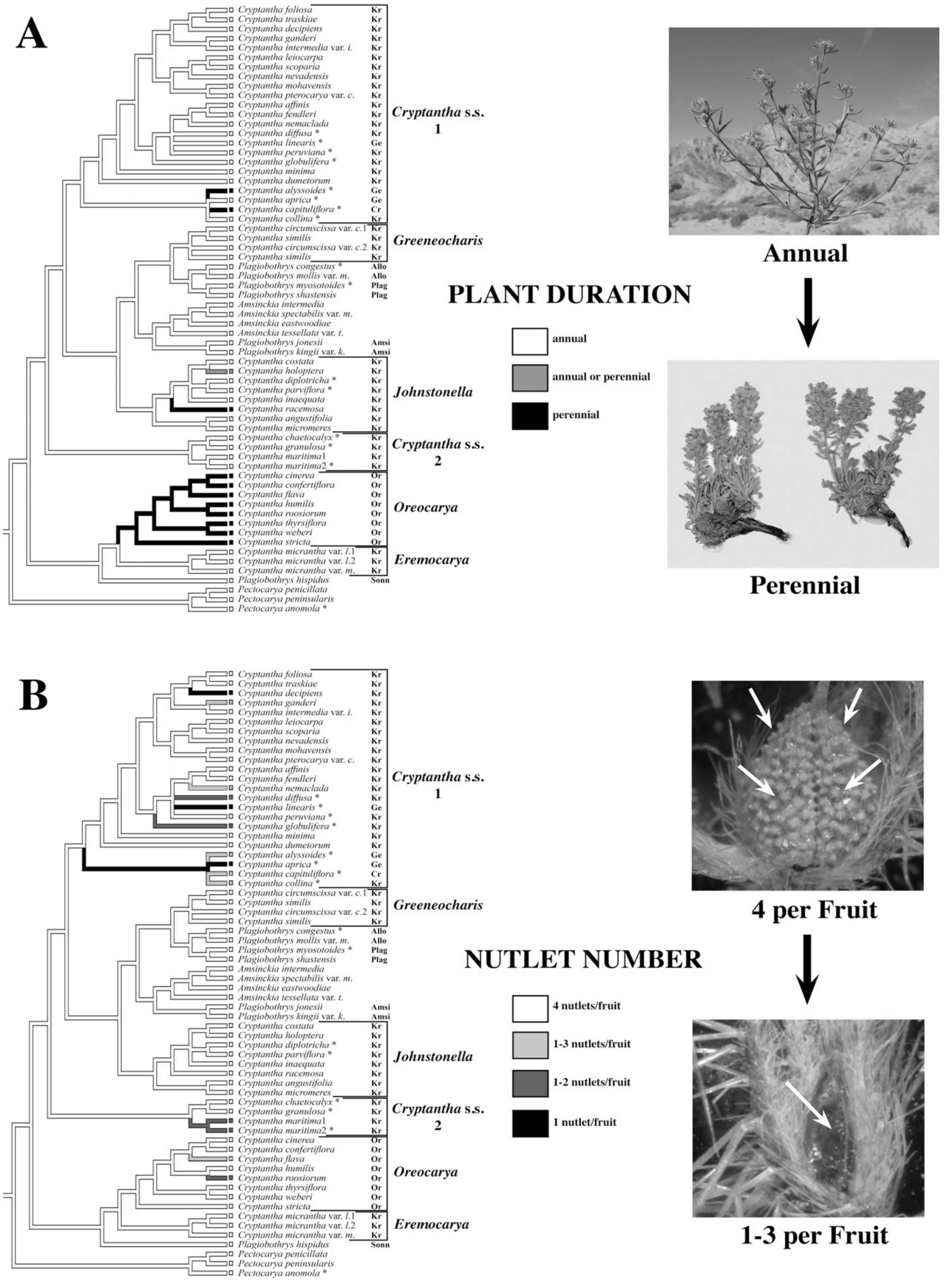

FIG. 3A and B. Character evolution, maximum likelihood tree shown. A. Plant duration (see Figs. 5A, 6D). Annual = white, perennial = black, annual or perennial = gray. Note that annual duration (illustrated by *C. maritima)* is ancestral for Cryptanthinae. Perennial duration (illustrated by *C. humilis*) is apomorphic for *Oreocarya* and evolved independently within *Johnstonella* and sections *Cryptantha* and *Geocarya* of *Cryptantha* s. s. 1. B. Nutlet number per fruit. Four nutlets/fruit = white, one nutlet/fruit = black, one-two nutlets per fruit = dark gray, one-three nutlets/fruit = light gray. Note that the ancestral condition for Crypanthinae is 4 nutlets per fruit (illustrated by *C. intermedia*). Reduction in nutlet number (illustrated by *C. ganderi*) occurred up to 10 times. Abbreviations as in Fig. 1.

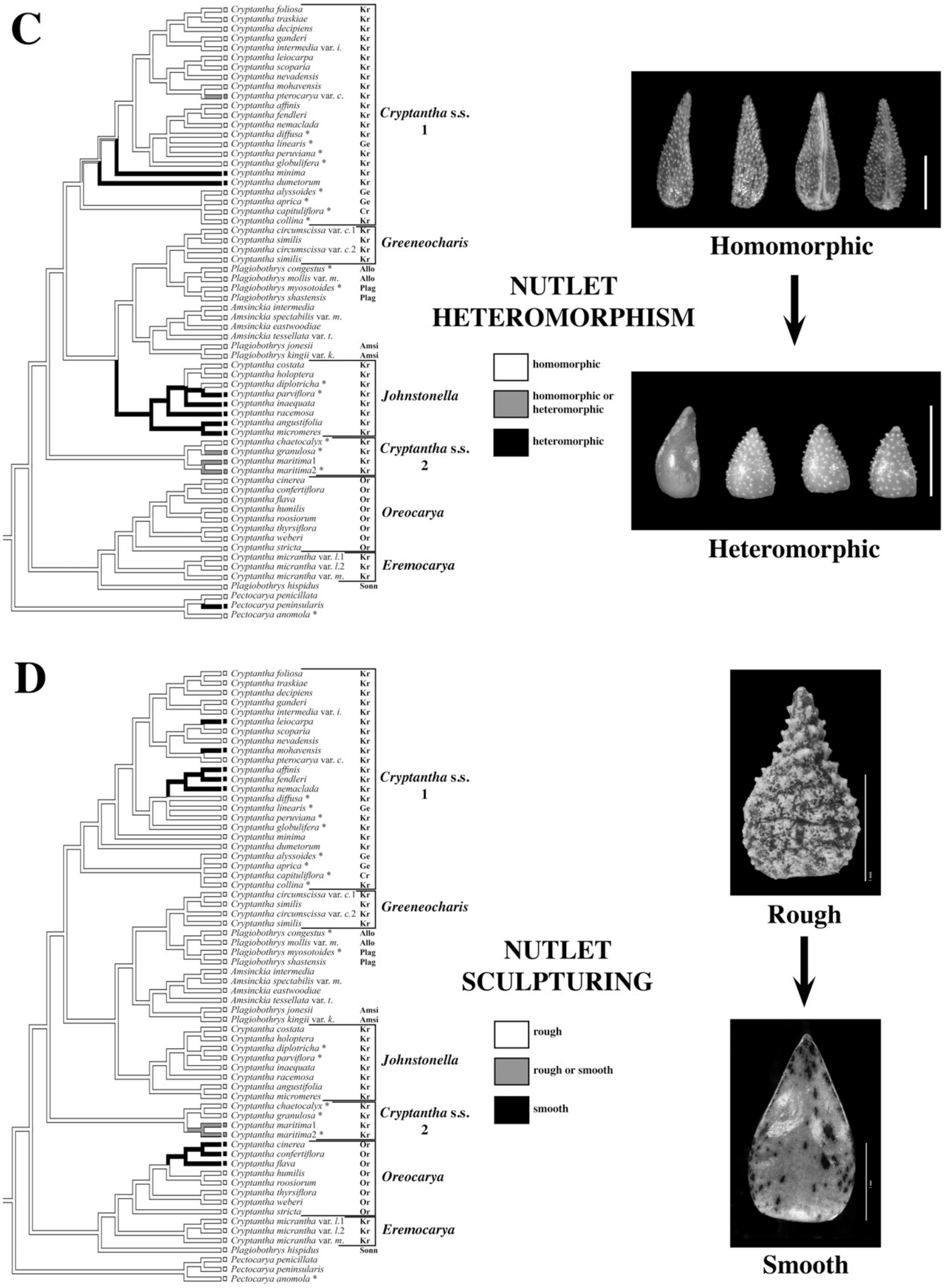

FIG. 3C and D. Character evolution, maximum likelihood tree shown. C. Nutlet heteromorphism. Homomorphic = white, heteromorphic = black, homomorphic or heteromorphic = gray. Note that homomorphic nutlets (illustrated by *C. scoparia*) are ancestral for Cryptanthinae. Heteromorphic nutlets (illustrated by *C. micromeres*) are apomorphic for *Johnstonella* and have evolved independently in the *Cryptantha* s. s. 1 and 2 clades, as well as in *Pectocarya peninsularis*. D. Nutlet surface sculpturing. Rough = white, smooth = black, rough or smooth = gray. Note that "rough" sculpturing (illustrated by *C. peruviana*) is ancestral for Crypanthinae. A "smooth" sculpturing (illustrated by *C. mohavensis*) has evolved independently in the *Cryptantha* s. s. 1, *Cryptantha* s. s. 2, and *Oreocarya* clades. Scale bars = 1 mm. Abbreviations as in Fig. 1.

Cryptanthinae: three times within *Cryptantha* s. s. 1, once within *Cryptantha* s. s. 2, and once within *Oreocarya*, the last an apomorphy for three sampled species (Fig. 3D).

