# Chromosome numbers in some cacti of Western North America — IX

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**Abstract:** Chromosome numbers are determined for 524 individuals belonging to 107 taxa, including nothotaxa, within Cactaceae. Chromosome morphology was uniform within and among species. Nine unnamed nothotaxa and one previously named nothotaxon, *Cylindropuntia* ×*vivipara*, have chromosome numbers reported for the first time, and new chromosome numbers are reported for three taxa. Five putative *Cylindropuntia* hybrids are reported here for the first time: *C. alcahes* var. *gigantensis* × *C. lindsayi*, *C. bernardina* × *C. echinocarpa, C. leptocaulis* × *C. ramosissima*, *C. echinocarpa* × *C. ramosissima*, and *C. echinocarpa* × *C. ganderi* var. *ganderi.* Two putative *Opuntia* hybrids of less-certain origin are reported here: *O. azurea* var. *discolor* × *O. rufida*, and *O. chlorotica* × *O. engelmannii*. Two putative hybrids are reported for *Echinocereus*: *E. arizonicus* subsp. *arizonicus* × *E. bonkerae* subsp. *bonkerae* and *E. coccineus* subsp. *coccineus* × *E. yavapaiensis*. All chromosome number determinations reported to date are tabulated for *Cylindropuntia*, *Grusonia*, and selected taxa within *Echinocereus*. The significance of these data is discussed, including apparent correlations among polyploidy, subdioecy, sexual reproduction, and apomixis. We introduce six new combinations, one nothospecies designation, and a lectotypification for one taxon.

**Keywords:** Cactaceae, *Cylindropuntia, Echinocereus, Grusonia*, *Opuntia*, chromosome numbers, evolution, polyploidy, hybridization, taxonomy, nomenclature

## INTRODUCTION

The cytogenetics of Cactaceae has been studied extensively over the previous century (Arakaki et al. 2007; Assis et al. 2003; Baker 2006, 2016; Baker & Pinkava 1987; Baker et al. 2009; Baker & Cloud-Hughes 2014; Bhattacharyya 1970, Cid & Palomino 1996; Cohen & Tel-Zur 2012; Cota & Phibrick 1994; Das et al. 1997, 1998a, 1998b; Donati 2011, 2017a, 2017b; Fenstermacher 2016; Gadella et al. 1979; Gutiérrez-Flores et al. 2018, Las Peñas et al. 2014, 2017; Majure et al. 2012a, 2012b, 2012c; Moreno et al. 2015; Negrón-Ortiz 2007; Palomino 2016; Parfitt 1987, 1997; Pinkava & McLeod 1971; Pinkava et al. 1973, 1977, 1985, 1992a, 1992b, 1998; Pinkava & Parfitt 1982; Powell & Weedin 2001, 2005; Ross 1981; Schlumpberger & Renner 2012; Ward 1984; Weedin & Powell 1978a, 1978b, 1980; Weedin et al. 1989, Wellard 2016). The general degree of polyploidy has been estimated for most genera (Pinkava et al. 1998). In this paper, we report additional chromosome determinations for North American cacti, including new counts for some taxa and putative hybrids. We also discuss correlations among polyploidy, apomixis, dioecy, and geographical distribution for *Cylindropuntia*, *Echinocereus*, and *Grusonia* and how these factors may have influenced their evolution.

## MATERIALS AND METHODS

Flower buds were collected from individuals occurring in native habitats or placed in cultivation (Southwest Botanical Research, Chino Valley and Tucson, Arizona and Desert Botanical Garden, Phoenix, Arizona). Buds were fixed in chloroform, 95% ethanol, and glacial acetic acid (3:3:1 or 0:3:1) for at least 24 hrs then transferred to 70% ethanol and refrigerated. In general, best results were obtained from buds transferred to 70% ethanol within 48 hrs. Anthers were squashed in acetocarmine and mounted in Hoyer's medium (Beeks 1955). Most squashes were done using a metal vise. Mitotic counts (2*n*) were obtained from root tips fixed and either stained directly with alcoholic hydrochloric acid-carmine (Snow 1963) or macerated in 1N HCL and stained with acetocarmine (Darlington and La Cour 1962). Voucher specimens (Appendix 1) are deposited in ASU unless otherwise stated. Most specimens included duplicates that will be distributed to various herbaria.

Morphological measurements, as necessary for identification and taxonomic review, were taken from both live and herbarium material. Herbarium material included specimens from ARIZ, ASC, ASU, BRY, DES, MICH, MO, NY, NMC, RENO, RM, RSA, SRSC, UNLV, UNM, US, UT, and UTEP.

**Table 1.** Tabulation of chromosome determinations to date for *Cylindropuntia*, by taxon, by ploidy level. Only reports that were vouchered with herbarium specimens are included. Approximate determinations are included.

| Taxon | 2× | 3× | 4× | 5× | 6× | 7× | 8× |
|---|---|---|---|---|---|---|---|
| *C. abyssi* (Hester) Backeberg | 5 | | | | | | |
| *C. abyssi* × *C. acanthocarpa* var. *acanthocarpa* | 1 | | | | | | |
| *C. acanthocarpa* var. *acanthocarpa** | 21 | | | | | | |
| *C. acanthocarpa* var. *ramosa*** | 38 | | | | | | |
| *C. acanthocarpa* var. *thornberi* | 15 | | | | | | |
| *C. acanthocarpa* var. *acanthocarpa* × *C. multigeniculata* | 3 | | | | | | |
| *C. acanthocarpa* var. *ramosa* × *C. spinosior* | 9 | | | | | | |
| *C. acanthocarpa* var. *acanthocarpa* × *C. whipplei* | 2 | | | | | | |
| *C. alcahes* (F. A. C. Weber) F. M. Knuth var. *alcahes* | 33 | 3 | | | | | |
| *C. alcahes* var. *burrageana* (Britton & J. N. Rose) Rebman | 1 | | | | | | |
| *C. alcahes* var. *gigantensis* Rebman | 3 | | | | | | |
| *C. alcahes* var. *mcgillii* Rebman | 4 | 2*** | | | | | |
| *C. alcahes* var. *gigantensis* × *C. lindsayi* | | | 1 | | | | |
| C. *anteojoensis* (Pinkava) E. F. Anderson × *C. leptocaulis* | | | 1 | | | | |
| *C. arbuscula* (Engelmann) F. M. Knuth | | | | | 10 | | |
| *C. arbuscula* × *C. leptocaulis* | | | | 1 | | | |
| *C. bernardina* (*C. californica* var. *parkeri*) | 8 | | | | | | |
| *C. bigelovii* | 30 | 74 | | | | | |
| *C. californica* var. *californica* | 3 | | | | | | |
| *C. californica* var. *rosarica* (G. E. Lindsay) Rebman | 4 | | | | | | |
| *C. californica* var. *parkeri* × *C. echinocarpa* | 1 | | | | | | |
| *C. calmalliana* (J. M. Coulter) F. M. Knuth | | | | | 8 | | |
| *C.* ×*campii* (M. A. Baker & Pinkava) Pinkava | | | 1 | | | | |
| *C.* ×*cardenche* (Griffiths) Pinkava & M. A. Baker | | | 2 | | | | |
| *C. cholla* (F. A. C. Weber) F. M. Knuth | 16 | 1 | 1 | | | | |
| *C. chuckwallensis* M. A. Baker & M. Cloud-Hughes | | | | | 13 | | |
| *C. ciribe* (Engelmann ex J. M. Coulter) Backeberg & F. M. Knuth | 6 | | | | | | |
| *C. davisii* (Engelmann & J. M. Coulter) F. M. Knuth | 2 | 1 | 3 | | | | |
| *C. delgadilloana* Rebman & Pinkava | 3 | | | | | | |
| *C.* ×*deserta* | 4 | | | | | | |
| *C. echinocarpa* | 45 | | | | | | |
| *C. echinocarpa* × *C. gander* var. *ganderi* | 1 | | | | | | |
| *C. echinocarpa* × *C. leptocaulis* | 1 | | | | | | |
| *C. echinocarpa* × *munzii* | 2 | | | | | | |
| *C. echinocarpa* × *ramosissima* | 1 | | | | | | |
| *C. fosbergii* (C. B. Wolf) Rebman, M. A. Baker & Pinkava | | 3 | | | | | |
| *C. fulgida* | 62 | 19 | | | | | |
| *C. gander* var. *catavinensis* | 6 | | | | | | |
| *C. gander* var. *ganderi* | 22 | | | | | | |
| *C.* ×*grantiorum* | 9 | | | | | | |
| *C. imbricata* var. *argentea* | 3 | | | | | | |
| *C. imbricata* var. *imbricata* | 28 | | | | | | |
| *C. imbricata* var. *rosea* (as *C. imbricata* var. *imbricata)* | 1 | | | | | | |
| *C. imbricata* var. *spinosior* | 83 | | | | | | |
| *C. imbricata* var. *spinitecta* | 4 | | | | | | |
| *C. imbricata* var. *imbricata* × *C. imbricata* var. *spinosior* | 1 | | | | | | |
| *C.* ×*kelvinensis* | 7 | 54 | | | | | |

| Taxon | 2× | 3× | 4× | 5× | 6× | 7× | 8× |
|---|---|---|---|---|---|---|---|
| *C. kleiniae* (DC.) F. M. Knuth | | | 10 | | | | |
| *C. kleiniae* × *C. leptocaulis* | | 4 | | | | | |
| *C. leptocaulis* | 27 | 4 | 8 | | | | |
| *C. leptocaulis* × *C. ramosissima* | 1 | | | | | | |
| *C. leptocaulis* × *C. spinosior* | 5 | | | | | | |
| *C. leptocaulis* × *C. thurberi* (Engelmann) F. M. Knuth | 1 | | | | | | |
| *C. leptocaulis* × *C. whipplei* | 8 | | | | | | |
| *C. lindsayi* (Rebman) Rebman | | | 1 | | | | |
| *C. molesta* (T. S. Brandegee) F. M. Knuth var. *molesta* | | | | | | | 8 |
| *C. molesta* var. *clavellina* (Engelmann) Rebman | | | | | | | 1 |
| *C. molesta* × *C. prolifera*? | | | | | 2 | 4 | |
| *C. multigeniculata* (Clokey) Backeberg | 17 | | | | | | |
| *C. multigeniculata* × *C. whipplei* | 1 | | | | | | |
| *C. munzii* | 21 | 1 | | | | | |
| *C.* ×*neoarbuscula* | 5 | | | | | | |
| *C.* ×*pallida* (J. N Rose) F. M. Knuth | | | 1 | | | | |
| *C. prolifera* (Engelmann) F. M. Knuth | 1 | 21 | | | 1 | | |
| *C. ramosissima* | 33 | 14 | | | | | |
| *C. sanfelipensis* (Rebman) Rebman | | | | | 5 | | |
| *C. santamaria* (E. M. Baxter) Rebman | 1 | | | | | | |
| *C. tesajo* (Engelmann ex. J. M. Coulter) F. M. Knuth | 11 | | | | | | |
| *C.* ×*tetracantha* (Toumey) F. M. Knuth | 6 | | | | | | |
| *C. thurberi* (Engelmann) F. M. Knuth | 7 | | | | | | |
| *C. tunicata* (Lehmann) F. M. Knuth | 2 | 1 | | | | | |
| *C. versicolor* | 17 | | | | | | |
| *C.* ×*viridiflora* (Britton & J. N. Rose) F. M. Knuth | 4 | | | | | | |
| *C. waltoniorum* Rebman | | | 2 | | | | |
| *C. whipplei* (Engelmann & J. M. Bigelow) var. *enodis* (Peebles) Backeberg | | | 42 | | | | |
| *C. whipplei* var. *whipplei* | 59 | | | | | | |
| *C. wolfii* | | | | | 7 | | |

*Includes *C. acanthocarpa* var. *coloradensis* (L. Benson) Pinkava.
**Previously published as *C. acanthocarpa* var. *major* (Engelmann & J. M. Bigelow) Pinkava or *Opuntia acanthocarpa* var. *major* (Engelmann & J. M. Bigelow) L. D. Benson.
***One chromosome determination originally published as *O. prolifera*.

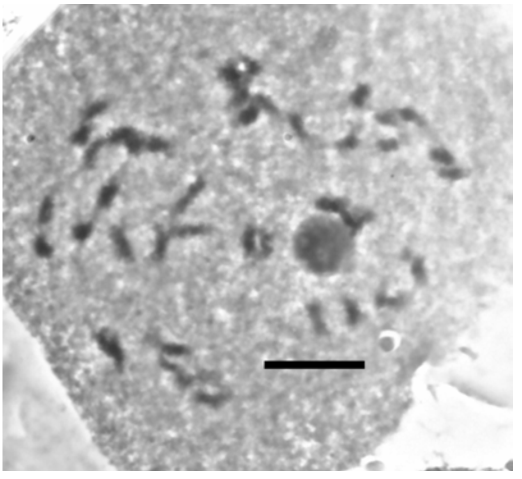

**Figure 1.** Diakenesis, *n* = 22 IIs (22 bivalents). *Echinocereus coccineus* subsp. *coccineus*, *Baker 14367.3*. Magnification bar in all figures is 10 micrometers.

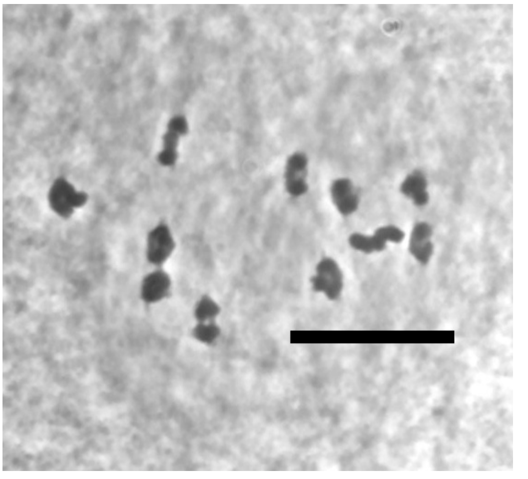

**Figure 2.** Early metaphase I, 11 IIIs (11 trivalents), *Cylindropuntia bigelovii*, *Baker 18510*. Note that triploids can easily be mistaken for diploids at this phase; there is an extra protuberance visible on at least three of the trivalents. This count was verified by examining cells from the same preparation that were in Anaphase I (see figure 4).

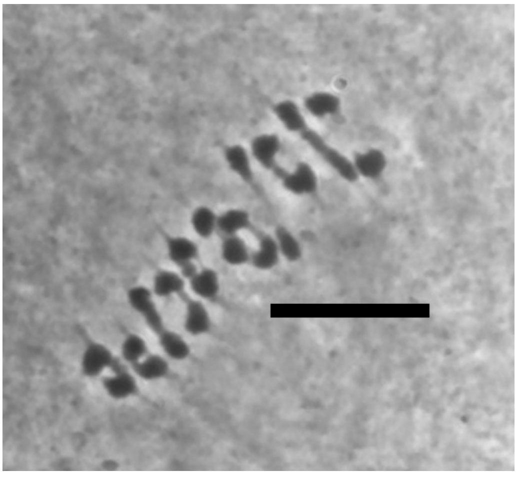

**Figure 3.** Late metaphase I, *n* = 22, *Echinocereus chloranthus* subsp. *chloranthus*, *Baker 18182.1*.

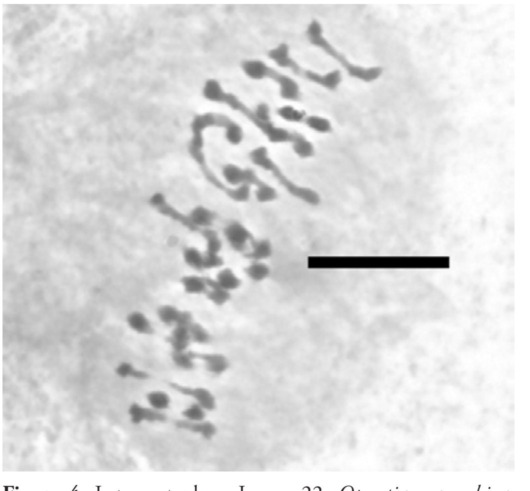

**Figure 4.** Late metaphase I, *n* = 22, *Opuntia macrorhiza*, *Baker 18204.3.*

## RESULTS

Chromosome counts are reported for 524 individuals representative of 107 taxa, including unnamed nothotaxa, from nine genera of cacti mostly from the western United States and northern Mexico. Chromosome morphology was uniform within and among species. Figures 1–10 show photomicrographs for a variety of meiotic phases, ploidy levels, and taxa. Images were made at the Desert Botanical Garden using a Motic Moticam Pro® 282A camera mounted on an Olympus CX41® phase contrast microscope. Images were stacked using Helicon Focus® 6.8. First-time chromosome counts (Appendix 1) are determined for nine interspecific hybrids. All hybrids were from native habitat and identified by their morphology, with nearly all characters observed being additive between the two putative parents. Demography was also a determining factor, with the apparently spontaneous hybrids consisting of one to few documented individuals. The first triploid chromosome determinations were made for *Opuntia basilaris* (*n* = 33/2) and *O. robusta* (*n* = 33/2), and the first hexaploid chromosome count was made for *O. macrocentra* (*n* = 33). Chromosome number determinations for the remaining taxa are in agreement with previously published reports.

## DISCUSSION

There are four genera in the Chihuahuan, Mojave, and Sonoran deserts and associated mountains for which polyploidy has played a crucial role in their evolution and geographic distribution: *Cylindropuntia*, *Echinocereus*, *Grusonia*, and *Opuntia*. Majure et al. (2012a, 2012b) have tallied chromosome determinations for *Opuntia* and discussed the evolutionary systematics of the genus. We therefore focus our discussion here on the other three genera.

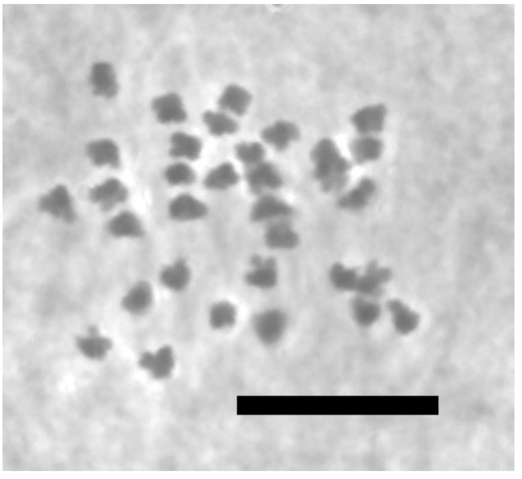

**Figure 5.** Early anaphase I, *n* = 33/3, it appears that 12 chromosomes are going to one pole and 21 to the other, note that if 11 would have gone to one pole and 22 to the other, the daughter cells would have been euploid, *Opuntia basilaris* var. *basilaris*, *Baker 18538*.

