

CHROMOSOME NUMBERS IN SOME CACTI OF
WESTERN NORTH AMERICA—VI, WITH
NOMENCLATURAL CHANGES

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ABSTRACT

Documented meiotic and mitotic chromosome counts are reported for 69 taxa, including interspecific hybrids, representing 11 genera of Cactaceae from the southwestern United States and northern Mexico. These include first reports for 16 taxa. New ploidy levels were determined for two additional taxa. These chromosome counts are all consistent with the base number for the Cactaceae, $x=11$.

Nomenclatural changes are: *Opuntia* \times *kelvinensis* V. Grant & K. Grant (pro sp.) (*O. fulgida* \times *O. spinosior*), *O.* \times *vaseyi* (J. Coulter) Britton & Rose (pro sp.) (*O. littoralis* \times *O. phaeacantha*), *O.* \times *occidentalis* Engelm. (pro sp.) (*O. littoralis* \times [*O. engelmannii* \times *O. phaeacantha*]), and *O. wolfii* (L. Benson) M. A. Baker, comb. et status nov.

RESUMEN

Se reportan conteos meióticos y mitóticos documentados de cromosomas para 69 taxa, representando 11 géneros de cactáceas del suroeste de los Estados Unidos y del norte de México. Estos incluyen los primeros reportes para 16 taxa. Nuevos niveles de ploidia fueron determinados para dos taxa adicionales. Estos conteos de cromosomas son todos consistentes con el número base para Cactaceae, $x=11$.

Cambios de nomenclatura son: *Opuntia* \times *kelvinensis* V. Grant & K. Grant (pro sp.) (*O. fulgida* \times *O. spinosior*), *O.* \times *vaseyi* (J. Coulter) Britton & Rose (pro sp.) (*O. littoralis* \times *O. phaeacantha*), *O.* \times *occidentalis* Engelm. (pro sp.) (*O. littoralis* \times [*O. engelmannii* \times *O. phaeacantha*]), y *O. wolfii* (L. Benson) M. A. Baker, comb. et status nov.

This report on chromosome numbers is part of a continuing effort to clarify taxonomic and evolutionary relationships among the Cactaceae. Polyploid chromosome numbers, especially in *Opuntia* and *Echinocereus*, aid in distinguishing closely related taxa and in verifying occurrences of hybridization. The base number of the family is established as $x=11$. Pinkava et al. (1985) reported that among the three subfamilies of Cactaceae the percentages of taxa known to include polyploids for the three subfamilies were: Pereskioideae—0.0% of 5 taxa; Opuntioideae—63.3% of 169 taxa; and Cactoideae—12.5% of 377 taxa.

METHODS

Flower buds were collected in developmental series from plants growing in native habitats or in cultivation. Buds were killed and fixed in chloroform, 95% ethanol and glacial acetic acid (0.6:3:1) for at least 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). Pollen stainability was based on 500+ grain samples stained in aniline blue in lactophenol (Maneval 1936).

RESULTS

Chromosome numbers were determined for 341 individual cacti representing 69 taxa in 11 genera (Table 1). First counts are reported for 14 taxa of 13 species plus two interspecific hybrids. New numbers are determined for two additional species, *Opuntia prolifera* and *Opuntia leptocaulis*.

The hexaploid number (Table 1) is new for *Opuntia prolifera*, previously known from diploid (Yuasa et al. 1973; Pinkava and Parfitt 1982) and triploid individuals (Yuasa et al. 1973). The triploid number for *Opuntia leptocaulis* is new. This species previously was known as diploid (Yuasa 1973; Pinkava et al. 1977, 1985) and tetraploid (Fischer 1962; Pinkava et al. 1973; Yuasa 1973; Conde 1975; Weedin and Powell 1978; and $2n=ca. 44$ by Ward 1984). The Sonoran Desert is now known to have both diploid and triploid individuals. Our diploid count from the Chihuahuan Desert (*Baker 5080 & Daniel*) is the first from that region.

New in our continuing series of studies are 26 taxa of which 16 were cytologically undescribed; the other 10 had been counted previously and all are consistent with our findings: 1) diploid *O. polyacantha* var. *trichophora* (Yuasa et al. 1973; Weedin and Powell 1978; Weedin et al. 1989); 2) *O. rosarica* (Yuasa et al. 1973); 3) hexaploid *O. stricta* var. *dillenii* (Carpio 1952; Yuasa et al. 1973); 4) diploid *O. strigil* (Weedin and Powell 1978; Weedin et al. 1989); 5) *Echinocereus engelmannii* var. *chrysoctrus* (Parfitt 1978); 6) *E. fendleri* var. *fendleri* (Weedin and Powell 1978); 7) *E. nicholii* (Parfitt 1987); 8) *Echinomastus warnockii* (Weedin and Powell 1978); 9) diploid *Coryphantha robertii* (Beard 1937, as *Escobaria runyonii*); and 10) *C. vivipara* var. *vivipara* (Fischer 1971).

Four of the above 10 taxa also have had discordant numbers reported: *O. polyacantha* var. *trichophora* as $2n=ca. 44$ (Weedin and Powell 1980); *O. stricta* var. *dillenii* as $2n=22$ (Spencer 1955) and as $2n=12, 22, 26, 36$, etc. (Sampathkumar and Navaneetham 1980a, b); *O. strigil* as $n=22$ (Weedin et al. 1989); and *Coryphantha vivipara* [var. *vivipara*] as $2n=44$ (Löve and Löve 1982).

TABLE I. 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 material. Percentages in parentheses after collector numbers represent pollen stainability. Collector names abbreviations: RA = R. Anthony; MAB = M. A. Baker; CMC = C. M. Christy; RKG = R. K. Gierisch; LAM = L. A. McGill; BDP = B. D. Parfitt; DJP = D. J. Pinkava; KLR = K. L. Roberts; AS = A. Sanders; NT = N. Trushell; RDW = R. D. Worthington.