Two other morphological features (unmapped) were also assessed with respect to our phylogenetic analyses (see Figs. 1, 2). First, heterostyly, a type of herkogamy in which the stamens and style vary inversely in height, is found in several *Amsinckia* species (including *A. spectabilis,* sampled here) and in several members of section *Oreocarya* (including *Cryptantha confertiflora* and *C. flava*, sampled here); thus, heterostyly is clearly derived within Cryptanthinae, having evolved at least twice. Second, cleistogamy, found only in members of section *Cryptantha* and *Geocarya* of South America, is clearly derived in Cryptanthinae, having evolved independently at least twice by our results.

Finally, we note that the amphitropic distribution of *Cryptantha* s. l., if explained via long distance dispersal, is best explained as unidirectional, from North to South America and has occured a minimum of four times in the complex with a possible single dispersal in the opposite direction in the *Cryptantha* s. s. 1 clade. Independent dispersals, from North to South America, are also evident in the genera *Pectocarya* and *Plagiobothrys* (see Fig. 2).

## Discussion

***Phylogenetic Analyses***—In all analyses, monophyly of the Cryptanthinae is supported, based on our sample of outgroup taxa. The genera *Amsinckia* and *Pectocarya* are maintained as strongly supported, monophyletic groups. *Plagiobothrys* is recovered as polyphyletic in all analyses, forming three to four separate clades. Although relationships among species of *Plagiobothrys* are beyond the scope of this study because of our limited sample size, we do note some patterns. Investigated species of *Plagiobothrys* section *Amsinckiopsis* are sister to genus *Amsinckia* in the Bayesian and maximum likelihood analyses, and species sampled from sections *Plagiobothrys* and *Allocarya* are each monophyletic and together form a strongly supported clade in all analyses. Finally, the one taxon sampled from section *Sonnea, Plagiobothrys hispidus,* is consistently placed sister to the clade of *Eremocarya* + *Oreocarya*, but with robust support only from the Bayesian analysis (PP = 0.97). We predict that an increased sample size of *Plagiobothrys* s. l. species (e.g. Guilliams and Baldwin 2010, 2011) will more definitively resolve these relationships.

*Cryptantha* s. l., as currently circumscribed, is also polyphyletic in all analyses, as is section *Krynitzkia*. Six major clades are consistently recovered, four corresponding to previously named genera. One of the clades is composed of one species with two taxa placed in section *Krynitzkia* by Johnston (1925): *C. micrantha* var. *m.* and *C. micrantha* var. *lepida* [sometimes treated as *C. lepida*]. This corresponds to the genus *Eremocarya,* as named and described by Greene (1887b; see Table 1). Taxa in this clade are diagnosed morphologically by having red-pigmented roots (Fig. 4A), an aerial branching system that is approximately equal in height and width (Fig. 4B), bracteate flowers (Fig. 4C), and a gynobase that is greater in height than mature nutlets with a persistent style (Fig. 4D). The *Eremocarya* clade is consistently placed sister to the *Oreocarya* clade.

The *Oreocarya* clade, with eight sampled taxa in our analyses, also forms a well supported monophyletic group. Greene (1887b) originally circumscribed the genus *Oreocarya* to include a subset of species from *Krynitzkia* (Table 1). Greene distinguished *Oreocarya* from *Krynitzkia* based on perennial duration, persistent fruiting calyx, and nutlets that lack a ventral keel (as found, e.g. in all *Plagiobothrys* species). The remaining *Krynitzkia* species were transferred by Greene and others to *Cryptantha*, as these workers saw no diagnostic differences between North American *Krynitzkia* and South American *Cryptantha,* the latter name having priority of publication. A monograph by Payson (1927) reduced the genus *Oreocarya* to a section of *Cryptantha,* in agreement with Johnston's treatment of South American *Cryptantha* (Johnston 1927). Payson reasoned that, after examining South American members of *Cryptantha,* there is "... not a single morphological character that will definitely separate *Oreocarya* and *Cryptantha* when the South American species are taken into account. Even in North America the primary character that has been used to separate the two groups was the biennial or perennial root in *Oreocarya* and the annual one in *Cryptantha.*" Also in 1927, Brand proposed the genus *Hemisphaerocarya* to encompass *C. cinerea* [*C. jamesii*] and four closely associated species because of the distinct, globular nutlets present in these taxa. Our results show that *C. cinerea* is

Fig. 4. Diagnostic and/or apomorphic features of resurrected genus *Eremocarya*. A,B. *Cryptantha micrantha* var. *micrantha*. A. Red-purple pigmented roots. B. Plants with short, wide aerial branching. C,D. *C. micrantha* var. *lepida*. C. Corollas. D. Fruit, with aposepalous calyx and four, homomorphic nutlets and elongate gynobase, bearing apical style. Scale bars = 1 mm.

nested well within the *Oreocarya* clade so that recognition of *Hemisphaerocarya* is unfounded. Despite Payson's comments, *Oreocarya* is well circumscribed from remaining *Cryptantha* s. l. by perennial plant duration with a persistent basal rosette of leaves (Fig. 5A,D), relatively large, showy flowers (Fig. 5B), persistent fruiting calyces, and nutlets with a sub-apical ventral groove (Fig. 5F,J) and a sculpturing that is either smooth (Fig. 5C,G) or rugulose to roughened (Fig. 5E, F, H-J). In addition, among *Cryptantha* s. l., heterostyly has evolved only in certain members of *Oreocarya.* As mentioned earlier, the recognition of *Oreocarya* as a distinct genus agrees with the classification used in two relatively recent floristic treatments (Abrams 1951; Weber 1987).

The *Cryptantha* s. s. 2 clade is strongly supported in all analyses, but its placement within Cryptanthinae varies. In the parsimony analysis this clade is placed sister to *Cryptantha* s. s. 1, but this placement is not robustly supported (Fig. 1). In both the likelihood and Bayesian analyses, the *Cryptantha* s. s. 2 clade is sister to a large clade composed of *Johnstonella, Amsinckia,* two clades of *Plagiobothrys* species,

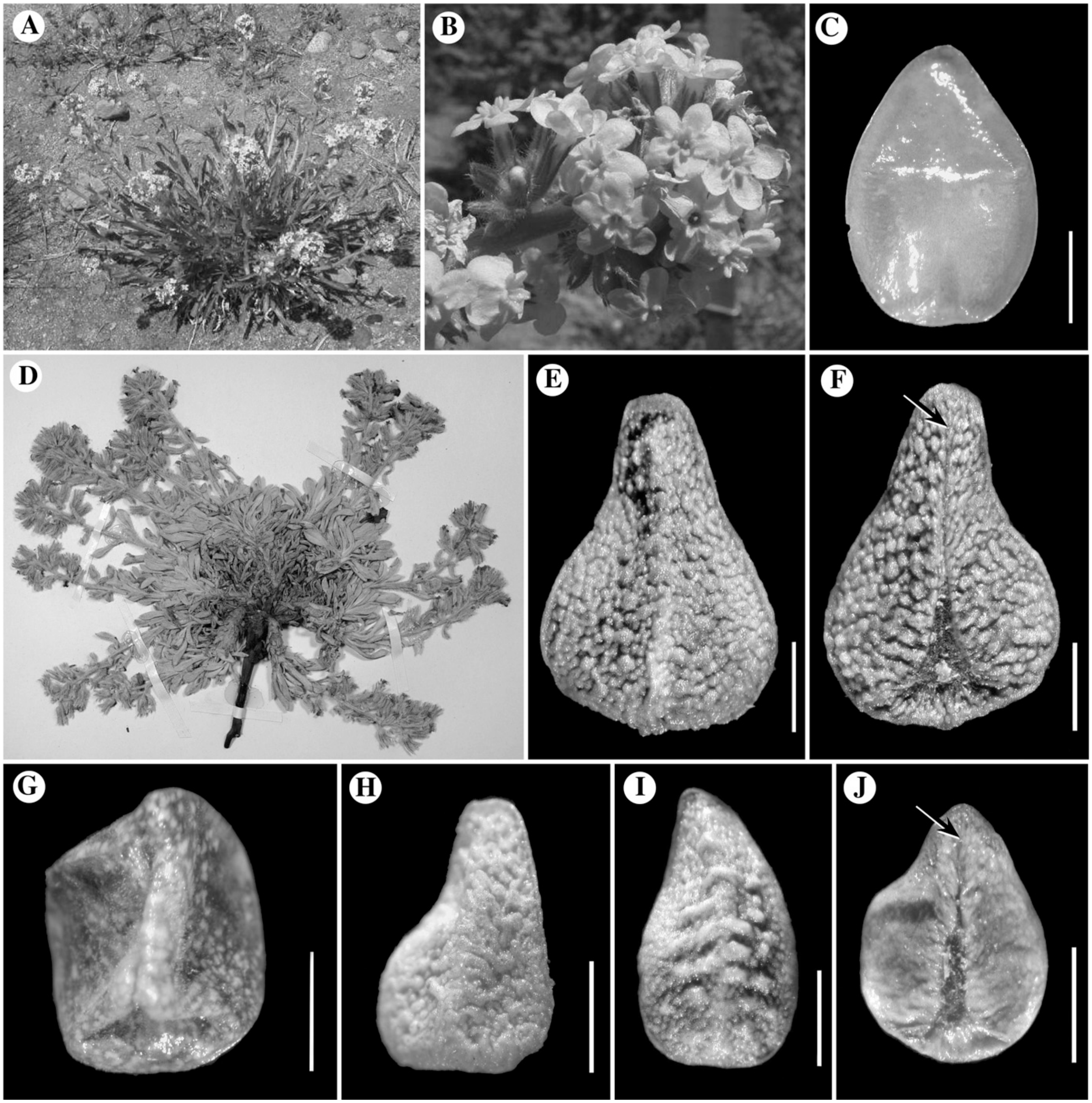

Fig. 5. Diagnostic and/or apomorphic features of resurrected genus *Oreocarya*. A-C. *C. confertiflora*. A. Plant, a perennial. B. Inforescence, showing large, showy flowers. C. Nutlet, dorsal view; note large size. D-F. *C. humilis*. D. Whole plant, herbarium sheet, showing perennial habit and persistent, basal leaves. E. Nutlet, dorsal view, showing rugulose sculpturing. F. Nutlet, ventral view; note subapical ventral groove (arrow). G. *C. cinerea*, nutlet, ventral view. H. *C. roosiorum*, nutlet, dorsal view, with rugulose sculpturing. I. *C. thyrsiflora*, nutlet, dorsal view, with rugulose sculpturing. J . *C. weberi*, nutlet, ventral view, showing sub-apical ventral groove (arrow). Scale bars = 1 mm.

and the *Cryptantha* s. s. 1 clade. We cannot identify any diagnostic morphological features for the *Cryptantha* s. s. 2 clade. Given its uncertain phylogenetic position and the fact that it may actually be sister to *Cryptantha* s. s. 1, we choose to retain these taxa within the genus *Cryptantha* s. s. (delimited here to encompass clades 1 and 2). Future studies with a greater sample size or additional molecular data will be needed to confirm the interrelationships of these two clades.