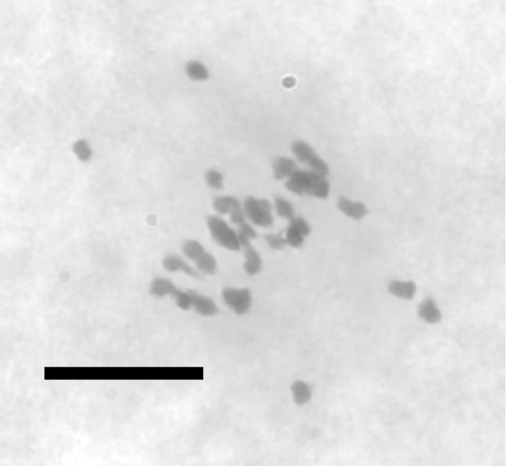

**Figure 6.** Early anaphase I, *n* = 33/3, a single chromosome from each of several trivalents has reached the poles before the other two, *Opuntia basilaris* var. *basilaris*, *Baker 18538*.

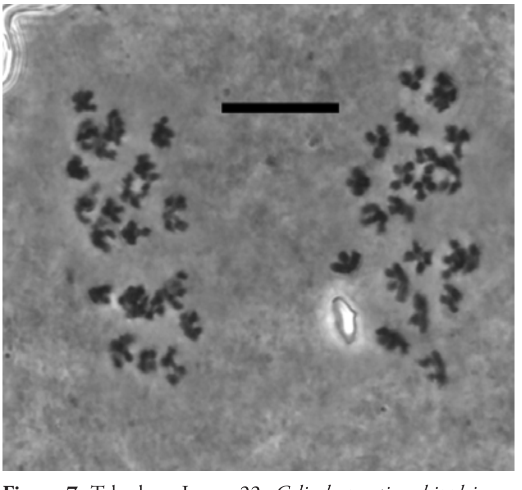

**Figure 7.** Telophase I, *n* = 22, *Cylindropuntia whipplei* var. *whipplei*, *Baker 16645.1* (Baker 2016).

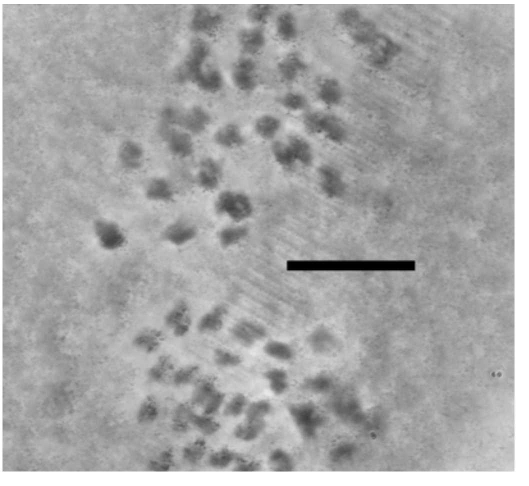

**Figure 8.** Telophase I, *n* = 33, *Cylindropuntia chuckwallensis*, *Baker 17719.4* (Baker & Cloud-Hughes 2014).

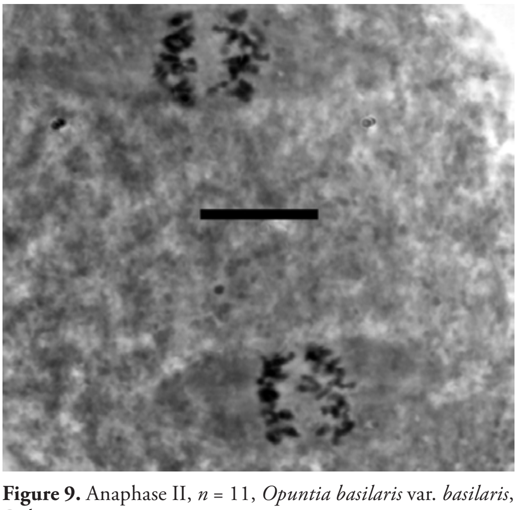

**Figure 9.** Anaphase II, *n* = 11, *Opuntia basilaris* var. *basilaris*, *Baker 18279*.

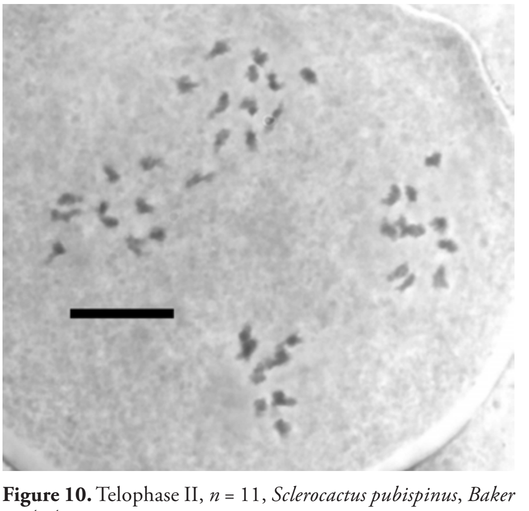

**Figure 10.** Telophase II, *n* = 11, *Sclerocactus pubispinus*, *Baker 17414.1*.

Chromosome numbers have been tallied, by taxon or putative hybrid, for this paper and all of the past literature available to the authors (Baker 2006, 2016; Baker & Cloud-Hughes 2014; Baker & Pinkava 1999; Baker et al. 2009; Beard 1937; Cloud-Hughes et al. 2015; Conde 1975; Cota & Philbrick 1994; Donati 2011, 2017a, 2017b; Fenstermacher 2016; Parfitt 1978, 1987, 1997; Pinkava & McLeod 1971; Pinkava & Parfitt 1982; Pinkava et al. 1973, 1977, 1985, 1992a, 1992b, 1998; Powell & Weedin 2001, 2005; Ralston & Hilsenbeck 1989, 1992; Rebman 1997: Rebman & Pinkava 2001; Ross 1981; Segura et al. 2007; Ward 1984; Weedin and Powell 1978a, 1978b, 1980; Weedin et al. 1989). We did not include chromosome determinations that were not vouchered with permanent herbarium specimens. Not all vouchers were reviewed, and consequently, some identifications may be incorrect. However, the data are generally robust in terms of repetition. Those taxa with one to few counts may be viewed as provisional and, assuming initial chromosome determinations are correct, may prove to encompass populations with multiple ploidy levels.

Nine hybrids are reported here for the first time, along with their chromosome numbers. These include four *Cylindropuntia*: *C. alcahes* (F.A.C. Weber) F. M. Knuth var. *gigantensis* Rebman × *C. lindsayi* Rebman; *C. bernardina* × *C. echinocarpa* (Engelmann & J. M. Bigelow) F. M. Knuth, *C. leptocaulis* (de Candolle) F. M. Knuth × *C. ramosissima* (Engelmann) F. M. Knuth; *C. echinocarpa* × *C. ramosissima*; and *C. echinocarpa* × *C. ganderi* (C. B. Wolf) Rebman & Pinkava var. *ganderi*; two *Opuntia*: *O. azurea* J. N. Rose var. *discolor* Weedin × *O. rufida*, and *O. chlorotica* Engelmann & J. M. Bigelow × *O. engelmannii* Salm-Dyck ex Engelmann; and two *Echinocereus*: *E. arizonicus* J. N. Rose ex Orcutt subsp. *arizonicus* × *E. bonkerae* Thornber & Bonker subsp. *bonkerae* and *E. coccineus* Engelmann subsp. *coccineus* × *E. yavapaiensis* M. A. Baker.

Five of these hybrids are known only from a single individual, and eight possess characters that are additive between the two putative parents, at least for the putative $F_1$ individuals. Several individuals occurred at the site for *C. leptocaulis* × *C. ramosissima,* and all appeared to be $F_1$. Populations of *C. bernardina* and *C. echinocarpa* appear to intergrade where the species come into contact with one another and so morphological intermediates are common. Several putative hybrid individuals occurred at the site of *O. chlorotica* × *O. engelmannii,* and a chromosome number of $n = 33$ was determined for three of these. Because *O. chlorotica* is known only as a diploid, including an individual at the hybrid site (*MAB18789*), and *O. engelmannii* is known only as a hexaploid in Arizona, including one at the hybrid site (*MAB18787*), the expected $F_1$ hybrid between the two species would be tetraploid ($n = 22$). For this reason, we hypothesize that the putative hexaploid hybrid may have originated from a union between an unreduced gamete from a triploid *O. chlorotica* and a normal gamete from *O. engelmannii.* Most characters appear additive, except that the putative hybrids have spines longer than either of the putative parents. This hypothesis requires the past or present occurrence of a triploid individual of *O. chlorotica,* and thus it would be of interest to further survey the area for such individuals. Triploids can be easily determined by viewing pollen, as triploid meiosis produces conspicuous micro- and macropollen grains (Baker & Pinkava 1987). Alternatively, hexaploid individuals of *O. chlorotica* may have been involved but this scenario would require two missing links. At least two individuals have been documented for *Echinocereus arizonicus* subsp. *arizonicus* × *E. bonkerae* subsp. *bonkerae*, including one at the *MAB17826* site and one at El Capitán, Gila County, Arizona, where a putative $F_2$ also occurred.

## *CYLINDROPUNTIA*

A summary of chromosome determinations reported to date for *Cylindropuntia* is presented in Table 1. For most taxa, several to many chromosome determinations have been made, and thus their ploidy levels are well-documented. Of the 33 apparently non-apomictic and non-hybrid *Cylindropuntia* taxa, 25 have been reported only as diploids. Five *Cylindropuntia* taxa are composed of both triploids and/or tetraploids, in addition to diploids. Five *Cylindropuntia* are strictly hexaploids. Odd-level polyploidy, e.g., triploidy and pentaploidy, is largely restricted to vegetatively cloning taxa. It has been suggested that the success of triploid apomixis lies in its ability to fix and maintain particularly adaptive genomes (Baker & Pinkava 1987). This is evidenced by triploid clones in *C. bigelovii* (Engelmann) F. M. Knuth, *C. fosbergii* (C. B. Wolf) Rebman, M. A. Baker, & Pinkava, *C. ×kelvinensis* (V. E. Grant & K. A. Grant P. V. Heath), and *C. prolifera* (Engelmann) F. M. Knuth that are often comprised of numerous ramets occurring over large areas. Some clones appear to include many thousands of ramets, but the extents of these clones are yet to be determined. Triploidy is known to occur sporadically in several other *Cylindropuntia* species, but the triploid individuals do not appear to have an advantage over the diploid or tetraploids in terms of abundance or occurrence within specialized habitats. Baker et al. (2009) suggested that triploidy may not be an evolutionary dead end, and may represent a punctuated evolutionary mechanism that involves producing rare haploid ($n = 11$) and diploid ($n = 22$) gametes. Given that aneuploidy is either lethal or plays little or no role in the modern evolution of Cactaceae (Pinkava et al. 1985), Baker et al. (2009) suggest that normal segregation of chromosome during meiosis, even without the assumption of meiotic drive (Furness & Rudall 2011), would produce euploid gametes at a frequency that would explain occasional outcrossing. There is also evidence that unreduced gametes from triploids may lead to genetic exchange. Baker & Pinkava (1999) suggest such an origin for *C. ×campii* (M. A. Baker & Pinkava) M. A. Baker & Pinkava, where triploid *C. bigelovii* is thought to have contributed an unreduced gamete ($n$ = 33) and diploid *C. acanthocarpa* (Engelmann & J. M. Bigelow) F. M. Knuth a reduced gamete ($n$ = 11) to form a tetraploid zygote. As expected, the morphology of the tetraploid hybrid reflects a much greater contribution from the putative parent *C. bigelovii*. The triploid species *C. fosbergii* is morphologically very similar to *C. bigelovii* and is suspected of originating from an $n$ = 22 *C. bigelovii* gamete combining with an $n$ = 11 gamete from another species (Parfitt & Baker 1993). Unfortunately, the other putative parent remains a mystery (Mayer et al. 2011).

Hajrudinović et al. (2016) found that triploids in *Sorbus* exhibited both ecological and reproductive success, perhaps even the capacity to tolerate endosperm imbalance. They suggest that *Sorbus* sexual–agamic complexes, composed of mixtures of cytotypes and the interacting sexual and asexual lineages, represent potential reservoirs of new biodiversity. The scenario of triploidy in *Populus tremuloides* Michx., a species with a dramatically different ecology, is surprisingly similar to that of *C. bigelovii* (Mock et al. 2012). Triploid clones of *P. tremuloides* comprise a high percentage of the clones within the geographic distribution of an otherwise diploid species. Triploidy is most common in the southwestern portion of the species range, where ecological values are low with respect to potential seedling survival. Similarly, triploid populations of *C. bigelovii* occur in areas of low rainfall or at the edges of the species distribution, where ecological values for seed germination would be low. The concept of triploids being involved in sexual reproduction has also been suggested for animals (Fakharzadeh et al. 2015).

Tetraploidy is found in several taxa of *Cylindropuntia*. However, only a single apparently non-hybrid taxon, *C. whipplei* (Engelmann & J. M. Bigelow) F. M. Knuth var. *enodis* (Peebles) Backeb., is consistently tetraploid. *Cylindropuntia ramosissima*, *C. davisii* (Engelmann & J. M. Bigelow) F. M. Knuth, *C. leptocaulis*, and *C. tunicata* (Lehmann) F. M. Knuth are also apparently non-hybrid taxa that are composed of diploid and tetraploid individuals. There are also triploid individuals known for *C. leptocaulis*. Both *C. leptocaulis* and *C. tunicata* are vegetatively apomictic. To date, there have been no taxonomic implications for chromosomal races within *C. ramosissima*, *C. davisii*, *C. leptocaulis*, or *C. tunicata*. Most tetraploid races that are presently classified within the same species, primarily based on morphology, are probably autotetraploids.

Morphological evidence for autoploid speciation has been presented by Baker (2016) for *C. whipplei* var. *enodis*. In the geographic area of sympatry between the diploid *C. whipplei* var. *whipplei* and the tetraploid *C. whipplei* var. *enodis*, individuals of the two cytotypes have similar mean morphological character values. Populations of *C. whipplei* var. *enodis* occurring geographically farther from those of typical *C. whipplei*, however, possess many significantly different mean character values than those of their diploid ancestor. The most consistent morphological differences are within populations of *C. whipplei* var. *enodis* that occur in lower and hotter habitats than those of the diploid. Lower transpiration rates have been documented in autopolyploids and may or may not be a factor in this case (Levin 1983). Autopolyploids also tend to have slower growth rates (Levin 1983), which may account for some of the diminutive sizes of stems and plant height in *C. whipplei* var. *enodis*. However, the hotter, drier habitat is probably the primary cause of their diminutive stature, and individuals grown in the common garden are generally larger than those occurring naturally (Baker pers. observ.). Slower growth rates may also be of adaptive value in hotter, drier habitats, which may be related, at least in part, to the degree of CAM photosynthesis (Monson 1989). Because of this ecological, geographical, and morphological correlation, *C. whipplei* var. *enodis* is recognized as a separate taxon from that of the typical variety (Baker 2016). The idea of niche separation resulting from the change in ploidy level has been discussed at length by Fowler and Levin (1984; 2016). Selection for niche separation may result from reduction of competition for resources and the reduction of pollination by pollen with the incorrect ploidy level. Also, the ability to invade new niches may be enhanced by increased heterozygosity in polyploids, including autopolyploids (Moody et al. 1993, Visger et al. 2016). With respect to *Cylindropuntia*, autoploidy leading to the evolution of a taxon has been documented only for *C. whipplei*. For the other species that include apparently autotetraploid races, no correlations have yet been recorded between ploidy level, and geography, morphology, and/or ecology.

There are several tetraploid taxa within *Cylindropuntia*, such as *C. kleiniae* (DC.) F. M. Knuth, *C. lindsayi* (Rebman) Rebman, and *C. waltoniorum* Rebman, that have no recorded apomorphic character states, are vegetatively apomictic, and are probably of hybrid origin (see Rebman 2015). There are also several isolated tetraploid individuals that appear to be of hybrid origin, which have not been named beyond being designated as hybrids between two putative parents. Fowler and Levin's (2016) model for establishment of polyploids suggests that one of the critical factors is the number of new polyploid individuals occurring within the same space and time. This may help to explain the high percentage of vegetatively apomictic polyploids in *Cylindropuntia*, in that they have the potential to clone and, thereby not only increase their numbers, but also potentially spread to new and more favorable habitats. Thus, tetraploidy appears to be correlated with the stabilization of hybrids and to a lesser extent the stabilization of unique genomes that have been more successful than their diploid counterparts within certain habitats. It has been shown that within certain plant taxa, hybrid individuals produce a much higher frequency of unreduced gametes than those of their parents (Whitton et al. 2008).