OPUNTIOIDEAE

- Opuntia acanthocarpa* Engelm. & J. Bigelow var. *coloradensis* L. Benson
n=11. Arizona. La Paz Co., T1S R18W, 2 km W of Signal Peak, MAB 7729, Maricopa Co., T7S R1E, Vekol Valley, MAB 7726A. Pima Co., SW of Ajo, near Lime Hill. T14N R6W S7 NW¼-S6 SW¼, BDP 3569 & Landrum (counted by Eggers).
- Opuntia acanthocarpa* var. *major* Engelm. & J. Bigelow
n=11. Arizona. Pinal Co., ESE of Florence, ca. 20 mi E of jct US 80-89 and 289, DJP 13811 et al., LAM 2287, 2288.
- Opuntia acanthocarpa* var. *major* × *Opuntia spinosior* (Engelm.) Toumey
*n=11. Arizona. Pinal Co., ESE of Florence, T6S R12E S11, LAM 2451 (92.7%); T6S R12E S30, LAM 2468 (yellow-fl.).
- Opuntia acanthocarpa* var. *thorneri* (Thornber & Bonker) L. Benson
n=11. Arizona. Yavapai Co., ca. 11 mi E from I-17 along Bloody Basin Rd, T10N R4E S28, NT 82-116, 82-122 & MAB.
- Opuntia arenaria* Engelm.
n=11. Texas. El Paso Co., frontage road along E side of I-10, 0.5 mi N of junction with N end of Mesa Drive, BDP 3473 (99.0%), 3475 (97.8%) & KLR.
- Opuntia aurea* E. Baxter
2n=6x=66. Arizona. Mohave Co., Cedar Ridge, T40N R6W S12, RKG 5072-0 (ca. 2n=66); SE of Lost Spring Mt., T41N R7W S35, RKG 5082.
Utah. Kane Co., 12.8 mi N of the jct US 89 & US 89A in Kanab, BDP 3618 & KLR.
- Opuntia basilaris* Engelm. & J. Bigelow var. *brachyclada* (Griffiths) Munz
n=11. California. Los Angeles Co., Trailhead at entrance to South Fork Campground, South Fork of Big Rock Creek, T4N R9W S33 NE¼, BDP 3596 & MAB.
- Opuntia basilaris* var. *heilii* Welsh & Neese
*n=11. Utah. Wayne Co.: ca. 12 mi W of Hanksville, T28S R9E S13 SW¼, Anderson 88-14.
- Opuntia basilaris* var. *treleasei* (J. Coulter) J. Coulter ex Toumey
2n=3x=33. California. Kern Co., NE of Bakersfield, T29S R28E S1, R. Lewis 1, 2, 8.
- Opuntia chaffeyi* Rose
*2n=4x=44. Mexico. Zacatecas, road from Nieves to Concepción del Oro, just N of Comacho on road to Cedros, Glass & Foster 4038, cultivated in Arizona by Parfitt as BDP 3612.
- Opuntia chlorotica* Engelm. & J. Bigelow
n=11. Arizona. Santa Cruz Co., T23S R12E S19, Ruby Rd, 5.5-5.7 mi W of jct AZ 289, BDP 4240, 4250 & CMC.
- Opuntia chlorotica* × *Opuntia santa-rita* (Griffiths & Hare) Rose
*n=11. Arizona. Santa Cruz Co., T23S R12E S19, Ruby Rd, 5.7 mi W of jct AZ 289, BDP 4245, 4251 & CMC (meiosis irregular).

TABLE I. CONTINUED

- Opuntia cholla* F. A. C. Weber
n=11. Mexico. Baja California, Mex Hwy 1, 60 mi SE of Cataviña, DJP 14226, et al.; 14.2 mi N of turn in center of El Rosario, DJP 14212, et al.
- Opuntia echinocarpa* Engelm. & J. Bigelow
n=11. Arizona. Maricopa Co., T1S R6W S10 SW¼, 4 mi N of Centennial Wash, 6 mi NW of Gila R., MAB 7734.
California. San Bernardino Co., W bank of Mojave River, Victorville, T5N R4W S35 SE ¼, MAB 7515 & BDP; 10 km E of Goffs, T11N R17E S35 NE¼, MAB 7507 & BDP. San Diego Co., 5.3 km NW of Imperial Co. line, T15S R8E S34 SW¼, MAB 7531 & BDP.
- Opuntia engelmannii* Salm-Dyck ex Engelm. var. *engelmannii*
n=33. Arizona. Yavapai Co., 112°42'W, 34°23'N, MAB 7547; T12N R5W S1 NE¼, MAB 7548; N of Sunset Rest Area along I-17, T10N R2E S14, BDP 3939.
- Opuntia fulgida* Engelm. var. *fulgida*
n=11. Arizona. Maricopa Co., T6S R3W S16, I-8, ca. 10 mi E of Gila Bend turnoff, MAB 7836, LAM 90-2, -3, -4, -6. Pima Co., Organ Pipe Cactus Nat'l. Mon.: ca. 1.5 km S of Diablo Mts., MAB 7829; Estes Canyon trail head, MAB 7835. Pinal Co., ESE of Florence, T5S R11E S17, MAB 3787 (97.4%), 3788; T5S R12E S34, DJP 13805 et al. (52.7%); T6S R12E S3, LAM 2459, 2460, DJP 13950, 13951 et al.; T6S R12E S11, MAB 3779, 3790, 3791, 3792; T6S R12E S13, MAB 3795 (99.4%), 3796, 3797, 3798, (75.0%), 3799 (85.4%); T6S R13E S29, MAB 3803 (97.4%), 3808; T9S R12E S12, MAB 3829; 42.6 mi E of jct US 80-89 and 289, DJP 13819 et al. (69.5%). Pinal Co., Peralta Canyon: T1N R10E S31, MAB 4593 (97.0%), 4588 (97.6%), 4589 (92.3%), 4590, 4591 (92.4%); T1S R9E S1, 4597 (62.4%), 4598 (84.7%); T1S R9E S11, MAB 4603 (90.4%), 4606 (91.8%); T1S R9E S12, MAB 4599 (45.9%), 4601, 4602 (98.5%); T1S R10E S6, MAB 4595 (95.2%).
2n=3x=33. Arizona. Pinal Co., ESE of Florence, T6S R12E S3, DJP 13807 (40.7%), 13807B, 13807C & LAM; T6S R12E S11, MAB 3704, 3705, 3770, 3772, 3778, 3793, 3794; T6S R12E S12, DJP 13954, 13955 (29.9%) & LAM; T6S R13E S29, MAB 3800, 3801, 3802, 3805, 3807.
- Opuntia fulgida* var. *mammillata* (A. C. V. Schott) J. Coulter
n=11. Arizona. Pinal Co., ESE of Florence: T9S R12E S12, MAB 3827, 3828; T9S R13E S21, MAB 3826. Pinal Co., Peralta Canyon: T1N R10E S31, MAB 4592 (94.1%), 4594 (94.6%); T1S R9E S11, MAB 4605 (80.8%).
- Opuntia imbricata* (Haw.) DC. var. *imbricata*
n=11. Mexico. Nuevo Leon, Huasteca Canyon, MAB 5050 & Daniel. Tamaulipas, Mex Hwy 101, 3 mi NNE of Juamave, MAB 5075 & Daniel.
- Opuntia imbricata* var. *imbricata* × *Opuntia spinosior* (Engelm.) Toumey
***n=11. New Mexico. Doña Ana Co., Organ Mtns., T24S R3E S12 SW¼, RDW 8300-8301-8302 (69.5%) (pop. voucher) (ASU, UTEP) (counted by Fillipi).
- Opuntia* × *kelvinensis* V. Grant & K. Grant (pro sp.)
n=11. Arizona. Pinal Co., ESE of Florence: T6S R12E S34, MAB 4318 (58.1%), DJP 13952 (44.6%) & LAM; T6S R13E S34, MAB 4340; ca. 20 mi E of jct US 80-89 and 289, DJP 13809 (78.7%), 13809A & LAM, LAM 2462 & DJP.
2n=3x=33. Triploid Morphotype A: Arizona. Pinal Co., ESE of Florence: T5S R12E S27, LAM 2454 (20.4%), DJP 13802 (16.1%) et al.; T5S R12E S28, LAM 2443, 2444, 2452, 2453 (20.2%) & DJP, DJP 13800 et al.; T5S R12E S34, DJP 13804 (20.7%) et al.; T6S R12E S3, LAM 2448 (20.0%), 2455 (15.3%), 2456 (21.6%), 2457

