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CHROMOSOME NUMBERS IN SOME CACTI OF WESTERN NORTH AMERICA

DONALD J. PINKAVA¹ AND MALCOLM G. MCLEOD

Pinkava, D. J. & M. G. McLeod (Department of Botany & Microbiology, Arizona State University, Tempe). Chromosome numbers in some cacti of western North America. *Brittonia* **23**: 171-176, 1971.—Documented chromosome numbers and meiotic behavior were recorded for 23 taxa of 18 species of Cactaceae of southwestern United States and adjacent Mexico. All taxa are diploid ($n = 11$) or polyploid ($n = 22, 33, 44$), and with regular meiotic behavior.

This investigation was undertaken to determine numbers and meiotic behavior of chromosomes of certain cacti, prior to initiating a breeding program (particularly in *Opuntia*) in an attempt to elucidate certain taxonomic problems. Chromosome counts of native cacti of southwestern United States and northwestern Mexico have been reported by Stockwell (1935), Takagi (1938), Katagiri (1952, 1953), Remski (1954), Fischer (1962), and Philbrick (1963). Cultivated *Opuntia ficus-indica* is reported as $n = 11$ from Puerto Rico (Spencer, 1955) and as $n = 44$ from South America (Carpio, 1952).

MATERIALS AND METHODS

Flower buds were collected in developmental series from plants growing in their native habitats (except *O. 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. Anthers were squashed in aceto-carmine and mounted in Hoyer's medium, according to the method of Beeks (1955). Illustrations are from camera lucida drawings. Voucher specimens, including habit photographs and chromosome drawings, are deposited in the Herbaria of Arizona State University (ASU) and of the Desert Botanical Garden (DES). Nomenclature follows that of Benson (1969) and Shreve & Wiggins (1964).

RESULTS AND DISCUSSION

Chromosome counts (Table I) and their corresponding illustrations (Figs. 1-23) were made for 23 taxa, including 12 of *Opuntia*, six of *Cereus*, two each of *Echinocereus* and *Mammillaria*, and one of *Ferocactus*. All taxa are diploid ($n = 11$) or polyploid ($n = 22, 33, 44$), consistent with proposed base number, $x = 11$.

Chromosome counts for ten species consistent with our findings were made by Carpio (1952) for *Opuntia ficus-indica*; by Remski (1954) for *Mammillaria macdougallii* and *M. wrightii*; by Stockwell (1935) for *Opuntia chlorotica*, *O. discata*, *O. phabacantha*, *Carnegiea gigantea*, *Lophocereus schottii*, *Echinocereus engelmannii*, and *Neomammillaria macdougallii*; and by Takagi (1938) for *Opuntia basilaris*. At variance with octoploid counts by Carpio (1952) and us, Spencer (1955) reported $2n = 22$ for *Opuntia ficus-indica*.

Except for minor variations, meiosis appears to be regular in all forty-five plants investigated. Multivalents are sometimes encountered (polyploid *Opuntia* species)