There are five *Cylindropuntia* taxa that are known only as hexaploids. One of these, *C. arbuscula* (En-

**Table 2.** Tabulation of chromosome determinations to date for selected taxa of *Grusonia* and *Micropuntia*, by taxon, by ploidy level. Only reports that were vouchered with herbarium specimens are included. Texas species were largely identified by Fenstermacher (pers. comm. 2016).

| Taxon | 2× | 3× | 4× | 5× | 6× |
|---|---|---|---|---|---|
| *G. aggeria* (Ralston & Hilsenbeck) E. F. Anderson | 52 | | | | |
| *G. aggeria* × *G. densispina* | | 3* | | | |
| *G. aggeria* × *G. grahamii* | | 1* | 5 | | |
| *G. agglomerata* (A. Berger) E. F. Anderson | | | 4 | | |
| *G. bradtiana* (J. M. Coulter) Britton and J. N. Rose | 1 | | | | |
| *G. bulbispina* (Engelmann) H. Robinson subsp. *bulbispina* | | | 2 | | |
| *G. bulbispina* subsp. *basileocephala* | | | 3 | | |
| *G. clavata* | 5 | | | | |
| *G. deinacantha* | | | 1** | | |
| *G. deinacantha* × *G. aggeria* | | 1** | | | |
| *G. deinacantha* × *G. grahamii* | | | 1** | | |
| *G. deinacantha* × *G. nigrispina* | | 1** | | | |
| *G. densispina* | | | 25 | | |
| *G. densispina* × *G. grahamii* | | | 1* | | |
| *G. emoryi* | | | 9 | | |
| *G. grahamii* (Engelmann) H. Robinson | | | 8 | 1* | |
| *G. invicta* (T. Brandegee) E. F. Anderson | 2 | | | | |
| *G. kunzei* (J. N. Rose) Pinkava | 4 | | | | |
| *G. halophila* | | | 10 | | |
| *G. moelleri* (A. Berger) E. F. Anderson | 22 | | | | |
| *G. parishii* | 7 | | | | |
| *G. robertsii* (Orcutt ex Britton & J. N. Rose) Pinkava | 1 | | | | |
| *G. schottii* | | | | | 4 |
| *G. wrightiana* (E. M. Baxter) E. M. Baxter | | | 4 | | |
| *M. pulchella* (Engelmann) M. P. Griffith | 5 | | | | |

*Not an exact count, possibly aneuploidy.
**Uncertain number of chromosome determinations and vouchers not specifically reported.

gelmann) F. M. Knuth, appears to reproduce asexually. Based on the lack of any apparent apomorphic characteristics, it is probably an allopolyploid with *C. leptocaulis* as one of its parents. Populations of this species are common and widespread geographically. Pentaploids, such as *C.* ×*neoarbuscula* (Griffiths) Backeberg & F. M. Knuth and *C.* ×*vivipara* (J. N. Rose) F. M. Knuth, with similar morphology are rare and very restricted geographically. The remaining four species of hexaploid *Cylindropuntia* are all gynodioecious and have a similar array of flower colors. The significance of these correlations has been reviewed by Baker and Cloud-Hughes (2014), who suggest that selection pressure for subdioecy may be greater in polyploids because of low self-incompatibility (Cohen & Tel-Zur 2012), probably resulting from an almost certainly low population size for incipient polyploids. Thus, the occurrence of pollen-sterility forces outcrossing, at least among certain individuals, and increases genetic exchange within the population.

There is a single octoploid *Cylindropuntia*, *C. molesta* (T. S. Brandegee) F. M. Knuth, including *C. molesta* var. *clavellina* (Engelmann) Rebman, which is also gynodioecious but vegetatively clonal. There is a single 7× chromosome determination for the genus, which is a putative hybrid between *C. molesta* and *C. prolifera*.

## *GRUSONIA* AND *MICROPUNTIA*

A summary of chromosome determinations made to date for *Grusonia* and *Micropuntia* is presented in Table 2. We follow the taxonomy of Stuppy (2002), who places *Corynopuntia* (F. Knuth) Stuppy as a subgenus within *Grusonia*. Bárcenas (2016) also recognizes *Grusonia* as including *Corynopuntia* but has provided ample DNA evidence to exclude *Micropuntia pulchella* (Engelmann) M. P. Griffith from the genus. However, to date, molecular analyses are conflicting as to whether *Corynopuntia* belongs within *Grusonia* (Bárcenas 2016, Griffith 2002, Griffith and Porter 2009, Wallace and Dickie 2002). *Micropuntia pulchella* has been reported five times as diploid. Eight species of *Grusonia* have been reported as diploids, eight species (nine taxa) as tetraploids, and only one species, *G. schottii* (Engelmann) H. Robinson, as a hexaploid. Unlike *Cylindropuntia*, only a single ploidy level has been reported for any one *Grusonia* species. Three *Grusonia* hybrids have been reported as tetraploid, a single hybrid as pentaploid, and four as triploids (Donati 2017b; Fenstermacher 2016). Thus, within *Grusonia*, more than half the taxa are polyploid. Pollen sterility occurs in at least four tetraploid species and most consistently in the one hexaploid species and has not been detected in any of the diploid species (Fenstermacher 2016; Baker pers. observ.).

### *ECHINOCEREUS*

A summary of chromosome determinations made to date for selected *Echinocereus* is presented in Table 3. Among the taxa tallied, ploidy levels appear to correlate closely with taxonomic lines, at least at the species level. Forty-seven of the taxa are reported as diploid, while only 12 taxa are tetraploid, and one is hexaploid. Odd-polyploids are confined to putative hybrids. Three of the 12 tetraploid taxa and the single hexaploid taxon are dioecious or subdioecious, and all are red-flowered, belonging to the section *Triglochidiatus*. Dioecy within *Echinocereus* was discussed at length by Hoffman (1992). The red color, long floral tube, and copious production of nectar in the flower of section *Triglochidiatus* correspond to hummingbird pollination syndrome (Scobell 2008). The evolution of this flower morphology may have been a result of populations being geographically isolated from one another, as hummingbirds would potentially be more effective at gene exchange among widely spaced populations than insect pollinators (Scobell 2008). In general, these dioecious or subdioecious populations occur in the northern portion of the geographic range of the genus, although pollen-sterile individuals have been recorded at the type locality of *E. polyacanthus* from Cusihuiriachi, Chihuahua, Mexico, which is in the southern portion of the range for section *Triglochidiatus* (Baker pers. observ.).

According to Cota and Philbrick (1994), populations of polyploid *Echinocereus* occur primarily within medium to high elevations, with the majority of populations occurring near 33° latitude; which is similar to distributional patterns of polyploid races in other flowering plants (Stebbins 1971).

## NOMENCLATURAL NOTES

Owing primarily to molecular and morphological work recently conducted by Lucas Majure, Marc Baker, and Michelle Cloud-Hughes, and the need for consistency in the generic names for the chromosome numbers reported in *Grusonia*, the following new combinations are made:

**_Cylindropuntia imbricata_ (Haworth) F. M. Knuth var. _spinosior_ M. A. Baker, Cloud-H. & Majure comb. nov.**

Basionym: *Opuntia whipplei* Engelmann & J. M. Bigelow var. *spinosior* Engelmann Proc. Amer. Acad. Arts 3: 307. 1856.

Type: "South of the Gila [Arizona]" Lectotype (Coulter 1896): Schott, no. 5, June 1855, MO 2015359! [MO 178850], DUPLICATE: POM 317797! [RSA0002239]

*Opuntia spinosior* (Engelmann) Toumey Bot. Gaz. 25: 119 (1898).

*Cylindropuntia spinosior* (Engelmann) F. M. Knuth, Kaktus-ABC [Backeberg & Knuth] 126. 1936.

*Grusonia spinosior* (Engelmann) Goodwyn ex G. D. Rowley, *Tephrocactus* Study Group 12(3): 45. 2006

*Opuntia spinosior* var. *neomexicana* Toumey, Bot. Gaz. 25: 119 (1898).

Type: Britton & Rose (1919): "Mr. Toumey writes that his original material of this variety came from the low foothills north of the Rillito River near Tucson". LECTOTYPE (Benson 1982): "Tucson, Toumey, Feb. 5 and Apr. 20, 1896, POM 83393 [RSA 0002234]. "Probable DUPLICATES [isolectotypes] (with the same dates but for 1895)": MO 2015360!, NY 02056648!, BH 000143324! [originally from US], UC 422713! [originally from US], UC108227! [originally from the Brandegee Herbarium].

**_Cylindropuntia imbricata_ (Haworth) F. M. Knuth var. _rosea_ (DC.) M. A. Baker comb. nov.**

Basionym: *Opuntia rosea* DC.

Type: De Candolle (1828a) does not name a type but made his description from a plate, labelled in pencil *Cactus subquadriflorus*, from flor. mex. ined, which he included in his Revue de la famille des Cactées, as plate 15, labelled as *Opuntia rosea* (De Candolle 1828b). HOLOTYPE (Arias-Montes et al. 1997; see Rowley 1994, Crook & Mottram 2002): figure of *Cactus quadrifolius* in Mociño, Fl. Mex. ined., DC. no. 406, preserved in the Hunt Institution for Botanical Documentation, Torner Collection of Sessé and Mociño biological illustrations, no. 880.

**_Cylindropuntia bernardina_ (Engelmann ex Parish ) M. A. Baker, Cloud-H. & Rebman comb. nov.**

Basionym: *Opuntia bernardina* Engelmann ex Parish, Bull. Torrey Bot. Club 19(3): 92. 1892

Type: Specimens distributed by the National Herbarium, ticketed "New Mexico, Geo. R. Vasey, February, 1881," were probably collected in Southern California, where Mr. Vasey was at that date.

LECTOTYPE: Designated here as G. R. Vasey, Feb. 1881, San Bernardino, California, US3046434,

**Table 3.** Tabulation of chromosome determinations to date for selected taxa of *Echinocereus*, by taxon, by ploidy level. Only reports that were vouchered with herbarium specimens are included.

| Taxon | 2× | 3× | 4× | 5× | 6× |
|---|---|---|---|---|---|
| *Echinocereus arizonicus* subsp. *arizonicus* | 12 | | | | |
| *Echinocereus arizonicus* subsp. *matudae* (Bravo-Hollis) J. Rutow | 2 | | | | |
| *Echinocereus arizonicus* subsp. *nigrihorridispinus* | 20 | | | | |
| *Echinocereus arizonicus* subsp. *arizonicus* × *E. bonkerae* subsp. *bonkerae* | 1 | | | | |
| *Echinocereus bonkerae* Thornber & Bonker subsp. *apachensis* (W. Blum & J. Rutow) A. D. Zimmerman. | 1 | | | | |
| *Echinocereus bonkerae* subsp. *bonkerae* | 13 | | | | |
| *Echinocereus chisoensis* W. T. Marshall [includes *E. reichenbachii* (Terscheck ex Walp.) Britton & J. N. Rose var. *chisoensis* (W. T. Marshall) L. D. Benson | 2 | | | | |
| *Echinocereus chloranthus* (Engelmann) F. A. Haage subsp. *chloranthus* [includes *E. viridiflorus* Engelmann var. *cylindricus* (Engelmann) Rümpler] | 20 | | | | |
| *Echinocereus chloranthus* subsp. *rhyolithensis* W. Blum & Mich. Lange | 2 | | | | |
| *Echinocereus cinerascens* (DC.) Engelmann ex J.N. Haage subsp. *cinerascens* | 2* | | | | |
| *Echinocereus cinerascens* subsp. *septentrionalis* N. Taylor | 1* | | | | |
| *Echinocereus coccineus* subsp. *coccineus* [includes *E. canyonensis* Clover & Jotter and *E. baker* W. Blum, Oldach & J. Oldach; *E. triglochidiatus* var. *melanocanthus* (Engelmann) L. D. Benson, in part] | | | 61 | | |
| *Echinocereus coccineus* subsp. *coccineus* × *E. yavapaiensis* | | | | 1 | |
| *Echinocereus coccineus* subsp. *paucispinus* (Engelmann) W. Blum, Mich. Lange, & Rutow [includes *E. coccineus* subsp. *transpecosensis* W. Blum, Oldach & J. Oldach, in part] | | | 3 | | |
| *Echinocereus coccineus* subsp. *rosei* [includes *E. coccineus* subsp. *transpecosensis* W. Blum, Oldach & J. Oldach, in part; *E. triglochidiatus* var. *gurneyi* L. D. Benson; *E. triglochidiatus* var. *neomexicanus* (Standley) W. T. Marshall, in part; *E. triglochidiatus* var. *melanocanthus* (Engelmann) L. D. Benson, in part] | | | 22 | | |
| *Echinocereus coccineus* subsp. *santaritensis* (W. Blum & Rutow) M. A. Baker | | | 37 | | |
| *Echinocereus dasyacanthus* Engelmann [including *E. pectinatus* var. *neomexicanus* J. M. Coulter and *E. pectinatus* var. *minor* (Engelmann) L. D. Benson, which may have been an introgressant form involving *E. coccineus* subsp. *rosei*] | | | 13 | | |
| *Echinocereus davisii* A. D. Houghton | 1 | | | | |
| *Echinocereus engelmannii* (Parry ex Engelmann) Rümpler subsp. *engelmannii* | | | 130 | | |
| *Echinocereus engelmannii* subsp. *engelmannii* morphologically intermediate to *E. engelmannii* subsp. *fasciculatus* [includes *E. boyce-thompsonii* Orcutt, in part] | | | 10 | | |
| *Echinocereus engelmannii* subsp. *fasciculatus* (Engelmann ex S. Watson) W. Blum & Mich. Lange [includes *E. boyce-thompsonii* Orcutt, in part] | | | 63 | | |
| *Echinocereus engelmannii* subsp. *fasciculatus* × *E. fendleri* var. *fendleri* | | 2 | | | |
| *Echinocereus enneacanthus* Engelmann subsp. *intermedius* (W. O. Moore) W. Blum & Mich. Lange [ including *E. enneacanthus* subsp. *brevispinus* N. P. Taylor, nom. inval.] | 2 | | | | |
| *Echinocereus enneacanthus* subsp. *enneacanthus* [includes *E. enneacanthus* var. *dubius* (Engelmann) L. D. Benson] | 6 | | | | |
| *Echinocereus fendleri* (Engelmann) F. Sencke ex J. N. Haage subsp. *fendleri* | 15 | | | | |
| *Echinocereus fendleri* subsp. *rectispinus* (Peebles) N. P. Taylor | 14 | | | | |
| *Echinocereus fitchii* Britton & J. N. Rose var. *albertii* (L. Benson) W. Blum & Mich. Lange [published as *E. reichenbachii* (Walpers) Haage var. *albertii* L.D.Benson] | 1 | | | | |
| *Echinocereus fitchii* subsp. *fitchii* [*E. reichenbachii* var. *fitchii* (Britton & J. N. Rose) L. D. Benson] | 2 | | | | |
| *Echinocereus knippelianus* Lieber [without subspecies] | 1 | | | | |

| Taxon | 2× | 3× | 4× | 5× | 6× |
|---|---|---|---|---|---|
| *Echinocereus laui* G. R. W. Frank | 1 | | | | |
| *Echinocereus leucanthus* N. P. Taylor | 1 | | | | |
| *Echinocereus ledingii* Peebles | 3 | | | | |
| *Echinocereus lindsayorum* J. Meyrán [asked Kanchi] | 1 | | | | |
| *Echinocereus ×lloydii* Britton & J. N. Rose | | | 5 | | |
| *Echinocereus maritimus* K. Schumann | 5 | | | | |
| *Echinocereus mojavensis* | 38 | | | | |
| *Echinocereus neocapillus* (Weniger) W. Blum & Mich Lange [*E. viridiflorus* var. *neocapillus* (Weniger) A. D. Zimmerman] | 2 | | | | |
| *Echinocereus nicholii* (L. Benson) B. D. Parfitt | 7 | | | | |
| *Echinocereus pacificus* (Engelmann) F.A. Haage subsp. *mombergerianus* (G. R. W. Frank) W. Blum & Rutow | | | 2 | | |
| *Echinocereus pacificus* subsp. *pacificus* | | | 1 | | |
| *Echinocereus papillosus* Linke ex F. A. Haage [includes *E. papillosus* var. *angusticeps* (Clover) W. T. Marshall, *E. papillosus* var. *papillosus*, and *E. blankii* F. Palmer var. *angusticeps* (Clover) L. Benson] | 2 | | | | |
| *Echinocereus pectinatus* (Scheidweiler) Engelmann subsp. *pectinatus* | 2 | | | | |
| *Echinocereus pectinatus* subsp. *wenigeri* (L. Benson) W. Blum & Rutow | 2 | | | | |
| *Echinocereus pensilis* (K. Brandegee) Purpus | 1 | | | | |
| *Echinocereus pentalophus* (DC.) F. A. Haage (without subsp.) | 2 | | | | |
| *Echinocereus pentalophus* subsp. *procumbens* (Engelmann) W. Blum & Mich. Lange [*E. procumbens* (Engelmann) Lemaire] | 1 | | | | |
| *Echinocereus poselgeri* Lemaire [with subsp.] | 1 | | | | |
| *Echinocereus reichenbachii* (Tercheck ex Walpers) Britton & J. N. Rose subsp. *baileyi* (J. N. Rose) N. P. Taylor | 1 | | | | |
| *Echinocereus reichenbachii* subsp. *perbellus* (Britton & J. N. Rose) N. P. Taylor [published as *E. reichenbachii* subsp. *reichenbachii*] | 2* | | | | |
| *Echinocereus reichenbachii* subsp. *reichenbachii* | 1 | | | | |
| *Echinocereus relictus* B. Wellard | 52 | | | | |
| *Echinocereus rigidissimus* (Engelmann) F. A. Haage subsp. *rigidissimus* [published as *E. pectinatus* var. rigidissimus (Engelmann) Rümpler in C.F.Förster] | 1 | | | | |
| *Echinocereus russanthus* Weniger | 7 | | | | |
| *Echinocereus salm-dyckianus* Scheer | | | 1* | | |
| *Echinocereus scheeri* (Salm-Dyck) Scheer subsp. *scheeri* | 1 | | | | |
| *Echinocereus schmollii* (Weingart) N. P. Taylor | 1 | | | | |
| *Echinocereus stoloniferus* W. T. Marshall [without subsp.] | 1 | | | | |
| *Echinocereus stramineus* (Engelmann) F. Seitz [without subsp.] | | | 1 | | |
| *E. triglochidiatus* Engelmann [includes *E. triglochidiatus* var. *gonacanthus* (Engelmann & J. M. Bigelow) Boissevain} | 6 | | | | |
| *E. triglochidiatus* morphologically and geographically intermediate to *E. mojavensis* | 4 | | | | |
| *Echinocereus viridiflorus* Engelmann subsp. *correllii* (L. Benson) W. Blum & Mich. Lange | 1 | | | | |
| *Echinocereus viridiflorus* subsp. *viridiflorus* | 5 | | | | |
| *Echinocereus viridiflorus* subsp. weedinii Leuck ex W. Blum & Mich. Lange | 1 | | | | |
| *Echinocereus yavapaiensis* | | | | | 32 |

*Identification made by Wolfgang Blum (pers. comm. 2016).

which is part of or at least a duplicate of the material seen by Parish. The lectotype by Benson (1982) is rejected: "Arid plains about San Bernardino and along the mountain bases", George Engelmann, November 9, 1880, MO2015324!, Duplicate POM 317796!, Possible duplicate (part of sheet), PH19855!.

