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Chromosome numbers in some cacti of western North America—III.¹

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PINKAVA, D. J., L. A. MCGILL, T. REEVES (Dept. Bot. and Microbiol., Arizona State Univ., Tempe, 85281), and M. G. MCLEOD (Dept. of Biol. Sci., California Polytechnic State Univ., San Luis Obispo, 93407). Chromosome numbers in some cacti of western North America—III. Bull. Torr. Bot. Club 104: 105-110, 1977.—Documented meiotic chromosome numbers are reported for 42 taxa in 36 species of 9 Cactaceae genera of southwestern United States and northern Mexico. First counts for 17 taxa belonging to 15 species are reported, including first counts for 3 genera (*Machaerocereus*, *Rathbunia* and *Sclerocactus*). Diploid and polyploid taxa, including one triploid, were observed, all consistent with the base number, $x = 11$.

This report is the third in a series of studies (cf. Pinkava & McLeod, 1971; Pinkava et al. 1973) that attempt to solve certain taxonomic problems in cacti. Polyploidy plays an important evolutionary role in Cactaceae, particularly in the tribe Opuntieae. As reported in our series thus far, 19 of 39 taxa (48.7%) of the Opuntieae and 5 of 38 taxa (13.2%) of the Cactaceae are polyploid. Two taxa are represented by both diploid and polyploid individuals.

Materials and methods. Flower buds were collected in developmental series from plants growing in their native habitats. Buds were killed and fixed in chloroform, ethanol, and glacial acetic acid (6 [or 4] : 3:1 v/v), transferred to 70% ethanol and refrigerated. Anthers were squashed in acetocarmine and mounted in Hoyer's medium according to the method of Beeks (1955). Voucher specimens are deposited in ASU. Nomenclature follows that of Benson (1969a, b, c), Britton and Rose (1919-1923), and Shreve and Wiggins (1964).

Results and discussion. Chromosome counts (Table 1) were made for 54 individuals belonging to 42 taxa of 36 species in 9 genera. Counts for 17 taxa belonging to 15 species are first reports, including first counts for 3 genera (*Machaerocereus*, *Rathbunia*, and *Sclerocactus*).

Newly counted in our series of studies are 25 taxa (including one count different from that previously reported for the species, *Opuntia leptocaulis*) which are illustrated (Figs. 1-26). Of this group, only 7 taxa had been published previously and all are consistent with our findings: *O. fragilis* (Bowden, 1945), *O. kleiniae* var. *tetracantha* (Fischer, 1962), *O. microdasys* (Katagiri, 1952, 1953), *O. polyacantha* (Stockwell, 1935), *O. rufida* (Katagiri, 1952, 1953), *Ferocactus rostris* Britt. & Rose (= *F. acanthodes* var. *acanthodes*) (Stockwell, 1935), and *Mammillaria microcarpa* (Remski, 1954). Individuals of *O. polyacantha* are also reported as diploids ($n = 11$) by Matsuura and Suto (1935) and as hexaploids ($n = \pm 33$) by Stockwell, 1935. *Opuntia leptocaulis* is reported here as $n = 11$ in the Sonoran Desert and as $n = 22$ (Conde, 1975; Fischer, 1962; Pinkava et al., 1973) in the Chihuahuan Desert. Careful study may reveal that more than one taxon is involved, as in the two varieties of *O. kleiniae*: diploid var. *tetracantha* in the Sonoran Desert and tet-

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Table 1. Chromosome counts of certain cacti of western North America.

