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# CHROMOSOME NUMBERS IN SOME CACTI OF WESTERN NORTH AMERICA—II

D. J. Pinkava, M. G. McLeod, L. A. McGill, and R. C. Brown

Pinkava, D. J., M. G. McLeod, L. A. McGill, & R. C. Brown (Department of Botany & Microbiology, Arizona State University, Tempe). Chromosome numbers in some cacti of western North America—II. Brittonia 25: 2–9. 1973.—Documented chromosome numbers and meiotic behavior are recorded for an additional 30 taxa representing 25 species of Cactaceae of southwestern United States and northern Mexico. Diploid and polyploid taxa including two triploids were observed, all of which indicate the same base number, x=11. Trisomism and inversions are reported for the first time in cacti.

This investigation is a continued effort (cf. Pinkava & McLeod, 1971) to unravel certain taxonomic problems in cacti, particularly problems relating to origins and hybridization. Sato (1958) noted in his list of chromosome counts for 214 species and six varieties of cacti that only 17.7% of the taxa were polyploid. Polyploidy is most frequent in *Mammillaria*, ranging from 4x to 24x in 12 species (Beard, 1937; Remski, 1954), and in *Opuntia*, ranging from 3x to 12x in about 23 species. Previous to our reports, the only other polyploids known were tetraploids: *Pterocactus kuntzei* Schum. (Covas & Hunziker, 1954), *Cephalocereus chrysacanthus* Britton & Rose, *C. royenii* Britton & Rose, *Trichocereus spachianus* Riccobono, *Notocactus submammulosus* Berger (Katagiri, 1952, 1953), *Mediocactus coccineus* (Salm-Dyck) Britton & Rose (Beard, 1937), *Echinocereus engelmannii* (Parry) Rümpler (Stockwell, 1935), and *Lobivia caespitosa* (Purpus) Britton & Rose (Diers, 1961). The primitive tribe, Pereskieae, is without reports of polyploid taxa.

# MATERIALS AND METHODS

Flower buds were collected from plants growing in their native habitats (except *Opuntia ficus-indica*, known only from cultivation) and from those transplanted to a research garden at Arizona State University and to the Desert Botanical Garden (DBG), Phoenix.

Buds were killed and fixed in ethanol and glacial acetic acid (3:1), transferred to 70% ethanol after 24 hours, and refrigerated. Recently we have obtained far superior fixation using chloroform-ethanol-glacial acetic acid (4:3:1) (Bradley, 1948). Anthers were squashed in aceto-carmine and mounted in Hoyer's medium according to the method of Beeks (1955). Percent pollen stainability is based on 500-grain samples stained in aniline blue in lactophenol. Illustrations are from camera lucida drawings. Voucher specimens, including habit photographs and chromosome figures, are deposited in the herbaria of Arizona State University (ASU) and of the Desert Botanical Garden (DES). Nomenclature follows that of Benson (1969a, b, c) and Shreve & Wiggins (1964).

## RESULTS AND DISCUSSION

Chromosome counts (Table I) were made from 83 plants belonging to 41 taxa of 33 species; those newly counted (30 taxa) since the first report (Pinkava & McLeod, 1971) are illustrated (Figs. 1–31). Of the latter, only five species had been previously counted, and all are consistent with our findings: *Opuntia leptocaulis* (Fischer, 1962),

Brittonia 25: 2-9. January-March, 1973.

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O. oricola (Philbrick, 1963), O. santa-rita (Stockwell, 1935), Ferocactus wislizenii (Katagiri, 1952, 1953), and Coryphantha vivipara (Remski, 1954).

It is anticipated that our studies of cactus morphology, chemistry, and chromosomes will provide clues to relatedness among certain taxa. Of particular interest are interploidal hybrids and aberrant chromosome behavior.