*Opuntia echinocarpa* var. *parkeri* J. M. Coulter, Contr. U.S. Natl. Herb. 3(7): 446

Type: "C. F. Parker of 1879 in Herb. Mo. Bot. Gard. San Diego County, California, east side of mountains facing desert. Specimens examined: California (*C. F. Parker* of 1879)". HOLOTYPE: C. F. Parker, Campo, San Diego County, on the eastern slope of the mountains, towards the desert, September 1879, on two sheets: MO39396!, MO39397!.

According to Benson (1982): "Coulter omitted the key word, 'Campo,' a town on the coastal rather than the desert watershed, and var. *parryi* occurs there, *Lindsay & Benson 16368*". However, the *Lindsay & Benson 16368* specimen has long (>20mm), narrow tubercles and 2–3 centrals well-differentiated from the radials, and therefore, belongs within *C. californica* var. *parkeri* (*C. bernardina*) (see Baker et al. 2012). Several other specimens collected in the vicinity of Campo, including *J. Rebman et al. 19752* (RSA, SD), *19758* (RSA, SD), and *19678* (SD), have also been identified as *C. californica* var. *parkeri*.

*Opuntia parkeri* Engelmann ex. J. M. Coulter, pro. syn., Contr. U.S. Natl. Herb. 3(7): 446, 1896, an illegitimate name (Art. 36) listed only in synonymy.

*Opuntia californica* (Torrey & A. Gray) Coville var. *parkeri* (J. M. Coulter) Pinkava, Haseltonia 4:103. 1996.

*Cylindropuntia californica* (Torrey & A. Gray) F. M. Knuth var. *parkeri* (J. M. Coulter) Pinkava, J. Arizona-Nevada Acad. Sci. 33:150. 2001.

*Cylindropuntia californica* subsp. *parkeri* (J. M. Coulter) Guzmán, Cactaceae Syst. Init. 16: 16. 2003.

***Cylindropuntia* ×*parryi* (Engelmann) F. M. Knuth pro. sp.,** Kaktus-ABC [Backeb. & Knuth] 124. 1936

***Opuntia parryi* Engelmann,** Amer. J. Sci. Arts ser. 2, 14: 339. 1852,

The original description was based on two taxa and the name represented a nomen nudum but was neotypified by L. Benson (1982).

Type: NEOTYPE designation (Benson 1982): San Felipe Valley, San Felipe Ranch 1/2 mile from the canyon of Banner Grade, San Diego Co., California, 2500 ft elevation, *Lyman Benson 16384*, July 14, 1963, "POM305014." The POM accession number was reported incorrectly and is actually POM311503. POM305014 is 2 miles north of the junction of the San Felipe Valley road and the Banner Grade road, San Diego Co., California, 2,000 ft elevation, *Lyman Benson 16145*, February 17 1962.

Both specimens are from approximately the same locality, with the neotype (POM311503) having been annotated by M. Baker, 19 October 2013, as *Cylindropuntia ganderi* var. *ganderi* morphologically intergrading with, *C. californica* var. *parkeri*. The mean number of spines per areole in *C. bernardina* (*C. californica* var. *parkeri*) is 7–8 and that for *Cylindropuntia ganderi* var. *ganderi* is 17–18. At least two of the stems of the neotype possess 12–15 spines per areole and are morphologically intermediate between the two taxa. Other stems on the specimen approach those of *C. bernardina*. It is possible that Benson may have collected more than one individual but, in any case, it is clear that the population from which Benson collected his material is composed of intergrading individuals. For this reason, we hereby designate the name *Opuntia parryi* Engelmann as applying to the nothotaxon, *C. bernardina* × *C. ganderi* var. *ganderi*.

***Grusonia bulbispina* (Engelmann) H. Robinson subsp. *basileocephala* (Donati) Majure, M. A. Baker & Cloud-H. comb. nov.**

Basionym: *Corynopuntia bulbispina* (Engelmann) F. M. Knuth subsp. *basileocephala* Donati, Piante Grasse 31(1): 17 (16–18; photos), 2011.

Type: HOLOTYPE: *Hinton et al. 29069*, "MEXICO. COAHUILA: Mpio. San Pedro de las Colonias, North of San Pedro, on alluvial plains, 850 m, June 2009". GBH29069; Isotype: MEXU.

***Grusonia deinacantha* (D. Donati) Majure, M. A. Baker & Cloud-H. comb. nov.**

Basionym: *Corynopuntia deinacantha* D. Donati, Webbia 72(1): 106. 2017.

Type: HOLOTYPE: Mexico, Coahuila: Mpo. Francisco I. Madero, south of Laguna del Rey, 1107 m above sea level, growing on gravelly plains and gentle slopes, 11 June 2009, *G. Hinton et D. Donati 29070*, GBH29070, isotype MEXU.

***Grusonia halophila* (D. Donati) Majure, M. A. Baker & Cloud-H. comb. nov.**

Basionym: *Corynopuntia halophila* D. Donati, Plant Biosystems 2017:9. 10 March 2017.

Type: HOLOTYPE: Mexico, Coahuila, San Pedro, North of San Pedro de Las Colonias, 817 m, loamy gypsum plains; 10 June 2009, *G. Hinton and D. Donati 29068*, GBH29068; isotype: MEXU.

## CONCLUSIONS

It is a common assertion that polyploids can have a selective advantage over diploids because of their novel genetic variation, including genomic variation (Soltis & Soltis, 2000; Leitch & Leitch, 2008; Flagel & Wendel, 2009). However, given that Pinkava et al. (1985, 1998) estimate only 28% of taxa within the Cactaceae are polyploid, it would appear that polyploidy within the family has a selective advantage only in certain circumstances. Even within *Cylindropuntia* and *Echinocereus*, where polyploidy is frequent, the majority of the taxa are diploid. It is apparent, however, that polyploidy has played a major role in the evolution of several taxa or groups of taxa. Because most cacti occur in harsh, arid conditions, it stands to reason that polyploidy within the family has been selected by factors inherent in the migration into new niches, as has been suggested for polyploids in general (Stebbins 1971).

One hypothesis that addresses the underlying genetic mechanism for the ability of polyploids to invade new habitats is that duplicated genes have the potential for subfunctionalization and/or neofunctionalization, and, because of a freedom from selective constraints, enable mutation-driven evolution of new copies (Dodsworth et al. 2016).

There is a strong correlation between dioecy or subdioecy within *Cylindropuntia*, *Echinocereus*, and *Grusonia*, and in all three genera the greatest degree of dioecy, measured primarily by the percentage of pollen-sterile individuals, occurs in the higher polyploids (e.g., Baker and Cloud-Hughes 2014). Glick et al. (2016) reviewed sexual systems with respect to polyploidy and concluded that the connection between ploidy and sexual system holds in some clades, although it may be affected by factors that differ from clade to clade. We have an excellent example of this among the genera *Cylindropuntia*, *Grusonia*, and *Echinocereus*. Although dioecy and subdioecy are confined to polyploids, pollen-sterile individuals are confined to hexaploids and a single octoploid in *Cylindropuntia*, and occur in both tetraploids and hexaploids in *Grusonia* and *Echinocereus*. Given these data, as well as those from other genera within the Cactaceae (Baker and Cloud-Hughes 2014), the correlation between polyploidy and sexual systems shows clearly that as polyploidy increases, so does the chance for subdioecy in these three groups. Most recently, Gutiérrez-Flores et al. (2018) have found a correlation between subdioecy and ploidy level in *Pachycereus pringlei* Britton & J. N. Rose. The chance formation of a polyploid individual from diploid individuals is a rare event, a fact which is evidenced by the large number of chromosome determinations for many diploid taxa, among which no triploids or tetraploid individuals have been documented. Therefore, polyploid species begin as one or, less likely, a few individuals that can reproduce only by self-fertilization or apomixis. Models developed by Fowler and Levin (2016) indicate that high selfing rates were critical in the establishment of polyploids. Thus, as the population of the new polyploid increases, inbreeding becomes a barrier to gene exchange. Miller and Venable (2000) proposed that the selection of male-sterile mutants occurs in response to inbreeding depression. Selection pressure for outbreeding has been suggested as a logical consequence for the low population size of incipient allopolyploids (Baker and Cloud-Hughes 2014), but probably also holds true for autopolyploids. It has also been suggested that polyploids have an increased fixed heterozygosity, leading to increased heterosis and a higher tolerance of selfing, perhaps even promoting the evolution of self-compatibility (Dodsworth et al. 2016). This may be true in some taxa, but the evolution of dioecy and subdioecy in the cactus genera discussed herein suggests otherwise.

Given the thousands of chromosome determinations reported for the North American cacti alone, one might ask, when is enough enough? Regardless, the ploidy levels of numerous taxa have only recently been sorted out (Baker & Cloud Hughes 2014, Fenstermacher 2016, Gutiérrez-Flores et al. 2018, Majure et al. 2012a, Wellard 2016), and many gaps remain in the knowledge of chromosome races of many taxa. Thus, there are indubitably many puzzle pieces yet to be discovered and basic field work and associated lab work are far from complete.

**FUTURE WORK**

Beyond the obvious need for further molecular studies within Cactaceae, there are many more straightforward approaches that would do much to increase our understanding of the evolutionary processes within the family, especially within those genera that exhibit polyploidy and/or apomixis. Although the apomictic production of seeds is rare among higher plants (Whitton et al. 2008), it may be especially important within the life cycles of many polyploid and/or hybrid taxa. The only known pentaploid *Echinocereus*, *E. coccineus* × *E. yavapaiensis*, produces seed, which is almost certainly agamospermous (Baker pers. observ.). There are several species of *Opuntia* that are suspected or known to produce seed apomictically (Baker et al. 2009, Garcia-Aguilar, and E. Pimienta-Barrios 1996, Vélez-Gutiérrez and Rodríguez-Garay 1996). Do gametes form through apospory and/or apogamy? How self-incompatible are individuals within taxa? There are many meiotic phenomena that are poorly known. For example, there is geographic evidence for the selection for meiotic drive in *Cylindopuntia*. Nearly all apomictic taxa and associated hybrids that occur on the mainland produce at least some seeds, while isolated insular species, such as *C. hystrix* (Grisebach) Areces of Cuba, and *C. caribaea* (Britton & J. N. Rose) F. M. Knuth of the Dominican Republic do not (Baker pers. observ.). With no other *Cylindropuntia* genes available for genetic exchange, there appears to be no selection pressure within these insular species to produce viable gametes. Because both species reproduce by means of vegetative cloning, there has also been little, if any, selection pressure to reproduce via apomictic seeds. Interestingly, both species still bear flowers and parthenogenetic fruits. Mainland species and hybrids that are vegetatively apomictic, on the other hand, nearly always produce at least a limited number of seeds, indicating some selection for gene exchange, unless seeds of mainland species just happen to be agamospermous, while those of the islands are not. These and other unanswered questions indicate that much lab, field, and experimental garden work remains to gain a better understanding of the evolutionary mechanisms in Cactaceae.

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**Appendix 1.** Chromosome numbers determined for certain cacti of western North America. Voucher specimens are on deposit at ASU unless otherwise noted. Symbols: * = first chromosome count for taxon, including nothotaxa, ** = new chromosome count for taxon. Because of the variable number of chromosomes in meiotic daughter cells, odd polyploid counts are denoted by the diploid number of chromosomes divided by two, for instance, triploid = *33/2,* pentaploid = *55/2.* Type localities are in bold. Note: some taxonomic corrections and addenda to earlier published chromosome reports are presented at the end of this table. Collector names: *MAB* = Marc A. Baker, other collectors are not abbreviated. The names of co-collectors have been omitted. All chromosome determinations were made by Marc A. Baker. Coordinates are given in latitude-longitude, WGS 84. *Coryphantha* were identified by Andrew Salywon and many *Opuntia* were identified by Raul Puente-Martinez and Lucas Majure.

*Coryphantha missouriensis* (Sweet) Britton & J. N. Rose

*n*=11. USA, ARIZONA, Yavapai Co.: 34.7800° N, 112.4433° W, Chino Valley, 9km south of the confluence of the Verde River and Granite Creek, MAB18302.

*Coryphantha sneedii* (Britton & J. N. Rose var. *sneedii*

*n*=11. **USA, NEW MEXICO**, Doña Ana Co. 32.2023° N, 106.5155° W, south end of Organ Mountains, 27km SE of Las Cruces, 8.4km NE of Bishop Cap, originally collected by *R. D. Worthington 35053, MAB16690.*

*Coryphantha vivipara* (Nuttall) Britton & J. N. Rose var. *deserti* (Engelmann ex S. Watson) W. T. Marshall

*n*=11. **USA, NEVADA**, Nye Co.: 36.6647° N, 116.2008° W, Spector Range, 110km NW of Las Vegas, 56km SE of Beatty, *MAB17072.2.*

*Coryphantha vivipara* (Nuttall) Britton & J. N. Rose var. *vivipara*

*n*=11. **USA, NEW MEXICO**, McKinley Co.: 35.4880° N, 108.1630° W, 51km east of Gallup, 4.5k SSW of Smith Lake, *MAB11900*; **NEVADA**, Lincoln Co.: 37.8912° N, 114.4162° W, Pioche Hills, 5km SSE of Pioche, *MAB16960.*

*Cylindropuntia acanthocarpa* (Engelmann & J. M. Bigelow) F. M. Knuth var. *acanthocarpa*

*n*=11. **USA, ARIZONA**, Mohave Co.: 35.1581° N, 113.6965° W, just SW of the Round Valley Interchange, junction of I-40 and Hwy 93, *MAB11621*; 35.0693° N, 114.2908° W, Sacramento Valley, 1.6km NE of Dripping Spring [as indicated by the topographic map], *MAB18081*; **CALIFORNIA**, Imperial Co.: 32.9452° N, 114.8558° W, 32km NW of Yuma, Arizona, 5km NW of the north end of Cargo Muchacho Mountains, *MAB17541.1*; 33.0938° N, 114.9100° W 19km west of the Colorado River, 58km ESE of Niland, 50k NW of Yuma, Arizona, *MAB18488*; San Bernardino Co.: 34.8381° N, 114.9844° W, 5km west of the Sacramento Mountains, 32km due west of Needles, 9km WSW of South Pass, **type locality for *Opuntia acanthocarpa* Engelmann & J. M. Bigelow var. *coloradensis* L. Benson**, *MAB167824.1*.

*Cylindropuntia acanthocarpa* var. *acanthocarpa* × *C. multigeniculata*

*n*=11. **USA, ARIZONA**, Mohave Co.: 35.3356° N, 114.3999° W, 35km NW of Kingman, Black Mountains, 2.8km NNE of Burns Spring, *MAB17668.1.*

*Cylindropuntia acanthocarpa* var. *ramosa* (Peebles) Backeberg × *C. versicolor* (J. M. Coulter) F. M. Knuth

*n*=11. **USA, ARIZONA**, Pima Co.: 32.2072° N, 111.0027° W, Tucson, south slope of Tumamoc Hill, *MAB8137.*

*Cylindropuntia acanthocarpa* var. *thornberi* (Thornber & Bonker) Backeberg

*n*=11. **USA, ARIZONA**, Yavapai Co.: 34.2514° N, 112.0552° W, along Bloody Basin Road, 850m east of the Agua Fria River, 50km SE of Prescott, *MAB17657.1;* 34.2761° N, 112.9053° W, 17km WNW of Antelope Peak, 50km SW of Prescott, *MAB18269.1*

*Cylindropuntia acanthocarpa* × *C. leptocaulis* (DC.) F. M. Knuth

*n*=11. **USA, ARIZONA**, Yuma Co.: 32.6000° N, 114.1000° W, north of Wellton Hills, ca. 50k east of Yuma and south of I-8, *MAB11275.*

*Cylindropuntia alcahes* var. *gigantensis* × *C. lindsayi*

**n*=22. **MEXICO, BAJA CALIFORNIA SUR,**: 26.2792° N, 111.9208° W, along road to San Isidrio; ca. 10 road miles east of the junction with road to Comondú, *MAB8731*.

*Cylindropuntia bigelovii* (Engelmann) F. M. Knuth

*n*=11. **USA, CALIFORNIA,** Inyo Co.: 36.2931° N, 117.3018° W, Panamint Valley, 13km SW of Pinto Peak, *MAB18286.1, MAB18286.3, MAB18286.4*; Riverside Co.: 33.6373° N, 115.4223° W, Chuckwalla Mountains, 4km west of Aztec Well, *MAB17728;* 33.6385° N, 115.4313° W, Chuckwalla Mountains, 5km west of Aztec Well, *MAB17729.*

*n*=33/2. **USA, ARIZONA**, Mohave Co.: 34.9485° N, 114.4124° W, 4km south of Boundary Cone, 20km west of Colorado River, *MAB16818*; 35.0376° N, 114.2785° W, east side of the Black Mountains, 900m SE of Gold Trail Spring, *MAB16819*; 34.9602° N, 114.4037° W, 2.7km south of Boundary Cone, 20km west of Colorado River, *MAB16821.1*; 35.0693° N, 114.2908° W, 25km SW of Kingman, 1.6km NE of Dripping Spring [as indicated by the topographic map], *MAB18078*. **CALIFORNIA**, Imperial Co.: 33.3555° N, 115.3233° W, Chocolate Mountains, along the Niland-Blythe Road, 73km SW of Blythe, *MAB18295*; 33.1882° N, 115.2934° W, Chocolate Mountains, south side, 1.7km west of Mammoth Wash, *MAB18501; MAB18506*; 33.3182° N, 115.3491° W, Chocolate Mountains, 2.8km SSW of Beal Well, *MAB18510*; 33.2071° N, 115.2583° W, Chocolate Mountains, above and west of Mammoth Wash, *MAB18494;* Riverside Co.: 33.9379° N, 116.5815° W, Coachella Valley, 3km NNE of I-10 and Hwy 62, *MAB16809.1*; 33.6710° N, 115.7220° W, 1km north of Chiriaco Summit, 48km east of Indio, upper bajada, *MAB17532*; 33.6215° N, 115.6765° W, Orocopia Mountains, 2.4km north of Red Canyon, 52km east of Indio, *MAB18288.1*; 33.4537° N, 115.2707° W, Chuckwalla Bench, 64km WSW of Blythe, 3.3km SSW of Augustine Pass, *MAB18290*; 33.4459° N, 115.2632° W, Chuckwalla Bench, 64km WSW of Blythe, 3.9km south of Augustine Pass, *MAB18291*; 33.6340° N, 115.3607° W, Chuckwalla Mountains, 3.3km WNW of Corn Spring, *MAB18296*; San Bernardino Co.: 34.8542° N, 114.8912° W, Sacramento Mountains, 7km NE of Camino, *MAB16822.1*; *MAB16822.2*; **NEVADA**, Clark Co.: 35.2135° N, 114.6732° W, 10km NNW of Bullhead City, 1.3km north of confluence of Pipe Springs and Dripping Springs Canyons, *MAB16812, MAB16812.2, MAB16812.3, MAB16812.4*; 35.1820° N, 114.6830° W, Newberry Mountains, 38km SSE of Searchlight, *MAB16858, MAB16858.1.*

*Cylindropuntia bernardina* See nomenclatural notes

*n*=11. **USA, CALIFORNIA**, Los Angeles Co.: 34.1081° N, 117.7148° W, Claremont, 300m south of the SE base of Indian Hill, *MAB18407*.

