

CHROMOSOME NUMBERS IN SOME CACTI OF WESTERN NORTH AMERICA—VII

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Abstract. Documented meiotic and mitotic chromosome numbers are reported for 91 taxa, including intergeneric and interspecific hybrids, representing 15 genera of Cactaceae from southwestern United States and northern Mexico. Chromosome counts are reported for the first time for 32 taxa and additional ploidy levels for five taxa. These chromosomes counts are all consistent with the base number for the Cactaceae, $x = 11$.

This report on chromosome numbers and behavior is part of an ongoing effort to clarify taxonomic evolutionary relationships among the Cactaceae, this time mostly for taxa from Lower California, Mexico. The taxonomic and geographic distribution of polyploid taxa in the Cactaceae is tabulated and includes previously published chromosome reports. Interspecific hybridization coupled with polyploidy, the perennial habit, and asexual reproduction all play a role in the complexity of the Cactaceae, particularly the genera *Opuntia*, *Echinocereus*, and *Mammillaria*.

Materials and Methods

Flower buds were collected in developmental series from plants growing in native habitats or placed into cultivation. Buds were killed and fixed in chloroform, 95% ethanol, and glacial acetic acid (6:3:1 or 0:3:1) for 24 hours, transferred to 70% ethanol, and refrigerated. Anthers were squashed in acetocarmine and mounted in Hoyer's medium (Beeks, 1955). Mitotic counts were obtained from root tips fixed, stained, and mounted according to the method of Parfitt (1979). Percent pollen stainability was based on 500⁺-grain samples stained with aniline blue in lactophenol (cotton blue) (Maneval, 1936).

Results

Chromosome numbers were determined for 346 individual cacti representing 91 taxa in 15 genera (Table 1). Many of these chromosome counts are the result of a biosystematic investigation of the chollas of Lower California (Rebman, 1995). First counts are determined for 14 species, 6 additional varieties, and 12 intergeneric and interspecific hybrids; new counts are determined for 5 additional taxa.

First counts for species and varieties include: *Opuntia abyssi*, *O. acanthocarpa* var. *acanthocarpa*, *O. alcahes* var. nov. A., *O. alcahes* var. nov. B., *O. calmanniana*, *O. clavellina*, *O. ganderi* var. nov. A., *O. molesta*, *O. munzii*, *O. pycnantha*, *O. tapona*, *O. tesajo*, *O. thurberi*, *Opuntia* (subgenus *Cylindropuntia*) sp. nov. A., *Coryphantha missouriensis* var. *missouriensis*, *Echinocereus engelmannii*

var. *purpureus*, *Mammillaria bocensis*, *M. goodridgei* var. *goodridgei*, and *M. standleyi*.

First counts for interspecific hybrids were obtained for: *Opuntia abyssi* × *O. acanthocarpa*, *O. arbuscula* × *O. leptocaulis*, *O. burrageana* × *O. lindsayi*, *O. ×congesta*, *O. echinocarpa* × *O. munzii*, *O. ×fosbergii*, *O. leptocaulis* × *O. whipplei*, *O. molesta* × *O. ?prolifera*, *O. ×multigeniculata*, *O. tesajo* × *O. ganderi*, *O. ×viridiflora*, and *Echinocereus fasciculatus* × *E. fendleri*. A first count is also reported for the intergeneric hybrid ×*Pachgerocereus orcuttii*.

Triploid number counts (Table 1) are new for *Opuntia alcahes*, previously reported only from a diploid individual (Yuasa et al., 1973). Triploid and tetraploid numbers are new for *Opuntia cholla*, previously reported as diploid (Pinkava and Parfitt, 1982; Pinkava et al., 1992; and Yuasa et al., 1973). Both diploid and triploid counts are new for *O. munzii* and *O. alcahes* var. nov. B.; both hexaploid and heptaploid counts are new for *O. molesta* × *O. ?prolifera*.

New in our continuing series of studies are 45 taxa (including 12 interspecific hybrids), of which 32 were cytologically undescribed. Thirteen others had been counted previously and all are consistent with our findings: 1) *Opuntia alcahes* (Yuasa et al., 1973); 2) *O. bigelovii* var. *ciribe* (Yuasa et al., 1973); 3) *O. clavata* (Yuasa et al., 1973); 4) *O. davisii* (Weedin et al., 1989); 5) *O. invicta* (Yuasa et al., 1973); 6) *O. macrorhiza* var. *pottsii* (Weedin & Powell, 1978); 7) *O. pulchella* (Yuasa et al., 1973); 8) *O. sanfelipensis* (Rebman, 1999); 9) *Echinocereus triglochidiatus* var. *mojavensis* (Cota & Philbrick, 1994); 10) *Ferocactus peninsulae* var. *peninsulae* (Cota et al., 1996); 11) *F. peninsulae* var. *townsendianus* (Cota et al., 1996); 12) *Mammillaria*

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Table 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; ** = new number for taxon; *** = mitotic counts from root tips (all other counts are from microsporogenesis). Percentages in parentheses after collectors' numbers represent pollen stainability. Abbreviations of collectors' names: MAB = M. A. Baker; DJF = D. J. Ferguson; WH = W. Hodgson; RJ = R. Johnson; LAM = L. A. McGill; BDP = B. D. Parfitt; DJP = D. J. Pinkava; JPR = J. P. Rebman; NT = N. Trushell; RDW = R. D. Worthington; TW = T. Wright. Note: some taxonomic corrections to earlier published chromosome reports in this series are presented at the end of this table.

OPUNTIOIDEAE*Opuntia abyssi* Hester

* n = 11. **Arizona.** Mohave Co.: T27N R10W S5, Peach Springs Canyon, *MAB 8102-A, -B, -E, -F* (60.1).

*** $2n$ = 22. **Arizona.** Mohave Co.: T27N R11W S25, Peach Springs Canyon, *MAB 4975-A* (94.8) & *J. Trushell*.

Opuntia abyssi \times *O. acanthocarpa*

* n = 11. **Arizona.** Mohave Co.: T27N R10W S5, Peach Springs Canyon, *MAB 8103*, (57.0).

Opuntia acanthocarpa Engelm. & J. M. Bigelow var. *acanthocarpa*

* n = 11. **Arizona.** Yavapai Co.: T13N R6W S18, 2.5 mi SSW of Hillside, *MAB 10702, 10703* (intermediate to var. *thornberi*).

Opuntia acanthocarpa var. *coloradensis* L. D. Benson

n = 11. **Arizona.** Maricopa Co.: T6S R3W S16, 1-8, ca. 8 mi E of Gila Bend, *MAB 8100, T6S R3W S13, 1-8*, ca. 11 mi E of Gila Bend, *MAB 8098* [both intermediate to var. *major*]. Yavapai Co.: T13N R6W S18, ca. 2.5 mi due SSW of Hillside, *MAB 10704* [intermediate to var. *thornberi*].

Opuntia acanthocarpa var. *major* Engelm.

n = 11. **Arizona.** Pima Co.: T12S R12E S20, Rattlesnake Pass, Tucson Mts. *MAB 8111, T14S R12E S9*, near Gates Pass, Tucson Mts, *MAB 8114, T12S R12E S29, Sanctuary Cove, MAB 8112, T14S R12E S8*, Tucson, *MAB et al. 7801* (93.8), *7802* (73.6) [all with unusual spination].

Opuntia acanthocarpa var. *thornberi* (Thornberi & Bonker) L. D. Benson

n = 11. **Arizona.** Pinal Co.: T1S R13E S33, Oak Flat, *MAB 4678* (80.5). Yavapai Co.: T10N R4E S16, 4 mi E of I-17 on Bloody Basin Rd., *NT 82-103, 82-105, 82-106* & *MAB*; T10N R4E S15, 10 mi E of I-17 on Bloody Basin Rd., *NT 82-109, 82-110, 82-112* & *MAB*.