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TABLE I
CHROMOSOME COUNTS OF CERTAIN CACTI OF WESTERN NORTH AMERICA

OPUNTIEAE	
<i>Opuntia acanthocarpa</i> Engelm. & Bigelow var. <i>major</i> (Engelm. & Bigelow) L. Benson	<i>n</i> = 11 ARIZONA: Maricopa Co.: NE section of White Tank Mts. Regional Park, <i>McLeod</i> 142, 19 Apr 1970. <i>Fig. 1.</i>
<i>Opuntia arbuscula</i> Engelm.	<i>n</i> = 33 ARIZONA: Maricopa Co.: NE section of White Tank Mts. Regional Park, <i>McLeod</i> 143, 19 Apr 1970. <i>Fig. 2.</i>
<i>Opuntia basilaris</i> Engelm. & Bigelow var. <i>basilaris</i>	<i>n</i> = 11 ARIZONA: Yavapai Co.: Hwy. 93, 27 mi NW of Wickenburg, <i>W. H. Earle</i> <i>DBG</i> 70-9704, 10 Mar 1970. <i>Fig. 3.</i>
<i>Opuntia bigelovii</i> Engelm.	<i>n</i> = 11 ARIZONA: Maricopa Co.: 0.3 mi N of Morning Star, <i>Dodge s.n.</i> , 20 Apr 1970. <i>Fig. 4.</i>
<i>Opuntia chlorotica</i> Engelm. & Bigelow	<i>n</i> = 11 ARIZONA: Maricopa Co.: NE section of White Tank Mts. Regional Park, <i>McLeod</i> 139, 19 Apr 1970. ARIZONA: Maricopa Co.: ca. 9 mi W of Jct. Vulture Mine Road, along US 60, <i>Pinkava</i> 4937, 4938, 25 Apr 1969. ARIZONA: Mohave Co.: Route 93, 3.25 mi NW of Yavapai County line, <i>Pinkava</i> 6500 (<i>Fig. 5</i>), 6502, 3 May 1969. ARIZONA: Yavapai Co.: 2 mi W of Congress, <i>Ganz</i> 222, 1 Aug 1965.
<i>Opuntia ficus-indica</i> (Linnaeus) Miller	<i>n</i> = 44 ARIZONA: Maricopa Co.: Desert Botanical Gardens, <i>McGill</i> <i>DBG</i> 149, 20 Apr 1970. CALIFORNIA: San Diego Co.: 100 yds W of US Hwy. 395, W side of Quince St. & N of Lincoln Ave., <i>G. Smith</i> <i>DLW</i> 279, May 1969. <i>Fig. 6.</i>
<i>Opuntia macrorhiza</i> Engelm. var. <i>macrorhiza</i>	<i>n</i> = 22 ARIZONA: Maricopa Co.: Christopher Creek, <i>Ganz</i> <i>GT</i> (<i>Fig. 7</i>), 204, 8 Apr 1965.
<i>Opuntia phaeacantha</i> Engelm. var. <i>discolor</i> (Griffiths) L. Benson & Walkington	<i>n</i> = 33 ARIZONA: Maricopa Co.: Humboldt Mt. & Seven Springs roads, <i>Ganz</i> 118, May 1965. ARIZONA: Maricopa Co.: Saguaro Lake, <i>Ganz</i> 152, May 1965. ARIZONA: Pinal Co.: 25 mi S of Casa Grande, <i>Ganz</i> 102, 3 Apr 1965. ARIZONA: Yavapai Co.: 5 mi SW of Jct. Route 93, along Route 71, <i>Pinkava</i> 3942, 3945, 3946 (<i>Fig. 8</i>), 25 Apr 1969. ARIZONA: Yavapai Co.: Route I-17, 9 mi N of Agua Fria River crossing, <i>Pinkava</i> 4951, 2 May 1969.
<i>Opuntia phaeacantha</i> Engelm. var. <i>laevis</i> (Coulter) L. Benson	<i>n</i> = 33 ARIZONA: Pinal Co.: along Route 80-89, 12 mi N of Pima County line, <i>E. Smith</i> , <i>Ganz</i> , & <i>Pinkava</i> 2399, 26 Nov 1965. <i>Fig. 9.</i>
<i>Opuntia phaeacantha</i> Engelm. var. <i>major</i> Engelm.	<i>n</i> = 33 ARIZONA: Mohave Co.: Pipe Springs, <i>Ganz</i> 177, 9 Jun 1965. ARIZONA: Pima Co.: 1.5 mi N of Madera Canyon turnoff, on Patagonia Hwy., <i>Ganz</i> 17, 23 Jun 1965. <i>Fig. 10.</i> ARIZONA: Pinal Co.: 11.65 mi S of Casa Grande, <i>Ganz</i> 101, 3 Apr 1965. ARIZONA: Yavapai Co.: ¼ mi N of Jct. Route 93, along Route 71, <i>McLeod</i> 144, 19 Apr 1970. ARIZONA: Yavapai Co.: 0.1 mi from Beaver Creek bridge near Montezuma Lake, <i>Ganz</i> 202, 21 Apr 1965.
<i>Opuntia phaeacantha</i> Engelm. var. <i>phaeacantha</i>	<i>n</i> = 35 ARIZONA: Apache Co.: 13 mi E of Vernon turnoff, on US 60, <i>Pinkava</i> A-2, 3 Jul 1965. <i>Fig. 11.</i> ARIZONA: Coconino Co.: 4 mi S of road to Glen Canyon Dam-Page, <i>Moore</i> , <i>Pinkava</i> , & <i>Lehto s.n.</i> , 6 Aug 1966. ARIZONA: Navajo Co.: 10 mi N of Heber, <i>Ganz</i> 209, 8 Jun 1965.
<i>Opuntia violacea</i> Engelm. var. <i>violacea</i>	<i>n</i> = 22 ARIZONA: Cochise Co.: 1 mi E of RR tracks in Dragoon, <i>Pinkava</i> 2331, 23 Jul 1965. ARIZONA: Cochise Co.: 10.3 mi S of Bowie, <i>Pinkava</i> 2341, 23 Jul 1965. Approaching var. <i>macrocentra</i> (Engelm.) L. Benson. <i>Fig. 12.</i>