*Cylindropuntia bernardina* × *C. echinocarpa*

**n*=11. **USA, CALIFORNIA**, San Bernardino Co.: 34.4044° N, 117.5801° W, San Gabriel Mountains, base of Horse Canyon, *MAB17938*.

*Cylindropuntia* ×*cardenche* (Griffiths) Pinkava & M. A. Baker *n*=22. **Mexico**, **San Luis Potosí**,: 22.1100° N, 100.9333° W, SE side of San Luis Potosí, 2km NNE of El Aguaje, *MAB12379.3.*

*Cylindropuntia chuckwallensis* M. A. Baker & M. A. Cloud-Hughes

*n*=33. **USA, CALIFORNIA**, Imperial Co.: 33.3555° N, 115.3233° W, Chocolate Mountains, along the Niland-Blythe Road, 73km SW of Blythe, *MAB18293*; Riverside Co.: 33.6366° N, 115.3688° W, Chuckwalla Mountains, 630m NE of Aztec Well, *MAB18297.1.*

*Cylindropuntia ×deserta* (Griffiths) Pinkava (= *C. acanthocarpa* var. *acanthocarpa* × *C. echinocarpa*)

*n*=11. **USA, ARIZONA,** Yavapai Co.: 34.0904° N, 113.0074° W, 1.5k SSW of Merrit Peak, ca. 17km SW of Congress, *MAB11274*; **NEVADA**, Clark Co.: 35.5120° N, 115.0349° W, Piute Valley, 11.5km WNW of Searchlight, 9km NE of Crescent Peak, *MAB17352.1, MAB17352.2, MAB17352.3*.

*Cylindropuntia delgadilloana* Rebman

*n*=11. **MEXICO, BAJA CALIFORNIA**: N30.9462° N, W115.9149° W, east of San Telmo, 23km east of Hwy 1, *MAB 18720* (voucher at BCMEX).

*Cylindropuntia echinocarpa* (Engelmann & J. M. Bigelow) F. M. Knuth

*n*=11. **ARIZONA**, Yuma Co.: 32.6802° N, 114.0519° W, Wellton Mesa, south end of Radar Hill, *M. Cloud-Hughes 509.2*; **CALIFORNIA**, Imperial Co.: 33.2151° N, 115.1860° W, Chocolate Mountains, Mammoth Wash, *MAB18500,* Riverside Co.: 33.6693° N, 115.7218° W, 900m north of Chiriaco Summit, 48km east of Indio, *MAB17699.2*; 33.8993° N, 114.6944° W, Big Maria Mountains, 12.5km WSW of Quien Sabe Point, *MAB17932* ; 33.8991° 116.7909° W, San Gorgonio River, 2km SW of Cabazon, *MAB18523*; San Bernardino Co.: 34.8381° N, 114.9844° W, 5km west of the Sacramento Mountains, 2km west of Homer Wash **lectotype locality for *Opuntia echinocarpa* Engelmann & J. M. Bigelow**, *MAB14290*; 35.4901° N, 115.6137° W, 3km SE of Pachalka Spring, south side of Clark Mountain, *MAB16794.1*; 34.8170° N, 116.3432° W, Cady Mountains, 15km west of Broadwell Lake, *MAB17020*; 35.5420° N, 115.4356° W, lower bajada on east side of Clark Mountain Range, 2.4km west of Ivanpah Lake, *MAB17292*; 35.6966° N, 116.6808° W, Owlshead Mountains, 2.4km south of the south end of Owl lake, *MAB18281*; 35.6384° N, 116.6488° W, 135m SSW of Owl Hole Springs, south side of the Owls Head Mountains, *MAB18283*; 34.0416° N, 116.5855° W, Morongo Valley and the town of Morongo Valley, *MAB18548*; **NEVADA**, Clark Co.: 36.4569° N, 114.7395° W, lower bajada to the NW of the Muddy Mountains, 48km NE of the center of Las Vegas, *MAB16858.2*; 36.0414° N, 115.5521° W, Spring Mountains, 4.5km NW of Mountain Springs, *MAB16948*; Lincoln Co.: 37.6151° N, 114.9985° W, just east of Pahroc Pass Summit, north end of South Pahroc Range, *MAB16963.2*; 35.8506° N, 115.5521° W, 3.8km west of the summit of Shenandoah Peak at the mouth of Keystone Wash, 50km SW of central Las Vegas, *MAB17547*.

*Cylindropuntia echinocarpa* × *C. ganderi* var. *ganderi*

**n*=11. **USA, CALIFORNIA**, San Diego Co.: 32.8167° N, 116.1288° W, 0330mS 2.5km ESE of Sweeney Pass, *MAB12784.*

*Cylindropuntia echinocarpa* × *C. munzii* (C. B. Wolf) Backeberg

*n*=11. **USA, CALIFORNIA**, Imperial Co.: 33.4278° N, 115.1493° W, south side of Chuckwalla Mountains, 3.8km SW of Graham Pass, *MAB17539*; 33.4195° N, 115.1576° W, south side of Chuckwalla Mountains, Bradshaw Trail, 1.4km east of its intersection with Graham Pass Road, *MAB17722.*

*Cylindropuntia echinocarpa* × *C. ramosissima*

**n*=11. **USA, NEVADA**, Clark Co.: 35.6293° N, 115.3358° W, Ivanpah Valley, lower bajada west of the Lucy Gray Mountains, *MAB18102.*

*Cylindropuntia fosbergii* (C. B. Wolf) Rebman, M. A. Baker, & Pinkava

*n*=33/2. **USA, CALIFORNIA**, San Diego Co.: 33.0178° N, 116.4395° W, Box Canyon, 70km ENE of central San Diego, *MAB17733*

*Cylindropuntia ganderi* var. *catavinensis* Rebman

*n*=11. **Mexico, Baja California**: 29.7350° N, 114.7920° W, 7km west of Cataviña, along Arroyo La Traveta, *MAB12330.*

*Cylindropuntia ganderi* var. *ganderi*

*n*=11. **USA, CALIFORNIA**, San Diego Co.: 32.8683° N, 116.2340° W, Tierra Blanca Mountains, 6.8km NE of Sombrero Peak, *MAB17696.*

*Cylindropuntia imbricata* (Haworth) F. M. Knuth var. *imbricata*

*n*=11. **USA, NEW MEXICO**, Eddy Co.: 32.0960° N, 104.6060° W, Yucca Canyon, south of Pack Trail, *MAB13073*; 32.3180° N, 104.8090° W, 750m north of Rawhide Canyon, 54km WSW of Carlsbad, *MAB16705.2*; Lincoln Co.: 33.7850° N, 105.7100° W, Jicarilla Mountains, Castle Garden Mesa, *MAB16189*; Sandoval Co.: 35.3101° N, 106.5323° W, 1.4km SE of Bernilillo, 1.4km SW of Santa Fé, *MAB16971.* Santa Fé Co: 35.6364° N, 105.9421° W, just south of Interstate 25 on south side of Rabbit Road, 5.5km south of the center of Santa Fé, **near the lectotype locality for *Opuntia arborescens* Engelmann in Wislizenus**, *MAB16974*.

*Cylindropuntia imbricata* var. *spinotecta* (Griffiths) M. A. Baker

*n*=11. **MEXICO, DURANGO**: 24.1050° N, 104.5717° W, Cinco de Mayo, 10km NE of Durango, **type locality for *Opuntia spinotecta* Griffiths**, *MAB12386.*

*Cylindropuntia ×kelvinensis* (V. E. Grant & K. A. Grant) P. V. Heath

*n*=11. **USA, ARIZONA**, Pima Co.: 31.4888° N, 110.4997° W, San Pedro Valley, Peck Canyon, *MAB17261.*

*n*=33/2. **USA, ARIZONA**, Pima Co.: 32.4413° N, 110.9682° W, Oro Valley, 7.9km NE of Buster Mountain, *MAB11284.*

*Cylindropuntia leptocaulis*

*n*=11. **USA, ARIZONA**, Graham Co.: 31.3101° N, 110.3505° W, above Triplet Wash, 10km ESE of San Carlos, *MAB17232.*

*Cylindropuntia leptocaulis* × *C. ramosissima*

**n*=11. **USA, ARIZONA**, Mohave Co.: 34.7249° N, 113.9496° W, SW flank of the Hualapai Mountains, 21km SW of the summit of Diamond Peak, *MAB17835.*

*Cylindropuntia leptocaulis* × *C. whipplei* (Engelmann & J. M. Bigelow) F. M. Knuth var. *whipplei*

*n*=11. **USA, ARIZONA**, Yavapai Co.: 34.8618° N, 112.0705° W, 10km north of Clarkdale, 0.7k ESE of the confluence of the Verde River with Sycamore Creek, *MAB8921.*

*Cylindropuntia munzii* (C. B. Wolf) Backeberg

*n*=11. **MEXICO, BAJA CALIFORNIA**: 29.6070° N, 114.3976° W, 21km SSW of Punta Final, 6.5km ESE of Cerro Tomás, *MAB18714* (voucher at BCMEX); 28.6304° N, 113.2515° W, 47km SE of Bahía de Los Angeles, 14km NW of San Rafael *MAB18715*, *MAB18716*; (voucher at BCMEX); **USA, CALIFORNIA**, Imperial Co.: 33.3555° N, 115.3233° W, Chocolate Mountains, along the Niland-Blythe Road, *MAB18294;* 33.3172° N, 115.3488° W, Chocolate Mountains, 18km (11 miles) NE of Niland, 2.8km SSW of Beal Well, **type locality of *Opuntia munzii* C. B. Wolf**, *MAB18483, MAB18485*; 33.3091° N, 115.3542° W, Chocolate Mountains, 2.8km SSW of Beal Well, 18km (11 miles)

NE of Niland, **type locality of *Opuntia munzii* C. B. Wolf**, *MAB18502, MAB18505*; 33.2073° N, 115.2503° W, Chocolate Mountains, Mammoth Wash, 24km ESE of Niland, 54km NNE of El Centro, *MAB18489, MAB18490.*

*Cylindropuntia ×neoarbuscula* (Griffiths) F. M. Knuth

*n*=55/2. **USA, ARIZONA**, Pima Co.: 31.9179° N, 110.9168° W, 33km south of central Tucson, along Santa Rita Road, *MAB10476.1.*

*Cylindropuntia ramosissima*

*n*=11. **USA, CALIFORNIA**, Riverside Co.: 33.4988° N, 115.1731° W, 57km WSW of Blythe, 4.2km NE of Chuckwalla Spring, *MAB17303*; San Bernardino Co.: 34.9140° N, 115.0480° W, 1.3km ESE of Goffs, north end of Piute Mountains, *MAB16688.2*, *MAB16688.3*; 34.8112° N, 116.3824° W, Cady Mountains, 18km WSW of Broadwell lake, *MAB17044*; 34.7109° N, 115.6737° W, NW base of Marble Mountains, 1km south of Brown Butte, *MAB17047.1*; *MAB17047.3*; 34.0142° N, 114.9571° W, 4km SW of the summit of Homer Mountain, 36km WNW of Needles, *MAB17243*; 34.8581° N, 116.2527° W, 16km NE of Pisgah Crater, 5.5km ESE of Cady Peak, *MAB18801*; 34.9767° N, 116.1183° W, just north of Bristol Mountains, 34km NE of Pisgah Crater, *MAB18803*; **NEVADA**, Clark Co.: 35.7297° N, 115.3016° W, 4.3km SSE of Jean, 2.6km west of the south end of Sheep Mountain, *MAB16920.1*; 36.0508° N, 115.3997° W, 400m NNE of the town of Blue Diamond, *MAB16949*; 35.6126° N, 115.3329° W, Ivanpah Valley, 4km SE of Roach Lake, *MAB18108.*

*n*=22. **USA, CALIFORNIA**, Riverside Co.: 33.4410° N, 114.7736° W, 800m north of Sand Wash, lower bajada to the east of the Mule Mountains, *MAB17298*; 33.4454° N, 114.7743° W, 2800m north of Sand Wash, lower bajada to the east of the Mule Mountains, *MAB17299*; 33.4611° N, 114.7862° W, 24km SW of Blythe, lower bajada to the east of the Mule Mountains, *MAB17300*; San Bernardino Co.: 34.8381° N, 114.9844° W, 5km west of the Sacramento Mountains, 9km WSW of South Pass, *MAB16701, MAB17049.1.*

*Cylindropuntia sanfelipensis* Rebman

*n*=33. **Mexico, Baja California**: 31.2972° N, 115.3537° W, Valle de Santa Clara, 58km NW of San Felipe, *MAB18713* (voucher at BCMEX).

C*ylindropuntia spinosior* (Engelmann) F. M. Knuth

*n*=11. **USA, ARIZONA**, Yavapai Co.: 34.5772° N, 112.5060° W, 5km NW of the center of Prescott, 7km SE of the summit of Granite Mountain, *MAB17133.*

*Cylindropuntia ×vivipara* (J. N. Rose)

**n*=55/2. **USA, ARIZONA**, Pima Co.:32.3366° N 111.0977° W, Tucson, 1km west of Silver Bell Road on Ina (Picture Rocks) Road *MAB7806.*

*Cylindropuntia whipplei* (Engelmann & J. M. Bigelow var. *enodis* Peebles

*n*=22. **USA, ARIZONA**, Mojave Co.: 36.4989° N, 113.4461° W, Little Hurricane Rim, 4.4km NNW of Poverty Knoll, *MAB17882.3.*

*Cylindropuntia wolfii* (L. D. Benson) M. A. Baker

*n*=33. **Mexico, Baja California**: 32.5798° N, 115.9743° W, Sierra Juarez, 45km west of Mexicali, *MAB17695.*

*Echinocereus arizonicus* subsp. *arizonicus* (Material collected under USFWS permit no. TE-43719A-1)

*n*=11. **USA, ARIZONA**, Gila Co.: 33.3394° N, 110.9086° W, Pinal Mountains, upper reaches of Copper Springs Canyon, *MAB17436*; 33.3037° N, 110.7949° W, Pinal Mountains, above and 270m west of Pinal Creek, *MAB17723*; Pinal Co.: 33.3783° N, 111.0980° W, 9.1km north of Superior, 2.6km NNW of Fortuna Peak, *MAB17526.1*, *MAB17526.2*; 33.4003° N, 111.1271° W, 12.4km NNW of Superior, 1.5km ESE of Black Spring, *MAB17528.*

*Echinocereus arizonicus* subsp. *nigrihorridispinus* W. Blum & Rutow

*n*=11. **USA, ARIZONA**, Cochise Co.: 31.4880° N, 109.0770° W, Peloncillo Mountains, 700m WSW of Miller Spring, *MAB17569.5*; Graham Co.: 33.3315° N, 110.0810° W, 65km NW of Safford, 1km west of Sweetmeat Draw and Yellow Jacket Road, *MAB11736*; Greenlee Co.: 33.1141° N, 109.0481° W, 750m north of Hwy 78, 13km east of the summit of Bushy Mountain, *MAB17827.1*, *MAB17827.2*; 33.4115° N, 109.3579° W, 3.3km SSE of Rose Peak, Route 666 between Hogtail Canyon and Hogtail Saddle, *MAB18444.1.*

*Echinocereus arizonicus* × *E. bonkerae*

**n*=11. **USA, ARIZONA**, Pinal Co.: 33.3604° N, 111.0318° W, upper reaches of Devils Canyon, 5km east of Fortuna Peak, *MAB17826.*

*Echinocereus bonkerae* subsp. *apachensis* (W. Blum & Rutow) A. D. Zimmerman

*n*=11. **USA, ARIZONA**, Gila Co.: 34.2556° N, 111.1843° W, Green Valley Creek, 12.7km ENE of Payson, *MAB17169.3.*

*Echinocereus bonkerae* subsp. *bonkerae*

*n*=11. **USA, ARIZONA**, Gila Co.: 34.2556° N, 111.1843° W, Green Valley Creek, 12.7km ENE of Payson, *MAB17169.1*; 33.1537° N, 110.6855° W, Mescal Mountains, 8km ESE of the summit of El Capitan Mountain, *MAB17689*; Greenlee Co.: 33.4077° N, 109.3510° W, 600m ESE of Hogtail Saddle on south side of Hwy 666 (191), 39km north of Clifton, *MAB17219.1*; Pinal Co.: 33.6070° N, 110.7510° W, Oracle, 1300m east of the junction of Mount Lemmon Road and the Oracle loop, *MAB16504.1*; Yavapai Co.: 34.2032° N, 111.8809° W, 25km SE of Cordes Junction, vicinity of Hutch Springs, *MAB8839.1*, *MAB8839.2.*

*Echinocereus chloranthus* (Engelmann) Rümpler subsp. *chloranthus*

*n*=11. **USA, NEW MEXICO**, Otero Co.: 32.7618° N, 105.5129° W, Sacramento Mountains, just west of Weed Road, above Park Canyon, *MAB18182.4*; 32.7161° N, 105.5515° W, Sacramento Mountains, Buck Canyon, *MAB18203.1.*

*Echinocereus chloranthus* (Engelmann) Rümpler subsp. *rhyolithensus* W.Blum & Mich.Lange

*n*=11. **USA, ARIZONA**, Greenlee Co.: 33.1097° N, 109.0681° W, Big Lue Mountains, along Coal Creek, *MAB17873.2.*

*Echinocereus coccineus* Engelmann subsp. *coccineus*

*n*=22. **USA, ARIZONA**, Greenlee Co.: 33.5701° N, 109.3320° W, 2.3km NNW of Stray Horse, 5.9km west of Sawed Off Mountain, *MAB17216.2*; La Paz Co.: 34.0012° N, 113.5091° W, Harcuvar Mountains, above and south of Dripping Spring, *MAB13696*; 33.8197° N, 113.3604° W, Harquahala Mountain, 1.2km NW of the summit, *MAB18274.3*, *MAB18274.4*, *MAB18274.5*; Mohave Co.: 35.1820° N, 113.4840° W, vicinity of Cactus Pass, 50km east of Kingman, *MAB11815.1*, *MAB11815.2*; 35.9217° N, 113.9133° W, north of Seligman, Grapevine Canyon, *MAB15161.3*; 35.1820° N, 113.4840° W, vicinity of Cactus Pass, 50km east of Kingman, along Willow Ranch Road, *MAB11815.2*; 35.7493° N, 113.3640° W, Peach Springs Canyon, south of Diamond Creek, *MAB8105*; Yavapai Co.: 35.2667° N, 112.4167° W, above and north of Ashfork Draw at SE end of Antolini Hill, 7.5km NW of Ashfork, *MAB15876.2*; 34.4286° N, 112.4284° W, Bradshaw Mountains, 200m WSW of Hassayampa Lake, *MAB14367.1, MAB14367.3, MAB17738.1; MAB17738.2*; *MAB17738.4*; *MAB17738.6, MAB17738.7*; 34.7208° N, 112.7677° W, NNE of Prescott, south of Horse Wash at the north base of Eagle Peak, *MAB12400*; 34.5074° N, 112.5298° W, 1.8km WNW of Wolverton Mountain, 7km SW of downtown Prescott, *MAB17279.2*; **NEW MEXICO**, Cibola Co.:

35.0209° N, 107.9707° W, 20km SW of Grants,.5km west of Gallo Peak*, MAB16994.3*, *MAB16994.4*.