Opuntia alcahes F. A. C. Weber

n = 11. **Mexico.** Baja California: 114°25'W, 29°42'N, Las Arrastras Wash, *MAB 8683* & *RJ*; 114°22'W, 29°34'N, Rte. 5, 2.1 mi NW of Las Arrastras Wash, *MAB 8690* & *RJ*; 113°16'W, 28°08'N, 1 km NW of El Premiado, *MAB 8778-A* & *RJ*; 113°10'W, 28°28'N, Valle San Rafael, 14.7 mi NW of El Progreso, *MAB 8780* & *RJ* (79.2); Rte. 1, 11.4 mi S of N limits of Camalú, *DJP et al. 11135* (41.8) (counted by T. Hensel); 4.8 mi E of Rte. 1 & El Rosario, *DJP et al. 11144* (15.7), *11145* (58.2) (both counted by T. Hensel); Rte. 1, 68 km S of Cataviña, *JPR 1145* & *Rice* (64.8); 115°30'W, 30°03'N, Rte. 1, ca. 25 km SE of El Rosario, *JPR 1225* & *Cota* (61.1); 114°43'W, 29°26'N, ca. 25 mi W of Rte. 1 near Cataviña along road to San José de la Piedra, *JPR 1321* & *Cordova*; 113°33'W, 28°55'N, ca. 2 mi S of Bahía de los Angeles, *JPR 1324* & *Cordova* (89.2); 114°12'W, 29°24'N, ca. 0.5 mi S of Misión Calamajue, *JPR 1611* & *Delgadillo*; 115°15'W, 30°01'N, km marker 108 of Rte. 1 between El Rosario & Cataviña, *JPR 2732* & *Vincent* (58.3). Baja California Sur: 113°03'W, 27°17'N, Rte. 1, 1 km NW of Palo Verde Wash, *MAB 8706* (91.4), *8707* (53.0) & *RJ*; 112°46'W, 27°19'N, just S of Rte. 1, Santa Maria Wash between Cerro Colorado & Cerro Guatamote, 8.3 mi ENE of Guamuchil & ca. 8 mi ENE of San Ignacio, *MAB 8711* & *RJ* (neotype); 112°07'W, 27°04'W, Rte. 1, 21.7 mi S of Santa Rosalia, *MAB 8716* & *RJ* (97.2); 112°12'W, 26°11'N, 4 mi NE of San Gregorio, *MAB 8757* & *RJ* (96.5); 111°13'W, 26°09'N, 3 km E of San Gregorio, *MAB 8763* & *RJ* (97.6); 112°30'W, 26°22'N, 7.4 mi N of San Juanico, *MAB 8769* & *RJ*; 112°48'W, 27°25'N, ca. 22 km N of San Ignacio, *MAB 12173* & *RJ*; 113°01'W, 27°36'N, San Francisco de la Sierra, *JPR et al. 1413* (88.0); 113°12'W, 27°29'N, E of Rte. 1 on road to San Francisco de la Sierra, *JPR 2357* & *Hirales* (91.3); 112°18'W, 27°24'N, 6 mi NNW of Santa Rosalia along Gulf, *Van Devender et al. 91-437* (photo).

*** $2n$ = 22. **Mexico.** Baja California Sur: Rte. 1, 27.7 mi E of San Ignacio turnoff, *DJP et al. 14103*.

** $2n$ = $3x$ = 33. **Mexico.** Baja California: 113°05'W, 28°19'N, A Japón, 5 mi W of El Progreso, *MAB 8779* & *RJ* (82.1). Baja California Sur: 112°46'W, 27°19'N, 8 mi ENE of San Ignacio, *MAB 8710* & *RJ* (26.9) (intermediate to var. nov. A.); 111°12'W, 26°07'N, 0.5 km W of San Gregorio, *MAB 8761* & *RJ* (22.2).

Opuntia alcahes var. nov. A.

* n : eq 11. **Mexico.** Baja California Sur: 111°47'W, 26°21'N, 12 mi W of Rte. 1 on road to San Isidro, *MAB 8726-A* & *RJ*; 111°49'W, 26°02'N, just NE of San Miguel Comondú, *MAB 8744* & *RJ* (56.3); 111°44'W, 26°22'N, just W of Rte. 1 & San Isidro, *JPR et al. 1409* (11.6).

Opuntia alcahes var. nov. B.

* n = 11. **Mexico.** Baja California: Rte. 1, 11.4 mi S of the northern limits of Camalu, *DJP et al. 11134* (counted by T. Hensel); Rte. 1, 3.4 mi N of El Rosario, *DJP et al. 11175* (93.1) (counted by T. Hensel); 17 mi E of Rte. 1 on road to San Telmo, *JPR 1136* & *Rice* (96.9); Rte. 1, ca. 8 mi N of El Rosario, *JPR 1219* & *Cota* (25.1) (holotype).

** $2n$ = $3x$ = 33. **Mexico.** Baja California: Rte. 1, 11.7 mi SE of El Rosario, *DJP et al. 9069* (orig. published as *O. prolifera* (Pinkava et al., 1992)); 115°55'W, 30°36'N, 2.3 mi E of Rte. 1 at Lázaro Cárdenas, *JPR 1650* & *Davis*.

Opuntia arbuscula Engelm.

n = 33. **Arizona.** Pima Co.: T13S R12E S3, 0.6 mi W of jct. Silverbell Rd. on Ina Road, *MAB et al. 7820*; T12S R12E S32, 1 mi NE of Safford Peak, *MAB et al. 7811*; T12S R12E S29, 1.5 km NE of Safford Peak, *MAB 8134*; T17N R14E S28, 3.5 mi SE of Sahuarita, *MAB et al. 10479*.

Table 1. Continued*Opuntia arbuscula* × *O. leptocaulis*

* $2n = 5x = 55$. **Arizona.** Pima Co.: T12S R12E S29, Tucson, Pima Farms Rd., near Sanctuary Cove, MAB et al. 7823.

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

$n = 11$. **Arizona.** Mohave Co.: T27N R10W S5, Peach Springs Canyon, MAB 8104. Yavapai Co.: T13N R6W S29, 2 km N of Hillside, MAB 10354.

Opuntia basilaris var. *longiareolata* (Clover & Jotter) L. D. Benson (including *O. basilaris* var. *beillii* Welsh & Neese).

$n = 11$. **Arizona.** Coconino Co.: 112°05'W, 36°05'N, Grand Canyon Natl. Park, near Bright Angel Campground, WH 7004 & Buchanan (pop. voucher) (DES).

Opuntia bigelovii Engelm. var. *bigelovii*

$n = 11$. **Arizona.** Gila Co.: T5S R15E S12, 2 km NNE of Winkleman, MAB 8116-B; Tonto Basin, Hwy. 188, 1 mi NW of jct. Hwy. 288, MAB 8285-A, -B, -C; Rte. 88, 3.7 mi W of jct. Hwy 288, J. Anderson s.n.; road to Cherry Creek, ca. 2 km E of Salt River, MAB 8195-A, -C; Campaign Creek, ca. 12 km S of Roosevelt, MAB 8142-A, -B, -C; just SE of Salt River diversion dam, MAB 8198; Tonto Basin, ca. 2 km SE of Dutchwoman Butte, MAB 8272-A, -B. Maricopa Co.: Tonto Basin, just SE of Roosevelt Dam, MAB 8276. Pinal Co.: T9S R9E S9, 2 km NW of Picacho Peak, MAB 8110, 8133; T2S R12E S2, 1 km N of Donkey Canyon, just E of Hwy. 77, MAB 8140. **Mexico.** Baja California: 113°27'W, 28°42'N, 20 mi S of Bahía de los Angeles, MAB 8782 & RJ. Baja California Sur: 112°47'W, 26°34'N, 35.2 mi N of San Juanico, MAB 8772-A & RJ.