In 1969, near Rosario, Baja California, L. A. McGill located a plant morphologically intermediate between diploid *Cereus cochal (Myrtillocactus cochal)* and tetraploid *C. emoryi (Bergerocactus emoryi)*, conforming to the original description by Moran (1962b) of × *Myrtgerocactus lindsayi* based on a specimen collected south of Rosario by Lindsay in 1959. As expected, chromosome analysis revealed this second known hybrid plant to be a triploid. The plant does not set seed, and pollen grains are nonstainable and of various sizes. In meiosis, 11 trivalents are usually formed, and subsequent anaphase I (Fig. 19) and anaphase II chromosome migration is very irregular. It is surprising to observe synapsed genomes of parental species that are so morphologically dissimilar. Also from near Rosario, another triploid, a cholla of unknown parentage, usually forms 11 trivalents at metaphase I. These hybrids are being investigated further.

Not only does the analysis help explain the sterility of these triploid hybrids, but it gives some insight to the understanding of another Baja California hybrid,  $\times$  Pachgerocereus orcuttii (Brandg.) Moran, a hybrid between Cereus pringlei (Pachycereus pringlei) and again C. emoryi (Bergerocactus emoryi) (Moran, 1962a). The genomes of these two tetraploid parental taxa must be similar since at least partial fertility and recombination are attained in their  $F_1$  progeny.

A remarkable prickly-pear grows in a region near Kingman, Arizona, and from Searchlight to Nipton, Nevada. It is a small, compact tree, about three to five feet in height; has numerous, prominent, reddish brown and yellow spines, some usually spiraling on older pads; and fits the original description and holotype (*Griffiths 10530*, US!) of *Opuntia curvospina* Griffiths (1916). Microsporogenesis of five Arizona specimens was investigated; all were tetraploid, all formed some multivalents, and all produced moderate to high pollen stainability (53.7–77.7%). An anaphase I bridge plus fragment (Fig. 4) was found in each of two plants (*Pinkava, Brown & McLeod 1082, 1088*; Table I), the first records of such an aberration in cacti. *Opuntia curvospina*, a taxon we recognize, has been included in *O. chlorotica* by Britton & Rose (1919–1923), and in the hexaploid *O. phaeacantha* complex by Benson (1969b). It is, perhaps, of hybrid origin from these two taxa.

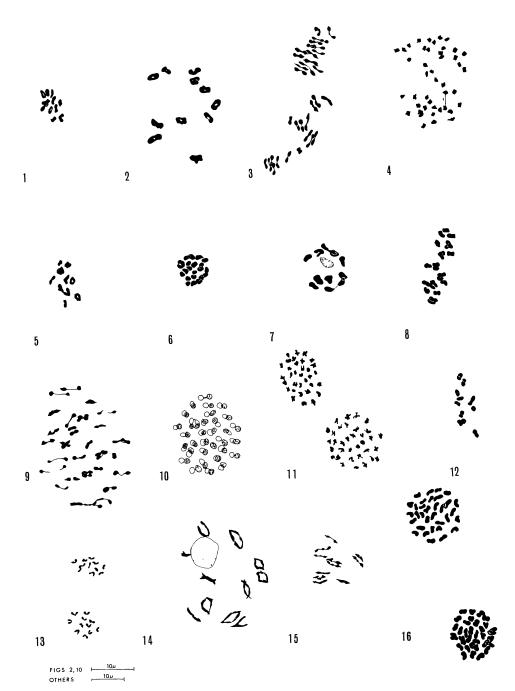
We also found a trisomic plant of the *O. phaeacantha* complex, an intermediate between varieties *discata* and *major*. A 33–34 chromosome separation at anaphase I is illustrated in Fig. 11. The univalent may be observed at metaphase I and often has aberrant migration behavior. A possible origin of trisomism is suggested by an anaphase I nondisjunction found in a somewhat similar plant (*McLeod 492*; Table I).

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FIGS. 1-31. Camera lucida drawings of meiotic chromosomes of cacti. Voucher specimens are cited in Table I. Spacing of chromosome groups adjusted in Figs. 11, 20. Fig. 1. Opuntia acanthocarpa var. coloradensis, metaphase I, n = 11. Fig. 2. O. acanthocarpa var. ganderi, diakinesis, n = 11. Fig. 3. O. aurea, metaphase I, n = 33. Fig. 4. O. curvospina, anaphase I, n = 22, inversion