TABLE I. CONTINUED

(20.0%); T6S R12E S11, *MAB* 3706 (16.4%), 3771, 3775, 4297, 4324; T6S R13E S19, *MAB* 4329 (20.0%), 4360 (30.1%); T6S R13E S29, *MAB* 3806, 4332 (20.6%), 4334, 4335 (23.2%), 4336 (31.4%); T6S R13E S34, *MAB* 4339; T6S R13E S28, *MAB* 3784 (26.4%); T6S R13E S35 *MAB* 4349, 4350; 1.7 mi NW of Bakerville Site Windmill near Cottonwood Hill, T7S R13E S2, *LAM* 1363 (19.0%).

Triploid Morphotype B: Arizona. Pinal Co., ESE of Florence: T4S R13E S1, *MAB* 4640 & *DJP*; T5S R12E S35, *DJP* 14002 & *LAM*; T6S R12E S3, *MAB* 4296 (17.7%), *DJP* 14003 & *LAM*; T6S R12E S11, *MAB* 4298 (23.2%), 4304, 4305 (18.2%), 4306 (12.8%), 4307 (14.4%), 4313 (28.6%), 4316 (59.1%), 4317 (31.5%), 4319 (33.6%), 4320 (42.2%), 4322 (38.6%), *LAM* 2450 (27.7%); 19.3 mi E of jct US 80-89 and 289, *LAM* 2285 (39.5%), *DJP* 13808 (23.0%) et al.

Opuntia kunzei Rose

* $2n=4x=44$. Arizona. La Paz Co., Hovatter Rd SW of I-10, *BDP* 3839 & *KLR*, (pop. voucher); US 60, 10 mi W of Gladden, T6N R12W S24, *MAB* 7614.

Opuntia leptocaulis DC.

$n=11$. Arizona. Maricopa Co., T1N R6W S28, Paloverde Power Plant, *MAB* 7737. Yavapai Co., Verde Valley, T13N R6E S30, *MAB* 7039 & *NT*; T10N R4E S15, 11 mi E of I-17 on Bloody Basin Rd, *NT* 82-154 & *MAB*; 0.5 km N of Rock Springs, T8N R2E S10, *MAB* 7545, 7546.

Mexico. Tamaulipas, Mex Hwy 101, 14 mi ENE of Jaumave, *MAB* 5080 & *Daniel*.

** $2n=3x=33$. Arizona. Yavapai Co., T6N R2E S10, *MAB* 4549 et al.

$2n=4x=44$. Texas. El Paso Co., Franklin Mts. NW of El Paso, *RDW* s.n. (ASU, UTEP).

Opuntia littoralis (Engelm.) Cockerell

$3n=6x=66$. California. Riverside Co., 5.1 mi W of I-15 at Temecula, *BDP* 3499 (42.9%) et al.; S of Riverside and Lake Mathews, *BDP* 3490 (67.6%) et al.

Opuntia macrocentra Engelm.

$2n=4x=44$. Arizona. Pima Co., T11S R9E S28, ca. 4 mi N of Silverbell, *Wiens* 90-RT-64-04 (counted by S. Gama).

New Mexico. Doña Ana Co., Bishop's Cap, T24S R3E S25, *RDW* 13592 (with up to 7 IV's) (ASU, UTEP).

Opuntia macrorhiza Engelm. var. *macrorhiza*

$2n=4x=44$. Arizona. Apache Co., Navajo Nation, Navajo Forest Rd 7700, E of Navajo Community College, 36°18'N, 109°9'W, *BDP* 3552 (77.1%) & *Reeves*.

Opuntia nicholii L. Benson

$2n=6x=66$. Arizona. Coconino Co., Hwy 89A, 14.9 mi W of road to Lee's Ferry, *BDP* 3634, 3635 & *KLR*.

Opuntia oricola Philbr.