Twenty-three sampled taxa of *Cryptantha* comprise our *Cryptantha* s. s. 1 clade with strong support in all analyses (Figs. 1, 2). This clade contains representatives of subgenera *Cryptantha* (one species sampled), *Geocarya* (three species sampled), and *Krynitzkia* (19 species sampled). Subgenera *Geocarya* and *Cryptantha* occur exclusively in South America and contain species with cleistogamous (and chasmogamous) flowers. In all analyses, two species of section *Geocarya, C. alyssoides* and *C. aprica*, form a well supported clade with the one sampled member of section *Cryptantha, C. capitulifora*, plus a species of section *Krynitzkia, C. collina.* The other *Geocarya* sampled, *C. linearis*, is nested within another clade of *Cryptantha* s. s. 1 (Figs. 1, 2). Members of subgenera *Geocarya* and *Cryptantha* must be sampled more extensively to evaluate their phylogenetic relationships, but our results support the fact that cleistogamy is a derived feature and may have evolved more than once in the complex. The taxa that have been classified in section *Krynitzkia*, distributed in both North and South America, form a polyphyletic assemblage in our analyses, found in both the *Cryptantha* s. s. 1 and *Cryptantha* s. s. 2 clades. Characters that have been used to diagnose *Krynitzkia* include an annual habit and fruits that detach easily as a unit at maturity. However, these features are shared with many other members of *Cryptantha* s. l. More extensive sampling is necessary to elucidate relationships in what has been called section (or subgenus) *Krynitzkia.*

The *Greeneocharis* clade of two species, *Cryptantha circumscissa* and *C. similis,* was found to be well-supported in all analyses (Figs. 1, 2). The genus *Greeneocharis* is diagnosed by having red-pigmented roots (Fig. 6A), a calyx that is basally synsepalous and cirscumscissile in fruit (Fig. 6B); a branched aerial stem system that is more or less as high as wide (Fig. 6D), and bracteate flowers (Fig. 6D); nutlets are not distinctive (Fig. 6C). The two species of *Greeneocharis* show a remarkable resemblance to *Eremocarya*, but these two groups are somewhat distantly related in our analyses (Figs. 1, 2). *Greeneocharis* is consistently sister to a clade of four species of the genus *Plagiobothrys* in all analyses (Figs. 1, 2), but without robust support. Interestingly, the only other known members of Cryptanthinae having circumscissile calyces, as found in *Greeneocharis*, occur in species of *Plagiobothrys.* Further research with additional *Plagiobothrys* taxa may ascertain if this similarity is via common ancestry.

Finally, the *Johnstonella* clade of eight sampled species is well supported in all analyses; these were all previously considered to be part of section or subgenus *Krynitzkia*, although *Cryptantha holoptera* of this clade was originally placed in the genus *Oreocarya* (Greene 1887b). The position of the *Johnstonella* clade varies, being either basal to the rest of Cryptanthinae (Fig. 1), or sister to a clade containing *Amsinckia, Greeneocharis,* and two separate *Plagiobothrys* clades (Fig. 2). The interrelationships of species within the *Johnstonella* clade vary somewhat, although in all analyses the North American *C. costata* and *C. holoptera* are sister taxa, as are the South American *C. diplotricha* and *C. parviflora* (Figs. 1, 2).

*Johnstonella* was described by Brand (1925), who included two species transferred from the genus *Cryptantha*: *Johnstonella racemosa* and *J. inaequata*. Brand diagnosed the genus as perennial, suffrutescent herbs with nutlets that are heteromorphic and with acute margins. The two species recognized by Brand were placed by Johnston (1925, 1927) in his series Angustifoliae, which contained a total of nine North American and two South American species (Table 3). One of the nine North American species in Angustifoliae was *C. micrantha*; however, this species clearly does not belong with the others (based on both morphological and molecular phylogenetic data), and we treat it in the genus *Eremocarya* (see above). Johnston (1925) diagnosed members of series Angustifoliae as having "4, muricate or tuberculate nutlets, dark with pale roughenings, triangular-ovate or triangular-oblong, with sides acute or knife-like or definitely winged, homomorphous or in most species decidedly heteromorphous with odd nutlet abaxial larger and sometimes slightly less roughened than the others; style definitely surpassing the nutlets."

Thus, we propose that the 10 species of Johnston's Angustifoliae (excluding *C. micrantha*) belong in the *Johnstonella*

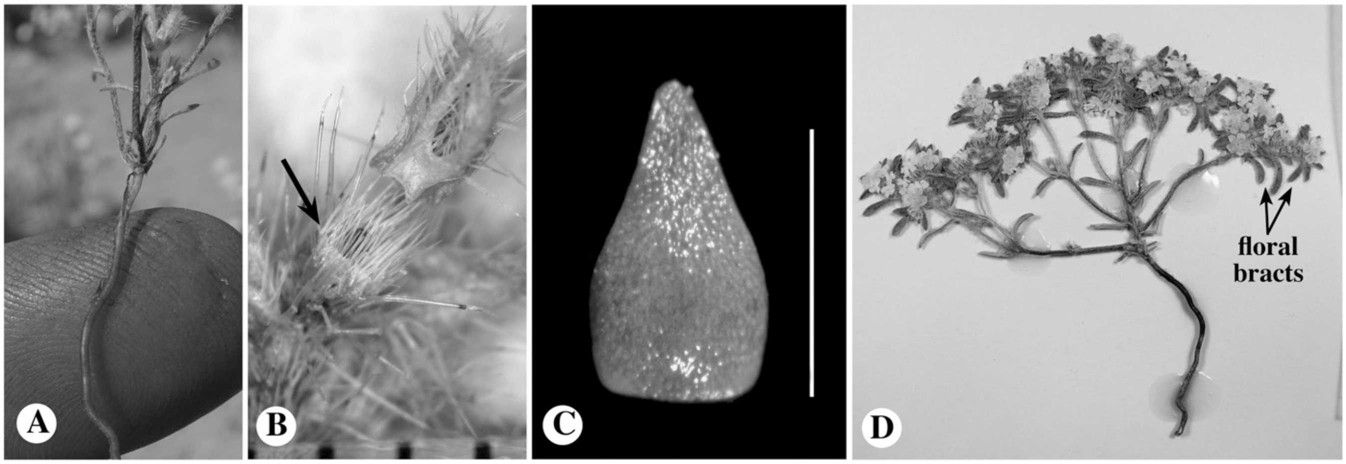

FIG. 6. Diagnostic and/or apomorphic features of resurrected genus *Greeneocharis*. A-C. *C. circumscissa* var. *circumscissa*. A. Red-purple pigmented roots. B. Circumscissile calyx; line of dehiscence at arrow. C. Nutlet, ventral view. D. *C. similis*, showing short, wide aerial branching and floral bracts. Scale bars = 1 mm.

TABLE 3. Species and varieties of *Cryptantha* resurrected or transferred to the genus *Johnstonella* with series classification and data for three key morphological traits. Bold taxa = sequenced for this study. * = South American distribution.

| *Cryptantha* taxon | Series (Johnston 1925, 1927) | Nutlet margin | Nutlet heteromorphism | Nutlet shape |
|---|---|---|---|---|
| *C. angelica* | Angustifoliae | Narrowly winged | Heteromorphic | Triangular-ovate |
| ***C. angustifolia*** | Angustifoliae | Rounded to angled | Heteromorphic (rarely Homo.) | Lance-ovate |
| ***C. costata*** | Angustifoliae | Narrowly winged | Homomorphic | Triangular-ovate |
| ***C. diplotricha**** | Angustifoliae | Narrowly winged | Homomorphic | Triangular-ovate |
| *C. echinosepala* | Maritimae | Rounded | Heteromorphic | Lance-ovate |
| *C. fastigiata* | (not classified) | Narrowly winged | Heteromorphic | Triangular-ovate |
| *C. grayi* var. *cryptochaeta* | Angustifoliae | Rounded | Homomorphic | Lance-ovate |
| *C. grayi* var. *grayi* | Angustifoliae | Rounded | Homomorphic | Lance-ovate |
| *C. grayi* var. *neseotica* | Angustifoliae | Rounded | Homomorphic | Lance-ovate |
| ***C. holoptera*** | Angustifoliae | Narrowly winged | Homomorphic | Triangular-ovate |
| ***C. inaequata*** | Angustifoliae | Narrowly winged | Heteromorphic | Triangular-ovate |
| ***C. micromeres*** | Maritimae | Angled | Heteromorphic | Lance-ovate to Ovate |
| ***C. parviflora**** | Angustifoliae | Angled | Heteromorphic | Lance-ovate to Ovate |
| *C. pusilla* | Angustifoliae | Narrowly winged | Homomorphic | Triangular-ovate |
| ***C. racemosa*** | Angustifoliae | Narrowly winged | Heteromorphic | Triangular-ovate |

clade (see Table 3), given the results of this study (Figs. 1, 2). Although we have sequence data for only seven of these species, we are confident that the others of Johnston's Angustifoliae belong in *Johnstonella*, given their similarity in nutlet morphology. In addition, we propose adding an additional three species to *Johnstonella*: *C. echinosepala, C. fastigiata,* and *C. micromeres*, the last of which was sampled here. *Cryptantha echinosepala* and *C. micromeres* were placed by Johnston (1925) in his series Maritimae, but resemble *Johnstonella* taxa in having heteromorphic, triangular-ovate nutlets with an angled to rounded nutlet margin (Table 3). *Cryptantha fastigiata* was described subsequent to Johnston's series classification; however, he noted that this species is similar to both *C. holoptera* and C. *inaequata*, and would likely have placed it in Angustifoliae. Morphological traits that distinguish *Johnstonella* include often heteromorphic nutlets with prominent, regularly spaced tubercles white in color, a rounded obtuse to acute, non-acuminate apex, and a margin that is often acute, rimmed, or narrowly winged (Table 3; see examples, Fig. 7).