TABLE I (cont'd)

CERECEAE	
<i>Cereus giganteus</i> Engelmann	
<i>n</i> = 11	ARIZONA: Maricopa Co.: NE section of White Tank Mts. Regional Park, <i>McLeod</i> 147, 25 Apr 1970. <i>Fig. 13</i> . ARIZONA: Maricopa Co.: White Tank Mts. Regional Park boundary on road from Canal Service road to Waterfall Canyon Trail, <i>Keil</i> 4604, 5 May 1969.
<i>Cereus greggii</i> Engelmann var. <i>transmontanus</i> Engelmann	
<i>n</i> = 11	ARIZONA: Pinal Co.: Maricopa, <i>Earle & Blakley s.n.</i> , 1952. <i>Fig. 14</i> .
<i>Cereus schottii</i> Engelmann var. <i>australis</i> K. Brandegee	
<i>n</i> = 11	MEXICO: Baja California Sur: La Paz, <i>G. Lindsay DBG</i> 270, Aug 1939. <i>Fig. 15</i> .
<i>Cereus schottii</i> Engelmann var. <i>schottii</i>	
<i>n</i> = 11	MEXICO: Baja California: El Arco, <i>Gates DBG</i> 92, prior to 1939. <i>Fig. 16</i> .
<i>Cereus schottii</i> Engelmann var. <i>schottii</i> forma <i>monstrosus</i> Gates	
<i>n</i> = 11	MEXICO: Baja California: Calmali, <i>G. Lindsay DBG</i> 289B, Aug 1939. <i>Fig. 17</i> .
<i>Cereus thurberi</i> Engelmann	
<i>n</i> = 11	ARIZONA: Pima Co.: Ajo, <i>G. Lindsay DBG</i> A425, 1939. <i>Fig. 18</i> .
<i>Echinocereus engelmannii</i> (Parry) Lemaire var. <i>acicularis</i> L. Benson	
<i>n</i> = 22	ARIZONA: Maricopa Co.: 50 yds E of Scottsdale road on Jomax road, <i>McLeod</i> 126, 17 Mar 1970. <i>Fig. 19</i> .
<i>Echinocereus fendleri</i> Engelmann var. <i>rectispinus</i> (Peebles) L. Benson	
<i>n</i> = 11	MEXICO: Sonora: 2.8 mi E of road from Cananea to Bacoachi, Jct. 6.5 mi N of Bacoachi, <i>McGill & Pinkava</i> 6445, 27 Mar 1970. <i>Fig. 20</i> . MEXICO: Sonora: 1.3 mi SSW of Cabullona, Route 19, <i>McGill & Pinkava</i> 6376, 26 Mar 1970.
<i>Ferocactus acanthodes</i> (Lemaire) Britton & Rose var. <i>vecontei</i> (Engelmann) Lindsay	
<i>n</i> = 11	ARIZONA: Maricopa Co.: NE section of White Tank Mts. Regional Park, <i>Pinkava & McLeod</i> 158, 11 Jul 1970. <i>Fig. 21</i> .
<i>Mammillaria gummiifera</i> Engelmann var. <i>macdougalii</i> (Rose) L. Benson	
<i>n</i> = 11	ARIZONA: Pima Co.: Gardner Canyon, near Onyx Cave, <i>Pinkava, Keil, & Lehto</i> 16619C, 15 Mar 1970. <i>Fig. 22</i> .
<i>Mammillaria wrightii</i> Engelmann	
<i>n</i> = 11	MEXICO: Sonora: near Mababi Ranch, ca. 20 mi NW of Bacoachi, <i>McGill & Pinkava</i> 6653B, 5 Jan 1970. <i>Fig. 23</i> .