$2n=6x=66$. California. Santa Barbara Co., Montecito, San Ysidro Canyon, 0.1 mi E of San Ysidro Ranch (topotype), *BDP* 3508 (72.1%) & *RA*. San Diego Co., S of Carlsbad, near Agua Hedionda Lagoon, *BDP* 3529 (50.7%) & *KLR*.

Opuntia parishii Orc.

* $n=11$. Arizona. Maricopa Co., Vekol Valley Rd, 6 mi S of I-8, *BDP* 4304, 4306, 4307. Mohave Co., vicinity of Cottonwood Wash, T34N R16W S11, *RKG* 5063A.

Opuntia parryi Engelm. var. *parryi*

$n=11$. California. Riverside Co., S of Riverside and Lake Matthews, *BDP* 3492 et al.

TABLE I. CONTINUED

Mexico. Baja California, 17.5 mi SW of turnoff to Rancho Mike from Mex Hwy 3, *DJP* 14182 et al.

Origin unknown. Cultivated at Rancho Santa Ana Bot. Gard., *MAB* s.n.

Opuntia parryi Engelm. var. *serpentina* (Engelm.) L. Benson

* $n=11$. California. San Diego Co., San Diego City, *Wolf* 9472, cultivated at Rancho Santa Ana Bot. Gard. as *RSA* 3373, *MAB* s.n.; Chula Vista, E Street Marsh, *BDP* 3520 & *KLR*; Telegraph Canyon, ca. 7 km E of ocean, T18S R1W S7 NE ¼, *MAB* 7522 & *BDP*.

Opuntia phaeacantha Engelm.

$2n=6x=66$. Arizona. Santa Cruz Co., T23S R12E S19, Ruby Rd, 5.7 mi W of jct AZ 289, *BDP* 4249 & *CMC*.

California. Riverside Co., CA 371 2.5 mi E of Anza and 1.8 mi W of CA 74, T7S R3E S13, *BDP* 3518 (88.2%) et al. San Bernardino Co., Cactus Flat, N side of San Bernardino Mtns., T3N R2E S30, *AS* 6600 et al.; N side of Baldwin Lake, ca. ¼ mi N of CA 18, road to Baldwin Mine, *AS* 6604, 6605 et al.

New Mexico. Luna Co., ca. 18 mi W of Columbus on Hwy 9, 1.7 mi E of Hermanas and 25 mi E of Hachita, *BDP* 3483 (94.6%) & *KLR*; N end of Florida Mts., T25S R8W SW ¼, *RDW* 11924.

Texas. El Paso Co., Three Sisters Hills, *RDW* 17899 (ASU, UTEP).

Opuntia polyacantha Haw. var. *trichophora* (Engelm. & J. Bigelow) J. Coulter

$n=11$. Texas. El Paso Co., Hueco Mtns., 32°54'45"N, 106°08'15"W, *RDW* 8068.

Opuntia prolifera Engelm.

$2n=3x=33$. California. Orange Co., Laguna Beach, *Stark* 139, cultivated at Rancho Santa Ana Bot. Gard., *MAB* s.n.; San Diego Co., Chula Vista, H Street 1.7 mi E of I-805, *BDP* 3521 & *KLR*; 0.5 km N of Batiquitos Lagoon, T12S R4E S28 SE ¼, *MAB* 7520 & *BDP*; ca. 4 km N of San Miguel Mt., *MAB* 7524 & *BDP*; Telegraph Canyon, ca. 7 km E of ocean, T18S R1W S7, *MAB* 7521 & *BDP*.

Mexico. Baja California, Mex Hwy 1, 19.3 mi S of San Vicente and 2.1 mi N of Colonel, *DJP* 9006 et al.; Mex Hwy 1, 11.7 mi SE of El Rosario, *DJP* 9069 et al.; 12.5 mi E of San Telmo, on fork to Rancho Buena Vista, *LAM* 514 & *Moulis*; 5.5 mi E of El Rosario, then 4.5 mi NE on left fork, *DJP* 8787 (45.8%), 9140, 9149, 9154 et al.; 8.3 mi on road to San Telmo from vicinity of Meling Ranch, *DJP* 14198 et al.

** $2n=6x=66$. Mexico. Baja California, 13 mi E of San Telmo, road to San Pedro Martir, *Gallagher* 82-46.

Opuntia ramosissima Engelm.

$n=11$. Arizona. La Paz Co., T4N R1W S4, US 60, W of Hope, *MAB* 7741, 7743. Maricopa Co., flats NE of Gila Bend Mts., *MAB* 7738. Mohave Co., US 93, ca. 19 mi S of Hoover Dam, *DJP* 14370 et al.

Mexico. Baja California Norte, Mex Hwy 5, 1.3 mi S of jct Mex Hwy 3, *DJP* 14130 et al.

$2n=4x=44$. Arizona. Maricopa Co., ca. 5 km NW of Gila R., T1S R6W, *MAB* 7735, 7736; flats NE of Gila Bend Mts., *MAB* 7732.

Opuntia rosarica G. Lindsay

$n=11$. Mexico. Baja California, 5.5 mi E of El Rosario, then 4.5 mi NE on left fork, *DJP* 12143, 12147 et al.

Opuntia rufida Engelm.

$n=11$. Texas. Hudspeth Co., S end of Quitman Mtns., *RDW* s.n.