Our results agree with those of Schwarzer (2007) in inferring that *Amsinckia* and *Pectocarya* are monophyletic. However, the cladogram of Schwarzer shows little resolution among the taxa of *Cryptantha* s. l., especially given that only one species of *Johnstonella* and one of *Oreocarya* were sequenced and representatives of *Eremocarya* and *Greeneocharis* were not included.

***Character Evolution and Biogeographic History***—The characters examined in this study are a subset of those traditionally used to delimit taxonomic groups within *Cryptantha* s. l. With regard to plant duration, previous taxonomists (Johnston 1925; Payson 1927; Higgins 1971) hypothesized that the perennial habit of *Oreocarya* was primitive, with the annual *Amsinckia, Cryptantha, Pectocarya,* and *Plagiobothrys* derived from perennial ancestors. This study clearly demonstrates that the perennial habit of *Oreocarya* is derived within Cryptanthinae and apomorphic for that group. Perennial duration may allow these plants to colonize or persist at higher elevations, where many *Oreocarya* occur. However, perenniality has also evolved independently in *Johnstonella* and some members of the *Cryptantha* s. s. 1 clades (Fig. 3A), which do not necessarily occur at high elevation.

Within subfamily Boraginoideae, each of the four ovary lobes generally develops into a 1-seeded nutlet. However, in *Cryptantha* s. l., many taxa consistently exhibit a reduction in number of nutlets per mature fruit, a feature used in the past to circumscribe species. This study reveals that reduction in nutlet number has occurred numerous times in Cryptanthinae, within *Oreocarya* and both the *Cryptantha* s. s. 1 and *Cryptantha* s. s. 2 clades (Fig. 3B). Interestingly, one clade of *Cryptantha* s. s. 1 characterized by reduction in nutlet number is that composed of species from sections *Geocarya* and *Cryptantha,* both of which have cleistogamous flowers. The adaptive significance of reduction in nutlet number is unclear, but could be related to resource allocation in that those taxa with fewer nutlets per fruit have either larger nutlets or more fruits per plant; however, this idea has not been tested.

Nutlet heteromorphism is a trait often weighted highly in the classification of groups within *Cryptantha* s. l. Our study shows that nutlet heteromorphism has evolved multiple times, within the *Johnstonella*, *Cryptantha* s. s. 1, and *Cryptantha* s. s. 2 clades, as well as in the genus *Pectocarya* (Fig. 3C). Although optimization of this character is variable (Fig. 3C), this feature apparently represents an apomorphy for the *Johnstonella* clade, which contains most of the heteromorphic taxa. The adaptive significance of heteromorphism may be related to the fact that the "odd" nutlet, which is usually larger and/or less ornamented, remains firmly attached to the gynobase, whereas the other three "consimilar" nutlets, which are usually smaller and often have rougher sculpturing, are easily detached. This differential attachment enables one propagule per fruit to remain nearer to the parent, and the other three to be more widely dispersed, a syndrome found in many other plants. The potential for germination and survivability of the large "odd" versus "consimilar" nutlets has not been studied.

Smooth nutlets are rare outside of *Cryptantha* s. l., and in our analysis, represent a derived feature, having evolved five to six times independently within the *Cryptantha* s. s. 1, *Cryptantha* s. s. 2, and *Oreocarya* clades (Fig. 3D). This goes against Payson (1927), who speculated that smooth nutlets are "more primitive than roughened ones." Roughened nutlets may be more adapted to animal dispersal (Grau 1983), but this has not been tested; the adaptive significance of smooth nutlets is unknown.

We note that heterostyly and cleistogamy are apomorphic floral features found in various *Cryptantha* s. l. taxa, and we discuss these features in a phylogenetic framework (not

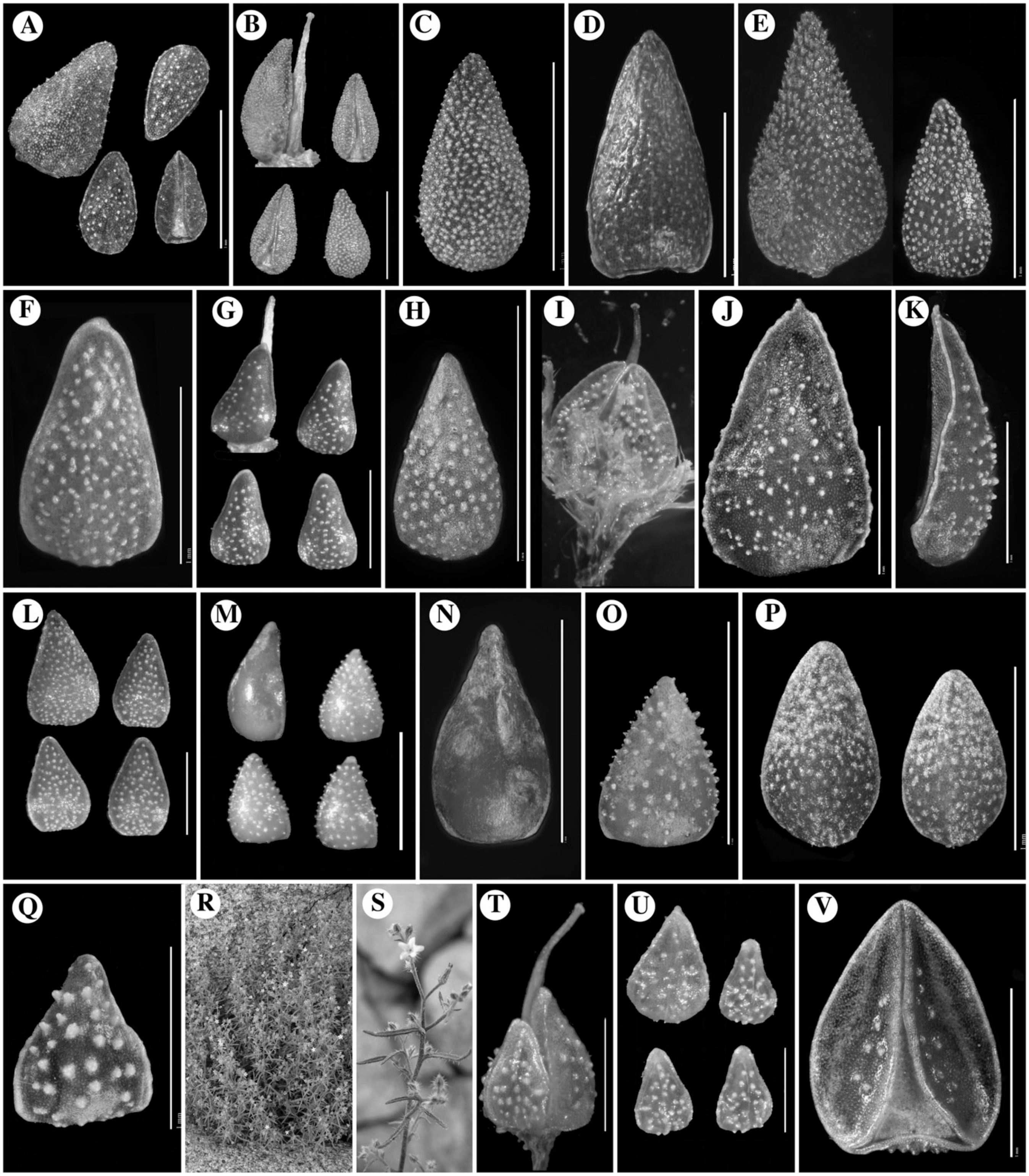

FIG. 7. Members of resurrected genus *Johnstonella*. A. *C. angelica*, with heteromorphic nutlets. B,C. *C. angustifolia*. B. Four, heteromorphic nutlets. C. One of three small nutlets, dorsal view. D. *C. costata,* one of four homomorphic nutlets, dorsal view. E. *C. echinosepala*, with heteromorphic nutlets, one small and one large shown, dorsal view. F. *C. diplotricha*, with homomorphic nutlets; dorsal view shown. G. *C. fastigiata*, heteromorphic nutlets of fruit shown, dorsal view. H. *C. grayi* var. *grayi*, with homomorphic nutlets, dorsal view shown. I-K. *C. holoptera*, with homomorphic nutlets. I. Fruit with four nutlets and projecting style. J. Nutlet, dorsal view. K. Nutlet, side view. L. *C. inaequata*, with heteromorphic nutlets of fruit shown, dorsal view. M-O. *C. micromeres*. M. Heteromorphic nutlets of fruit, dorsal view. N. Large, relatively smooth nutlet, dorsal view. O. One of three small, rough nutlets, dorsal view. P. *C. parviflora*, with heteromorphic nutlets, one of each size shown, dorsal view. Q. *C. pusilla,* one of four homomorphic nutlets shown, dorsal view. R-V. C. *racemosa.* R,S. Plant in the field. T. Fruit, showing heteromorphic nutlets and projecting style. U. Four nutlets of fruit. V. Large nutlet, ventral view. Scale bars = 1 mm.

illustrated). Heterostyly is found in several species of *Oreocarya,* as well as in some members of the genus *Amsinckia* (Ornduff 1976; Ray and Chisaki 1957; Schoen et al. 1997). It has long been known as an outcrossing mechanism (Baker 1966; Yeo 1975; Barrett et al. 2000), and has been studied in detail in some members of *Oreocarya* (Casper 1985).