*Echinocereus coccineus* subsp. *coccineus* × *E. yavapaiensis*

**n*=55/2. **USA, ARIZONA***,* Yavapai Co.: 34.4283° N, 112.4283° W, Bradshaw Mountains, 400m WSW of Hassayampa Lake*., MAB14367.2*.

*Echinocereus coccineus* subsp. *rosei* (Wooton & Standley) W. Blum & Rutow

*n*=22. **USA, NEW MEXICO***,* Lincoln Co.: 33.6767° N, 105.9283° W, 18.5km west of Carrizozo Peak, 6.1km NW of Carrizozo*, MAB16242*; **TEXAS***,* Culberson Co.: 31.8833° N, 104.8667° W, summit of Guadalupe Peak*, MAB13086.2*; *MAB13086.3*; Lincoln Co.: 33.2000° N, 105.0610° W, 54km WSW of Roswell, 1.5km east of Border Hill between Twin Butte and Monuments Canyons*, MAB16665.2*.

*Echinocereus coccineus* subsp. *santaritensis* (W. Blum & Rutow) M. A. Baker

*n*=22. **USA, ARIZONA***,* Cochise Co.: 31.4280° N, 110.4427° W, Canelo Hills, 500m east of Parker Canyon Lake, *MAB13383.1*; 31.8945° N, 109.9715° W, 520m NW of Cochise Peak, 14km west of Pearce, *MAB15392*; Gila Co.: 33.2859° N, 110.8632° W, Pinal Mountains, 2.7km WSW of Signal Peak, *MAB17686.2*; 33.2838° N, 110.8584° W, Pinal Mountains, 2.3km SW of Signal Peak, *MAB17686.1*; Pinal Co.: 33.3342° N, 110.8887° W, Pinal Mountains, 3km south of Granite Point*, MAB17289.1*, *MAB17289.4, MAB17289.5*; 33.3378° N, 110.9064° W, Pinal Mountains, 3.3km SSW of Granite Point, *MAB17290.1*; *MAB17290.3*; 33.4180° N, 111.1693° W, 15 NNW of Superior, 1km SSE of Roger Spring, *MAB17529.1*; 33.4394° N, 111.0842° W, west fork of Pinto Creek 900m WNW of its confluence with Rock Creek, NE end of Sawtooth Ridge, 16km north of Superior, *MAB17724.2*, *MAB17724.3*, *MAB17724.5*; 33.4410° N, 111.0610° W, west fork of Pinto Creek, FS Rd 287(A). *MAB13701.2*; Santa Cruz Co.: 31.4683° N, 111.2250° W, 1km SSE of Ruby Peak, east of Ruby, *MAB13422.1*.

*Echinocereus engelmannii* subsp. *engelmannii*

*n*=22. **USA**, **ARIZONA**, Coconino Co.: 35.9190° N, 111.6540° W, south rim of the Little Colorado Gorge, 11km SW of Shadow Mountain, *MAB16530.2*; La Paz Co.: 34.0233° N, 113.5150° W, 6.6km SSE of Black Butte, 69km SSW of Bagdad, *MAB16149.2*; Maricopa Co.: 33.7245° N, 112.2362° W, 1km west of the New River, 1.9km south of West Wing Mountain, **type locality for *Echinocereus engelmannii* (Parry ex Engelmann) Rümpler var. *acicularis* L. D. Benson**, *MAB16465.3, MAB16465.5*; 33.7093° N, 112.2508° W, 3.4km SE of Caldewood Butte, 2.8km west of New River, **type locality for *Echinocereus engelmannii* (Parry ex Engelmann) Rümpler var. *acicularis* L. D. Benson**, *MAB16632.6*; 32.8763° N, 113.2198° W, Sentinel Plain, 7.3km WSW of Sentinel Peak, *MAB18721.1*, *MAB18721.2*; Mohave Co.: 35.1650° N, 119.5422° W, Cactus Pass area, 1.6km SSE of the summit of Tin Mountain, **near type locality for *Cereus engelmannii* Parry ex Engelmann var. *variegatus* Engelmann and J. M. Bigelow**, *MAB16456.6, MAB16456.7*; 36.6407° N, 114.0170° W, Lime Kiln Canyon, 19km SSE of Mesquite, *MAB16762.2, MAB16762.3*; 35.1742° N, 113.7853° W, pass between Peacock and Hualapai Mountains, *MAB16799*; 34.6378° N, 113.5713° W, along the Big Sandy River, 1.7km SSW of its confluence with Sycamore Creek, *MAB16805.1*; 36.7952° N, 113.2834° W, 43km SE of St. George, Utah, along Navajo Trail *MAB17887.1*; 35.1350° N, 113.5220° W, Aquarius Mountains, 1.3km south of Willow Creek, **type locality for *Cereus engelmannii* Parry var. *variegatus* Engelmann & J. M. Bigelow,** *MAB16644.3*, *MAB16644.4*; Yavapai Co.: 34.3450° N, 112.2217° W, 7km north of Cleator, 1km west of Cedar Canyon, *MAB14566.3, MAB14566.6*; 34.2514° N, 112.0552° W, along Bloody Basin Road, 50km SE of Prescott, *MAB17656*; **CALIFORNIA**, Imperial Co.: 33.2151° N, 115.1860° W, Chocolate Mountains, Mammoth Wash, *MAB18499*; Riverside Co.: 33.5749° N, 116.4940° W, Ribbonwood, north end of the Santa Rosa Mountains, *MAB17464.1*; 33.6190° N, 116.6220° W, along Morris Ranch Road, 400m north of Kenworthy Station, **type locality for *Cereus munzii*** Parish, *MAB17354.4*; 33.6213° N, 116.6189° W, along Morris Ranch Road, 640m NNE of Kenworthy Station, **type locality for *Cereus munzii* Parish**, *MAB17368.1*; San Bernardino Co.: 35.4180° N, 115.8100° W, 3km ESE of Solomans Knob, 29km NE of Baker, *MAB16739.1*; 34.8170° N, 116.3432° W, 61km east of Barstow, 15km west of Broadwell Lake, *MAB17019*; 35.1537° N, 115.3554° W, 765m NNE of Government Spring, 3.2km SSE of the summit of Pinto Mountain, *MAB17521.2*; 35.7131° N, 116.8895° W, Owlshead Mountains, 12km ENE of the summit of Brown Mountain *MAB18284.1, MAB18284.2, MAB18284.3*; San Diego Co.: 33.0920° N, 116.4880° W, 1350m WSW of Scissors Crossing, **neotype locality of *Cereus engelmannii* Parry ex Engelmann**, *MAB17698.1*; 34.6820° N, 116.5040° W, 3km south of Silver Bell Mine, 36km ESE of Barstow *MAB16673.1*; **NEVADA**, Clark Co.: 35.2025° N, 114.6683° W, 10km NNW of Bullhead City, at confluence of Pipe Springs and Dripping Springs Canyons, *MAB16814*; 36.4261°N, 115.1619° W, 300m NE of Gass Spring, 3.2km NNE of the summit of Gass Peak, *MAB17842.2*; 36.4085° N, 114.1209° W, 44km south of Mesquite, 3km south of Devils Throat, *MAB16860*; Lincoln Co.: 37.4236° N, 115.3737° W, Pahranagat Range, 900m south of Hancock Summit, *MAB18110.1*; **UTAH**, Juab Co.: 39.6177° N, 113.9396° W, Deep Creek Range, 120km WNW of Delta *MAB16772.1, MAB16772.3, MAB16772.4, MAB16772.5*; Tooele Co.: 39.9455° N, 113.0508° W, east slope of the Dugway Range, 3km NE of Dugway Ridge, *MAB 16773.1, MAB16773.3, MAB16773.5*; Nye Co.: 38.5668° N, W117.5490° W, Shoshone Mountains, 1km SSW of Rojo Spring, *MAB18912.1*.

*Echinocereus engelmannii* subsp. *fasciculalatus*

*n*=22, **ARIZONA**, Coconino Co.: 35.5317° N, 113.2383° W, just WNW of the entrance to Grand Canyon Caverns, north side of Route 66, *MAB16177*; Graham Co.: 32.8667° N, 109.5184° W, 4.7km SW of the confluence of the Gila River and Bonita Creek, 18km ENE of Safford*,* **neotype locality for *Mammillaria fasciculata*** Engelmann, *MAB16180.3*; Pinal Co.: 32.5250° N, 110.7033° W, Nugget Canyon, 12km SSE of Oracle, *MAB16272.2, MAB16272.2*; 32.5950° N, 110.7283° W, Ray Spring Hill, 4km east of Oracle *MAB16273.3*; Yavapai Co.: 34.2761° N, 112.9053° W, 17km WNW of Antelope Peak, 16km SSW of Hillside *MAB18270.2*; 34.4083° N, 112.7050° W, 2.5k east of the confluence of Kirkland Creek and Skull Valley Wash, 1k south of the village of Kirkland *MAB12396.2*; 34.4503° N, 112.6939° W, 3.8m NNE of Kirkland, 23km SW of Prescott, *MAB18300.5, MAB18300.1*.

*Echinocereus fendleri* (Engelmann) Rümpler subsp. *fendleri*

*n*=11. **USA, ARIZONA**, Apache Co.: 34.0899° N, 109.3949° W, 10km WSW of Eagar, 6.4km east of the summit of Antelope Mountain *MAB17206.2*; Navajo Co.: 34.0631° N, 109.8868° W, above Bull Cienega Spring, 1.8km east of the summit of Cooley Mountain, *MAB17179.5;* Yavapai Co.; 34.9816° N, 112.3889° W, 500m west of the confluence of Limestone and Hell Canyons, 1.2km WNW of Drake, *MAB18529.1*.

*Echinocereus fendleri* (Engelmann) Rümpler subsp. *rectispinus* (Peebles) Taylor

*n*=11, **USA**, **ARIZONA**; Cochise Co.: 31.3680° N, 109.1450° W, 9km west of the New Mexican border, 3.9km north of the Mexican border *MAB16467.3;* 31.9575° N, 109.1479° W, 5km north of Portal, 5km SE of Harris Mountain *MAB17226*; Graham Co.: 31.5911° N, 109.8544° W, Pinaleño Mountains, Stockton Pass, along Hwy 266 *MAB17228*.

*Echinocereus mojavensis* (Engelmann & J. M. Bigelow) Rümpler

*n*=11. **USA, ARIZONA,** Coconino Co.: 35.2293° N, 111.6108° W, south side of Elden Mountain, 1.4km south of Devils Head, *MAB17736.1*; 35.2644° N, 111.0086° W, Canyon Diablo, 4.2km SSW of the confluence of Canyon Diablo Wash and the Little Colorado River, **near the lectotype locality of *Cereus mojavensis* var. *zuniensis* Engelmann & J. M. Bigelow**, *MAB14054.1*; Mohave Co.: 36.6407° N, 114.0170° W, Lime Kiln Canyon, 19km SSE of Mesquite *MAB16761.1*; **CALIFORNIA**, Inyo Co.: 37.2935° N, 118.1678° W, White Mountains, 1.5km SW of Westgard Pass, *MAB17749.2*; San Bernardino Co.: 35.1550° N, 115.2230° W, Lanfair Valley, ca. 10km north of Hackberry Mountain, **type locality for *Cereus mojavensis* Engelmann & J. M. Bigelow**, *MAB13758*; 35.1167° N, 115.4000° W, Black Canyon, Mid Hills, 7km NE of the top of Columbia Mountain, **type locality for *Echinocereus sandersii* Orcutt**, *MAB13957.1, MAB13957.2*; **UTAH,** Millard Co.: 38.6755° N, 113.9351° W, east slope of the Mountain Home Range, 20km SSE of Garrison, *MAB17787.3*; San Juan Co.: 37.0574° N, 110.5839° W, 80km ENE of Page, Arizona, 20km SSW of the summit of Monitor Butte *MAB17274*; 38.4790° N, 109.3506° W, Brumley Ridge, 20km SE of Moab, **neotype locality of *Echinocereus phoeniceus* Rümpler var. *inermis* K.Schum**, *MAB17582.1*, *MAB17582.2*; 38.4700° N, 109.3525° W, Brumley Ridge, 20km SE of Moab, **neotype locality of *Echinocereus phoeniceus* Rümpler var. *inermis* K.Schum**, *MAB17584.1, MAB17584.3, MAB17585.1, MAB17585.2,* 37.9435° N, 109.4920° W, Abajo Mountains, 2.3km WNW of Jackson Spring, *MAB17594*, *MAB17595.1, MAB17595.2*.

*Echinocereus relictus* Wellard

*n*=11. **USA**, **ARIZONA**, Mohave Co.: 36.8500° N, 113.6550° E, 58km WSW of Colorado City, Maple Canyon, *MAB16138.1*, *MAB16138.2*, *MAB16138.3*, *MAB16138.4*, *MAB16138.6*; 36.9200° N, 113.6617° E, 57km W of Colorado City, E of Purgatory Canyon, *MAB16137.1*, *MAB16137.2*; 36.9374° N, 113.6402° W, 20km SSW of St. George, Utah, 4km north of the summit of Mokaac Mountain, *MAB17789.2*; **UTAH**, Washington Co.: 37.1483° N, 113.6067° W, just NNW of St. George, between Halfway Wash and City Creek, *MAB16139.1*, *MAB16139.2*, *MAB16139.4*.

*Echinocereus russanthus* D. Weniger

*n*=11. **USA, TEXAS,** Brewster Co.: 29.3655° N, 103.0507° W, 900m NNE of Roys Peak, 95km south of Marathon, *MAB18623.3*.

*Echinocereus triglochidiatus* Engelmann

*n*=11. **USA, NEW MEXICO,** McKinley Co.: 35.0654° N, 108.7140° W, Cheama Canyon, 7km east of Dowa Yalanne Mountain, *MAB17830.3*

*Echinocereus triglochidiatus* Engelmann (with morphology intermediate to *E. mojavensis*)

**n*=11. **USA, ARIZONA**. Apache Co. : 35.4107° N, 109.4840° W, 1.5km SE of Wide Ruins, 34km SSE of Ganado, *MAB17596.1*; 35.4752° N, 109.3970° W, 29km SSE of Ganado, 500m north of Oak Ridge, *MAB17598.1, MAB17598.2, MAB17598.3*.

*Echinocereus yavapaiensis* M. A. Baker

*n*=33. **USA, ARIZONA**. Maricopa Co.: 33.8964° N, 111.9856° W, Elephant Mt., 750 m SE of Burro Spring, *Hunkins 370* (DES); Yavapai Co.: 34.2750° N, 112.2667° W, 3km east of Cleator, just north of Crazy Basin Creek, *MAB13153.2*; 34.3450° N, 112.2217° W, 7km north of Cleator, 1km west of Cedar Canyon, *MAB14565.2*; 33.9500° N, 112.5217° W, Wickenburg Mountains, 750m west of the summit of Red Picacho, *MAB15794.3*; 34.2237° N, 112.0944° W, Badger Spring Wash, 160m NNW of its confluence with Agua Fria River, *MAB17674.2*.

*Grusonia clavata* (Engelmann) H. Robinson

*n*=11. **USA, NEW MEXICO**, Sandoval Co.: 35.3101° N, 106.5323° W, 1.4km SW of Santa Fé, 2.5km east of the Rio Grande River, **near the Lectotype locality for *Opuntia clavata* Engelmann**, *MAB16972*.

*Grusonia densispina* (Ralston & R. A. Hilsenbeck) Pinkava in Rebman

*n*=22. **USA, TEXAS**, Brewster Co.: 29.0650° N, 103.1130° W, Big Bend National Park, 20km SW of Boquillas, Solis junction, this is a confirmation of a chromosome determination made by Fenstermacher (2016) for a clone under the number *Fenstermacher 2212*. *MAB16637;* 29.0646° N, W103.1138° W, 2.4km NNW of Solis Landing, 1.4km NW of Solis (historic) at the Mexican border, a clone of *Fenstermacher 2215*, *MAB18417*.

*Grusonia emoryi* (Engelmann) Pinkava

*n*=22. **USA, ARIZONA**, Gila Co.: 33.3815° N, 110.4744° W, 28km east of Globe, 2km west of Sevenmile Wash, *MAB17267.3*; **NEW MEXICO**, Hidalgo CO: 32.6684° N, 108.9560° W, 14.5km south of Steeple Rock, 42km NW of Lordsburg, **near the neotype locality for *Opuntia stanlyi* Engelmann in Emoryi**, *MAB17876.5*; 32.6455° N, 108.9831° W, 5km SSE of Virden, 42km NW of Lordsburg, **near the neotype locality for *Opuntia stanlyi* Engelmann in Emoryi** *MAB17877.2*.