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bridge plus fragment. Fig. 5. O. echinocarpa, metaphase I, n=11. Fig. 6. O. erinacea var. erinacea, metaphase I, n=22. Fig. 7. O. fulgida var. fulgida, diakinesis, n=11. Fig. 8. O. leptocaulis, metaphase I, n=22. Fig. 9. O. littoralis var. vaseyi, metaphase I, n=33. Fig. 10. O. oricola, metaphase I, n=33. Fig. 11. O. phaeacantha var. discata, telophase I, 2n=3311+11 (trisomic). Fig. 12. O. ramosissima, metaphase I, n=11. Fig. 13. O. spinosior, telophase I, n=11. Fig. 14. O. violacea var. santa-rita, diplotene, n=11. Fig. 15. O. whipplei var. whipplei, metaphase I, n=11. Fig. 16. O. hybrid, telophase I, n=33. Fig. 17. Cereus cochal, metaphase I, n=11.

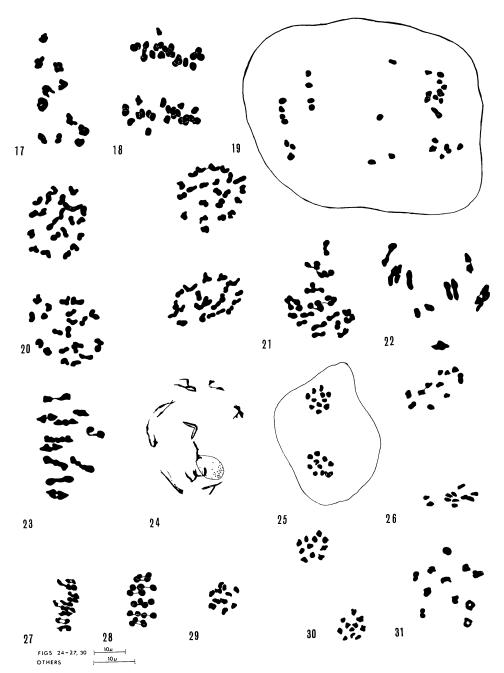


Fig. 18. C. emoryi, telophase I, n=22. Fig. 19. C. cochal  $\times$  C. emoryi, telophase I, 3n=33 (triploid). Fig. 20. C. pringlei, telophase II, n=22. Fig. 21. Echinocereus triglochidiatus var. melanocanthus, metaphase I, n=22. Fig. 22. Ferocactus fordii var. fordii, metaphase I, n=11. Fig. 23. F. gracilis var. gracilis, metaphase I, n=11. Fig. 24. F. viridescens, diplotene, n=11. Fig. 25. F. wislizenii, telophase I, n=11. Fig. 26. Neolloydia johnsonii, telophase I, n=11. Fig. 27. Ancistrocactus uncinatus var. wrightii, metaphase I, n=11. Fig. 28. Pediocactus sileri, metaphase I, n=11. Fig. 29. Coryphantha minima, metaphase I, n=11. Fig. 30. C. strobiliformis, telophase I, n=11. Fig. 31. C. vivipara var. arizonica, diakinesis, n=11.

#### TABLE I

#### CHROMOSOME COUNTS OF CERTAIN CACTI OF WESTERN NORTH AMERICA

#### OPUNTIEAE

Opuntia acanthocarpa Engelmann & Bigelow var. coloradensis Benson

n = 11 Arizona: Maricopa Co.: 8.3 mi W of Vulture Mine Road, along Rte. 60, Pinkava, Brown & McLeod 1065. Fig. 1.

Opuntia acanthocarpa Engelmann & Bigelow var. ganderi (C. B. Wolf) Benson

n = 11 Mexico: Baja California: Rte. 2, 52.3 mi W of jct. main route to Mexicali, L. McGill & Pinkava 8677 (Fig. 2), 8678.

Opuntia acanthocarpa Engelmann & Bigelow var. major (Engelmann & Bigelow) Benson

n = 11 Arizona: Yavapai Co.: 7.9 mi NE of Yavapai County line, along Rte. 71, Pinkava, Brown & McLeod 1070.

Opuntia aurea Baxter

n = 33 Arizona: Mohave Co.: just N of Pipe Spring National Monument, Brown & McLeod 425. Fig. 3.