2 $n = 3x = 33$. **Arizona.** La Paz Co.: T1S R18W, 2 km W of Signal Peak, MAB 7729-A; ca. 1 mi W of Crystal Hill Campground, Kofa Wildlife Refuge, B. Warner s.n. Maricopa Co.: T3N R8E S18, 3 km N of Stewart Mt., MAB 8121; SE of Roosevelt Dam, MAB 8279; T6S R3W S13, ca. 11 mi E of Gila Bend, MAB 8096; T5N R3E S12, Paradise Valley, MAB 11664; T6S R3W S16, 8 mi E of Gila Bend, MAB 8099. Pima Co.: T14S R12E S11, Tucson Mts., MAB 8113-A, -B, -C; 8115-A, -B, -C; T12S R14E S30, MAB 8138-B, -C. Pinal Co.: T1N R8E S11, 6 km NE of Apache Junction, MAB 4945; T5S R6E S9, ca. 8 mi N of Casa Grande, MAB 8108-A, -C. **California.** Riverside Co.: T8S R17E S28, above Chuckawalla Well, MAB 4943 & Daniel; T9S R17E S2, S of Graham Pass, MAB 4938 & Daniel. **Mexico.** Baja California: 113°48'W, 29°01'N, 18.2 mi W of Bahía de los Angeles, MAB 8784 & RJ 12.6 mi E of San Telmo as the junction of the roads to the observatory & Meling Ranch, Hensel 334 & Garmon; 115°22'W, 31°17'N, Rte. 3, ca. 33 km W of jct. Rte. 5, JPR 1287 & Cordova.

Opuntia bigelovii var. *citrina* (Engelm.) W. T. Marshall

$n = 11$. **Mexico.** Baja California Sur: 111°53'W, 26°20'N, ca. 22 mi W of Rte. 1 along the road to San Isidro, MAB 8727, 8728 & RJ(87.4); 111°53'W, 26°17'N, ca. 25 mi W of Rte. 1 on road to San Isidro, MAB 8730 & RJ; 111°55'W, 25°57'N, Cerro Sombrerito, ca. 2 km S of Rio Comondú, MAB 8736-A (90.4), 8736-B & RJ (90.8); 111°56'W, 25°58'N, 64 km N of Ciudad Insurgentes & 13.7 mi E of Francisco Villa, JPR 1686 & Davis (92.8) (neotype).

Opuntia burrageana Britton & Rose × *O. lindsayi* J. Rebman

* $n =$ ca. 22. **Mexico.** Baja California Sur: 111°08'W, 24°44'N, S of Ciudad Constitución, a few mi NE of La Fortuna, JPR 1701 & Davis.

Opuntia californica (Torr. & A. Gray) Coville var. *californica* (Engelm.) Pinkava (= *O. parryi* Engelm. var. *serpentina* (Engelm.) L. D. Benson).

$n = 11$. **Mexico.** Baja California: 116°33'W, 32°33'N, 1 mi E of Rte. 3 at km marker 39 between Tecate and Ensenada, S of Valle Las Palmas, JPR 2622 (71.7).

Opuntia californica var. *parkeri* (J. M. Coulter) Pinkava (= *O. parryi* Engelm. var. *parryi*)

$n = 11$. **Mexico.** Baja California: Sierra San Pedro Martir, 11.8 mi SW of Rte. 3 on road to Rancho Mike MAB 3699 (69.3); 0.2 mi SW on turnoff to Rancho Mike from Rte. 3, DJP et al. 14171; 10 mi W of Ejido Heroes de la Independencia at km marker 78 of Rte. 3 between Ensenada & San Felipe, JPR 1188 & Cota; 115°57'W, 32°01'N, Sierra Juárez, 2.5 mi SW of Laguna Hanson & 0.3 mi NE of El Asarradero, JPR 2776 & Rebman.

Opuntia calmalliana J. M. Coulter

* $n = 33$. **Mexico.** Baja California: 113°40'W, 28°05'N, 16 mi WNW of El Arco, MAB 8774 & RJ; 113°25'W, 28°07'N, at ruins of Calmali, MAB 8775, 8776 & RJ. Baja California Sur: 113°30'W, 27°44'N, Rte. 1, 37.3 mi SE of B. C. border, MAB 8704, 8705 & RJ; 113°14'W, 27°27'N, 4 km E of Rte. 1 on road to San Francisco de la Sierra, JPR et al. 1421 (92.1).

Opuntia cholla F. A. C. Weber

$n = 11$. **Mexico.** Baja California: 114°10'W, 28°42'N, 4.2 mi W of Rte. 1 along road to Santa Rosalilita, MAB 8697 & RJ (44.4) (pop. voucher); 114°01'W, 28°30'N, just S of El Tomatal, MAB 8702 & RJ; Rte. 1, 5.5 mi E of El Rosario & 4.5 mi NE to Rancho, DJP 8791 & LAM (92.7). Baja California Sur: Rte. 1, 13 km SE of San Ignacio, JPR 1164 & Rice (86.5); 109°58'W, 24°02'N, beach area S of La Ventana, JPR et al. 1365, 1366; 111°56'W, 25°58'N, 64 km N of Ciudad Insurgentes & 13.7 mi E of Francisco Villa, JPR 1688 & Davis (73.0); 111°44'W, 24°35'N, 2 mi N of Puerto Cayuca, JPR 1700 & Davis; 111°08'W, 24°44'N, E of Rte. 1 and a few mi NE of La Fortuna, JPR 1702 & Davis; 110°19'W, 24°17'N, Pichilingue area, N of La Paz, JPR et al. 1705.

** $2n = 3x = 33$. **Mexico.** Baja California: 115°55'W, 30°36'N, 2.3 mi E of Rte. 1 in Lázaro Cárdenas, JPR 1651 & Davis.

** $n = 22$. **Mexico.** Baja California Sur: 110°26'W, 23°40'N, 7 mi NW of El Carrizal Agua Blanca Resort, JPR et al. 1385.