Cleistogamy is restricted to members of South American sections *Cryptantha* and *Geocarya* of our *Cryptantha* s. s. 1 clade, having evolved twice in our analyses. As with other cleistogamous plants, this feature may be an adaptation enabling plants to reproduce in the absence of pollinators (Grau 1983; Calviño and Galetto. 2003). In section *Geocarya* the highly specialized cleistogamous flowers (“cleistogenes,” sensu Grau 1983) found at ground level may enable the plant to reproduce even if aerial branches are eaten or damaged; in addition, the nutlets of these cleistogenes are considerably larger than those of chasmagamous flowers above, giving seedlings of the former an advantage in their desert habitat (Grau 1983).

Finally, the mostly unidirectional, long-distance dispersal from North to South America supported in this study agrees with scenarios of other American amphitropically distributed taxa (Raven 1963; Grau 1983; Moore et al. 2006). This is most strongly evidenced by our sampling of *C. maritima* from both North and South American localities. These accessions are resolved as monophyletic with strong support, making vicariance a highly unlikely scenario to explain current patterns of distribution and supporting the notion of a relatively recent dispersal event (Raven 1963; Grau 1983). However, formal biogeographic analyses with a substantially greater sample size, particularly of South American taxa, are needed to corroborate this trend.

## Taxonomic Treatment

As discussed earlier, one of the major results of this study is that the genus *Cryptantha* s. l., as circumscribed in recent treatments, is polyphyletic. Although “backbone” relationships of major clades are not always supported in our analyses, we do have good evidence that several members of *Cryptantha* s. l. are more closely related to species of other genera than to other *Cryptantha* s. l. species. One solution to maintaining genera that are monophyletic is to lump all four previously recognized genera, *Amsinckia, Cryptantha, Pectocarya,* and *Plagiobothrys* (and, most likely, the genus *Harpagonella*, not analyzed in this study) into one, large genus of approximately 500 species, which would be called *Cryptantha* by priority of publication. However, this classification would not reflect the diversity in vegetative, floral, and especially fruit morphology that characterizes the major clades denoted here. Thus, we propose to retain *Amsinckia, Pectocarya,* and *Plagiobothrys* (plus *Harpagonella* for now) and to resurrect four genera, *Eremocarya, Greeneocharis, Johnstonella,* and *Oreocarya*. The taxa within our designated *Cryptantha* s. s. 1 clade remain in the genus *Cryptantha,* given that sequenced members of section (subgenus) *Cryptantha* (containing the type of the genus) are nested within this clade. Although members of our *Cryptantha* s. s. 2 group fall into a clade separate from *Cryptantha* s. s. 1 in two of the three anlayses, the interrelationships of these two clades are without robust support. Thus, we retain both the *Cryptantha* s. s. 1 and *Cryptantha* s. s. 2 groups within a reduced *Cryptantha* s. s. genus (see examples in Fig. 8).

***Characterizations and New Combinations*—**The following are diagnostic features of the four proposed resurrected genera. New combinations are given for certain taxa, as required by the International Code of Botanical Nomenclature (McNeill et al. 2006).

EREMOCARYA Greene, Pittonia 1:58. 1887b.

*Eremocarya* is characterized by plants with a red-pigmented root, a branched aerial stem system that is more or less as high as wide, bracteate flowers, a gynobase that is greater in height than the mature nutlets, and a persistent style. Greene (1887b), in validly publishing the genus name, cited two species: the (here designated) type *Eremocarya micrantha* (Torrey) Greene (basionym *Eritrichium micranthum* Torr., Rep. U.S. Mex. Bound., Bot. [Emory] 141. 1859) and *Eremocarya lepida* (A. Gray) Greene (basionym *Eritrichium micranthum* Torr. var. *lepidum* A. Gray, Syn. Fl. N. Amer. 2 (1): 193. 1878). Subsequently, MacBride changed *Eremocarya lepida* in rank, to *Eremocarya micrantha* (Torr.) Greene var. *lepida* MacBr., Proc. Amer. Acad. Arts 51: 545. 1916. Given that there are already validly published names in *Eremocarya*, whether treated as a single species with two varieties (which we recognize here; see Kelley et al. 2012) or as two species, no new combinations are needed.

GREENEOCHARIS Gürke & Harms, Nat.Pflanzenfam. [Engler & Prantl] Regist. 460. 1899. [*Piptocalyx* Torr., ined., non *Piptocalyx* Oliv. ex Benth.; *Wheelerella* G. B. Grant, ined.]

The genus *Greeneocharis* is characterized by plants with a red-pigmented root, a branched aerial stem system that is more or less as high as wide, bracteate flowers, and a calyx that is basally synsepalous and cirscumscissile in fruit. A name exists in the genus for only the type species, *Greeneocharis circumscissa* (Hook. & Arn.) Ryd., Bull. Torrey Bot. Club 36: 677. 1909 (basionym *Lithospermum circumscissum* Hook. & Arn., Bot. Beechey Voy. 370. 1840). Two new combinations are needed for a variety and for a second species, all previously named as members of *Cryptantha*.

1. **Greeneocharis circumscissa** (Hook. & Arn.) Ryd. var. **rosulata** (J. T. Howell) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha circumscissa* (Hook. & Arn.) I. M. Johnst. var. *rosulata* J. T. Howell, Leafl. W. Bot. 6: 104. 1951.—TYPE: U. S. A. California: Inyo Co., Cottonwood Lakes, 12 Aug 1949, *Howell 26227* (holotype: CAS).
2. **Greeneocharis similis** (K. Mathew & P. H. Raven) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha similis* K. Mathew & P. H. Raven, Madroño 16: 168. 1962.—TYPE: U. S. A. California: San Bernardino Co., Mohave Desert, U.S. Highway 395, 8.7 mi n Adelanto, 29 Mar 1958, *H. Lewis and K. Mathew 1113* (holotype: RSA; isotype: UC).

OREOCARYA Greene, Pittonia 1: 57. 1887b.

*Oreocarya* circumscribes a morphologically well-defined group of plants, diagnosed as perennials with a persistent basal rosette of leaves, relatively large flowers, persistent calyces, and relatively large nutlets with a sub-apical ventral groove and smooth, rugulose, to roughened sculpturing. Greene (1887b), in validly publishing the genus name, cited nine species. Of these, we exclude *Oreocarya holoptera* Greene from the genus and treat it as a synonym of *Johnstonella holoptera* (below). Of the remaining eight species cited by