Opuntia basilaris Engelmann & Bigelow var. basilaris

n = 11 Arizona: Maricopa Co.: 8.3 mi W of Vulture Mine Road, along Rte. 60, Pinkava, Brown & McLeod 1064.

Opuntia curvospina Griffiths

n = 22 Arizona: Mohave Co.: vicinity of Duval Mine, along Rte. 93, McLeod 452; Pinkava, Brown & McLeod 1082 (Fig. 4), 1088, 1089, 1090.

Opuntia echinocarpa Engelmann & Bigelow

n = 11 Arizona: Maricopa Co.: Eagle Eye Boulevard at Aguila, 2.5 mi S of Rte. 60, Pinkava, Brown & McLeod 1067. Fig. 5.

Opuntia erinacea Engelmann & Bigelow var. erinacea

n = 22 Arizona: Mohave Co.: Duval Mine Road, 2.2 mi E of Rte. 93, MacIntyre & McLeod 367. Fig. 6.

Opuntia ficus-indica (Linnaeus) Miller

n=44 Arizona: Maricopa Co.: along 67th Avenue, ¾ mi N of Rte. 60-70-89-93, Glendale, Brown & McGill 459. Elongate-pad form.

California: Orange Co.: Cook's Corner, Trabuco Canyon, Santa Ana Mts., Walkington, G. Smith, Pinkava & McLeod 305. Spiny form called O. "megacantha."

Opuntia fulgida Engelmann var. fulgida

n=11 Arizona: Pima Co.: 6.5 mi E of Continental, along Madera Canyon road, Walkington, G. Smith, Pinkava & McLeod 487. Fig. 7.

Opuntia leptocaulis DeCandolle

n = 22 Mexico: Coahuila: Bolson de Mapimí, Rancho Acatita, S of Laguna del Rey, L. McGill & Keil 8062. Fig. 8.

Opuntia littoralis (Engelmann) Cockerell var. vaseyi (Coulter) Benson & Walkington

n=33 CALIFORNIA: Orange Co.: Black Star Road to Flying B Ranch, Pinkava & McLeod 436 (DLW 385); El Modena along ridge road (possibly intermediate to var. austrocalifornica Benson & Walkington), Pinkava & McLeod 444 (DLW 319) (Fig. 9); El Modena saddle at E end of hill, Pinkava & McLeod 446.

Opuntia macrorhiza Engelmann var. macrorhiza

n = 22 Arizona: Coconino Co.: 8.6 mi W of Jacob Lake, Moore, Pinkava & Lehto 7193A; NW corner, jct. Paradise Road and Cedar Avenue, Flagstaff, R. K. Brown 210.

ARIZONA: Yavapai Co.: Lynx Lake, Pinkava, Brown, McGill & McLeod 1104.

Opuntia oricola Philbrick

n = 33 California: Orange Co.: Fullerton, Euclid Avenue, ½ mi N of Bastanchury, Walkington, G. Smith, Pinkava & McLeod 290 (DLW 62). Fig. 10.

Opuntia phaeacantha Engelmann var. discata (Griffiths) Benson & Walkington

n = 33 Arizona: Maricopa Co.: 0.2 mi N of jct. New River and Cave Creek roads, Ganz 106; unpaved extension of Greenway Road, White Tank Mts. Regional Park, McLeod 368, 492 (all approaching var. major).

### Table I (Continued)

#### OPUNTIEAE

ARIZONA: Mohave Co.: ca. 20 mi N of Wikieup, along Rte. 93, Pinkava, Brown & McLeod 1091.

ARIZONA: Santa Cruz Co.: Patagonia, Ganz 216.

ARIZONA: Yavapai Co.: ¼ mi E of jct. Rte. 93, along Rte. 71, *Pinkava 3948* (approaching var. *major*).

California: San Diego Co.: along Rte. S2 near jct. Rte. 78, *Pinkava 8639* (approaching var. *major*).

2n = 33<sub>II</sub> + 1<sub>I</sub> Arizona: Mohave Co.: ¼ mi N of old Kingman Road, along Rte. 93, *Pinkava*, Brown & McLeod 1073 (approaching var. major). Fig. 11.