Table 1. Continued

- Opuntia clavata* Engelm.
 $n = 11$. **New Mexico.** Bernadilla Co.: W Albuquerque, S of I-40, *DJF 1138-B*.
- Opuntia clavellina* Engelm.
 $*n = ca. 44$. **Mexico.** Baja California Sur: 111°47'W, 25°32'N, 7.5 km E of Col. Purísima on road between Purísima & San Javier, *JPR et al. 1393* (58.7).
- Opuntia × congesta* Griffiths (*Opuntia acanthocarpa* var. *thornberi* × *O. whipplei*)
 $*n = 11$. **Arizona.** Yavapai Co.: T10N R4E, 10.5 mi E from I-17 along Bloody Basin Rd., *NT 82-114 & MAB* (51.0).
- Opuntia davisii* Engelm. & J. M. Bigelow
 $n = 22$. **New Mexico.** Hidalgo Co.: T27S R19W S16, 1.5 km from center of Animas, *MAB 10896-B* (pop. voucher).
- Opuntia echinocarpa* Engelm. & J. M. Bigelow (incl. *O. wigginsii* L. D. Benson)
 $n = 11$. **Arizona.** Maricopa Co.: T1S R6W S10, 4 mi N of Centennial Wash, *MAB 7733* (77.1). La Paz Co.: T3N R18W S9, Hwy. 95 S of Quartzsite, *MAB 7728*. Yuma Co.: W of AZ 95, ca. 2 mi N of Gila River crossing, *LAM 90-1*; T7S R21W S12, 30 km N of Yuma, *MAB 8128*.
- Opuntia echinocarpa* × *O. munzii* C. B. Wolf
 $*n = 11$. **California.** Riverside Co.: T8S R17E S33, *MAB 4941 & Daniel*.
- Opuntia engelmannii* Salm-Dyck ex Engelm. var. *engelmannii*
 $n = 33$. **Arizona.** Yavapai Co.: T16N R1E S24, Woodchute Wilderness Area, ca. 9 km W of Jerome, *MAB 9369*. **New Mexico.** Bernadillo Co.: E Albuquerque, *DJF 1170-D*.
- Opuntia engelmannii* var. *flavispina* (L. D. Benson) B. D. Parfitt & Pinkava
 $n = 33$. **Arizona.** Pima Co.: Organ Pipe Cactus Natl. Mon., Quitobaquito Springs, *MAB 8788*. Yavapai Co.: T9N R9W S18, NE of the Harcuvar Mts., *MAB 11066 & TW*.
- Opuntia × fosbergii* C. B. Wolf (*O. bigelovii* var. *bigelovii* × *O. ?ganderi*)
 $*2n = 3x = 33$. **California.** San Diego Co.: T14S R7E S35, Carrizo Valley, *MAB 4922* (7.8).
- Opuntia fulgida* Engelm. var. *fulgida*
 $n = 11$. **Arizona.** Maricopa Co.: just S of Waddell Dam at Lake Pleasant, *JPR 1444*. Pima Co.: T14S R12E S8, Tucson, *MAB et al. 7816*.
- Opuntia ganderi* (C. B. Wolf) J. Rebman & Pinkava
 $n = 11$. **California.** San Diego Co.: T15S R8E S33, ca. 1 km SE of Sweeney Pass, *MAB 7529* (67.1), 7530 (86.6). **Mexico.** Baja California: San Matias Pass, 2 mi E of San Matias, *MAB 3698* (97.0); 114°25'W, 29°47'N, Rte. 5, 3 km W of Bahía San Luis Gonzaga, *MAB 8681* (95.5), 8682 & *RJ*; 114°25'W, 29°42'N, Rte. 5, Las Arrastras Wash, *MAB 8683* (96.4), 8685 & *RJ*; 114°22'W, 29°34'N, Rte. 5, 2.1 mi NW of Las Arrastras Wash, *MAB 8691 & RJ*; Rte. 2, 52.3 mi W of jct. with main rte. to Mexicali, *DJP 8677* (89.5), 8678 (74.1) & *LAM* (intermediate with *O. californica* var. *parkeri*); Rte. 3, 6.6 mi SE of San Matias, *DJP et al. 14167*; 115°17'W, 31°16'N, ca. 1 mi S of Rte. 3 on the road to Col. San Pedro Martir, *JPR 2549*.
- Opuntia ganderi* var. nov. A.
 $*n = 11$. **Mexico.** Baja California: 114°02'W, 29°03'N, road to Bahía de los Angeles, 8.2 mi E of its junction with Rte. 1, *MAB 8785 & RJ*; Rte. 1, ca. 10 mi SE of San Agustín, *DJP et al. 14220* (96.9); 114°43'W, 29°26'N, ca. 25 mi W of Rte. 1 on the road to San José de la Piedra, *JPR 1322 & Cordova*; 114°46'W, 29°47'N, near Rte. 1, 5 mi NNW of Cataviña, *Van Devender et al. 91-346*.
- Opuntia imbricata* (Haw.) DC. var. *imbricata*
 $n = 11$. **New Mexico.** Chaves Co.: T8S R26E S21, 30 km NE of Roswell, *MAB 10895*. Dona Ana Co.: Las Cruces, I-10, 1.6 mi W of Rio Grande bridge, *RDW 19075*. **Oklahoma.** Cimarron Co.: Hwy. 325, 7.7 mi E of Kenton, *BDP et al. 5129*.
- Opuntia invicta* Brandegee
 $n = 11$. **Mexico.** Baja California Sur: 112°51'W, 27°14'N, 4.2 mi S of San Ignacio, *MAB 8773 & RJ*. **Origin unknown.** Cultivated: Universidad Autónoma de Baja California garden, just N of Ensenada, Mexico, *JPR 2502*.
- Opuntia × kelvinensis* V. E. Grant & K. A. Grant (*O. fulgida* × *O. spinosior*)
 $n = 11$. **Arizona.** Pima Co.: T13S R11E S34, Tucson, *MAB et al. 7803*; T13S R13E S30, Tucson, *MAB et al. 7810* (98.2); T13S R11E S28, Tucson, *MAB et al. 7812* (58.6). Pinal Co.: T6S R13E S19, SE of Florence, *MAB 4327* (photo only).
- Opuntia leptocaulis* DC.
 $n = 11$. **Arizona.** Mohave Co.: T13N R15W, bajada west of McCracken Mts., *MAB et al. 10779*; T15N R12W S29, Signal Rd. 15 km S of Wikieup, *MAB 10781, 10782*. Pima Co.: T14S R13E S6, Tucson, Las Lomas area, *MAB 7817*; T12S R12E S35, Tucson, just S of Silverbell Rd., *MAB 7819*. Yavapai Co.: T13N R6W S29, 2 km N of Hillside, *MAB 10358*; T13N R6W S16, 6 km NNW of Hillside, *MAB 10362*.
- $2n = 3x = 33$. **Arizona.** Pima Co.: T13S R11E S28, Tucson, *MAB et al. 7814*; T12S R12E S29, Tucson, Pima Farms Rd. near Sanctuary Cove, *MAB et al. 7824, MAB 8237*.
- Opuntia leptocaulis* × *O. whipplei*
 $*n = 11$. **Arizona.** Yavapai Co.: T10N R4E S15, 10 mi E of I-17 on Bloody Basin Rd., *NT 82-108 & MAB*; T13N R6W S29, 2 km N of Hillside, *MAB 10357, 10862, 10865*; T18N R3E S16, Sycamore Canyon Wilderness, *MAB 10270*.
- Opuntia macrocentra* Engelm.
 $n = 22$. **New Mexico.** Dona Ana Co.: Las Cruces, I-10, 1.6 mi W of Rio Grande bridge, *RDW 19073*. Grant Co.: T17S R16W S5, 1 km NNE of Mangas Springs, *MAB 11627 & TW*.

Table 1. Continued*Opuntia macrorhiza* Engelm. var. *macrorhiza*

$n = 22$. **Kansas.** Harper Co.: Hwy. 2, 0.3 mi NE of Chiskaskia River & 8.3 mi NE of East Sand Creek, *BDP 5112A, 5112B*. **Missouri.** Reynolds Co.: County Road N, 5.1 mi E of road to Johnson's Shut-ins State Park, *BDP 5110*. **New Mexico.** Guadalupe Co.: I-40, 5 mi W of Hwy. 84 jct., *DJP 1376-A*; Hwy. 91, 1 mi N of Puerto de Luna, *DJP 1367-B*. **Texas.** Hartley Co.: Hwy. 54, 2 mi SW of Dalhart, *DJP 1374*.

Opuntia macrorhiza var. *pottsii* (Salm-Dyck) L. D. Benson

$n = 22$. **Arizona.** Cochise Co.: San Simon Valley, on Portal-Rodeo Rd., *LAM 6182*.

Opuntia molesta Brandegee

* $n = 44$. **Mexico.** Baja California: 113°10'W, 28°28'N, Valle San Rafael, 14.7 mi NW of El Progreso, *MAB 8781 & RJ*; Rte. 1, 5.5 mi E of El Rosario & 4.5 mi NE to Rancho, *DJP 8786 & LAM* (69.9); 4.8 mi E of Rte. 1 & El Rosario, *DJP et al. 11149* (30.9), *11160* (60.1), *11161* (16.7); Rte. 1, 3 mi N of Cataviña, *JPR 1142* (17.6), *1144 & Rice* (13.0). Baja California Sur: Rte. 1, near San Ignacio turnoff, *DJP et al. 14098*.

Opuntia molesta \times *O. ?prolifera*

* $n = 33$. **Mexico.** Baja California: Rte. 1, 11.7 mi SE of El Rosario, *DJP et al. 9068*; 5.5 mi E of El Rosario & 4.5 mi NE on left fork, *DJP et al. 9137* (31.7).

** $2n = 7x = 77$. **Mexico.** Baja California: Rte. 1, 11.7 mi SE of El Rosario, *DJP et al. 9066* (0.9); 5.5 mi E of El Rosario & 4.5 mi NE on left fork, *DJP et al. 9148* (51.1); 12.6 mi E of San Telmo *DJP et al. 11185*; 5.5 mi E of El Rosario & 4.5 mi NE of Rte. 1, *DJP et al. 12144* (13.9).