OPUNTIEAE	
<i>Opuntia basilaris</i> Engelm. & Bigel. var. <i>basilaris</i> n = 11	CALIFORNIA: Kern Co.: 1.5 mi NE of Caliente store, <i>McLeod 1223</i> ; San Bernardino Co.: Ca. 1.5 mi SW of Parker Dam, <i>Reeves 353</i> .
* <i>Opuntia basilaris</i> Engelm. & Bigel. var. <i>brachyclada</i> (Griffiths) Munz n = 11	CALIFORNIA: San Bernardino Co.: 5 mi W of Rte. I-15 along Rte. 138, <i>McLeod 1233, 1234</i> (Fig. 1), <i>1235</i> .
* <i>Opuntia basilaris</i> Engelm. & Bigel. var. <i>treleasei</i> (Coulter) Toumey n = 11 3n = 33	CALIFORNIA: Kern Co.: 1.5 mi NE of Caliente store, <i>McLeod 1224</i> (Fig. 2). CALIFORNIA: Kern Co.: 1.5 mi NE of Caliente store, <i>McLeod 1220</i> (Fig. 3).
* <i>Opuntia broadiana</i> (Coulter) Brandegee n = 11	MEXICO: Coahuila: Rte. 40, 1.6 mi W of Paila, <i>McGill, Reeves, Nash & Pinkava P13469</i> (Fig. 4).
<i>Opuntia chlorotica</i> Engelm. & Bigel. n = 11	ARIZONA: Maricopa Co.: Sierra Estrella Mts. Regional Park, <i>Sundell & Sundell 500</i> .
<i>Opuntia curvospina</i> Griffiths n = 22	NEVADA: Clark Co.: Rte. 68, ca. 16 mi W of Searchlight, <i>Reeves & Pinkava P12037</i> (topotype).
<i>Opuntia echinocarpa</i> Engelm. & Bigel. n = 11	CALIFORNIA: Riverside Co.: dirt road overlooking Whitewater, <i>Reeves & Pinkava P11764</i> .
<i>Opuntia fragilis</i> Nutt. n = 33	ARIZONA: Coconino Co.: Flagstaff, NW corner of Cedar Rd. and Paradise Dr., <i>Brown & Brown RKB380</i> (Fig. 5).
<i>Opuntia kleiniae</i> DC, var. <i>tetracantha</i> (Toumey) Marshall n = 11	MEXICO: Sinaloa: 0.8 mi from Tobora, Rte. 15, <i>Pinkava, et al. P12919</i> (Fig. 6).
† <i>Opuntia leptocaulis</i> DC. n = 11	ARIZONA: Maricopa Co.: Cave Creek, <i>Smith 1647</i> (Fig. 7).
<i>Opuntia macrorhiza</i> Engelm. var. <i>macrorhiza</i> n = 22	ARIZONA: Coconino Co.: Flagstaff, NW corner of Cedar Rd. and Paradise Dr., <i>Brown & Brown RKB381</i> .
<i>Opuntia cf. microdasys</i> (Lehmann) Pfeiffer n = 11	MEXICO: Coahuila: ca. 63 mi S of Monclova, Rte. 57, <i>Pinkava 10533</i> (Fig. 8). Red-glochid form.
* <i>Opuntia nicholii</i> L. Benson n = 33	ARIZONA: Coconino Co.: Lee's Ferry, <i>Nash & Nash 92</i> (Fig. 9); 1 mi N of jctn. Rtes. 89 & 89A, <i>Brown & McLeod M418</i> .
<i>Opuntia oricola</i> Philbrick n = 33	MEXICO: Baja California: Rte. 1, 18.5 mi S of San Vicente, <i>McGill & Pinkava P8778</i> ; ca. 6 mi W of Rosario toward Punta Baja, <i>McGill, Nash, & Pinkava P9161</i> . (Both intermediate to <i>O. phaeacantha</i> complex).
* <i>Opuntia parryi</i> Engelm. var. <i>parryi</i> n = 11	MEXICO: Baja California: just E of E1 Condor, Rte. 2, <i>McGill, Nash & Pinkava P8989</i> (Fig. 10).
<i>Opuntia phaeacantha</i> Engelm. var. <i>discata</i> (Griffiths) Benson & Walkington n = 33	ARIZONA: Yavapai Co.: Prescott, at Thumb Butte, <i>Brown RKB385</i> .
<i>Opuntia phaeacantha</i> Engelm. var. <i>major</i> Engelm. n = 33	ARIZONA: Coconino Co.: Flagstaff, <i>Brown & Brown RKB379</i> . CALIFORNIA: San Luis Obispo Co.: Cuyama Valley, Rte. 166, <i>McLeod 1237</i> .
<i>Opuntia polyacantha</i> Haw. var. <i>polyacantha</i> 2n = 20 _{II} + 1 _{IV}	COLORADO: Fremont Co.: N rim, Royal Gorge, <i>Keil 10700</i> (Fig. 11).
<i>Opuntia rufida</i> Engelm. n = 11	MEXICO: Coahuila: Cuatro Ciénegas basin, Sierra de San Marcos, <i>Pinkava 10395</i> (Fig. 12).
* <i>Opuntia stenopetala</i> Engelm. n = 11	MEXICO: San Luis Potosi: 18 mi ESE of El Huizache, Rte. 80, <i>McGill, Brown, & Pinkava P9673</i> (Fig. 13).
<i>Opuntia violacea</i> Engelm. var. <i>santa-rita</i> (Griffiths & Hare) L. Benson n = 11	ARIZONA: Pima Co.: W base of Baboquivari Peak, <i>Lehto, Brown, Nash, & Pinkava P10658</i> .
* <i>Opuntia versicolor</i> Engelm. n = 11	ARIZONA: Pima Co.: along Tanque Verde Rd., 9.1 mi E of jctn. Catalina Hwy., <i>Lehto, Hensel, & Pinkava P10877</i> (Fig. 14).