*Grusonia parishiorum* (Orcutt) Pinkava

*n*=11. **USA**, **NEVADA,** Clark Co.:35.7470° N, 115.3243° W, Ivanpah Valley, 3.7km south of Jean, *MAB16823*; N35.8522° N, 115.4342° W, Goodsprings Valley, 2km north of Goodsprings, *MAB17321*; 35.8853° N, 115.6859° W, 3.2km east of the summit of Black Butte, 58km SW of central Las Vegas, *MAB17548*; **CALIFORNIA**, San Bernardino Co.: 36.6020° N, 115.4790° W, Ivanpah Valley, 8km east of Keany Pass, *MAB11652*.

*Grusonia robertsii* Rebman

*n*=11. **MEXICO, BAJA CALIFORNICA SUR**: 27.3241° N, 113.1295° W, SW base of Cerro Las Mulas, 1.5km west of the intersection of Hwy 1 and the road to Punta Abreojos, near the type locality for the taxon; *MAB18718* (voucher at BCMEX). Chromosome number, habit, stem and fruit morphology, and frequency of individuals suggest that this represents a spontaneous hybrid between *Cylindropuntia alcahes* var. *alcahes* and *Grusonia invicta* (Brandegee) E. F. Anderson, both of which occur at his location. However, we are reluctant to assign nothospecies status to what would be the first intergeneric hybrid between these two genera until we have results from DNA analyses.

*Grusonia wrightiana* E. M. Baxter

*n*=22. **USA, ARIZONA**, La Paz Co.: 34.1432° N, 113.5001°, Butler Valley, 15km SE of Alamo, the former settlement at the crossing of the Bill Williams River, Near the type locality of *Opuntia stanlyi* Engelmann [ex B. D. Jackson] var. *peeblesiana* L. Benson, *MAB17601.1*.

*Mammillaria heyderi* Muehlenpfordt var. *meiacantha* (Engelmann) L. D. Benson

*n*=11. **USA, NEW MEXICO**, Otero Co.: 32.7560° N, 105.5251° W, Sacramento Mountains, above Park Canyon, *MAB18183.1*; Sandoval Co.: 35.6500° N, 106.8667° W, west of Peñasco Canyon, approximately 1.4k due north of Los Pinos Arroyo, *MAB13549*.

*Mammillaria tetrancistra* Engelmann

*n*=11. **USA, ARIZONA**, La Paz Co.: 34.2810° N, 103.4380° W, 2km south of Santa Maria River, just west of Grapevine Springs, *MAB16621*; **NEVADA**, Nye Co.: 36.8256°

N, 116.4837° W, 26km ESE of Beatty, 7.3km NW of Busted Butte, *MAB18129*.

*Micropuntia pulchella*

*n*=11. **USA, NEVADA**, Churchill Co.: 39.4945° N, 118.7512° W, 560m north of the summit of Rattlesnake Mountain, 3.3km NE of central Fallon, *MAB17778.1;* Esmeralda Co.: 37.9448° N, 118.2210° W, north end of White Mountains, 3.5km NW of Pinyon Hill, 65km NNE of Bishop, *MAB17773.2*; Lyon Co,: 38.8095° N, 119.2237° W, just SW of Wilson Canyon, 80m north of Walker River, 20km SW of Yerington, **near the lectotype locality of *Opuntia pulchella* Engelmann**, *MAB17776.4*.

*Opuntia austrina* Small

*n*=11. **USA, FLORIDA**, St. Lucie Co.: 27.3672° N, 80.2881° N, 9.6km south of Ft. Pierce along South Indian Drive, originally collected by *L. Benson15379*, 1 September 1954, cultivated in the greenhouse at the Desert Botanical Gardens (1994-0023-01-1), Phoenix, Arizona; stems rooted and grown in greenhouse at Chino Valley, Arizona, *MAB17935*.

*Opuntia aurea* McCabe ex E. M. Baxter

*n*=33. **USA, ARIZONA**, Mohave Co.: 36.8950° N, 112.7474° W, SW side of the town of Kaibab, 22km SE of Colorado City. *MAB16538.1*; **UTAH**, Washington Co.: 37.0483° N, 113.0900° W, Big Plain, 5km west of the Vermillion Cliffs, *MAB13665*; 37.1720° N, 113.2670° W, Little Creek Mountain, just north of Little Creek, *MAB14093.1* (apparently introgressed with *O. polyacantha*).

*Opuntia austrina* Small

*n*=11. **USA, Florida**, St. Lucie Co.: 27.3672° N, 80.2881° W, 9.6km south of Ft. Pierce, along South River Drive, originally collected by *L. Benson15379*, cultivated at the Desert Botanical Garden, Phoenix, Arizona, and then at our garden in Chino Valley, Arizona, *MAB16935*.

*Opuntia azurea* J. N. Rose var. *parva* A. M. Powell & Weedin

*n*=11. **USA, TEXAS**, Brewster Co.: 29.3870° N, 1103.0754° W, McKinney Springs, 3.5km NNW of Roys Peak, *MAB18620*.

*Opuntia azurea* J. N. Rose var. *discolo*r J. F. Weedin × *O. rufida* Engelmann

**n*=11. **USA, TEXAS**, Presidio Co.: N29.2960° N, 103.9434° W, Big Hill, SE end of Santana Mesa, 33km west of Terlingua, **at the type locality of *Opuntia azurea* J. N. Rose var. *discolo*r J. F. Weedin**, *MAB18628.2*.

*Opuntia basilaris* Engelmann & J. M. Bigelow var. *basilaris*

*n*=11. **USA, CALIFORNIA**, Kern Co.: 35.5688° N, 118.5852° W 2.6km NE of Delonegha Hot Springs, just west of Little Creek, *MAB18511.1*; 35.5683° N, 118.5846° W, Kern Canyon, 2.6km NE of Delonegha Hot Springs, *MAB18511.2*; 35.5263° N, 118.0874° W, Bird Spring Canyon, 5.7km SE of Bird Spring Pass, *MAB18517*; 35.5540° N, 118.2011° W, SW base of Scodie Mountain, 5.3km SW of Skinner Peak, *MAB18516*; 35.3020° N, 118.5912° W, 3km ENE of Caliente, 39km ESE of central Bakersfield, *MAB18540*; 35.0538° N, W118.3448° W, east base of the Tehachapi Mountains, 16km west of Mohave, *MAB18568.1*; Los Angeles Co.; 34.7727° N, 118.7986° W, Peace Valley, along the San Andreas Rift, *MAB18520.2;* 34.7715° N, 118.7970° W, Peace Valley, along the San Andreas Rift, *MAB18520*; 34.6576° N, 118.3359° W, north side of Portal Ridge, 18km WSW of central Lancaster, *MAB18519*; 34.6582° N, 118.3366° W, 1.8km east of Johnson Summit, north side of Portal Ridge, *MAB18518*; 34.5916° N, 118.4484° W San Francisquito Canyon, junction of Cherry Canyon, *MAB18503;* Riverside Co.: 33.4480° N, 114.7943° W, 28km SW of Blythe, 400m north of Sand Wash, *MAB17280*; 33.8993° N, 114.6944° W, Big Maria Mountains, 12.5km WSW of Quien Sabe Point, *MAB17929.1, MAB17929.2*; 33.8291° N, 114.7089° W, Big Maria Mountains, 16km SW of Quien Sabe Point, *MAB17933*; 33.6215° N, 115.6765° W, Orocopia Mountains, 2.4km north of Red Canyon, *MAB18289*; San Bernardino Co.: 34.8220° N, 116.3771° W, Cady Mountains, 18km west of Broadwell Lake, *MAB17021*; 34.2053° N, 114.5091° W, 6.3km ENE of Vidal Junction, 8km SSW of Savahia Peak, *MAB18272*; 35.6393° N, 116.6478° W, Owl Hole Springs, south side of the Owlshead Mountains, *MAB18279*; 35.7110° N, 116.8889° W, Owlshead Mountains, 12km ENE of the summit of Brown Mountain, *MAB18282*; 35.5791° N, 115.4181° W, west edge of Ivanpah Lake, 10km SSW of Primm, Nevada, *MAB17294*; San Diego Co.: 32.8683° N, 116.2340° W, Tierra Blanca Mountains, 6.8km NE of Sombrero Peak, *MAB17697*; **NEVADA**, Clark Co.: 35.2135° N, 114.6732° W, 10km NNW of Bullhead City, 1.3km north of confluence of Pipe Springs and Dripping Springs Canyons, *MAB16813*; 36.2935° N, 115.8218° W, Spring Mountains, above Wheeler Wash, 11.4km WNW of the summit of Charleston Peak, *MAB18126.3*; 35.6057° N, 115.3343° W, bajada on the west side of the Lucy Gray Mountains, 4.3km SE of the south end of Roach Lake, *MAB18277*.

***n*=33/2. **USA, CALIFORNIA,** Kern Co.: 35.5263° N, 118.0874° W, 1.5km SSE of Isabella main dam, 2km west of the town of Lake Isabella, *MAB18538, MAB18539*.

*Opuntia basilaris* var. *treleasei* (J. M. Coulter) Toumey
(Material collected under USFWS permit no. (TE009018-4) and CDFW permit no. (2081(a)-15-015-RP))

*n*=11. **USA, CALIFORNIA**, Kern Co.: 35.3020° N, 118.5912° W, 3km ENE of Caliente, 39km ESE of central Bakersfield, *MAB18540*; Los Angeles Co.; 34.7713° N, 118.7972° W, Peace Valley, along the San Andreas Rift, *MAB18520.1*; 34.7727° N, 118.7986° W, Peace Valley, along the San Andreas Rift, *MAB18520.2*.

*Opuntia basilaris* var. *brachyclada* (Griffiths) Munz

*n*=11. **USA, CALIFORNIA**, San Bernardino Co.: 34.3804° N, 117.5953° W, San Gabriel Mountains, Horse Canyon, *MAB17939.1*.

*Opuntia* ×*charlestonensis* Clokey

*n*=55/2. **USA, ARIZONA**, Mohave CO.: 36.8860° N, 113.6630° W, 1km east of Black Rock Gulch, 2.4km south of Pocket Hill, *MAB16711*; 36.9011° N, 113.6947° W, between Black Rock and Purgatory canyons, 5km west of Mokaac Mountain, *MAB16968.2*; 36.6407° N, 114.0170° W, Lime Kiln Canyon, 19km SSE of Mesquite, *MAB16759.1*; **NEVADA**, Clark Co.: 36.2750° N, 115.6283° W, Spring Mountains, Kyle Canyon, *MAB16451.2*; 36.2710° N, 115.5990° W, Spring Mountains, Kyle Canyon, 2km east of Fletcher Canyon, *MAB16566.2*, *MAB16566.6*; 36.2760° N, 115.5800° W, Kyle Canyon, 2.5km WNW of its confluence with Telephone Canyon, *MAB16569.1*; 36.2703° N, 115.6371° W, Spring Mountains, just east of Stanley B. Springs, at the Griffith Mine [Leroy Mining Claim], **type locality for the species**, *MAB17741.1*, *MAB17741.2, MAB17741.3*, *MAB17741.4*, *MAB17741.5*.

*Opuntia chlorotica*

*n*=11. **USA, ARIZONA**, Yavapai Co.: 34.1745° N, 113.0286° W, along Alamo Road (north branch), near its junction with Hwy 93, *MAB18789*.

**Opuntia chlorotica* × *O. engelmannii* (see also *MAB18787, MAB18787*)

*n*=33. **USA, ARIZONA**, Yavapai Co.: 34.1686° N, 113.0377° W, along Alamo Road, 2.8km WNW of its junction with Hwy 93, *MAB18784*; 34.1679° N, 113.0346° W, along Alamo Road, 2.5km WNW of its junction with Hwy 93, *MAB18785*; *MAB18786*.

*Opuntia cuija* (Griffiths & Hare) J. N. Rose in Britton & J. N. Rose *n*=11. **MEXICO, QUERÉTERO**: exact location unknown, originally collected by *Hernandez s. n.*, and accessioned at the Desert Botanical Garden, Phoenix, Arizona, as 1987-0850-10-6, *MAB19109*.

*Opuntia curvispina* Griffiths

*n*=22. **USA, ARIZONA**, Mohave Co.: 35.7508° N, 114.2153° W, White Hills, 13km SE of Senator Mountain, *MAB13647*; 35.1935° N, 113.8824° W, north bajada of Hualapai Mountain, 2.8km ESE of Rattlesnake Hill, *MAB16726*; 35.1742° N, 113.7853° W, pass between Peacock and Hualapai Mountains, *MAB17524*; 35.1410° N, 113.5510° W, Aquarius Mountains, along Willow Creek *MAB16646*; 35.7733° N, 114.2333° W, 66km ESE of Boulder City, 8km SE of the confluence of White Elephant and Hualapai Wash *MAB15367*; **NEVADA**, Clark Co.: 35.5010° N, 115.0710° W, Piute Valley, 4km WNW of Searchlight, **near the type locality for the species, as *O. curvospina***, *MAB16754.1*, *MAB16754.2*.

*Opuntia cymochila* Engelmann & J. M. Bigelow

*n*=22. **USA, NEW MEXICO**, Quay Co.: 35.1156° N, 103.8939° W, 17km WSW of Tucumcari, 350m south of Interstate 40, **type locality for the species**, *MAB16988.1, MAB16988.3*; 35.1500° N, 103.1900° W, east of San Jon, east of Tucumcari, *MAB17012, MAB17013, MAB17014*; **OKLAHOMA**, Custer Co.: 35.4826° N, 99.1041° W, I-40, ca. 2-3mi on frontage road, north side of I-40, *MAB17011*; **TEXAS**, Potter Co.: 35.5596° N, 101.9453° W, 2.8km SW of John Ray Butte, 40km north of the center of Amarillo, *MAB16985.1.*; 35.6187° N, 101.8346° W, west end of Red Draw, 12km west of Lake Meredith on the Canadian River, *MAB16980;* 35.5596° N, 101.9453° W, 2.8k m SW of John Ray Butte, west side of Hwy 87, *MAB16984.1*; *MAB16984.3*; *MAB16984.4*.

*n*=33. **USA, TEXAS**, Potter Co.: 35.5596° N, 101.9453° W, 2.8km SW of John Ray Butte, west side of Hwy 87, *MAB16985.2*; 35.6187° N, 101.8346° W, west end of Red Draw, 12km west of Lake Meredith on the Canadian River, *MAB16981.1*.

*Opuntia decumbens* Salm-Dyck

*n*=33. **MEXICO, BAJA CALIFORNIA SUR,** 23.5417° N, 110.0750° W Santa Gertrudis, 15k NE of Todos Santos, *MAB12139*; **SONORA**: 27.0212° N, 109.0145° W, Near Alamos, above Aduana, *MAB11148*.

*Opuntia engelmannii* s. l. (Excluding *O. cuija*)

*n*=11. **MEXICO, COAHUILA**: 27.0500° N, 101.9333° W, NE of Cuatro Cienegas, ca. 11km west of Lamadrid, *MAB12811*.

*Opuntia engelmannii* var. *engelmannii*

*n*=33. **USA, ARIZONA**, Gila Co.: 33.387° N, 110.889°W, 4km east of Needle Mtn., 1.5km W of Miami, *T. Wright 1169.1*; Mohave Co.: 34.6538° N, 113.5826° W, along the Big Sandy River, 1.3km SSW of its confluence with Sycamore Creek, 6km south of Wikieup, **near the type locality of *Opuntia magnariensis* Griffiths**, *MAB16808*; 34.6489° N, 113.5823° W, 830m west of the Owen's Cemetery, 7km SSE of Wikieup, **near the type locality of *Opuntia magnariensis* Griffiths**, *MAB18699*; Yavapai Co.: 34.5357° N, 112.4607° W, 1km SE of the Prescott Courthouse, 2.8km NE of Kuhne Hill, *MAB17276*; 34.4202° N, 111.5692° W, 6km WNW of Strawberry, 0.5km SW of Fossil Springs, *MAB12948*; 34.2542° N, 112.2988° W, eastern flank of the Bradshaw Mountains, Muldoon Gulch, *MAB13725.1*, *MAB13725.2*; 34.3050° N, 112.2450° W, Turkey Creek, 3.3km NNW of Cleator, *MAB14894*; 34.9320° N, 112.8410° W, 2.6km west of summit of Indian Peak, 1km NNE of Walnut Creek Station, **near the type locality of *Opuntia procumbens* Engelmann & J. M. Bigelow**, *MAB16643.2*; N34.1679° N, 113.0346° W, along Alamo Road, 2.5km WNW of its junction with Hwy 93, *MAB18787*; **NEW MEXICO**, Otero Co.: 32.7820° N, 105.9228° W, mouth of San Andres Canyon, west base of the Sacramento Mountains, **near the type locality for *Opuntia dillei* Griffiths**, *MAB18582*.

*Opuntia engelmannii* var. *lindheimeri* (Engelmann) Parfitt & Pinkava

*n*=33. **USA, NEW MEXICO**, Eddy Co.: 32.2430° N, 104.7410° W, Guadalupe Mountains, 50km WSW of Carlsbad, *MAB13368*.

*Opuntia engelmannii* var. *engelmannii* × *O. phaeacantha*

*n*=33. **USA, ARIZONA**, Mohave Co.: 34.6378° N, 113.5713° W, along the Big Sandy River, 8km south of Wikieup, **near the type locality for *Opuntia magnarenensis* Griffiths**, *MAB16803*; 36.6407° N, 114.0170° W, Lime Kiln Canyon, 19km SSE of Mesquite, *MAB16759.2*; Pima Co.: 31.0006° N, 110.5798° W, historic site of Pantano railroad stop, 13km ESE of Vail, 38km SE of downtown Tucson, **type locality for *Opuntia eocarpa* Griffiths and *O. recurvospina* Griffiths**, *MAB17105.1*; **CALIFORNIA**, San Bernardino Co.: 35.5828° N, 115.6117° W, 6.7km NNW of the summit of Clark Mountain, 55km NE of Baker, *MAB17543.1*; **NEW MEXICO**, McKinnley Co., 35.0769° N, 108.7693° W, 7km east of Zuni, 1km SE of Black Rock Reservoir, **near the type locality of *Opuntia zuniensis* Griffiths,** *MAB16999.2*.

*Opuntia leucotricha* DC.

*n*=11. **MEXICO**, **ZACATECAS**: 23.6517° N, 103.5900° W, east of Durango, ca. 5k ENE of Sombrerete, *MAB12382.*

*Opuntia littoralis* (Engelmann) Cockerell

*n=33.* **Mexico, Baja California Sur**: 27.5933° N, 113.0133° W, Sierra San Francisco, 0.5km south of San Francisco, *MAB15197*.