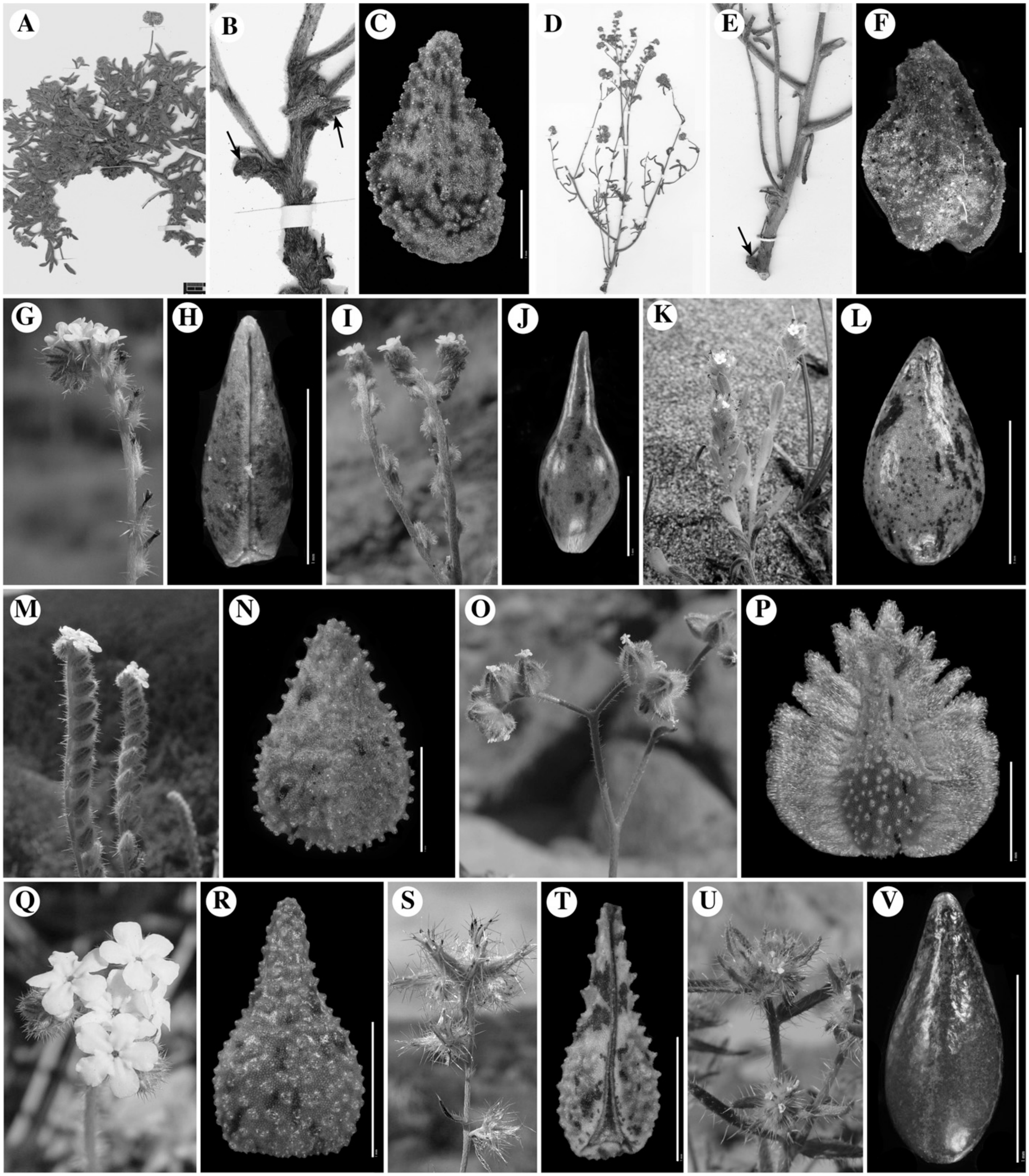

FIG. 8. Exemplars of *Cryptantha* s. s. A-C. Section *Cryptantha*. *C. capituliflora*. A. Whole plant of herbarium specimen. B. Fruits of cleistogamous flowers (arrow). C. Nutlet of chasmogamous flower, dorsal view. D-F. Section *Geocarya*. *C. aprica*. D. Whole plant from herbarium specimen. E. Nutlets of cleistogamous flower (arrow), ground-level of plant. F. Nutlet of chasmogamous flower, dorsal view. G-T. Section *Krynitzkia* (from *Cryptantha* s. s. 1 clade). G,H. *C. clevelandii* var. *c*. G. Inflorescence unit, a circinate, scorpioid cyme. H. Nutlet, ventral view. I,J. *C. flaccida*. I. Inflorescence. J. Nutlet, dorsal view. K-L. *C. leiocarpa* (type species of *Krynitzia*). K. Whole plant in field. L. Nutlet, dorsal view. M,N. *C. muricata* var. *m*. M. Inflorescence. N. Nutlet, dorsal view. O,P. *C. pterocarya* var. *p*. O. Inflorescence. P. Winged nutlet, dorsal view. Q,R. *C. intermedia* var. *i*. Q. Flowers, close-up. R. Nutlet, dorsal view. S,T. *C. nevadensis* var. *nevadensis*. S. Inflorescence. T. Nutlet, ventral view. U,V. Section *Krynitzkia* (from *Cryptantha* s. s. 2 clade). *C. maritima*. U. Inflorescence, showing floral bracts. V. Nutlet, dorsal view. Scale bars = 1 mm.

Greene, we here designate the generic type as *Oreocarya virgata* (Porter) Greene, Pittonia 1: 57. 1887b (basionym: *Eritrichium virgatum* Porter, Prelim. Rep. U.S. Geol. Surv. Montana [Hayden] 479. 1870; TYPE: *C. C. Parry 288*, GH). Most of the approximately 62 described species of *Cryptantha* section or subgenus *Oreocarya* have validly published names in the genus *Oreocarya* (see Payson 1927; Abrams 1951; Higgins 1971; Weber 1987). Twenty-one taxa known to us, however, require new combinations.

3. **Oreocarya atwoodii** (L. C. Higgins) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha atwoodii* L. C. Higgins, Southw. Naturalist 19(2): 127. 1974.—TYPE: U. S. A. Arizona: Coconino Co., 7 mi N of junction of hwy 89 and 164 on hwy 89, 20 May 1970, *N. D. Atwood 2624* (holotype: BRY).

4. **Oreocarya barnebyi** (I. M. Johnst.) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha barnebyi* I. M. Johnston, J. Arnold Arbor. 29: 240. 1948.—TYPE: U. S. A. Utah: Uintah Co., 30 mi east of Ouray, 17 Jun 1947, *H. D. D. Ripley & R. C. Barneby 8748* (holotype: GH).

5. **Oreocarya compacta** (L. C. Higgins) R. B. Kelley, comb. nov. Basionym: *Cryptantha compacta* L. C. Higgins, Great Basin Naturalist 28: 196–197. 1968.—TYPE: U. S. A. Utah: Millard Co., ca. 8 mi west of Desert Range Experimental Station Headquarters along Hwy 21, 100 m west of pass at north end of the Needle Range, 18 Jun 1968, *L. C. Higgins 1613* (holotype: BRY; isotypes: GH, LL, MO, NY, RSA, UTC).

6. **Oreocarya crassipes** (I. M. Johnst.) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha crassipes* I. M. Johnston, J. Arnold Arbor. 20: 397. 1939.—TYPE: U. S. A. Texas: Brewster Co., 6.5 miles east of Agua Fria Springs, 13 Apr 1936, *V. L. Cory 18613* (holotype: GH).

7. **Oreocarya creutzfeldtii** (S. L. Welsh) R. B. Kelley, comb. nov. Basionym: *Cryptantha creutzfeldtii* S. L. Welsh, Great Basin Naturalist 42: 203. 1982.—TYPE: U. S. A.: Utah, Emery Co., T21S, R6E, S22, ca 1.5 mi nw hwy 10, along dirt road at Muddy Creek historical marker, on slope S of canal, 6,400 ft, 14 May 1981, *S. L. Welsh 20470* (holotype: BRY; isotypes: CAS, NY, RSA, UC).

8. **Oreocarya fulvocanescens** (S. Wats.) Greene var. **nitida** (Greene) R. B. Kelley, comb. nov., stat. nov. Basionym: *Oreocarya nitida* Greene, Pl. Baker. [Greene] 3: 21. 1901.—TYPE: U. S. A.: Colorado, Mesa County, Gunnison Watershed, Deer Run, 11 Jun 1901, *C. F. Baker 95* (holotype: RSA; isotypes: E, MO, NY, RM, UC, US).

9. **Oreocarya grahamii** (I. M. Johnst.) R. B. Kelley, comb. nov. Basionym: *Cryptantha grahamii* I. M. Johnston, J. Arnold Arbor. 18: 23. 1937.—TYPE: U. S. A. Utah: Uinta Co., bench west of Green River north of mouth of Sand Wash, 4,500 ft, 28 May 1933, *E. H. Graham 7924* (holotype: GH).

10. **Oreocarya hypsophila** (I. M. Johnst.) Hasenstab & M. G. Simpson. comb. nov. Basionym: *Cryptantha hypsophila* I. M. Johnston, J. Arnold Arbor. 20: 395. 1939.—TYPE: U. S. A. Idaho: Blaine Co., crest of high ridge, head of Boulder Creek, Sawtooth National Forest, Sawtooth Mountains, 11,000 ft, 6 Aug 1937, *J. W. Thompson 14129* (holotype: GH; isotype: WTU).

11. **Oreocarya johnstonii** (L. C. Higgins) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha johnstonii* L. C. Higgins, Great Basin Naturalist 28: 195. 1968.—TYPE: U. S. A. Utah: Emery Co., from Woodside to Castle Dale, 25 May 1968, *L. C. Higgins 1310* (holotype: BRY; isotypes: CAS, GH, NY).

12. **Oreocarya ochroleuca** (L. C. Higgins) R. B. Kelley, comb. nov. Basionym: *Cryptantha ochroleuca* L. C. Higgins, Great Basin Naturalist 28: 197–198. 1968.—TYPE: U. S. A.: Utah: Garfield Co., on outcrop 100 m south of Red Canyon Campground in southwestern Garfield Co., 21 Jul 1968, *L. C. Higgins 1788* (holotype: BRY; isotypes: GH, NY).

13. **Oreocarya roosiorum** (Munz) R. B. Kelley, Hasenstab, and M. G. Simpson, comb. nov. Basionym: *Cryptantha roosiorum* Munz, Aliso 3: 124. 1955.—TYPE: U. S. A.: California: Inyo Co., crest of Inyo Mts., 3 mi east of Badger Flat, 10,600 ft, 13 Aug 1953, *J. C. Roos & A. R. Roos 6015* (holotype: RSA; isotypes: CAS, GH).

14. **Oreocarya schoolcraftii** (Tiehm) R. B. Kelley, comb. nov. Basionym: *Cryptantha schoolcraftii* Tiehm, Brittonia 38(2): 104. 1986.—TYPE: U. S. A.: Nevada, Washoe Co., Yellow Hills area, 1 road mile N of Bernards Corall, 23 Jun 1984, *A. Tiehm 8775* (holotype: NY; isotypes: CAS, MO, RSA).

15. **Oreocarya semiglabra** (Barneby) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha semiglabra* Barneby, Leafl. W. Bot. 3: 197. 1943.—TYPE: U. S. A. Arizona: Coconino Co., 2 miles E of Fredonia, 5 Jun 1942, *Ripley and Barneby 4829* (holotype: CAS; isotype: GH).

16. **Oreocarya shackletteana** (L. C. Higgins) R. B. Kelley, comb. nov. Basionym: *Cryptantha shackletteana* L. C. Higgins, Great Basin Naturalist 29: 28. 1969.—TYPE: U. S. A.: Alaska, Southeast Fairbanks Co., on steep south-facing slope of Eagle Bluff, about 1 mile northwest of Eagle, 26 July 1968, *S. L. Welsh and G. Moore 8629* (holotype: BRY).

17. **Oreocarya sobolifera** (Payson) R. B. Kelley, comb. nov. Basionym: *Cryptantha sobolifera* Payson, Ann. Missouri Bot. Gard. 14: 305. 1927.—TYPE: U. S. A.: Montana, Glacier Co., upper Marias Pass, 6,000 ft, 10 Sep 1909, *M. E. Jones s. n.* (holotype: RSA; isotype: GH).

18. **Oreocarya subcapitata** (Dorn & Lichvar) R. B. Kelley, comb. nov. Basionym: *Cryptantha subcapitata* Dorn & Lichvar, Madroño 28(3): 159. 1981.—TYPE: U. S. A.: Wyoming; Fremont Co.; Just west of Boysen Dam, 23 Jun 1980, *R. D. Dorn 3459* (holotype: RM; isotype: NY).

19. **Oreocarya suffruticosa** (Torrey) Greene var. **arenicola** (L. C. Higgins & S. L. Welsh) R. B. Kelley, comb. nov. Basionym: *Cryptantha cinerea* (Greene) Cronquist var. *arenicola* L. C. Higgins & S. L. Welsh, Great Basin Naturalist 46: 255. 1986.—TYPE: USA: Utah. Kane County. T41S, R5W, S26, Johnson Canyon, Lone Pine Point, 1,830 m, 6 Jun 1984, *L. C. Higgins 14296* (holotype: BRY).