Table 1—(Continued)

CACTEAE

- Cereus cochal* Orcutt (= *Myrtillocactus cochal* (Orcutt) Britt. & Rose)
 n = 11 MEXICO: Baja California: Rte. 1, ca. 19.3 mi S of San Vicente, McGill, Nash, & Pinkava P9014.
- Cereus emoryi* Engelm. (= *Bergerocactus emoryi* (Engelm.) Britt. & Rose)
 n = 22 MEXICO: Baja California: Rte. 1, 18 mi S of San Vicente, McGill & Pinkava P8845; Rte. 1, 3.5 mi N of El Rosario, McGill & Pinkava P8776.
- **Cereus pecten-aboriginum* Engelm. (= *Pachycereus pecten-aboriginum* (Engelm.) Britt. & Rose)
 n = 11 MEXICO: Sonora: Rte. 15, 57 mi N of Sonora-Sinaloa line, Pinkava, et al., 12798 (Fig. 15).
- ***Machaerocereus gummosus* (Engelm.) Britt. & Rose
 n = 11 MEXICO: Baja California: turnoff from Rte 1, ca. 30 mi S of Calamu, McGill, Nash, & Pinkava P9037 (Fig. 16).
- ***Rathbunia alamosensis* (Coulter) Britt. & Rose
 n = 11 MEXICO: Sonora: 27.3 mi SE of Guaymas, Rte 15, Reeves & Lehto L18590 (Fig. 17).
- **Echinocactus polycephalus* Engelm. & Bigel.
 n = 11 NEVADA: Nye Co.: Specter Mts., Nevada Test Site, Nash 160 (Fig. 18).
- Echinocereus engelmannii* (Parr.) Lemaire var. *acicularis* L. Benson
 n = 22 ARIZONA: Maricopa Co.: Utery Mt. region NE of Phoenix, Woodhouse s.n.
- **Echinocereus maritimus* (Jones) Schumann
 n = 11 MEXICO: Baja California: Rte. 1, ca. 19 mi S of San Vicente, Moulis & McGill McG501 (Fig. 19).
- **Echinocereus triglochidiatus* Engelm. var. *gonacanthus* (Engelm. & Bigel.) Boissvain
 n = 11 COLORADO: Fremont Co.: N rim, Royal Gorge, Keil 10699 (Fig. 20).
- Echinocereus triglochidiatus* Engelm. var. *melanocanthus* (Engelm.) L. Benson
 n = 22 ARIZONA: Apache Co.: near Black River, Forest Service Rd. 25, Nash 295.
- **Echinocereus viridiflorus* Engelm. in Wisliz. var. *cylindricus* (Engelm.) Engelm. ex Rümpler in Förster
 n = 11 TEXAS: Jeff Davis Co.: ca. 7 mi S of Ft. Davis, Rte 118, Pinkava P10605 (Fig. 21).
- **Echinocereus viridiflorus* Engelm. in Wisliz. var. *viridiflorus*
 n = 11 COLORADO: El Paso Co.: S of Colorado Springs, Rte 115, Keil 10695 (Fig. 22).
- Ferocactus acanthodes* (Lemaire) Britt. & Rose var. *acanthodes*
 n = 11 CALIFORNIA: Riverside Co.: 0.5 mi W of Whitewater, Pinkava & Reeves R392 (Fig. 23).
- Ferocactus acanthodes* (Lemaire) Britt. & Rose var. *lecontei* (Engelm.) Lindsay
 n = 11 ARIZONA: Maricopa Co.: Cave Creek, Smith 1625, 1728.
- Ferocactus gracilis* Gates var. *gracilis*
 n = 11 MEXICO: Baja California: NE edge of Laguna Chapala, Hensel & Reeves R462; Rte. 1, ca. 23 mi S of El Rosario, Pinkava & Reeves R467; Arroyo de El Rosario S of El Rosario, Pinkava & Reeves R426.
- **Ferocactus pringlei* (Coulter) Britt. & Rose
 n = 11 MEXICO: Nuevo Leon: 6.7 mi E of jctn. Rte. 57 at San Roberto, Pinkava P10551 (Fig. 24).
- Ferocactus viridescens* (Nutt. in T. & G.) Britt. & Rose
 n = 11 MEXICO: Baja California: Rte. 23, Punta Banda, Pinkava & Reeves R419.
- ***Sclerocactus whipplei* (Engelm. & Bigel.) Britt. & Rose var. *intermedius* (Peebles) L. Benson
 n = 11 NEW MEXICO: San Juan Co.: Large Canyon, Wynhoff 279 (Fig. 25).
- Coryphantha vivipara* (Nutt.) Britt. & Rose var. *arizonica* (Engelm.) Marshall
 n = 11 ARIZONA: Coconino Co.: Flagstaff, NW corner of Cedar Rd. and Paradise Dr., Brown RKB393.
- Mammillaria microcarpa* Engelm.
 n = 11 ARIZONA: Maricopa Co.: Cave Creek, just S of city limits, Reeves 398, 399 (Fig. 26).