*Opuntia macrocentra* s. l.

***n*=33. **USA, ARIZONA**, Cochise Co.: 31.3570° N, 109.1250° W, 38km east of Douglas, 8k west of the New Mexican border, *MAB11344*; **NEW MEXICO**, Chaves Co 33.2740° N, 104.0570° W, 45km ESE of Roswell, 4km east of Loco Draw, 22km west of Mescalero Ridge, *MAB16666.3*.

*Opuntia macrocentra* Engelmann var. *macrocentra*

*n*=22. **USA, NEW MEXICO**, Chaves Co.: 33.2740° N, 104.0570° W, 4km east of Loco Draw, 22km west of Mescalero Ridge, *MAB16666.1*; Eddy Co.: 32.1110° N, 104.5630° W, Slaughter Canyon, Carlsbad Caverns National Park, *MAB13098*; Lincoln Co.: 33.7430° N, 104.9590° W, above (north side) Middle Arroyo, 56km NW of Roswell, *MAB16672*.

*Opuntia macrocentra* Engelmann var. *minor* M. S. Anthony

*n*=22. **USA, TEXAS**, Terrell Co.: 30.0580° N, 102.2350° W, 18km ESE of Sanderson, just west of the old Mofeta Railroad stop, *MAB16613.1, MAB16613.2*.

*Opuntia macrorhiza* Engelmann

*n*=11. **USA, NEW MEXICO**, Chaves Co.: 33.5840° N, 103.7897° W, ENE of Roswell, 15km SE of Railroad Mountain, *MAB15682*; 33.4490° N, 103.8600° W, 45km SSW of Kenna, 11km NNW of Mescalero Point, *MAB16640.3*.

*n*=22. **MEXICO, CHIHUAHUA**: 28.4367° N, 108.4983° W, between Maycoba, Sonora and Yepachic, *MAB14359*; **USA, ARIZONA**, Navajo Co.: 34.3271° N, 110.3130° W, Indian Well Spring, 300m north of Butler Point, *MAB17178.1, MAB 17178.2*; Yavapai Co.: 34.4659° N, 113.4385° W, Bradshaw Mountains, 3.2km west of the summit of Spruce Mountain, **near the type locality of *Opuntia loomisii* Peebles**, *MAB17438.1*; *MAB17438.2*; *MAB17438.3*; **COLORADO**, Weld Co.: 40.1908° N,104.3703° W, probably just north of Roggen, 80km ENE of Boulder, 37km SE of Greeley, material originally collected by *L. Benson 16106* and cultivated at the Desert Botanical Garden, Phoenix, Arizona (1994-0030), material planted in the garden in Chino Valley, Arizona, *MAB18673*; **NEW MEXICO**, Colfax Co.: 36.7775°

N, 104.8918° W, just west of Bracket Canyon, 42km SW of Ratón, *MAB12554*; Otero Co.: 32.7161° N, 105.5515° W, Sacramento Mountains, Buck Canyon, *MAB18204.3, MAB18204.1.* Quay Co.: 35.1156° N, 103.8939° W, 17km WSW of Tucumcari, 350m south of Interstate 40, **type locality for *Opuntia cymochila* Engelmann & J. M. Bigelow**, *MAB16987.3*, *MAB16988.1*.

*Opuntia martiniana* (L. D. Benson) B. D. Parfitt

*n*=22. **USA, ARIZONA**, Mohave Co.: 35.1742° N, 113.7853° W, pass between Peacock and Hualapai Mountains, **near the type locality of *Opuntia macrocentra* var. *martiniana* L. D. Benson**, *MAB16788.1*; *MAB16925*, *MAB17235*, *MAB17353.1*, *MAB17353.2*.

*Opuntia occidentalis* Engelmann & J. M. Bigelow

*n=33.* **USA, CALIFORNIA:** Los Angeles Co.: 34.1118° N, 117.7124° W, Claremont, 100m south of the SE base of Indian Hill, *MAB18409*; **MEXICO, Baja California:** 30.1292° N, 115.7750° W, 3k due east of the Pacific Ocean, 6.6mi north of El Rosario, *MAB12117*.

*Opuntia phaeacantha* Engelmann

*n*=33. **USA, ARIZONA,** Gila Co.: 33.387° N, 110.889° W, 4k east of Needle Mtn., ca. 1.5k SW of Miami, *T. Wright 1619.1*; Greenlee Co.: 33.4077° N, 109.3510° W, 600m ESE of Hogtail Saddle on south side of Hwy 666 (191), *MAB17218*; Maricopa Co.: 32.5600° N, 112.6367° W, Sauceda Mountains, Ryans Canyon, *MAB15240*; Mohave Co.: 36.4139° N, 113.6406° W, Shivwits Plateau, 14km WNW of the top of Poverty Mountain, *MAB13657*; 35.1742° N, 113.7853° W, pass between Peacock and Hualapai Mountains, **near the type locality for *Opuntia superbospina* Griffiths**, *MAB16798.1*, *MAB16798.2*, *MAB16782, MAB16783*; 36.6407° N, 114.0170° W, Lime Kiln Canyon, 19km SSE of Mesquite, *MAB16759.3*; Navajo Co.: 35.9833° N, 110.0583° W, east end of Low Mountain, *MAB16247*; 36.5875° N, 110.4707° W, Long House Valley, 25km SW of Kayenta, *MAB17579*; N36.6832° N, 110.5334°, Betatakin Canyon, 120m SE of Betatakin ruin, ooriginally collected by *Susan Holiday 887*, under permit no. NAVA-2012-SCI0002, cultivated in garden, Chino Valley, Arizona, *MAB18576*; Yavapai Co.: 34.6102° N, 111.9107° W, ca. 500m east of Hwy 279, 7km NNW of Camp Verde, *MAB13676*; 34.5357° N, 112.4607° W, 1km SE of the Prescott Courthouse, 2.8km NE of Kuhne Hill, *MAB17277.3, MAB17277.4, MAB17277.5;* 34.283° N, 112.490° W, SSW of Prescott, 3.3km SSW of Battleship Butte, *MAB15000*; 34.949° N, 112.858° W, 900m south of Juniper Spring, SE-facing slope, *MAB14199*; **CALIFORNIA**, San Bernardino Co.: 35.4310° N, 115.5290° W, Mescal Range, 4km south of Mountain Pass, *MAB16750*; 35.2090° N, 115.3324° W, south slope of the New York Mountains, 2.6km SSW of Drum Peak, *MAB17523.1*; 35.5828° N, 115.6117° W, 6.7km NNW of the summit of Clark Mountain, 55km NE of Baker, *MAB17543.2*; 35.5169° N, 115.6309° W, 3.7km SW of the summit of Clark Mountain, 100m south of Pachalka Spring, *MAB17555.1*; 35.2856° N, 115.2585° W, New York Mountains, just below mine to NE of Keystone Canyon, *MAB18117*; 34.9121° N, 115.5729° W, 82km west of Needles, 2.1km ESE of Foshay Spring, *MAB17608*; Riverside Co.: 33.8991° N, 116.7909° W, San Gorgonio River, 2km SW of Cabazon, *MAB18524*; 34.2147° N, 117.4062° W, Devore, Cajón Wash, 14km NW of central San Bernardino, *MAB18546, MAB18547;* **NEVADA**, Clark Co.: 36.2760° N, 115.5800° W, Kyle Canyon, 2.5km WNW of its confluence with Telephone Canyon, *MAB16569.4*; 36.2717° N, 115.5833° W, Kyle Canyon, 5km south of Angel Peak, *MAB16589*; Lincoln Co.: 37.8980° N, 114.4150° W, SE end of Pioche Hills, 4.5km SE of Pioche, *MAB17628*; **NEW MEXICO**, Chaves Co.: 33.5700° N, 103.9160° W, 3.5km north of Presler Lake, 59km ENE of Roswell, *MAB16661.2*, *MAB16661.3*; Cibola Co.: 37.9870° N, 107.9520° W, 4km south of Gallo Peak, Bonita Canyon, *MAB16660.1*, *MAB16660.2*, *MAB16660.3*; 35.0209° N, 107.9707° W, 13km SW of San Rafael, 1.5km west of Gallo Peak, *MAB16993.1*; *MAB16996*; Guadalupe Co.: 34.9501° N, 104.6846° W, 1km SE of the Pecos River, 0.8km north of Santa Rosa, *MAB16989.2*; 35.0696° N, 104.2391° W, 200km east of Albuquerque, 6km east of the south end of Mesa del Gato, *MAB17017*; Lincoln Co.: 33.144° N, 104.984° W, 51km SW of Roswell, Monument Canyon, *MAB16663.3*; 33.8233° N, 105.6783° W, Jicarilla Mountains, 3km NE of Blue Hill, *MAB16186*; 33.7850° N, 105.7100° W, Jicarilla Mountains, Castle Garden Mesa, *MAB16187*; 33.1440° N, 104.9840° W, 51km SW of Roswell, Monument Canyon, *MAB16664*; McKinley Co.: 35.0720° N, 108.7670° W, Cheama Canyon, 12km east of Zuni, **near the type locality of *Opuntia zuniensis* Griffiths**, *MAB16671*; Otero Co.: 32.9917° N, 105.4950° W, Sacramento Mountains, Crooked Canyon, *MAB16279*; Sandoval Co.: 35.3101° N, 106.5323° W, 1.4km SW of Santa Fé, 2.5km east of the Rio Grande River, *MAB16970.2*; 35.5586° N, 106.2981° W, Majada Mesa, 3.8km SSE of Peña Blanca, **near the type locality of *Opuntia phaeacantha* Engelmann**, *MAB16973.1*; *MAB16973.3*; Santa Fé Co: 35.6364° N, 105.9421° W, 5.5km south of the center of Santa Fé*, MAB16975;* **TEXAS**, Potter Co.: 35.6187° N, 101.8346° W, west end of Red Draw, 12km west of Lake Meredith on the Canadian River, *MAB16977*; *MAB16980; MAB16982*; 35.6350° N, 101.8242° W, 1.2km north of Red Draw, 14km west of Lake Meredith on the Canadian River, *MAB16983*; **UTAH**, Washington Co.: 37.4340° N, 113.9910° W, 14km north of Motoqua, 2.8km west of the summit of Mineral Mountain, along Slaughter Creek (an upper fork of Beaver Dam Wash), **type locality for *O. phaeacantha* var. *castorea***, *MAB16658*, *MAB16658.2*; **MEXICO**; Sonora: 28.39158° N, 109.12769° W, 3.6km north of Santa Ana on road to Mexico 16, originally collected by *T. Van Devender 96-206*, cultivated in Chino Valley, Arizona, *MAB17477*.

*Opuntia pinkavae* B. D. Parfitt

*n*=44. **USA, ARIZONA**, Mohave Co.: 36.6419° N, 113.3416° W, 9km west of Hurricane Cliffs, 500m north of Sunshine Draw, *MAB18095.1*.

*Opuntia polyacantha* Haworth var. *erinacea* (Engelmann & J. M. Bigelow) B. D. Parfitt

*n*=22. **USA**, **ARIZONA**, Mohave Co.: 36.9203° N, 113.6635° W, just west of Dinner Flat, 1.4km north of Pocket Hill, *MAB18099.1*; 35.0635° N, 114.2258° W, Sacramento Valley, 400m east of Secret Pass Wash, *MAB16778.2*; **CALIFORNIA**, Riverside Co.: 33.6404° N, 116.5949° W, San Jacinto Mountains, Goff Flat, 16km SSE of Idyllwild, 12km NW of Ribbonwood, **type locality for *O. erinacea* Engelmann & J. M. Bigelow var. *paucispina* Dunkle**, *MAB17379.2*; San Bernardino Co.: 35.1537° N, 115.3554° W, 765m NNE of Government Spring, 3.2km SSE of the summit of Pinto Mountain, *MAB17522.1*; 34.7028° N, 116.8224° W, Ord Mountains, 400m SW of Aztec Spring, **neotype locality of *Opuntia ursina* Weber in Bois**, *MAB17940.1, MAB17940.2*; 33.5766° N, 116.4492° W, SSW of Palm Desert, Pinyon Flat, *MAB17001*; **NEVADA**, Clark Co.: 35.7017° N, 114.8867° W, 30km south of Boulder City, Eldorado Mountains *MAB15144*; Nye Co.: 39.1611° N, 116.7051° W, Little Smoky Valley, on the east side of the Antelope Range, *MAB18161.2*; Nye Co.: 38.8634° N, 117.4933° W, Shoshone Mountains, 4km north of Black Mountain, *MAB18138.2*.

*Opuntia polyacantha* var. *hystricina* (Engelmann & J. M. Bigelow) B. D. Parfitt

*n*=22. **USA, ARIZONA**, Apache Co.: 36.4304° N, 109.3115° W, 4 miles WNW of Lukachukai, north of Bad Bug (Buck) Butte, *MAB17007*, *MAB17008*; 36.3914° N, 109.7481° W, 8 miles west of Many Farms, *MAB17009*;

36.5400° N, 109.0600° W, 43km SW of the town of Shiprock, New Mexico, 1.75 mi. SSE of Red Rock, *MAB17018*.

*Opuntia polyacantha* var. *polyacantha*

*n*=11. **USA, NEW MEXICO**, Cibola Co.: 35.2981° N, 108.1032° W, Bluewater State Park, campground, *MAB17005*; Guadalupe Co.: 35.0696° N, 104.2391° W, 200km east of Albuquerque, 6km east of the south end of Mesa del Gato, *MAB17015*; San Juan Co.: 36.6410° N, 108.0320° W, just west of Horn Canyon, 8k south of the San Juan River, *MAB11719*.

*n*=33. **USA, UTAH,** San Juan : 38.4700° N, 109.3525° W, Brumley Ridge, 950m south of Mill Creek, *MAB17588.1*.

*Opuntia pubescens* Wendland

*n*=22. (In some cells, two univalents not pairing during Meiosis I). **MEXICO, SAN LUIS POTOSÍ**: 22.0603° N, 100.4972° W, 50km ESE of the center of San Luis Potosí, Santa Catarina, *MAB18124*.

*Opuntia robusta* H. L. Wendland ex Pfeiffer

***n*=33/2. **MEXICO, ZACATECAS**: 23.6517° N, 103.5900° W, east of Durango, ca. 5k ENE of Sombrerete, *MAB12384*.

*Opuntia tortispina* Engelmann & J. M. Bigelow

*n*=33. **USA, NEW MEXICO**, Chaves Co.: 33.2740° N, 104.0570° W, 4km east of Loco Draw, 22km west of Mescalero Ridge, *MAB16667.2*, Eddy Co. 32.661° N, 104.375° W, 1km south of Fourmile Draw, 20km south of the center of Artesia, MAB16616.1; **TEXAS,** Potter Co.: 35.6187° N, 101.8346° W, 147km north of the center of Amarillo, 12km west of Lake Meredith on the Canadian River, **near the type locality for species**, *MAB16979*; 35.5596° N, 101.9453° W, 2.8km SW of John Ray Butte, west side of Hwy 87, *MAB16985.3*.

*Opuntia vaseyi* (J. M. Coulter) Britton & J. N. Rose

*n*=33. **USA, CALIFORNIA,** Los Angeles Co.: 34.1096° N, 117.7124° W, Claremont, 300m south of the SE base of Indian Hill, *MAB18408;* 34.1081° N, 117.7147° W, Claremont, 300m south of the SE base of Indian Hill, *MAB18405*; 34.1081° N, 117.7148° W, Claremont, 300m south of the SE base of Indian Hill, *MAB18406, MAB18406.1*; 34.1118° N, 117.7122° W Claremont, 100m south of the SE base of Indian Hill, *MAB18410*; San Bernardino Co.: **USA, CALIFORNIA**, San Bernardino Co.: 34.0318° N, 117.1386° W, Crystal Springs area (historic), 4km SE of Redlands, *MAB18373*, *MAB18549*; 34.1857° N, 117.4346° W, Lytle Creek, 15km NW of central San Bernardino, *MAB18545*; 34.4064° N, 117.2471° W, Hesperia, 890m west of the western edge of the Mojave River, **near the type locality of *Opuntia mojavensis* Engelmann & J. M. Bigelow var. *mojavensis***, *MAB18754*; 34.3156° N, 117.4890° W, San Gabriel Mountains, 20km SW of Hesperia, **near the type locality of *Opuntia mojavensis* Engelmann & J. M. Bigelow var. *mojavensis***, *MAB18542, MAB18543*.

*Salmiopuntia salmiana* (J. Parmentier ex Pfeiffer) Guiggi

*n*=22. **USA, ARIZONA**, Yavapai Co.: 34.7808° N, 112.4439° W, Material (DBG 2001 0048 0102) obtained from the Desert Botanical Gardens, Phoenix, Arizona and cultivated in greenhouse at Chino Valley, Arizona, *MAB18351*.

*Sclerocactus cloveriae* K. Heil subsp. *brackii* K. D. Heil and J. M. Porter

*n*=11. **USA, NEW MEXICO**, San Juan Co.: 36.6620° N, 108.0070° W, 18km ESE of Farmington, *MAB11726*.

*Sclerocactus parviflorus* Clover & Jotter

*n*=11. **USA, NEW MEXICO**, Sandoval Co.: 35.6500° N, 106.8667° W, west of Peñasco Canyon, approximately 1.4k due north of Los Pinos Arroyo, *MAB13550*; San Juan Co.: 36.8040° N, 108.4980° W, north of Waterfall, just east of the Hogback, *MAB12420.1*.

*Sclerocactus pubispinus* (Engelmann) L. D. Benson

*n*=11. **USA, NEVADA**, White Pine Co.: 39.1345° N, 114.2904° W, Snake Range, Horse Canyon, *MAB17414.1*.

*Sclerocactus whipplei* (Engelmann & J. M Bigelow) Britton & J. N. Rose

*n*=11. **USA, ARIZONA**, Navajo Co.: 35.7917° N, 110.1217° W, 15km west of Jeddito Wash, NE of Jeddito, *MAB12655*.

## Errata for chromosome determinations reported in this series

Pinkava et al. (1998): *MAB8105*, published as *Echinocereus triglochidiatus* var. *mojavensis*, *n*=11, change to *E. coccineus* subsp. *coccineus*, *n*=22; *MAB8683*, *n*=11, change from *Cylindropuntia alcahes* to *C. munzii*.