TABLE I. CONTINUED

- Opuntia santa-rita* (Griffiths & Hare) Rose
 $n=11$. Arizona. Santa Cruz Co., T23S R12E, Ruby Rd ca. 5 mi W of jct AZ 289, BDP 4241, 4244 & CMC.
 Origin unknown. Cultivated at Payne Hall, Arizona State Univ. campus, DJP 14368, 14369 (crested forms).
- Opuntia spinosior* (Engelm.) Toumey
 $n=11$. Arizona. Gila Co., 1 km N of Young, T9N R14E S20, MAB 7038 & NT. Pinal Co., Oak Flat: T1S R6E S20, MAB 4684 (96.5%), 4685 (82.7%), 4690 (95.2%); T1S R13E S28 SW¼, MAB 4672 (96.8%), 4673 (96.9%), 4688 (89.9%), 4691 (92.1%); T1S R13E S20, MAB 4674 (96.4%), 4680 (97.0%), 4682 (66.6%), 4683 (95.1%), 4687 (96.6%), 4689 (94.2%); T1S R13E S33 NE¼, MAB 4677. Pinal Co., ESE of Florence: T6S R12E S3, MAB 3663, LAM 2446 (98.0%), 2447 (98.5%), 2449 (95.0%), 2461; T6S R12E S11, MAB 3774, 4302, 4309, 4312; T6S R12E S10, LAM 2464; T6S R12E S13, LAM 2466 (yellow-fl.); T6S R12E S12, DJP 13815 (98.5%), 13816 (92.8%) et al. (both yellow-fl.); T6S R13E S19, MAB 4314; T6S R13E S29, MAB 3674, 3676, 4331, 4333; T6S R13E S34, MAB 4337, 4341, 4342, 4343, 4344; T6S R13E S28, MAB 3780 (yellow-fl.), 3781; T6S R13E S35, MAB 4346, 4347, 4352; T7S R13E S12, MAB 4354, 4355, 4356; ca. 20 mi E of jct US 80-89 and 289, LAM 2463 (96.5%), 2465 & DJP (87.9%).
 New Mexico. Luna Co., Florida Mtns., Mahoney Park, T25S R8W S26 SW¼, RDW 8124 (counted by Fillipi).
- Opuntia stricta* (Haw.) Haw. var. *dillenii* (Ker Gawler) L. Benson
 $n=33$. Origin unknown. Cultivated at Desert Botanical Gard. as DBG 80-291-03, Zimmerman s.n.
- Opuntia strigil* Engelm.
 $n=11$. Texas. Terrell Co., 2.5 mi E of Sanderson, RDW 8007 (ASU, UTEP) (counted by Fillipi).
- Opuntia × vaseyi* (J. Coulter) Britton & Rose (pro sp.)
 $2n=6x=66$. California. Riverside Co., NNW of Lake Elsinore in Temescal Wash, BDP 3495 (66.6%) et al.; Pauba Valley, CA 79 crossing of Temecula River, 4.6 mi E of jct with road to Pala, BDP 3502 (67.7%), 3503 (27.9%) et al. San Diego Co., Chula Vista, H Street 1.1 mi E of I-805, BDP 3526 (63.6%) & KLR. Ventura Co., W of Thousand Oaks ¼ mi N of Camarillo Park exit from US 101, BDP 3507 (80.8%) & RA.
- Opuntia whipplei* Engelm. & J. Bigelow
 $n=11$. Arizona. Mohave Co., head of Lime Kiln Canyon, T37N R16W S4, RKG 5064A. Yavapai Co., T10N R3W S24 NE¼, ca. 3 mi SE of Wagoner, MAB 7826.
- Opuntia wolfii* (L. Benson) M. A. Baker
 $*2n=6x=66$. California. Imperial Co., T16S R9E S32 SE¼, 1 km SW of Sugarloaf Mt. (type locality), MAB 7533 (86.1%), 7534 & BDP. San Diego Co., T15S R8E S34, 3-4 km SE of Sweeney Pass, MAB 4917, MAB 7532 & BDP.

CACTOIDEAE

- Carnegiea gigantea* (Engelm.) Britton & Rose
 $n=11$. Arizona. Pima Co., Organ Pipe Cactus Nat'l. Mon., ca. 1.5 km S of Diablo Mts., MAB 7831.
- Coryphantha robbinsorum* (W. Earle) A. Zimmerman
 $*n=11$. Origin unknown. Cultivated at Desert Bot. Gard., Epple s.n. (DES).

TABLE I. CONTINUED

- Coryphantha robertii* A. Berger
 $n=11$. Texas. Val Verde Co., ca. 10 mi NW of Del Rio at Amistad Reservoir, RDW 8260, cultivated by Worthington as RDW 13879 (ASU, UTEP) (pop. voucher) (counted by Fillipi).
- Coryphantha vivipara* (Nutt.) Britton & Rose var. *vivipara*
 $n=11$. Colorado. Pueblo Co., Univ. of Southern Colorado, Pueblo, N of heating plant, BDP 3661 & KLR.
- Echinocereus bonkeriae* Thornber & Bonker
 $n=11$. Arizona. Gila Co., jct US 60 and road to Chrysolite Mine, 110°32'W, 33°43'N, MAB 4659 & BDP. Maricopa Co., vicinity of Sunflower, BDP 3214 (DES), Nash 106 (ASU, DES); T6N R9E S9 NW¼, BDP 3729 & Bricker. Yavapai Co., Forest Service Rd 269, 16-20 mi E of I-17 en route to Bloody Basin, BDP 3604, 3605 (counted by Eggers), 3606, 3607 (counted by Eggers), 3608 (counted by Eggers), 3609, 3611 & KLR.
- Echinocereus engelmannii* (C. Parry ex Engelm.) Lemaire var. *acicularis* L. Benson
 $2n=4x=44$. Arizona. Pima Co., 15.1 mi SSW of AZ 85 on Bates Well Rd, BDP 3562 & Landrum; Organ Pipe Cactus Nat'l. Mon., below base of Alamo Canyon, MAB 7788; Organ Pipe Cactus Nat'l. Mon., headwaters of Aguajita Wash, MAB 7772A, 7792, 7796; ca. 4 mi N of Silver Bell on Ragged Top Peak, Wiens s.n., cultivated at Desert Bot. Gard. as DBG-1989-0195-0101, Zimmerman s.n.
- Echinocereus engelmannii* var. *chrysoctrus* (Engelm. & J. Bigelow) Engelm. ex Ruempler
 $2n=4x=44$. Arizona. Mohave Co., Alamo Rd, 18.4 mi S of jct with Signal Rd (near type locality), BDP 4184, 4185 & CMC. California. San Bernardino Co., N of Ord Mt., ca. 1 mi N of Aztec Spring, T7N R1E S1 SE¼, BDP 3591 & MAB (counted by Eggers).
- Echinocereus engelmannii* var. *engelmannii*
 $*2n=4x=44$. California. San Diego Co., W of Ocotillo, on E side of mts. Mountain Springs exit on south side of I-8, BDP 3599 & MAB.
- Echinocereus engelmannii* var. *howei* L. Benson
 $*2n=4x=44$. California. San Bernardino Co., T10N R19E S31 NE¼ (topotype), MAB 7503, 7504 & BDP.
- Echinocereus engelmannii* var. *variegatus* (Engelm. & J. Bigelow) Engelm. ex Ruempler
 $2n=4x=44$. Arizona. Coconino Co., US 89a below Vermilion Cliffs, 0.8 mi E of Cliff-Dwellers Lodge, BDP 3983, 3984 & KLR. Mohave Co., near Signal, BDP 4179, 4182 & CMC.
- Echinocereus fasciculatus* (Engelm. ex B. D. Jackson) L. Benson var. *boyce-thompsonii* (Orc.) L. Benson
 $2n=4x=44$. Arizona. Yavapai Co.: Forest Rd 269, 20.5 mi E of I-17 en route to Bloody Basin, BDP 3617 & KLR (pop. voucher).
- Echinocereus fasciculatus* var. *fasciculatus*
 $2n=4x=44$. Arizona. Graham Co., T6S R28E S29/30, 1.6 mi E of Sanchez (near type locality), BDP 4212 & CMC. Pima Co., Tucson, near Agua Caliente Regional Park BDP 3918, 3919 & Bricker.
- Echinocereus fendleri* (Engelm.) Ruempler var. *fendleri*
 $n=11$. Arizona. Apache Co., T11N R24E S29, near jct US 60 & AZ 6 toward St.