* First report of chromosome count for this taxon.

** First report of chromosome count for this genus.

† Chromosome count different from that previously reported for the species.

raploid var. *kleinii* in the Chihuahuan Desert (Fischer, 1962).

The triploid specimen of *O. basilaris* var. *treleasei* (McLeod 1220, Table 1) differs not at all in its morphology from diploid members of the same population, except for its larger size. Meiotic configura-

tions were usually 11 trivalents at metaphase I. The most likely explanation of its origin is in the union of a reduced gamete (n) and an unreduced gamete ($2n$) of the same taxon yielding an autotriploid. Unfortunately, mature pollen grains were unavailable for stainability or germination

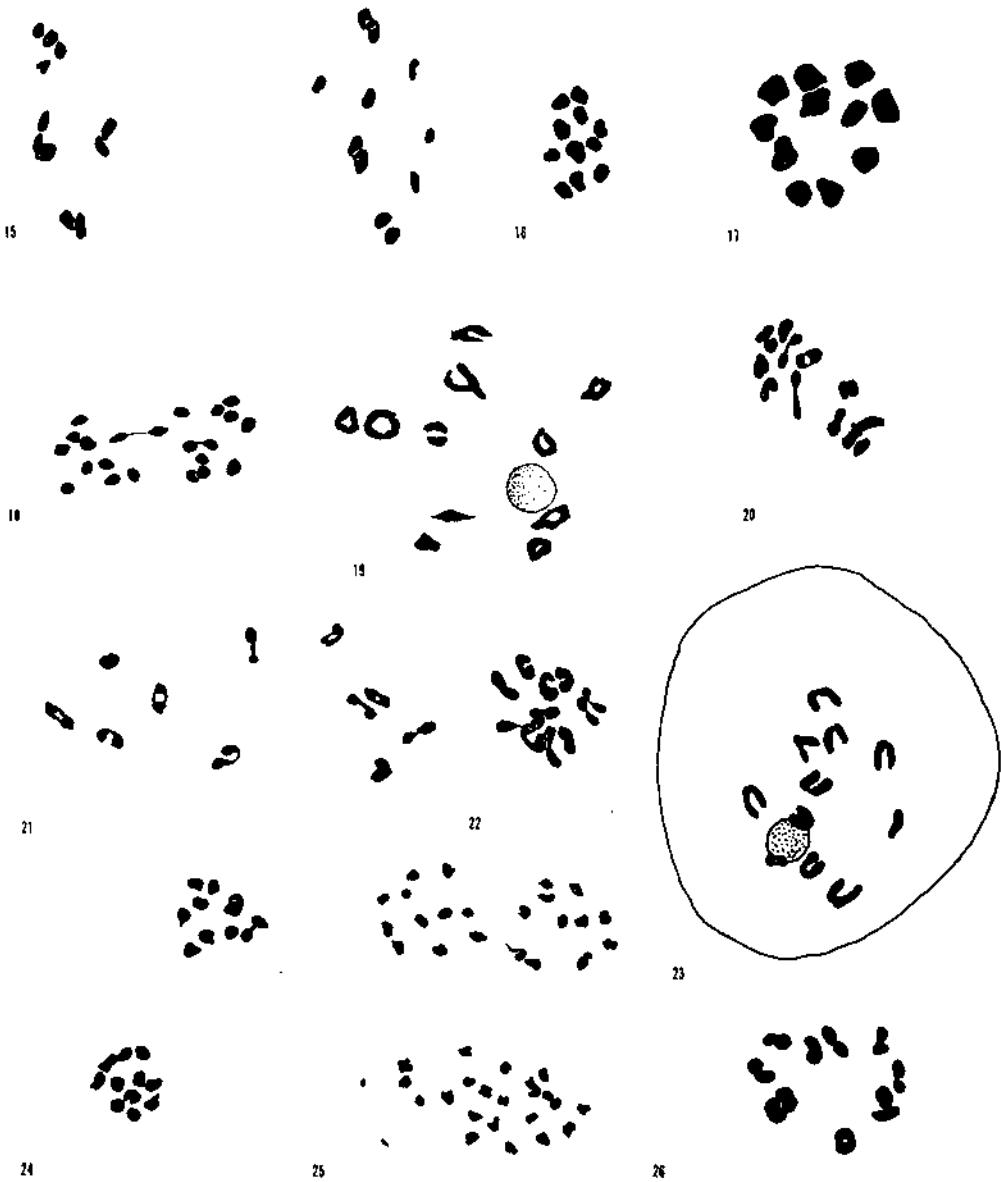
tests. No tetraploid individuals of *O. basilaris* are known.