Opuntia \times *multigeniculata* Clokey (*O. echinocarpa* \times *O. whipplei*)

* $n = 11$. **Nevada.** Clark Co.: T22S R59E S8, just N of Blue Diamond, *MAB et al. 11374-A, -B*; T22S R59 S8, just NW of Blue Diamond *MAB 4969-A & J. Trushell* (27.8).

Opuntia munzii C. B. Wolf

* $n = 11$. **California.** Riverside Co.: T9S R17E S2, *MAB 4940 & Daniel*; T8S R17E S28, above Chuckawalla Well, *MAB 4942 & Daniel* (87.4). **Mexico.** Baja California: 115°03'W, 31°25'N: just SW of jct. of Rtes. 3 & 5, Llano de Chiner, *MAB 8646 & RJ*; 114°58'W, 31°16'N: Rte. 5, 10.9 mi S of jct. with Rte. 3, *MAB 8647 & RJ*; 0.5 mi S of Rte. 3, just N of Laguna Diablo, *DJP et al. 14159* (12.1).

** $2n = 3x = 33$. **Mexico.** Baja California: 115°16'W, 31°18'N: Rte. 3, at km marker 170, *JPR 2543*.

Opuntia pphaecantha Engelm.

$n = 33$. **Arizona.** Coconino Co.: 111°42'W, 35°58'N, Little Colorado River drainage basin, *Joyal 2213*. Yavapai Co.: T12N R4W S6, 0.5 km SW of Kirkland, *MAB 10701*; T15N R10W S32, 500 m E of Mohave Co. line, *MAB et al. 10788*. **New Mexico.** Bernadillo Co.: W Albuquerque, *DJP 1138-A*; E Albuquerque, *DJP 1170-C, -F, -J*. Dona Ana Co.: Las Cruces, I-10, 1.6 mi W of Rio Grande bridge, *RDW 19072, 19074*; T24S R3E S24, 1.2 mi NNE of Bishop Cap, *RDW 17919*; E Potrillo Mts., *RDW 20888*. Guadalupe Co.: I-40, 5 mi W of jct. Hwy. 84, *DJP 1376-B*. Luna Co.: T25S R7W S5, Little Florida Mts., South Canyon, *RDW 19171*. Rio Arriba Co.: Hwy. 74, 3 mi N of jct. Hwy. 582, *DJP 94-32, 94-33* (both with irregular meiosis); Rio Grande Valley, jct. Hwys. 72 and 582, *DJP 94-29*. **Oklahoma.** Texas Co.: Hwy. 3, 0.7 mi E of Chiquita Creek & 11.5 mi S, *BDP et al. 5120*, near entrance to Hardesty Park, *BDP et al. 5121*.

Opuntia prolifera Engelm.

2 $n = 3x = 33$. **Mexico.** Baja California: 5.5 mi E & 4.5 mi NE on left fork, *DJP et al. 9149* (18.2); 9 km N of Punta Cabras, W of Santo Tomás, *JPR 1129* (4.4), *1130* (17.8); Rte. 3, at km 122, N of Valle de Trinidad, *JPR 1192 & Cota* (8.4); 115°47'W, 30°12'N, Rte. 1, at km marker 39, S of San Quintín, *JPR 1424* (4.3); 115°55'W, 30°36'N, 4 mi N of the military base at L & 2.3 mi E of Rte. 1, *JPR 1650 & Davis*.

Opuntia pulchella Engelm.

$n = 11$. **California.** Mono Co.: Fish Lake Valley, just N of Inyo Co. line, *MAB 7052*.

Opuntia pycnantha Engelm.

* $n = 11$. **Mexico.** Baja California Sur: 111°32'W, 24°26'N, E of Punta Chale, *JPR 1389*.

Opuntia ramosissima Engelm.

$n = 11$. **Arizona.** Mohave Co.: T13N R15W S17, SW of Wikieup, *MAB et al. 10780*; T13N R15W, W of McCracken Mts., *MAB et al. 10778*. **Nevada.** Clark Co.: T22S R60E S5, ca. 15 km SW of central Las Vegas, *MAB et al. 11371*. **Mexico.** Baja California: Rte. 5, 1.3 mi S of jct. 3, *DJP et al. 14130*.

Opuntia rosarica G. E. Linds.

$n = 11$. **Mexico.** Baja California: 115°54'W, 30°46'N, ca. 3.5 km E of Santo Domingo, *JPR 1213 & Cota* (29.1); 115°30'W, 30°04'N, ca. 82 km S of San Quintín along Rte. 1, *JPR 1644 & Delgadillo*.

Opuntia sanfelipensis J. Rebm

$n = 33$. **Mexico.** Baja California: 115°22'W, 31°17'N: Rte. 3, ca. 20 mi ESE of Lázaro Cárdenas, *MAB 8642 & RJ*; 115°14'W, 31°18'N: Rte. 3, 16 mi W of jct. with Rte. 5, *MAB 8643 & RJ*.

Opuntia santa-rita (Griffiths & Hare) Rose

$n = 11$. **Arizona.** Santa Cruz Co.: ca. 2 mi E of Sycamore Canyon entrance, *JPR 1827*.

Opuntia spinosior (Engelm.) Toumey

$n = 11$. **Arizona.** Cochise Co.: near Cochise Stronghold, *JPR 1816*. Pima Co.: T13S R11E S34, Tucson, *MAB et al. 7804*; T12S R12E S35, Santa Cruz River floodplain, W of Tucson, *MAB et al. 7807*. Pinal Co.: T6S R13E S19, Barkerville Rd., SE of Florence, *MAB 4326*; S29, *MAB et al. 11371*. Yavapai Co.: T13N R6W S29, 2 km N of Hillside, *MAB 10356*.

Opuntia tapona Engelm.

* $n = 11$. **Mexico.** Baja California Sur: 111°43'W, 26°03'N, 2 km E of San José Comondú, *MAB 8755 & RJ*; 111°11'W, 25°34'N, 11.4 mi SE of Rte. 1 along the road to Agua Verde, *JPR 1661*.

Table 1. Continued*Opuntia tesajo* Engelm.

*n = 11. **Mexico.** Baja California: 115°03'W, 31°25'N, just SW of the junction of Rte. 3 & Rte. 5, Llano de Chinero, MAB 8646 & RJ; 114°12'W, 28°40'N, 2 km E of Rosalilita, MAB 8698 & RJ; 113°44'W, 28°58'N, 11.7 mi W of Bahía de los Angeles, MAB 8783 & RJ; Rte. 3, near Ejido San Matias, JPR 1194 & Cota (68.6); 113°42'W, 28°58'N, ca. 12 mi W of Bahía de los Angeles, JPR 1323 & Cordova; 114°12'W, 29°27'N, ca. 1.5 mi N of Misión Calamajue, JPR 1615 & Delgadillo (73.2) (neotype); 115°16'W, 31°18'N, Rte. 3, 3.5 mi E of the turn to Laguna Diablo, JPR 2542; 113°59'W, 28°39'N, E of Rosarito on road to Misión San Borja, JPR 2634 & Hodgson (90.0); 115°12'W, 31°21'N, Rte. 3, 17.6 km W of jct. Rte. 5, Van Devender et al. 19-138; 115°13'50" W, 29°58'30" N, 1.6 mi E of Misión San Fernando Velicata, Van Devender 91-215 & Van Devender.

Opuntia tesajo × *O. ganderi*

*n = 11. **Mexico.** Baja California: 13.4 mi E of San Matias & 1.7 mi S of Rte. 3, JPR et al. 1467.

Opuntia thurberi Engelm.

*n = 11. **Mexico.** Sonora: 27°00'N, 108°47'W, 14 km ESE of Alamos, El Guayabo crossing of Rio Cuchujaqui, MAB et al. 10441, 10443; 27°02'N, 108°57'W, La Huerta, 1.8 km NNE of Alamos, MAB et al. 10370; 108°54'W, 26°51'N, ca. 22 km SSE of Alamos, MAB et al. 10375; 27°04'N, 109°02'W, near El Carrizal, MAB et al. 10447; 27°04'N, 109°17'W, 17 km E of Navajoa on road to Alamos, MAB et al. 10450. Sinaloa: Rte. 15, 0.8 mi from Tobora, DJP et al. 12919 (orig. publ. as *O. kleiniae* var. *tetracantha*) (Pinkava et al. 1977).