and one instance of anaphase I non-disjunction was detected (*O. violacea*). Flowers of *Cereus schottii* forma *monstrosus* are staminate, but with regular microsporogenesis.

Excellent results were obtained from buds collected from 7:50 AM to 11:15 PM. Surprisingly, chromosome material from buds collected and kept under refrigeration for three years was comparable in quality to current collections.

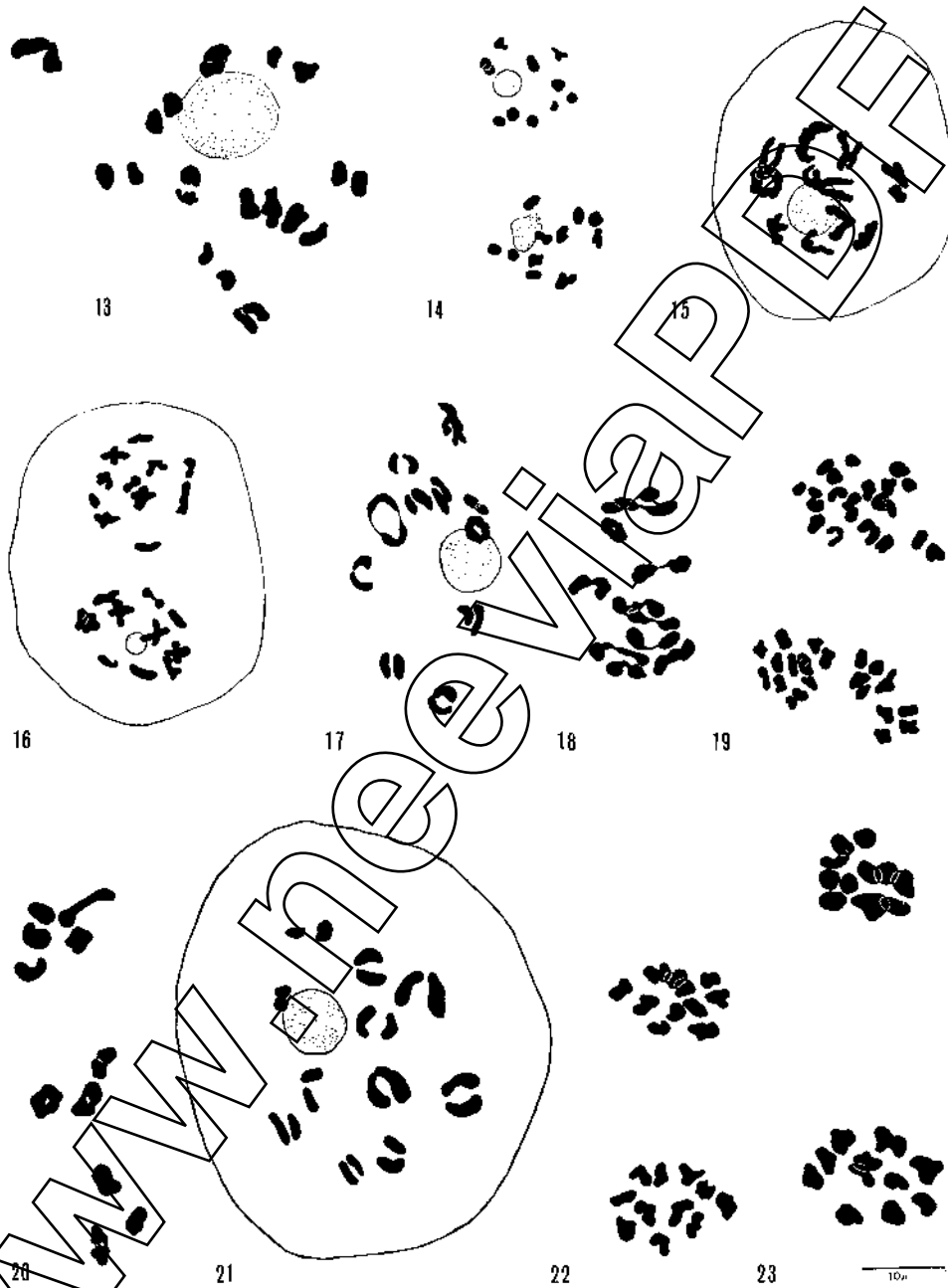
Aneuploid somatic counts have been cited for eleven species as $2n = 24$ by Beard (1937), $2n = 18$ by Stockwell (1935); $2n = 24$ by Sugiura (1931); and $2n = 18, 20, 24$, and 38 by Takagi (1938). All of these species but two—*Echinocactus aprieus* Arechavaleta, $2n = 38$ (Takagi, 1938) and *Neomammillaria* sp., $2n = 24$ (Sugiura, 1931)—have been counted more recently as diploids, $2n = 22$.

