

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 chasmogamous 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 analyses, 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. *lepida* 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.

GRENEOCHARIS 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 circumsessile 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, Leaf. 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