Opuntia versicolor Engelm. ex J. M. Coulter

n = 11. **Mexico.** Sonora: ca. 11.5 km ESE of Empalme, MAB et al. 10369.

Opuntia × *viridiflora* Britton & Rose (*O. imbricata* var. *imbricata* × *O. whipplei*)

*n = 11. **New Mexico.** Santa Fe Co.: Ft. Marcy Hill, Santa Fe, NT 83-15 & MAB.

Opuntia whipplei Engelm. & J. M. Bigelow

n = 11. **Arizona.** Apache Co.: Steamboat Canyon, MAB 4748; T9N R29E S7, ca. 8 km NE of Springerville, MAB 11429 & TW. Coconino Co.: Kaibab Natl. Forest, 0.9 mi E on For. Serv. Rd. 234 from jct. 234/646, NT 82-183. Mohave Co.: T39N R9W S8, just E of Hurricane Cliffs, NT 82-202 & MAB; T40N R6W S19, NT 82-194 & MAB; T38N R11W S14, road to Mt. Trumbull, NT 82-195 & MAB. Yavapai Co.: T15W R2W S31, NT 82-165 & MAB; T21N R11W S20, Cactus Pass, MAB 10868; T13N R6W S29, 2 km N of Hillside, MAB 10815; T20N R6W S15, Yavapai Co. Rd. #3, 2 km E of Turkey Canyon, MAB 11872; T18N R1E S28, 4.2 km SSE of Red Butte, NW of Jerome, TW 1529 & MAB.

n = 22. **Arizona.** Mohave Co.: T24N R13W S24, Hwy. 6, 6.5 km W of Truxton, NT 82-206 & MAB; T25N R11W S8, Peach Springs Canyon, NT 82-208 & MAB; T24N R19W S9, 28 mi NW of Kingman, MAB 4974-A & J. Trushell; T20N R13W S3, 3.8 mi N on road to Hackberry from Hwy. 93, NT et al. 84-6.

Opuntia (subgenus *Cylindropuntia*) sp. nov. A.

*n = 11. **Mexico.** Baja California: 115°13'W, 31°03'N, ca. 0.5 mi W of the junction of road to Agua Caliente and the road to Laguna Diablo, JPR 2566 (85.8).

Pereskia *porteri* (F. A. C. Weber) Britton & Rose

n = 55. **Mexico.** Baja California Sur: Rte. 1, between La Paz and San José del Cabo, JPR 2855.

CACTOIDEAE*Bergerocactus emoryi* (Engelm.) Britton & Rose

n = 22. **Mexico.** Baja California: ca. 3 mi S of Punta Baja, W of El Rosario, JPR 917.

Carnegiea gigantea (Engelm.) Britton & Rose

n = 11. **Arizona.** Maricopa Co.: Desert Botanical Garden in Papago Park, Phoenix, M. Chamberland s.n.

Coryphantha missouriensis (Sweet) Britton & Rose var. *missouriensis*

*n = 11. **Arizona.** Yavapai Co.: T16N R2W S4, Chino Valley, MAB 8574.

Echinocereus bonkerae Thornber & Bonker

n = 11. **Arizona.** Yavapai Co.: T10N R4E S36, near Hutch Springs, just W of Bloody Basin, MAB 8839 & TW.

Echinocereus engelmannii (Parry ex Engelm.) Rümpler var. *acicularis* L. D. Benson

n = 22. **Arizona.** Maricopa Co.: T6S R3W S13, I-8, ca. 11 mi E of Gila Bend, MAB 8097.

Echinocereus engelmannii var. *engelmannii*

n = 22. **Mexico.** Baja California: 9 mi S of Rte. 3 on road to Mike's Sky Ranch, JPR 1093 & Rice; 115°15'W, 30°05'N, 4.5 mi E of Rte. 1 near Rancho Peña, JPR 1640 & Delgadillo; 115°34'W, 31°16'N, 3 mi S of Rte. 3 and 2.3 mi S on road to El Tepi, JPR 2653.

Echinocereus engelmannii var. *purpureus* L. D. Benson

*n = 11. **Arizona.** Mohave Co.: T40N R13W S23, N edge of Black Rock Canyon, Gierisch 5040.

Echinocereus fasciculatus (Engelm.) L. D. Benson × *E. fendleri*

*2n = 3x = 33. **Arizona.** Yavapai Co.: T16N R1E S12, Woodchute Mt., 10 km WNW of Jerome, MAB 9102; T18N R2W S16, S of Ash Fork, 5.5 km SW of Rock Butte, MAB 11610 & TW.

Echinocereus fendleri (Engelm.) Rümpler var. *rectispinus* (Peebles) L. D. Benson

n = 11. **Arizona.** Cochise Co.: T24S R31E S1, 3.7 km N of Mexico, 9 km W of New Mexico, MAB 11335 & TW. **New Mexico.** Grant Co.: T17S R21W S11, 6 km NW of Steeple Rock, MAB 11634 & TW.

Echinocereus maritimus (M. E. Jones). K. Schum.

n = 11. **Mexico.** Baja California: ca. 3 mi S of Punta Banda, W of El Rosario, JPR 918.

Echinocereus triglochidiatus Engelm. var. *mojavensis* (Engelm. & J. M. Bigelow) L. D. Benson

n = 11. **Arizona.** Coconino Co.: T40N R3E S20, Vicinity of Corral Valley, Paria Plateau, Gierisch 5056. Mohave Co.: T27N R10W S5, Peach Springs Canyon, MAB 8105. **California.** San Bernardino Co.: T17N R13E S16, 5 km N of Clark Mt., MAB 7509 & BDP.