Although morphology of chromosomes of the species investigated is quite uniform, chromosome studies should aid in detecting certain interspecific hybrids and in the understanding of their origin. Only three taxa having odd-number chromosome complements (somatic) are on record, all $2n = 33$ and all in *Opuntia*: in *O. oricola* Philbrick, interpreted as a haploid state of a hexaploid parent by Philbrick (1963); in *O. kleiniae* DC. var. *kleiniae*, interpreted by Fischer (1962) as possible hybrids involving *O. leptocaulis*; and in *O. vulgaris* Miller var. (?) as reported by Katagiri (1953), apparently the same plant reported earlier (Katagiri, 1952) as *O. monacantha* Haw. var. *variegata* Cels. The latter two cases require further investigation.



FIGS. 2, 4
OTHERS: 10μ

FIGS. 1-23. Camera lucida drawings of meiotic chromosomes of cacti. Voucher specimens are cited in Table I. Fig. 1. *Opuntia acanthocarpa* var. *major*, diakinesis, $n = 11$. Fig. 2. *O. arbuscula*, diakinesis, $n = 33$. Fig. 3. *O. basilaris* var. *basilaris*, diakinesis, $n = 11$. Fig. 4. *O. bigelovii*, diakinesis, $n = 11$. Fig. 5. *O. chlorotica*, diakinesis, $n = 11$. Fig. 6. *O. ficus-indica*, diakinesis, $n = 44$. Fig. 7. *O. macrorhiza* var. *macrorhiza*, prophase II, $n = 22$. Fig. 8. *O. phaeacantha* var. *discata*, metaphase I, $n = 33$. Fig. 9. *O. phaeacantha* var. *laevis*, diakinesis, $n = 33$. Fig. 10. *O.*



O. phaeacantha var. *major*, anaphase I, $n = 33$. Fig. 11. *O. phaeacantha* var. *phaeacantha*, metaphase II, $n = 33$. Fig. 12. *O. violacea* var. *violacea*, metaphase II, $n = 22$. Fig. 13. *Cereus giganteus*, diakinesis, $n = 11$. Fig. 14. *C. greggii* var. *transmontanus*, prophase II, $n = 11$. Fig. 15. *C. schottii* var. *australis*, diakinesis, $n = 11$. Fig. 16. *C. schottii* var. *schottii*, prophase II, $n = 11$. Fig. 17. *C. schottii* var. *schottii* forma *monstruosus*, diakinesis, $n = 11$. Fig. 18. *C. thurberi*, metaphase I, $n = 11$. Fig. 19. *Echinocereus engelmannii* var. *acicularis*, telophase I, $n = 22$. Fig. 20. *E. fendleri* var. *rectispinus*, diakinesis, $n = 11$. Fig. 21. *Ferocactus acanthodes* var. *lecontei*, diakinesis, $n = 11$. Fig. 22. *Mammillaria gummifera* var. *macdougalii*, telophase I, $n = 11$. Fig. 23. *M. wrightii*, telophase I, $n = 11$.

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