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Chromosome Numbers in some Cacti of Western North America—V

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ABSTRACT. Documented meiotic and mitotic chromosome numbers and behavior are reported for 62 taxa representing 11 genera of Cactaceae from the southwestern United States and northern Mexico. Chromosome numbers for 12 species and six natural interspecific hybrids are first counts. New numbers were determined for four additional species. Chromosome counts of diploid and polyploid taxa, including triploid and pentaploid hybrids, are all consistent with the base number, $x = 11$. Translocations are reported for the first time in the Cactaceae.

The Cactaceae comprise a large and complex assemblage of New World succulent perennials. Much of the complexity, particularly in the Opuntioideae, arises from hybridization and polyploidy. The base number of the Cactaceae is $x = 11$ and probably paleotetraploid (Lewis 1980). Lewis (1980) reports only 14% of the known species of cacti are secondary polyploids. Sato (1958) noted in his list of chromosome counts for 214 species and six varieties of cacti that 17.7% of the taxa were polyploid. In our five-part series on chromosome numbers and behavior in western North American cacti, we have determined that polyploidy occurs in 37 of 68 taxa of Opuntioideae (52.4%) and in 14 of 72 taxa of Cactoideae (19.4%), including hybrids and taxa represented by both diploid and polyploid individuals. No polyploidy is known for the most primitive subfamily, Pereskioideae. This report on chromosome numbers, hybridization, and polyploidy is an attempt to clarify taxonomic and evolutionary relationships among the Cacteceae.

MATERIALS AND METHODS

Flower buds were collected in developmental series from plants growing in native habitats or in cultivation. Buds were killed and fixed for 24 hours in chloroform, 95% ethanol, and glacial acetic acid (6:3:1), transferred to 70% ethanol, and refrigerated. Anthers were squashed in acetocarmine and mounted in Hoyer's medium (Beeks 1955). Percent pollen stainability was based on 500-grain samples stained in aniline blue in lactophenol (Maneval 1936). The mitotic count (*Pereskiopsis porteri*) was obtained from root tips fixed, stained, and mounted according to the method of Parfitt (1979). Nomenclature follows that of Benson (1982), Britton and Rose (1919-1923), Bravo-Hollis (1978), Gibson and Horak (1978), Hunt (1967), and Pilbeam (1981).

RESULTS

Chromosome numbers were determined for 183 individual cacti representing 62 taxa in 11 genera (table 1). First counts are reported for 12 species and six natural, interspecific hybrids; new counts are determined for four additional species.

Not previously reported in our five-part series are counts for 33 taxa (figs. 1-36). At variance with these counts are a hexaploid count for *Opuntia schottii* (Yuasa et al. 1973) and diploid counts for *O. fulgida* var. *fulgida* (Pinkava et al. 1973), *O. ramosissima* (Pinkava et al. 1973), and *O. stanlyi* (Yuasa et al. 1973). In this five-part series as a whole, chromosome numbers have been determined for 438 individuals of 149 taxa in 98 species in 21 genera (sensu Hunt 1967) of cacti.

DISCUSSION

One specimen (*Ruffner 27*) of *Opuntia leptocaulis* was found to possess two translocations (fig. 10) coupled with only 35.4% pollen stainability. This is the first report of translocations in the Cactaceae. *Opuntia leptocaulis* is a widespread and variable taxon, thus far appearing as a tetraploid in the Chihuahuan Desert (Fischer 1962; Conde 1975; Pinkava et al. 1977; Weedin and Powell 1978) and as a diploid in the Sonoran Desert (Pinkava et al. 1977; table 1). It is believed to hybridize with other species, forming triploid hybrids with *O. kleiniae* var. *kleiniae* (Fischer 1962; Pinkava and Parfitt 1982) and forming diploid hybrids with *O. acanthocarpa* (table 1, fig. 2), *O. spinosior* (table 1, fig. 11), and *O. whipplei* var. *whipplei* (Trushell pers. comm.).