TABLE I. CONTINUED

- Johns, *Abbot & Abbot s.n.*, cultivated at Desert Bot. Gard. as 1984-0782-01-04, Zimmerman *s.n.*
- Echinocereus fendleri* var. *rectispinus* (Peebles) L. Benson
n=11. Arizona. Santa Cruz Co., T22S R10E S26, ca. 8.5 mi SE of Arivaca, *BDP 4191 & CMC*; T22S R11E S32, 12 mi SE of Arivaca, *BDP 4199 & CMC*.
- Echinocereus ledingii* Peebles
n=11. Arizona. Graham Co., Pinaleno Mtns., 8 mi above jct of Swift Trail & US 666; above Noon Creek, *Valenciano 002, 004, 006*.
- Echinocereus nicholii* (L. Benson) Parfitt
n=11. Arizona. Pima Co., Organ Pipe Cactus Nat'l. Mon., headwaters of Aguajita Wash, *MAB 7793*; Organ Pipe Cactus Nat'l. Mon., below base of Alamo Canyon, *MAB 7789*.
- Echinomastus erectocentrus* (J. Coulter) Britton & Rose var. *erectocentrus*
n=11. Arizona. Pima Co., ca. 16 mi SE of Oracle, T11S R16E S12, *Hodgson 4527* (ASU, DES).
- Echinomastus warnockii* (L. Benson) Glass & Foster
n=11. Texas. Brewster Co., Hwy 170, 6.2 mi E of Lajitas, *RDW 8021*. Hudspeth Co., Indio Mtns., Upper Echo Canyon, 30°47'N, 104°59'40"W, *RDW 13563* (UTEP, ASU).
- Ferocactus cylindraceus* (Engelm.) Orc. var. *lecontei* (Engelm.) H. Brav.-Holl. (*F. acanthodes* var. *lecontei* (Engelm.) G. Lindsay)
n=11. Arizona. Pima Co., SW of Ajo. 9.4 mi SSW of AZ 85 on Bates Well Rd, then 2.4 mi W, then 0.5 mi NNW to Lime Hill, T14N R6W S6/7, *BDP 3568 & Landrum*.
- Lophocereus schottii* (Engelm.) Britton & Rose
n=11. Arizona. Pima Co., Organ Pipe Cactus Nat'l. Mon., T18S R5W S14 NW¼, east hill of Dos Lomitas, *MAB 7831A*.

In this six-part series as a whole, chromosome numbers have been determined for 773 individuals of 165 taxa in 106 species in 21 genera of cacti.

DISCUSSION

In Arizona, hybridization between *Opuntia spinosior* and *O. fulgida* was first cited in the literature by Britton and Rose (1919–1923). In 1936 Peebles described a population of hybrids near Sacaton. Benson (1969) cited two collections from near Tucson. Grant and Grant (1971), after a detailed study of populations near Kelvin, considered *O. fulgida* × *O. spinosior* to be an agamosperous microspecies, naming it *O. kelvinensis*. Baker and Pinkava (1987) studied a large population near Florence cytologically and morphometrically and found *O. kelvinensis* to consist of a few diploid individuals and many triploid plants, largely apomictic. The triploid hybrids were segregated into morphotypes A and B, both more similar to

TABLE I. CONTINUED

- Mammillaria carmenae* Castañeda
n=11. Origin unknown. Obtained from Abbey Garden and cultivated in Arizona State Univ. greenhouse, *BDP s.n.*
- Mammillaria heyderi* Muehlenpf. var. *bullingtoniana* Castetter, Pierce & Schwerin
n=11. Arizona. Cochise Co., along AZ 90, 6 mi S of I-10, *Clark 1494 & BDP*; AZ 90, 8.6 mi N of jct with AZ 90/82, *Clark 1497 & BDP*.
 New Mexico. Luna Co., Red Mountain, ca. 9 mi WSW of Deming, T24S R10W S17, *RDW 12999* (ASU, UTEP) (counted by Fillipi).
- Mammillaria heyderi* var. *macdougalii* (Rose) L. Benson
n=11. Arizona. Pinal Co., Mt. Lemmon Rd, 17.5 mi from AZ 77, *BDP 4175 et al.*
- Pediocactus peeblesianus* (Croizat) L. Benson var. *fickesieniae* L. Benson
n=11. Arizona. Mohave Co., Main Street Valley, T38N R11W S22/23, *RKG 5054*.
- Sclerocactus* cf. *spinosior* (Engelm.) Woodruff & L. Benson
n=11. Arizona. Coconino Co., vicinity of Corral Valley, Paria Plateau, T40N R4E S20, *RKG 5055*.
- Sclerocactus parviflorus* Clover & Jotter var. *intermedius* (Peebles) Woodruff & L. Benson
n=11. Arizona. Mohave Co., Cedar Ridge, T40N R6W S12, *RKG 5045A*; vicinity of Cane Beds, T41N R5W S8, *RKG 5048*.
- Stenocereus thurberi* (Engelm.) F. Buxbaum
n=11. Arizona. Pima Co., Organ Pipe Cactus Nat'l. Mon., ca. 1.5 km S of Diablo Mts., *MAB 7830*.
- Correction.**
Echinocereus dasyacanthus (Engelm.) N. P. Taylor
n=22. Texas. El Paso Co., Franklin Mtns., *RDW 10290* (fig. 22), identified by A. Zimmerman; originally published as *E. pectinatus* (Scheidw.) Engelm. var. *minor* (Engelm.) L. Benson (Pinkava et al., 1985).