20. **Oreocarya suffruticosa** (Torrey) Greene var. **laxa** (J. F. Macbr.) R. B. Kelley, comb. nov. Basionym: *Oreocarya multicaulis* (Torr.) Greene var. *laxa* J. F. Macbr., Contr. Gray Herb. 48: 35. 1916.—TYPE: MEXICO: Chihuahua, near Paso del Norte, 20 Sep 1886, *C. G. Pringle 776* (holotype: GH; isotypes: E, LL, MICH, MO, NY, PHIL, US).

21. **Oreocarya suffruticosa** (Torrey) Greene var. **pustulosa** (Rydb.) R. B. Kelley, comb. nov., stat. nov. Basionym: *Oreocarya pustulosa* Rydb., Bull. Torrey Bot. Club 40: 480. 1913.—TYPE: USA: Utah. Hammond Canyon, Elk Mountains, 31 Jul 1911, *P. A. Rydberg 9320* (holotype: NY).

22. **Oreocarya suffruticosa** (Torrey) Greene var. **setosa** (M. E. Jones) R. B. Kelley, comb. nov. Basionym: *Krynitzkia multicaulis* var. *setosa* M. E. Jones, Contr. W. Bot. 13: 4. 1910.—TYPE: U. S. A.: Utah, near Fort Cove, 27 Jun 1901, *M. E. Jones s. n.* (holotype: RSA).

23. **Oreocarya welshii** (K. H. Thorne & L. C. Higgins) R. B. Kelley, comb. nov. Basionym: *Cryptantha welshii* K. H. Thorne & L. C. Higgins, Great Basin Naturalist 42(2): 196. 1982.—TYPE: U. S. A.: Nevada, Nye County, ca. 2.1 miles from Sunnyside, down Hot Creek Campground Road, 5 Jun 1979, *K. H. Thorne 578* (holotype: BRY; isotypes: NY, WTU).

JOHNSTONELLA Brand, Repert. Spec. Nov. Regni Veg. 21: 249. 1925.

*Johnstonella* consists of plants with nutlets that are usually triangular or ovate (rarely lance-ovate) in shape, usually have a “knife-like,” sharply angled, and often narrowly-winged (rarely rounded) margin, the nutlets of most species are heteromorphic in size and shape. The nutlet sculpturing often consists of prominent, regularly spaced, whitish tubercles, although in some taxa the tubercles are smaller and more numerous. Two species, one with two varieties, have existing names in *Johnstonella*: *J. racemosa* (I. M. Johnston) Brand (designated the type for the genus; see Johnston 1925) and *J. inaequata* (Watson) Brand (Brand 1925). *Johnstonella racemosa* is perennial in duration, which is rare in the Cryptanthinae outside of *Oreocarya*. (A variety of this species, *J. racemosa* var. *lignosa* (I. M. Johnst.) Brand, has not been recognized as different in recent treatments.) New combinations are needed for eleven species (one with three varieties), recognized here as members of this genus (see earlier discussion).

24. **Johnstonella angelica** (I. M. Johnston) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha angelica* I. M. Johnst., Proc. Calif. Acad. Sci. ser. 4, 12: 1143. 1924.—TYPE: MEXICO. Baja California: Angel de la Guarda Island, opposite Pond Island, 30 Jun 1921, *Johnston 4221* (holotype: CAS; isotypes: CAS, GH, UC, US).

25. **Johnstonella angustifolia** (Torrey) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Eritrichium angustifolium* (Torrey) Greene, Pacif. Rail. Rep. 5: 363. 1857.—TYPE: U. S. A. Arizona: Yuma Co., Fort Yuma, 1853, *Thomas* (holotype: NY).

26. **Johnstonella costata** (Brandegee) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha costata* Brandegee, Bot. Gaz. 27: 453. 1899.—TYPE: U. S. A. California: San Diego Co., Borrego Springs, 18 Apr 1859, *J. S. Brandegee* (holotype: UC).

27. **Johnstonella diplotricha** (Phil.) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Eritrichium diplotrichum* Phil., Anales Mus. Nac., Santiago de Chile 1891: 57.—TYPE: ARGENTINA. Los Andes: between Antofagasta and Calalaste, Jan 1885, *F. Philippi* (holotype: MS; isotypes: GH).

28. **Johnstonella echinosepala** (J. F. Macbr.) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha echinosepala* J. F. Macbr., Contr. Gray Herb. 56: 57. 1918. —TYPE: MEXICO. Lower California [Baja California Sur]: Magdalena Island, 1 Mar 1913, *C. R. Orcutt 15* (holotype: GH).

29. **Johnstonella fastigiata** (I. M. Johnston) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha fastigiata* I. M. Johnst., J. Arnold Arbor. 20: 388. 1939.—TYPE: MEXICO. Baja California Norte [Baja California], Las Animas Bay. 3 Mar 1921, *I. M. Johnston 3505* (holotype: GH).

30. **Johnstonella grayi** (Vasey & Rose) Hasenstab & M. G. Simpson var. **cryptochaeta** (J. F. MacBr.) Hasenstab & M. G. Simpson, comb. nov., Basionym: *Cryptantha micromeres* (A. Gray) Greene var. *cryptochaeta* J. F. Macbr., Contr. Gray Herb. 1916. n. ser. 48: 46.—TYPE: MEXICO. Baja California [Sur]: San Jose del Cabo, Jun 1897, *A. W. Anthony 347* (holotype: GH).

31. **Johnstonella grayi** (Vasey & Rose) Hasenstab & M. G. Simpson var. **grayi**, comb. nov. Basionym: *Krynitzkia grayi* Vasey & Rose, Proc. U. S. Natl. Mus. 11: 596. 1888.—TYPE: MEXICO. Baja California [Sur]: Lagoon Head, 6–15 Mar 1889, *E. Palmer 801* (holotype: NY; isotype: GH, UC).

32. **Johnstonella grayi** (Vasey & Rose) Hasenstab & M. G. Simpson var. **nesiotica** (I. M. Johnston) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Cryptantha grayi* (Vasey & Rose) J. F. Macbr. var. *nesiotica* I. M. Johnst., Proc. Calif. Acad. Sci. ser. 4, 12: 1146. 1924.—TYPE: MEXICO. Baja California Sur: San Francisco Island, 30 May 1921, *I. M. Johnston 3947* (holotype: CAS; isotypes: GH, UC, US).

33. **Johnstonella holoptera** (A. Gray) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Eritrichium holopterum* A. Gray, Proc. Amer. Acad. Arts 12: 81. 1877.—TYPE: U. S. A. Arizona: La Paz Co., Ehrenberg, 1876, *Palmer* (holotype: GH).

34. **Johnstonella micromeres** (A. Gray) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Eritrichium micromeres* A. Gray, Proc. Amer. Acad. Arts 19: 90. 1883.—TYPE: U. S. A. California: Santa Cruz Co., Santa Cruz, *M. E. Jones 2472* (holotype: GH).

35. **Johnstonella parviflora** (Phil.) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Eritrichium parviflorum* Phil., Fl. Atacam. 39. 1860.—TYPE: CHILE. Caldera, Dec 1853, *Philippi* (holotype: MS).

36. **Johnstonella pusilla** (Torrey & A. Gray) Hasenstab & M. G. Simpson, comb. nov. Basionym: *Eritrichium pusillum* Torr. & A. Gray, Pacif. Rail. Rep. 2: 171. 1856.—TYPE: U. S. A. Texas: Midland Co., Llano Estacado, 30 Mar 1852, *Pope* (holotype: NY).

## A KEY TO THE GENERA OF THE CRYPTANTHINAE

A key to the genera of the Cryptanthinae is presented here, modified (in part) from Kelley (2012) and Kelley et al. (2012). We note that the genus *Plagiobothrys* s. l. is polyphyletic in our study and will likely require segregation into separate genera in the future.

1. Nutlets spreading . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
    2. Calyx lobes in fr unequal, upper 2 >> others, partly fused, arched over 1 nutlet, with 5–10 stout spines each with hooked bristles; nutlets . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Harpagonella*

2\. Calyx lobes in fr ± equal or, if unequal, upper 2 > others, free, not arched over 1 nutlet, without spines but with hooked or straight prickles; nutlets gen 4 . . . . . . . . *Pectocarya*
1\. Nutlets ± erect . . . . . . . . 3
3\. Corolla tube, limb orange or yellow (red-orange); cotyledons 2-lobed; cleistogenes not present . . . . . . . . *Amsinckia*
3\. Corolla white, rarely yellow; cotyledons not usually lobed, if lobed cleistogenes present . . . . . . . . 4
4\. Nutlets with a ventral (adaxial) keel . . . . . . . . *Plagiobothrys* s. l.
4\. Nutlets with a ventral (adaxial) groove (*Cryptantha* s. l.) . . . . . . . . 5
5\. Plants annual, gen wider than tall, often rounded to cushion-like; taproot red or purple when dry (often staining herbarium paper); floral bracts present . . . . . . . . 6
6\. Calyx basally fused, tubular, tube circumscissile in fruit; gynobase < nutlet . . . . . . . . *Greeneocharis*
6\. Calyx of distinct sepals, intact in fruit; gynobase > nutlet . . . . . . . . *Eremocarya*
5\. Plants annual, biennial, or perennial, gen taller than wide, rarely rounded to cushion–like; taproot usually not red or purple when dry; flower bracts absent or rarely present . . . . . . . . 7
7\. Plants biennial or perennial; vegetative leaves basal or tufted; nutlets smooth, rugulose, or variously roughened, apically broadly rounded to obtuse,ventral groove apex well below nutlet apex . . . . . . . . *Oreocarya*
7\. Plants annual or rarely biennial or perennial; vegetative leaves generally cauline, rarely basal; nutlets smooth, papillate, tuberculate, or muricate, apically narrowly acute to acuminate, ventral groove apex almost to nutlet apex . . . . . . . . 8
8\. Plants annual, rarely biennial (perennial in *J. racemosa*); flowers always chasmogamous; nutlets ovate or triangular-ovate, often heteromorphic in size and sculpturing, margin angled (rarely rounded), often narrowly winged, densely or sparsely tuberculate, tubercles usually whitish . . . . . . . . *Johnstonella*
8\. Plants annual; flowers chasmogamous or cleistogamous; nutlets lanceolate, lance-ovate, or ovate, usually homomorphic, margin rounded or angled, not winged (except *C. oxygona, C. pterocarya* with generally toothed to undulate wings), smooth or papillate/tuberculate, if tuberculate, tubercles gen. not whitish . . . . . . . . *Cryptantha* s. s.