The hybrid, *Opuntia acanthocarpa* × *O. leptocaulis*, is intermediate between the putative parents in stem diameter and branching pattern, perianth segment length and color (in ours, yellow vs. yellow-orange or yellow-green), fruit size and color (green vs. tan or red), and seed size. The hybrid resembles *O. acanthocarpa* in having slightly tuberculate and wedge-shaped fruits often bearing 1–3 persistent spines and resembles *O. leptocaulis* in having only 1–4 spines per stem areole and somewhat fleshy fruits that occasionally proliferate. Percentage of pollen stainability is low (table 1).

The hybrid, *Opuntia leptocaulis* × *O. spinosior*, is intermediate between its putative parents in overall size, stem diameter, number of spines (3–4) per stem areole, perianth segment length and color (in ours, faded purple vs. yellow-green or bright purple), and fruit size and color (yellow with red blush at base vs. red or yellow). It resembles *O. spinosior* in having an irregularly whorled branching pattern and moderately tuberculate fruits.

Opuntia spinosior is another cholla that hybridizes with other diploid taxa: *O. acanthocarpa* var. *major* (table 1, fig. 3; Benson 1969, 1982; Pinkava and Parfitt 1982), *O. leptocaulis* (table 1, fig. 11), and *O. versicolor* (table 1, fig. 17; Grant and Grant 1971b).

The hybrid, *Opuntia acanthocarpa* var. *major* × *O. spinosior*, is intermediate between its putative parents in branching patterns, width and length of stem tubercles, amount of uniformity of spine lengths in an areole, and perianth color (brick red vs. yellow-orange or bright purple). The fruits often bear 1–3 persistent spines and are somewhat wedge-shaped with elongate lowermost tubercles (as in *O. acanthocarpa*), but are somewhat fleshy (as in *O. spinosior*).

Grant and Grant (1971b) described the hybrid, *O. spinosior* × *O. versicolor*, and found percentages of morphologically good pollen for four individuals from a population at Houghton Road (east of Tucson) to be 42%, 57%, 91%, and 97%. We found percentages of pollen stainability for seven hybrids from a population about 30 km southeast of Florence (north-northeast of Tucson) ranged from 21.0 to 90.9% ($\bar{x} = 50.7\%$).

Opuntia bigelovii var. *bigelovii*, which reproduces primarily from vegetative propagules (easily detached stem segments), appears to be mostly a triploid (table 1; Pinkava and McLeod 1971; Pinkava and Parfitt 1982). Percentages of pollen stainability are low, ranging from 1.0 to 17.2% ($\bar{x} = 9.1\%$ based on seven triploid individuals) and 0.9 to 46.1% ($\bar{x} = 14.0\%$ on 11 presumed triploid individuals from Maricopa County, Arizona). Surprisingly, two diploid individuals morphologically indistinguishable from triploid individuals were found growing together in Pinal County (table 1, fig. 6), each with higher seed set (germinability unknown) than the nearly sterile triploids but with low percent pollen stainability (12.4% for *Baker 4586A*). Because these diploids may be secondarily derived, further investigation is planned.

Opuntia fulgida var. *fulgida* is now known in apparently indistinguishable diploid and triploid forms (table 1, fig. 8). We hypothesize that these are autotriploids that arose via the union of reduced and unreduced gametes. This is further supported by the role of *O. fulgida* in the origin of *O. kelvinensis.* The common mode of polyploidy is through the formation and sexual functioning of cytologically unreduced gametes (deWet 1980).