## Opuntia phaeacantha Engelmann var. laevis (Coulter) Benson

n = 33 ARIZONA: Pima Co.: 7.2 mi W of jct. Hidden Springs Ranch road on Madera Canyon road, at waterfall, Santa Rita Mts., McPherson & McLeod 1095 (approaching var. discata); 9.2 mi W of jct. Hidden Springs Ranch road, Pinkava, Brown & McLeod 389.

## Opuntia phaeacantha Engelmann var. major Engelmann

n = 33 Arizona: Cochise Co.: 3.8 mi E of Fort Bowie turnoff Rte. 186, *Pinkava, Brown & McLeod 403*.

ARIZONA: Gila Co.: road to Young, just S of jct. Rte. 288 and A+ road, McLeod 1060.

ARIZONA: Mohave Co.: 6.2 mi S of Kingman, Hualapai Mts., McLeod 280, Walkington, G. Smith, Pinkava & McLeod 331.

ARIZONA: Pima Co.: Rte. 83, along Mountain-view Road turnoff, Ganz, E. Smith & Pinkava 2407B; 6 mi S of Rte. I-10, on Rte. 83, L. McGill, Newell & McLeod 176.

Mexico: Baja California: Rte. 2, just E of El Condor, L. McGill, Nash & Pinkava 8990.

#### Opuntia phaeacantha Engelmann var. phaeacantha

n = 33 Arizona: Coconino Co.: 7 mi S of Wupatki National Monument, along road from Sunset Crater, Brown 451.

# Opuntia ramosissima Engelmann

n = 11 Arizona: Mohave Co.: just W of Tooman Road, off Rte. 68, near Kingman, McLeod 455. Fig. 12.

# Opuntia spinosior (Engelmann) Toumey

n=11 Arizona: Graham Co.: ca. 20 mi S of Safford, Rte. 666, Lehto 17463 (Fig. 13);
 2 mi SE of Solomon, McLeod, Brown & Pinkava 8643.

ARIZONA: Pima Co.: 6.5 mi E of Continental, along Madera Canyon road, Mc-Pherson & McLeod 1096.

# Opuntia violacea Engelmann var. santa-rita (Griffiths & Hare) Benson

n = 11 Arizona: Cochise Co.: 1 mi E of Silver Creek Bridge, 16 mi E of Douglas, McPherson & McLeod 1101.

ARIZONA: Santa Cruz Co.: 4 mi SW of Patagonia, Pinkava, Brown & McLeod 396. Fig. 14.

### Opuntia violacea Engelmann var. violacea

n=22 Arizona: Graham Co.: 2 mi SE of Solomon, Pinkava, Brown & McLeod 405, 406.

New Mexico: Socorro Co.: 53 mi N of Truth or Consequences, McLeod 380.

# Opuntia whipplei Engelmann & Bigelow var. whipplei

n = 11 Arizona: Coconino Co.: 7 mi S of Wupatki National Monument, along road from Sunset Crater, Brown 450.

ARIZONA: Mohave Co.: along Rte. 93, 37 mi NW of jct. Rte. 71, McLeod 133. Fig. 15.

Opuntia hybrid (= 0. "occidentalis-demissa" complexes; see Benson, 1969c, pp. 164ff).

n = 33 California: Orange Co.: just SE of Cook's Corner, Trabuco Canyon, Santa Ana Mts., Pinkava & McLeod 304 (DLW 36). Fig. 16.

### TABLE I (Continued)

#### CEREEAE

Cereus cochal Orcutt [= Myrtillocactus cochal (Orcutt) Britton & Rose]

n=11 Mexico: Baja California: 3.5 mi N of Rosario, Rte. 1, L. McGill & Pinkava 8814 (Fig. 17), 8824, L. McGill, Nash & Pinkava 9059; 18.5 mi S of San Vicente, L. McGill & Pinkava 8772; ca. 5 mi E of El Socorro, L. McGill, Nash & Pinkava 9039.

Cereus emoryi Engelmann [= Bergerocactus emoryi (Engelmann) Britton & Rose]

n = 22 Mexico: Baja California: 3.5 mi N of Rosario, Rte. 1, L. McGill & Pinkava 8827 (Fig. 18); 10.7 mi S of Halfway House, Rte. 1, L. McGill, Nash & Pinkava 9196

Cereus cochal Orcutt X C. emoryi Engelmann (= X Myrtgerocactus lindsayi Moran)

3n = 33 Mexico: Baja California: near Rosario, L. McGill & Pinkava 8783. Fig. 19.