Cytological observations provide insights as to origins and relationships of

polyploid taxa. Odd-ploid interspecific hybrids have been recorded: *Cereus cochal* ($2n = 22$) \times *C. emoryi* ($4n = 44$) yielding a sterile hybrid ($3n = 33$) (Pinkava *et al.*,



Figs. 1-26. Camera lucida drawings of meiotic chromosomes of cacti. Voucher specimens are cited in Table 1. Spacing of chromosome groups adjusted in Figs. 3, 12, 13. Fig. 1. *Opuntia basilaris* var. *brachyelada*, metaphase I, $n = 11$. Fig. 2. *O. basilaris* var. *treleasei*, metaphase I, $n = 11$. Fig. 3. *O. basilaris* var. *treleasei*, anaphase I, $3n = 33$ (triploid). Fig. 4. *O. bradtiana*, metaphase I, $n =$

13 μm

11. Fig. 5. *O. fragilis*, telophase I, $n = 33$. Fig. 6. *O. kleintiae* var. *tetracantha*, diakinesis, $n = 11$. Fig. 7. *O. leptocaulis*, diakinesis, $n = 11$. Fig. 8. *O. cf. microdasys*, prophase II, $n = 11$. Fig. 9. *O. nicholii*, metaphase I, $n = 33$. Fig. 10. *O. parryi* var. *parryi*, telophase I, $n = 11$. Fig. 11. *O. polyacantha* var. *polyacantha*, metaphase I, $2n = 20_{11} + 1_{17}$. Fig. 12. *O. rufida*, telophase I, $n = 11$. Fig. 13. *O. stenopetala*, telophase II, $n = 11$. Fig. 14. *O. versicolor*, metaphase I, $n = 11$. Fig. 15. *Cereus pecten-aboriginum*, telophase I, $n = 11$. Fig. 16. *Machaerocereus gummosus*, metaphase I, $n = 11$. Fig. 17. *Rathbunia alamosensis*, metaphase I, $n = 11$. Fig. 18. *Echinocactus polycephalus*, anaphase I, $n = 11$. Fig. 19. *Echinocereus maritimus*, diakinesis, $n = 11$. Fig. 20. *E. triglochidiatus* var. *gonacanthus*, metaphase I, $n = 11$. Fig. 21. *E. viridiflorus* var. *cylindricus*, diakinesis, $n = 11$. Fig. 22. *E. viridiflorus* var. *viridiflorus*, metaphase I, $n = 11$. Fig. 23. *Ferocactus acanthodes* var. *acanthodes*, diakinesis, $n = 11$. Fig. 24. *F. pringlei*, telophase I, $n = 11$. Fig. 25. *Sclerocactus whipplei* var. *intermedius*, telophase II, $n = 11$. Fig. 26. *Mammillaria microcarpa*, metaphase I, $n = 11$.

1973); and *Opuntia ficus-indica* ($8n = 88$) \times *O. phaeacantha* var. *major* ($6n = 66$) yielding a hybrid ($7n = 77$) with irregular meiosis (McLeod 1975). An even-ploid interspecific hybrid was postulated for a cross between *O. chlorotica* ($2n = 22$) and *O. phaeacantha* var. *major* ($6n = 66$), yielding apparently *O. curvospina* ($4n = 44$), though more evidence is needed in this case to confirm the putative parents (Pinkava *et al.*, 1973). Additional triploid taxa from Baja California and San Luis Potosí, Mexico, are still under investigation.

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