O. spinosior than to *O. fulgida*, morphotype A more so than morphotype B. Voucher specimens (Table 1) document these types of hybrids for which Baker and Pinkava herein propose the following:

Opuntia × *kelvinensis* V. Grant & K. Grant (pro sp.) (*O. fulgida* Engelm. × *O. spinosior* [Engelm.] Toumey).—*O. kelvinensis* V. Grant & K. Grant, *Evolution* 25:154–155. 1971.—TYPE: USA, Arizona, Pinal Co., just southeast of Kelvin, 15 Jun 1970, V. Grant 70-29 (holotype, TEX!).

Opuntia echinocarpa Engelm. & Bigelow var. *wolfii* L. Benson from Imperial Co. (type locality) and San Diego Co., California were found to be hexaploid. These differ from all other dry-fruited chollas of southern California (which are all 2x or 4x) in having the following combination of characters: shrubby habit, dense and strict branching pattern, with thick stem segments (2.5–4 cm in diameter), and bronze

flowers bearing bronze- to red-purple filaments. Baker herein proposes the following new combination and lectotypification:

Opuntia wolfii (L. Benson) M. A. Baker, comb. et stat. nov.—*O. echinocarpa* Engelm. & Bigel. var. *wolfei* L. Benson, Cact. Succ. J. 41:33. 1969.—TYPE: USA, California, Imperial Co., base of Mountain Springs Grade, W edge of Colorado Desert, U.S. 80 W of El Centro, 12 Jun 1938, Carl B. Wolf 9429 (lectotype here designated, RSA 20700!; isolectotype, UC 592967! [box] and photo ASU 155254!, US [box]).

In the original protologue, Benson cited two different specimens as "holotype" [syntypes]: the specimen prepared in the field by Wolf (*Wolf 9429*); and a specimen later prepared (12 Apr 1954, *Balls 19004* RSA!, CAS! and photo ASU!, UC) from cultivated material (RSA propagation no. 3201) of Wolf's collection. The original, field-collected specimen is here chosen as lectotype.

Pinkava and Parfitt (1988) recognized as species the following two taxa that were treated (Benson 1969a, 1982) as varieties of *O. stanlyi* Engelm. ex B. D. Jackson (a superfluous name for *O. emoryi* Engelm.): diploid *O. parishii* and tetraploid *O. kunzei* (Table 1). *Opuntia stanlyi* var. *peeblesiana* L. Benson (1969a) was typified by a specimen of *O. kunzei*, and therefore is a synonym of that species. *Opuntia kunzei* consists of relatively robust plants, with very spiny fruits, from La Paz, western Pima and Yuma counties, Arizona. Benson's (1969a, 1982) concept of var. *peeblesiana* also included some specimens of *O. parishii* from Pima and Pinal counties, Arizona (relatively small plants, with spineless fruits). These south-central Arizona populations represent a southeastward disjunction of *O. parishii*; this species also has a southwestward disjunction in the vicinity of Joshua Tree National Monument, California.

Benson (1982) recognized five varieties comprising *Opuntia basilaris*. Two of these are consistently diploid: var. *basilaris* (Parfitt 1978; Pinkava and McLeod 1971; Pinkava et al. 1973, 1977), and var. *brachyclada* (Pinkava et al. 1977; Table 1). The var. *treleasei* is triploid (Pinkava et al. 1977; Table 1) except for one diploid report (Pinkava et al. 1977). *Opuntia basilaris* var. *aurea* (McCabe ex E. Baxter) W. Marshall is hexaploid (Pinkava et al. 1973; Pinkava and Parfitt 1982; Table 1); we treat it as *O. aurea*, specifically distinct from *O. basilaris*. Two recently described varieties remain under study: diploid var. *heilii* (Table 1), which may not be distinct from var. *basilaris*, and octoploid var. *woodburyi* W. Earle (Pinkava and Parfitt 1982), which is not closely related to *O. basilaris*. We consider the cytologically unknown var. *longiareolata* (Clover & Jotter) L. Benson as an aberrant form of var. *basilaris*.

Benson (1982) recognized five varieties of *Opuntia violacea* Engelm.; three of these—var. *macrocentra* (Engelm.) L. Benson, var.

violacea and var. *castetteri* L. Benson—were reduced to synonymy under *O. macrocentra* by Pinkava and Parfitt (1988). They consider the remaining two taxa as distinct diploid species: *O. santarita* and *O. gosseliniana* F. A. C. Weber. *Opuntia macrocentra* has two ploidy levels that apparently are not separable morphologically. From El Paso, TX, to central Arizona all nine chromosome counts are tetraploid (Table 1; Pinkava and McLeod 1971; Pinkava et al. 1973, 1985); from Alpine, TX, to the Rio Grande of Big Bend National Park, all eleven counts are diploid (Pinkava and Parfitt 1982; Pinkava et al. 1985; Weedon et al. 1978, 1989).