Table 1. Continued

- Echinomastus erectocentrus* (J. M. Coulter) Britton & Rose var. *erectocentrus*
n = 11. **Arizona.** Cochise Co.: Huachuca Mts., near Miller Peak, LAM 5104-A.
- Ferocactus peninsulae* (Engelm. ex F. A. C. Weber) Britton & Rose var. *peninsulae*
n = 11. **Mexico.** Baja California: 2 mi S of the town at Bahía de los Angeles, JPR 1325 & Cordova.
- Ferocactus peninsulae* var. *townsendianus* (Britton & Rose) N. P. Taylor
n = 11. **Mexico.** Baja California Sur: 111°55'W, 24°59'N, 3.1 mi N of the road to San Carlos on road to Lopez Mateos, JPR et al. 2804.
- Lophocereus schottii* (Engelm.) Britton & Rose var. *australis* (K. Brandegee) Borg
n = 11. **Mexico.** Baja California Sur: 109°58'W, 24°02'N, S of La Ventana, JPR et al. 1367.
- Lophocereus schottii* var. *schottii*
n = 11. **Mexico.** Baja California: 115°22'W, 31°05'N, near Rancho Las Animas, JPR 2550 (flowers greenish-yellow). Baja California Sur: 111°55'W, 24°59'N, 3.1 mi N of the road to San Carlos on road to Lopez Mateos, JPR 2801 (flowers pink).
- Mammillaria bocensis* Craig.
n* = 11. **Mexico. Sonora: 109°16'W, 26°31'N, Camahuiroa, between Agiabampo and Las Bocas, MAB 10458.
- Mammillaria brandegeei* (J. M. Coulter) K. Brandegee
n = 11. **Mexico.** Baja California: 115°45'W, 30°04'N, "Petrified Forest" area W of El Rosario, JPR 2181.
- Mammillaria dioica* K. Brandegee
n = 33. **Mexico.** Baja California: 115°50'W, 30°34'N, ca. 7 mi E of Rte. 1 at San Quintín, JPR 1290 & Cordova; 115°29'W, 31°18'N, Rte. 3, at San Matias Pass, JPR 2092 & Hirales; 116°39'W, 31°52'N, Cerro el Vigia, Rte. 1, N of Ensenada, JPR 2095 & Resendiz; 116°44'W, 31°54'N, San Miguel Arroyo, Rte. 1 (libre), JPR 2100 & Resendiz; 116°39'W, 31°38'N, S of Punta Banda, JPR 2144 & Hirales; 115°29'W, 31°19'N, Rte. 1, at San Matias Pass, JPR 2275 & Delgadillo; 114°41'W, 29°42'N, 6.3 mi S. of Cataviña, JPR 2294 & Hirales.
- Mammillaria goodridgei* Scheer var. *goodridgei*
n* = 11. **Mexico. Baja California: 115°14'W, 28°17'N, Cedros Island, near El Faro, JPR et al. 2472.
- Mammillaria lewisi* H. E. Gates
n = 11. **Mexico.** Baja California Sur: 113°12'W, 27°29'N, E of Rte. 1 on road to San Francisco de la Sierra, JPR 2359 & Hirales.
- Mammillaria louisae* G. E. Linds.
n = 11. **Mexico.** Baja California: 115°48'W, 30°18'N, Rte. 1, S of San Quintín near Ejido Valle Tranquilo, JPR 2287 & Hirales.
- Mammillaria standleyi* Orcutt
n* = 11. **Mexico. Sonora: 108°58'W, 26°59'N, 4 km SW of Alamos, MAB 10417 & Steinmann.
- Myrtillocactus cochal* (Orcutt) Britton & Rose
n = 11. **Mexico.** Baja California: ca. 3 mi S of Punta Baja, W of El Rosario, JPR 912 & Marsh; 115°46'W, 29°59'N, 3 mi S of Punta Baja, SW of El Rosario, JPR 2209.
- ✗ *Myrtillocactus lindsayi* Moran
 $2n = 3x = 33$. **Mexico.** Baja California: ca. 3 mi S of Punta Baja, W of El Rosario, JPR 947 & Marsh.
- ✗ *Pachycereus orcuttii* (K. Brandegee) Moran
 $*, **2n = 44$. **Mexico.** Originally from Baja California near El Rosario; cultivated at the Huntington Botanical Garden, JPR 2875 (live; photo voucher only).
- Pachycereus pecten-aboriginum* (Engelm.) Britton & Rose
n = 11. **Mexico.** Sonora: Minas Nuevas, 7.7 km NW of Alamos, MAB et al. 10446.
- Pachycereus pringlei* (S. Watson) Britton & Rose
n = 22. **Mexico.** Baja California: 3.3 mi S of the town at Bahía de los Angeles, JPR 950 & Marsh; 114°45'W, 29°46'N, 6 km N of Cataviña, JPR 2501 & Delgadillo.
- Stenocereus thurberi* (Engelm.) Buxb. var. *thurberi*
n = 11. **Mexico.** Baja California Sur: 111°55'W, 24°59'N, 3.1 mi N of the road to San Carlos on road to Lopez Matcos, JPR et al. 2800.

Corrections

- Coryphantha delaetiana* (Quehl) A. Berger
n = 11. **Mexico.** Chihuahua: Rte. 45, ca. 10 mi S. of Ciudad Camargo, DJP 9256, 9258, LAM & R. C. Brown (fig. 20), identified by Allan Zimmerman; originally published as *C. salm-dyckiana* (Pinkava & Parfitt, 1982).
- Mammillaria celsiana* Lem.
n = 11. **Mexico.** San Luis Potosí: road to Balneario de Lourdes, DJP 9632, LAM & R. C. Brown (fig. 34), originally published as *M. muehlenpfordtii* Förster (Pinkava & Parfitt, 1982).
- Sclerocactus sileri* (L. D. Benson) K. D. Heil & J. M. Porter
n = 11. **Arizona.** Coconino Co.: vicinity of Corral Valley, Paria Plateau, T40N R4E S20, Gierisch 5053, identified by Ken Heil; originally as *S. cf. spinosior* (Engelm.) Woodruff & L. D. Benson (Pinkava et al., 1992).

Table 2 Taxonomic and geographic distribution of polyploid taxa in the Cactaceae

Data tabulated from published reports and edited by Pinkava (unpubl.). The 37 genera with only diploid numbers are collectively presented at end of tabulation. Generic delimitation modified slightly from Hunt and Taylor (1990). Note: percent polyploidy (P_x) is based on the number of taxa with polyploidy divided by the total taxa with chromosome counts. Symbols: P_x = polyploid state at any level ($\geq 3x$), including taxa with diploid and polyploid individuals; N = North American, including West Indies; S = South American; T = North and South American; * = monospecific taxa.

Taxon	Geographic distribution	Total taxa	Species	Additional sspp./vars. + hybrids	Taxa (P_x)	Percent (P_x)	Levels (P_x)
PERESKIOIDEAE	T	16	15	1	0	0.0	—
<i>Maihuenia</i>	S	2	2	0	0	0.0	—
<i>Pereskia</i>	T	14	13	1	0	0.0	—
OPUNTIOIDEAE	T	199	146	53	128	64.3	—
<i>Opuntia</i> s.l.	T	193	140	53	123	63.7	—
<i>Austrocylindropuntia</i>	S	7	7	0	6	85.7	4–6, 10, 11
<i>Brasiliopuntia*</i>	S	2	1	1	0	0.0	—
<i>Consolea</i>	N	3	3	0	2	66.7	612
<i>Corynopuntia</i> (incl. <i>Micropuntia</i> *)	N	10	10	0	5	50.0	46
<i>Cumulopuntia</i>	S	1	1	0	1	100.0	6
<i>Cylindropuntia</i>	N	61	31	30	28	45.9	3–8
<i>Grusonia*</i>	N	1	1	0	0	0.0	—
<i>Miqueliopuntia*</i>	S	1	1	0	1	100.0	ca. 20
<i>Opuntia</i> s.s.	T	94	73	21	67	71.3	3–8
<i>Tephrocactus</i>	S	13	12	1	8	61.5	3–6, 8, 13, 19, 30
<i>Pereskiopsis</i>	N	3	3	0	3	100.0	10
<i>Pterocactus</i>	S	1	1	0	1	100.00	4
<i>Quiabentia</i>	S	1	1	0	1	100.0	10
<i>Tacinga</i>	S	1	1	0	0	0.0	—
CACTOIDEAE	T	435	376	59	56	12.9	—
<i>Ariocarpus</i>	N	3	3	0	1	33.3	ca. 4
<i>Bergerocactus*</i>	N	1	1	0	1	100.0	4
<i>Blossfeldia*</i>	S	1	1	0	1	100.0	6
<i>Cephalocereus</i>	T	3	3	0	2	66.7	4
<i>Escobaria</i>	N	20	13	7	3	15.0	4
<i>Echinocereus</i>	N	57	25	32	19	33.3	4
<i>Echinopsis</i>	S	9	9	0	2	22.2	4
<i>Gymnocalycium</i>	S	7	7	0	1	14.3	4
<i>Mammillaria</i>	N	127	119	8	14	11.0	4, 6, 8, 24
<i>Melocactus</i>	T	2	2	0	1	50.0	4
× <i>Myrtgerocactus*</i>	N	1	1	0	1	100.0	3
× <i>Pachgerocereus*</i>	N	1	1	0	1	100.0	4
<i>Pachycereus</i>	N	3	3	0	1	33.3	4
<i>Parodia</i> (incl. <i>Notocactus</i>)	S	3	3	0	2	66.7	ca. 4, 4
<i>Rebutia</i>	S	5	5	0	2	40.0	4
<i>Rhipsalis</i>	T	42	42	0	1	2.3	4, 8
<i>Selenicereus</i>	S	8	8	0	1	12.5	4
<i>Thelocactus</i>	N	2	1	1	1	50.0	4
<i>Trichocereus</i>	S	3	3	0	1	33.3	4
37 genera	T	137	126	11	0	0.0	—
CACTACEAE	T	650	537	113	184	28.3	—

lewisiana (Remski, 1954); and 13) *M. louisae* (Johnson, 1980).