Cereus pringlei S. Watson [= Pachycereus pringlei (S. Watson) Britton & Rose]

n = 22 Mexico: Baja California: 5.5 mi E + 5.4 mi NE of Rosario, L. McGill & Pinkava 8793 (Fig. 20); Rte. 1, 20-30 mi S of Rosario, L. McGill, Nash & Pinkava 9073.

Cereus schottii Engelmann var. australis K. Brandegee

n = 11 Mexico: Sonora: 7.7 mi N of Kino Bay highway (from Hermosillo) at jct 1.3 mi E of La Manza, Pinkava, Brown, L. McGill & McLeod 956.

Cereus schottii Engelmann var. schottii

n=11 Mexico: Baja California: 5.5 mi E + 5.4 mi NE of Rosario, L. McGill & Pinkava 8785; Rte. 1, 3.9 mi SE of Progresso + 2.4 mi S on road to Santa Catarina, L. McGill, Nash & Pinkava 9118.

Echinocereus triglochidiatus Engelmann var. melanocanthus (Engelmann) Benson

n = 22 Arizona: Yavapai Co.: ca. ½ mi E from Rte. I-17, along Stoneman Lake turnoff, Brown & McLeod 433. Fig. 21.

Ferocactus fordii (Orcutt) Britton & Rose var. fordii

n = 11 Mexico: Baja California: 3.5 mi N of Rosario, Rte. 1, L. McGill & Pinkava 8823. Fig. 22.

Ferocactus gracilis Gates var. gracilis

m=11 Mexico: Baja California: ca. 15 mi NE of Rosario, L. McGill & Pinkava 8795 (meiosis aberrant) (Fig. 23); Rte. 1, 3.9 mi SE of Progresso + 2.4 mi S on road to Santa Catarina, L. McGill, Nash & Pinkava 9116; 5.5 mi E + 5.4 mi NE of Rosario, L. McGill, Nash & Pinkava 9152.

Ferocactus viridescens (Nuttall) Britton & Rose

n = 11 Mexico: Baja California: 2.8 mi N of San Vicente, Rte. 1, L. McGill & Pinkava 8752. Fig. 24.

Ferocactus wislizenii (Engelmann) Britton & Rose

n=11 Arizona: Pima Co.: NW corner of jct. Rte. I-19 and Pima Mine Road, Pinkava, Lehto, Brown & McLeod 608, 609 (Fig. 25); 3 mi E of Houghton Road exit from Rte. I-19, L. McGill & McLeod 245, 246 (approaching F. acanthodes).

Neolloydia johnsonii (Parry) Benson

n=11 Arizona: Yavapai Co.: rest area, W side Rte. 93, along Joshua Tree Parkway, flowers yellow, *Pinkava*, *Brown*, *L. McGill & McLeod 996*. Fig. 26.

Ancistrocactus uncinatus (Galeotti) Benson var. wrightii (Engelmann) Benson

n = 11 Texas: Culberson Co.: 1 mi N of Kent, Cazier s.n. Fig. 27.

Pediocactus sileri (Engelmann) Benson [= Utahia sileri (Engelmann) Britton & Rose]

n = 11 Arizona: Mohave Co.: 6 mi W of Fredonia toward Pipe Spring National Monument, McLeod & Brown 417. Fig. 28.

Coryphantha minima Baird

n = 11 Texas: Brewster Co.: Rte. 385, 4 mi S of Marathon, R. McGill DBG 61-6887. Fig. 29.

Coryphantha strobiliformis (Poselger) Orcutt

n = 11 Texas: Presidio Co.: 1.4 mi N of Cibola Creek in Shafter, along Rte. 67, L. McGill & Keil 7751. Fig. 30.

Coryphantha vivipara (Nuttall) Britton & Rose var. arizonica (Engelmann) Marshall

n = 11 ARIZONA: Yavapai Co.: ca. 1 mi E from Rte. I-17, along Stoneman Lake turnoff, Pinkava 8641. Fig. 31.

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