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Appendix 1. Taxon, collector/collection number, sample number (if more than one of a given taxon), herbarium accession, and GenBank accession numbers for specimens sequenced and analyzed in this study.

*Amsinckia eastwoodiae* J. F. Macbride, *Helmkamp 6530* (SD 148214), JQ513391, JQ582293; *Amsinckia intermedia* Fisch. & C. A. Mey., *Simpson 2791* (SDSU 17575), JQ513392, JQ582294; *Amsinckia spectabilis* Fisch. & C. A. Mey. var. *microcarpa* (Greene) Jeps. & Hoover, *Helmkamp 8336* (SD 178190), JQ513393, JQ582295; *Amsinckia tessellata* A. Gray var. *t.*, *Hendrickson 525* (SD 173641), JQ513394, JQ582296; *Cryptantha affinis* (A. Gray) Greene, *Reiser s. n.* (SDSU 12421), JQ513395, JQ582297; *Cryptantha alyssoides* (A. DC.) Reiche, *Tiellier 5210* (CONC 156553), JQ513396, JQ582298; *Cryptantha angustifolia* (Torrey) Greene, *Simpson 8III98A* (SDSU 13030), JQ513397, JQ582299; *Cryptantha aprica* (Phil.) Reiche, *Teillier 1057* (MO 3636210), JQ513398, JQ582300; *Cryptantha capituliflora* (Clos) Reiche, *Kalin Arroyo 991122* (CONC 166914), JQ513399, JQ582301; *Cryptantha chaetocalyx* (Phil.) I. M. Johnst., *Munoz 2745* (MO 4317604), JQ513400, JQ582302; *Cryptantha cinerea* (Greene) Cronquist, *Rebman 2994* (SD 137256), JQ513401, JQ582303; *Cryptantha circumscissa* (Hook. & Arn.) I. M. Johnst. var. *circumscissa* 1, *Reiser s. n.* (SD 134493), JQ513402, JQ582304; *Cryptantha circumscissa* (Hook. & Arn.) I. M. Johnst. var. *circumscissa* 2, *Simpson 3108* (SDSU 18627), JQ513403, JQ582305; *Cryptantha collina* (Phil.) Reiche, *Zollner 8570* (MO 2614248), JQ513404, JQ582306; *Cryptantha confertiflora* (Greene) Payson, *Christie 229* (SD 140881), JQ513405, JQ582307; *Cryptantha costata* Brandegee, *Sanders 6173* (SD 124729), JQ513406, JQ582308; *Cryptantha decipiens* (M. E. Jones) A. A. Heller, *Rebman 11397* (SD 171652), JQ513407, JQ582309; *Cryptantha diffusa* (Phil.) I. M. Johnst., *Munoz 2745* (MO 4317604), JQ513408, JQ582310; *Cryptantha diplotricha* (Phil.) Reiche, *Zollner s. n.* (MO 2415685), JQ513409, JQ582311; *Cryptantha dumetorum* (A. Gray) Greene, *Sanders 7028* (SD 125659), JQ513410, JQ582312; *Cryptantha fendleri* (A. Gray) Greene, *Hogan s. n.* (COLO 457666), JQ513411, JQ582313; *Cryptantha flava* (A. Nels.) Payson, *Anderson DA9905* (COLO 499734), JQ513412, JQ582314; *Cryptantha foliosa* (Greene) Greene, *Rebman 6803* (SD 155048), JQ513413, JQ582315; *Cryptantha ganderi* I. M. Johnst., *Barth 183* (SD 169361), JQ513414, JQ582316; *Cryptantha globulifera* (Clos) Reiche, *Martinez 31492* (CONC 124411), JQ513415, JQ582317; *Cryptantha granulosa* (Ruiz & Pav.) I. M. Johnst., *Weigend 2000/642* (MO 6045195), JQ513416, JQ582318; *Cryptantha holoptera* (A. Gray) J. F. Macbr., *Helmkamp 2588* (SD 144002), JQ513417, JQ582319; *Cryptantha humilis* (A. Gray) Payson, *Honer 1089* (RSA 682210), JQ513418, JQ582320; *Cryptantha inaequata* I. M. Johnst., *Boyd 2221* (RSA 457775), JQ513419, JQ582321; *Cryptantha intermedia* (A. Gray) Greene var. *i.*, *Hasenstab 16* (SDSU 18348), JQ513420, JQ582322; *Cryptantha leiocarpa* (Fischer & C.A. Mey.) Greene, *Helmkamp 8417* (RSA 710334), JQ513421, JQ582323; *Cryptantha linearis* (Colla) Greene, *Kalin Arroyo 993602* (CONC 163475), JQ513424, JQ582326; *Cryptantha maritima* (Greene) Greene 1, *Simpson 3043* (SDSU 18446), JQ513425, JQ582327; *Cryptantha maritima* (Greene) Greene 2, *Biurrun 6185* (SI 87769), JQ513426, JQ582328; *Cryptantha micrantha* (Torr.) I. M. Johnst. var. *lepida* (A. Gray) I. M. Johnst. 1, *Wolfinger 12* (SD 189566), JQ513422, JQ582324; *Cryptantha micrantha* (Torr.) I. M. Johnst. var. *lepida* (A. Gray) I. M. Johnst. 2, *Simpson 2816* (SDSU 17572), JQ513423, JQ582325; *Cryptantha micrantha* (Torr.) I. M. Johnst. var. *m., Rebman 11358* (SD 168431), JQ513427, JQ582329; *Cryptantha micromeres* (A. Gray) Greene, *Lauri 401* (SDSU 16695), JQ513428, JQ582330; *Cryptantha minima* Rydberg, *Freeman 14292* (COLO 503599), JQ513429, JQ582331; *Cryptantha mohavensis* (Greene) Greene, *Gross 2273* (RSA 712528), JQ513430, JQ582332; *Cryptantha nemaclada* Greene, *Sanders 20412* (RSA 614189), JQ513431, JQ582333; *Cryptantha nevadensis* A. Nels. & P. B. Kennedy var. *nevadensis*, *Gregory 1305* (SD 172713), JQ513432, JQ582334; *Cryptantha parviflora* (Phil.) Reiche, *van der Werff 20532* (MO 6128118), JQ513433, JQ582335; *Cryptantha peruviana* I. M. Johnst., *van der Werff 20513* (MO 6128115), JQ513434, JQ582336; *Cryptantha pterocarya* (Torrey) Greene var. *cycloptera* (Greene) J. F. Macbr., *Burch 1IV95B* (SDSU 14135), JQ513435, JQ582337; *Cryptantha racemosa* (A. Gray) Greene, *Rebman 6305* (SDSU 15452), JQ513436, JQ582338; *Cryptantha roosiorum* Munz, *DeDecker 4846* (RSA 346621), JQ513437, JQ582339; *Cryptantha scoparia* A. Nels., *DeDecker 5977* (RSA 626035), JQ513438, JQ582340; *Cryptantha similis* K. Mathew & P. H. Raven, *Henrickson 17339* (RSA 272392), JQ513439, JQ582341; *Cryptantha similis* K. Mathew & P. H. Raven, *Sanders 21776* (RSA 660941), JQ513440, JQ582342; *Cryptantha stricta* (Osterhout) Payson, *Orthner 977* (COLO 475416), JQ513441, JQ582343; *Cryptantha thyrsiflora* (Greene) Payson, *Holt 744* (COLO 521709), JQ513442, JQ582344; *Cryptantha traskiae* I. M. Johnst., *Junak SN597* (SD 171991), JQ513443, JQ582345; *Cryptantha weberi* I. M. Johnst., *Rondeau s. n.* (COLO 467583), JQ513444, JQ582346; *Cynoglossum occidentale* A. Gray, *Howe 5108* (SDSU 2648), JQ513446, JQ582347; *Hackelia floribunda* (Lehm.) I. M. Johnst., *Reveal 2390* (SD 103849), JQ513445, JQ582347; *Myosotis discolor* Pers., *Ahart 9593* (JEPS 103365), JQ513447, JQ582358; *Myosotis laxa* Lehm., *Ahart 13408* (JEPS 110466), JQ513448, JQ582359; *Pectocarya anomola* I. M. Johnston, *van der Werff 20623* (MO 6128114), JQ513449, JQ582348; *Pectocarya penicillata* (Hook. & Arn.) A. DC., *Lauri 189* (SDSU 16855), JQ513450, JQ582349; *Pectocarya peninsularis* I. M. Johnst., *Barth 135* (SD 169347), JQ513451, JQ582350; *Phacelia crenulata* S. Watson var. *minutiflora* (Munz) Jeps., *Guilliams 570* (SDSU 19853), JQ513452, JQ582360; *Phacelia distans* Benth., *Guilliams 692* (SDSU 19859), JQ513453, JQ582361; *Plagiobothrys congestus* (Wedd.) I. M. Johnston, *Beck s. n.* (MO 5183035), JQ513454, JQ582351; *Plagiobothrys hispidus* A. Gray, *Taylor 16824* (UC 1731379), JQ513455, JQ582352; *Plagiobothrys jonesii* A. Gray, *Sanders 27585* (RSA 709039), JQ513456, JQ582353; *Plagiobothrys kingii* (S. Watson) A. Gray var. *k., Honer 992* (RSA 680594), JQ513457, 0; *Plagiobothrys mollis* (A. Gray) I. M. Johnst. var. *mollis, Ahart 9211* (JEPS 102650), JQ513458; *Plagiobothrys myosotoides* (Lehm.) Brand, *van der Werff 20645* (MO 6128112), JQ513459, JQ582356; *Plagiobothrys shastensis* A. Gray, *Ahart 11672* ( JEPS 107359), JQ513460, JQ582357.