Discussion

In this seven-part series (Pinkava & McLeod, 1971; Pinkava & Parfitt, 1982; Pinkava et al., 1973, 1977, 1985, 1992), chromosome numbers have been determined for 1118 individuals of 209 taxa (including 25 interspecific and two intergeneric hybrids), 123 species, and 21 genera of cacti.

The complexity of cacti is heightened by evolutionary processes of natural intergenetic and interspecific hybridization, polyploidization, and apomixis (not only via vegetative propagules, but also adventive embryony (see, e.g., Davis, 1966)). In our studies, interspecific and intergeneric hybrids are determined by intermediacy in several morphological characters, such as flower color and size, fruit shape, texture, and spination, etc., reduced pollen stainability, the proximity of putative parents, and

overlapping flowering periods, at least in some years. Hopefully, future DNA and chemical analyses will confirm our hybrid proposals. The vast majority of these natural hybrids, particularly in the genus *Opuntia* Mill. sensu lato, are known mostly in regions where both parents presently grow, but some occur with only one parent and are currently disjunct from the other parent (e.g., *O. ×multigeniculata* and *O. ×viridiflora*).

Although polyploidy occurs in only about 28% of all cacti investigated thus far, it does play an important role in the evolution of the subfamily Opuntioideae (64.3%) but much less so in the Cactoideae (12.9%) and not at all in Pereskioideae (0.0%) (Table 2). Most polyploidy in cacti occurs in three genera, *Opuntia* sensu lato (Opuntioideae), *Echinocereus* Engelm., and *Mammillaria* Haw., (Cactoideae). The remaining genera in the Cactoideae from which polyploidy is known have taxa that are mostly at triploid and tetraploid levels. The highest levels of ploidy occur in the South American taxa—*Austrocylindropuntia* (11x), *Miqueliopuntia* (ca. 20x), and *Tephrocactus* (30x) (Opuntioideae)—and in North American *Mammillaria* (24x) (Cactoideae) (Table 2).

We believe unreduced gametes account for most of the origins of polyploid cacti (at least in *Opuntia* s.l.) because we have found: 1) macropollen positively staining with cotton blue in diploid species; 2) many taxa (e.g., *Opuntia basilaris*, *O. prolifera*, *O. alcahes*, *O. fulgida*, and *O. leptocaulis* in the Sonoran Desert) that are 2x and 3x, but not 4x, suggesting that triploid individuals are produced from the union of a reduced gamete (1x) and an unreduced gamete (2x) and then reproduce vegetatively, rather than from 2x × 4x hybridizations; and 3) interspecific and intergeneric hybrids derived from parents with different ploidy levels show genome dosage effects on character expression, being more similar to the parent of higher genome dosage than to the parent of lower dosage, e.g., a) an unreduced 3x gamete of triploid *Opuntia bigelovii* var. *bigelovii* × a reduced 1x gamete of diploid *O. acanthocarpa* var. *major*, yielding a yet to be described tetraploid hybrid; b) a partially reduced 2x gamete of triploid *O. bigelovii* var. *bigelovii* × a reduced gamete of diploid *O. ganderi*, yielding a triploid hybrid called *O. ×fosbergii*, in both cases the hybrid resembling more the *O. bigelovii* var. *bigelovii* parent than the other respective parent; c) a reduced 1x gamete of diploid *O. spinosior* × an unreduced 2x gamete of a diploid individual of *O. fulgida*, yielding a triploid hybrid called *O. ×kelvinensis*. All three examples demonstrate that triploid hybrids are not all evolutionary dead ends.

Hybridization and polyploidization play an important role in the evolution of cacti, espe-

cially the subfamily Opuntioideae, and cytogenetic analyses have been very useful in evaluating taxonomic hypotheses (e.g., *Opuntia ×kelvinensis* and *O. ×fosbergii*). Counting chromosomes of several individuals of a single taxon has also proven fruitful because many taxa have more than one chromosome number (see Table 1; e.g., *Opuntia alcahes*, *O. bigelovii* var. *bigelovii*, *O. cholla*, *O. leptocaulis*, and *O. whipplei*). Because many cactus taxa are not yet known cytogenetically, and other taxa are only known from one or few counts, continued chromosome evaluation will help to resolve many of the taxonomic dilemmas still present in the Cactaceae.

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Literature Cited

- Beeks, R. M. 1955. Improvements in the squash technique for plant chromosomes. *Aliso* 3:131–134.
- Cota, J. H., and C. T. Philbrick. 1994. Chromosome number variation and polyploidy in the genus *Echinocereus* (Cactaceae). *Amer. J. Bot.* 81:1054–1062.
- Cota, J. H., J. P. Rebman, and R. S. Wallace. 1996. Chromosome numbers in *Ferocactus* (Cactaceae: Cactoideae). *Cytologia* 61:411–417.
- Davis, G. L. 1966. Systematic Embryology of the Angiosperms. Wiley & Sons, Inc., New York.
- Hunt, D., and N. Taylor (eds). 1990. The genera of Cactaceae: progress towards consensus. Report of the IOS Working Party, 1987–1990. Bradleya 8:85–107.
- Johnson, M. A. T. 1980. Further cytological investigations in *Mammillaria prolifera* and three other *Mammillaria* species. *Cact. Succ. J. (Great Britain)* 42:43–47.
- Maneval, W. E. 1936. Lactophenol preparations. *Stain Technol.* 11:9–11.
- Parfitt, B. D. 1979. *Acacia glandulifera* (Leguminosae): distribution and chromosome number. *Madroño* 26:103.
- Pinkava, D. J., M. A. Baker, B. D. Parfitt, M. W. Mohlenbrock and R. D. Worthington. 1985. Chromosome numbers in some cacti of western North America—V. *Syst. Bot.* 10:471–483.
- Pinkava, D. J., L. A. McGill, T. Reeves and M. G. McLeod. 1977. Chromosome numbers in

- some cacti of western North America—III. Bull. Torrey Bot. Club 104:105–110.
- Pinkava, D. J., and M. G. McLeod. 1971. Chromosome numbers in some cacti of western North America. Brittonia 23:171–176.
- Pinkava, D. J., M. G. McLeod, L. A. McGill and R. C. Brown. 1973. Chromosome numbers in some cacti of western North America—II. Brittonia 25:2–9.
- Pinkava, D. J., and B. D. Parfitt. 1982. Chromosome numbers in some cacti of western North America—IV. Bull. Torrey Bot. Club 109:121–128.
- Pinkava, D. J., B. D. Parfitt, M. A. Baker and R. D. Worthington. 1992. Chromosome numbers of some cacti of western North America—VI, with nomenclatural changes. Madroño 37:98–113.
- Rebman, J. P. 1995. Biosystematics of *Opuntia* subgenus *Cylindropuntia* (Cactaceae), the chollas of Lower California, Mexico. Ph.D. dissertation. Arizona State University, Tempe, Arizona.
- Rebman, J. P. 1999. A new cholla (Cactaceae) from Baja California, Mexico. Haseltonia 6; in press.
- Remski, M. F. 1954. Cytological investigation in *Mammillaria* and some associated genera. Bot. Gaz. 116:163–171.
- Weedin, J. F., and A. M. Powell. 1978. Chromosome numbers in Chihuahuan Desert Cactaceae. Trans-Pecos Texas. Amer. J. Bot. 65:531–537.
- Weedin, J. F., A. M. Powell and D. O. Kolle. 1989. Chromosome numbers in Chihuahuan Desert Cactaceae. II. Trans-Pecos Texas. Southwest. Nat. 34:160–164.
- Yuasa, H., H. Shimizu, S. Kashiwal, and N. Kondo. 1973. Chromosome numbers and their bearing on the geographic distribution in the subfamily Opuntioideae (Cactaceae). Report of the Institute of Breeding Research, Tokyo University—Agriculture 4:1–10.