In California there are two hexaploid hybrid complexes, *Opuntia occidentalis* (Pinkava et al. 1973) and *O. vaseyi* (Table 1), each involving numerous genetic segregates making identifications exceedingly difficult and somewhat arbitrary. *Opuntia occidentalis* is not a synonym of *O. ficus-indica* (L.) Miller as proposed by Benson and Walkington (1965) but apparently does include most of hybrid population "occidentalis" described by them. Parfitt herein proposes the following two changes:

Opuntia* × *occidentalis Engelm. & J. Bigelow (pro sp.) (*O. littoralis* [Engelm.] Cockerell × [*O. engelmannii* Salm-Dyck ex Engelm. × *phaeacantha* Engelm.]).—*O. occidentalis* Engelm. & J. Bigelow, Proc. Amer. Acad. 3:219. 1856.—TYPE: USA, California, near Los Angeles (Benson [1982] places it near Cucamonga, 43 mi E of Los Angeles, San Bernardino Co.), 19 Mar 1854, J. M. Bigelow (lectotype designated by Benson and Walkington [1965], MO 2015200!; photos, ASU!, DS!, MO!, POM!, US!).

Opuntia* × *vaseyi (J. Coulter) Britton & Rose (pro sp.) (*O. littoralis* × *O. phaeacantha*).—*O. mesacantha* Raf. var. *vaseyi* J. Coulter, Contr. U.S. Natl. Herb. 3:431. 1896.—*O. littoralis* (Engelm.) Cockerell var. *vaseyi*—Benson & Walkington, Ann. Mo. Bot. Gard. 52:268. 1965.—TYPE: USA, Arizona, Yuma Co., Yuma (presumably a labelling error [see Britton and Rose 1919–1923]), 1881, G. R. Vasey s.n. (lectotype designated by Benson and Walkington [1965], US 62105!; photos, ASU!, POM, NY!, US!; isolectotype, PH).

Coulter's syntype (AZ, Ft. Verde, Jun 1883, *H. H. Rusby 624* NY!, photo ASU!) is a different taxon, *O. chlorotica* Engelm. & J. Bigelow.

These two nothospecies may be distinguished from related species by the following key (Parfitt 1991):

KEY TO THE FLESHY-FRUITED PRICKLY-PEARS OF CALIFORNIA

- a. Areoles more than 38 per ovary; base of plant a single erect trunk; branches ascending.

- b. Ovary with well defined tubercles when fresh, areole wool dark brown; stem glochids 0–1 mm long, inconspicuous; mature plants more than 3 m tall (octoploid). *O. ficus-indica*
- b'. Ovary smooth, areole wool tan; stem glochids 2–12 mm long, conspicuous; mature plants less than 2.5 m tall.
- c. Style red or pink when fresh; longest spines 19–25(–28) mm long; seeds 3.5–4 mm in diameter; southwestern California Floristic Province (hexaploid). *O. oricola*
- c'. Style white when fresh; longest spines (24–)32–47 mm long; seeds 3 mm in diameter; southeastern California Floristic Province northward and eastward to desert mountains (diploid). *O. chlorotica*
- a'. Areoles fewer than 36 per ovary; base of plant generally obscured by several spreading to decumbent branches (hexaploids).
- b. Style and filaments white.
- c. Stem segments more than 15 cm wide; perianth all yellow; fruit red-purple throughout. *O. engelmannii*
- c'. Stem segments less than 14 cm wide; perianth yellow with red base; fruit externally red-purple, internally green. *O. phaeacantha*
- b'. Style pink and filaments yellow, or, if either style or filaments white then the other colored.
- c. Stem segments more than 15 cm wide. *O. × occidentalis*
- c'. Stem segments less than 15 cm wide.
- d. Stem segments obovate; major spines usually flat, 1–4 per areole. *O. × vaseyi*
- d'. Stem segments oblong-elliptic or narrowly obovate; major spines usually round, 4–11 per areole. *O. littoralis*

Three of the above names for fleshy-fruited species of *Opuntia* in California (Parfitt 1991) represent substantial changes from the concepts of Benson (1982). For names used in Table 1, these changes are as follows: 1) *O. engelmannii* var. *engelmannii* (*O. phaeacantha* var. *discata* (Griffiths) L. Benson & Walkington, not *O. ficus-indica*); 2) *O. littoralis* (*O. littoralis* var. *littoralis*); and 3) *O. phaeacantha* (*O. littoralis* var. *piercei* (Fosb.) L. Benson, *O. phaeacantha* var. *major* Engelm.); and *O. × vaseyi* (*O. littoralis* var. *austrocalifornica* L. Benson and var. *vaseyi* (J. Coulter) L. Benson).

All five varieties of *Echinocereus engelmannii* reported here are tetraploid, two are first reports (vars. *engelmannii* and *howei*) and all are in agreement with earlier counts for the species (Parfitt 1978; Pinkava et al. 1977, 1985; Pinkava and McLeod 1971; Pinkava and Parfitt 1982; Stockwell 1935). Varieties *armatus*, *munzii*, and *purpureus* remain uncounted; var. *nicholii* is diploid and is considered a distinct species (Parfitt 1987). Specimens of var. *howei* from the type locality (Table 1) have multicolored spines, not all yellow as stated by Benson (1982). However, in spine number and robustness they correspond to Benson's description of the taxon. Varieties *howei* and *armatus* may be only minor variants of var. *chrysoctrus*.

CONCLUSIONS

Repeated counting of chromosomes in some species has revealed taxonomically useful variation in ploidy level, particularly in species

groups already known to include polyploids. Careful comparison between morphology and chromosome number often leads to easier identification of previously unrecognized evolutionary lineages. When taxa of different ploidy levels hybridize, the progeny have intermediate ploidy levels in addition to morphological intermediacy.

Furthermore, our studies of *Opuntia* show that usually in 3x interspecific hybrids pollen stainability is about 20–25%; in 2x, 4x, 5x, and 6x interspecific hybrids, about 60–65%. For nonhybrid taxa, pollen stainability is about 85–95%. Besides hybridity, several factors may affect stainability percentages (e.g., inversions, translocations, and gametophytic lethal alleles); thus, sometimes results are difficult to interpret. In *Opuntia*, the meiotic chromosomes of triploid interspecific hybrids regularly form 11 trivalents per cell, rather than combinations of bivalents and univalents observed for interspecific hybrids in other families. We also caution against using seed set as an indicator of sexual fertility; adventive embryony in *Opuntia* has been reported for several taxa (see e.g., Davis 1966).

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