Opuntia kelvinensis, as it is now named, has long been considered a hybrid between *O. fulgida* and *O. spinosior* (Peebles 1936; Benson 1940, 1950, 1969, 1982; Grant and Grant 1971a). The predominant form (which includes the type of *O. kelvinensis*), as we interpret it, is a triploid (table 1, fig. 9). *Opuntia spinosior* is a sexual species characterized by normal *Polygonum*-type gametogenesis and embryogenesis (Baker and Pinkava 1983), high percent pollen stainability and seed set, non-proliferating fruits, and rigidly attached stem segments that do not, or but rarely, serve as vegetative propagules. The available evidence strongly suggests that *O. fulgida* provided the unreduced gamete (as it apparently did in forming autotriploid *O. fulgida*) and *O. spinosior* the reduced gamete in the formation of *O. kelvinensis*. Hence the genomic formula becomes SFF for autoallotriploid *O. kelvinensis*, which is morphologically closer to *O. fulgida* than to *O. spinosior* (Pinkava and McGill 1979).

Also discovered were two interspecific pentaploid hybrids (table 1, fig. 4) putatively formed between hexaploid *Opuntia arbuscula* and diploid *O. spinosior* (or its triploid derivative *O. kelvinensis*), with the assumption that the former parent provided the 3*x* gamete (AAA) and the latter provided the 2*x* gamete (unreduced SS or partially reduced 2/3 SFF). The hybrids resemble *O. spinosior* (or *O. kelvinensis*) by the tuberculate fruits but resemble *O. arbuscula* in the 1-4 spines per stem areole, and in fruit size, shape, and color. Percentage of pollen stainability (58.4% for *Baker 4325* and 65.3% for *Baker 4310*) is higher than expected for these hybrids.

Three putative prickly-pear hybrids were found (but not analyzed). One, a tetraploid similar to *O. robusta* (table 1, fig. 15), has very irregular meiosis and a low percentage of pollen stainability (14.5%). The other two hybrids are diploid, probably involving diploid forms of *O. chihuahuensis* and *O. lindheimeri* (see table 1 and figs. 7, 12).

In *Echinocereus*, seven species and eight additional taxa (37.2% of reported taxa) are polyploid, all tetraploid (table 2). Included herein by Hunt (1967) is monotypic, tetraploid *Bergerocactus* Britton & Rose. Our first count of $n = 22$ for *E. fasciculatus* var. *boyce-thompsonii* makes it the third of the three varieties of that species to be recognized as tetraploid. Similarly, our first count of $n = 22$ for *E. pectinatus* var. *minor* makes it the second of five reported varieties to be tetraploid.

Our tetraploid and hexaploid counts for *Mammillaria dioica* confirm both the earlier tetraploid reports by Remski (1954), Lenz in Munz and Keck (1959), and Johnson (1980), and a hexaploid report by Johnson (1980). Diploid individuals are not known.

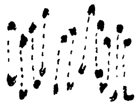
CONCLUSIONS

The significance of polyploidy in the evolution of cacti is reflected in its frequency within taxa as summarized in table 2. In the Cactaceae, 154 of 551 reported taxa (27.9%) are recorded

⟶

FIGS. 1-20. Camera lucida drawings of meiotic and mitotic (fig. 18 only) chromosomes of cacti. Voucher specimens are cited in table 1. Spacing of chromosome groups per cell adjusted in figs. 4, 14, and 20. 1. *Opuntia acanthocarpa* var. *thornberi*, anaphase I, $n = 11$. 2. *O. acanthocarpa* × *O. leptocaulis*, metaphase I, $n = 11$. 3. *O. acanthocarpa* × *O. spinosior*, metaphase I, $n = 11$. 4. *O. arbuscula* × *O. spinosior* or *O. kelvinensis*, metaphase II, $2n = 5x = 55$. 5. *O. arenaria*, prophase II, $n = 11$. 6. *O. bigelovii* var. *bigelovii*, anaphase I, $n = 11$. 7. *O.* aff. *chihuahuensis*, diakinesis, $n = 11$. 8. *O. fulgida* var. *fulgida*, anaphase I, $2n = 3x = 33$. 9. *O. kelvinensis*, anaphase I, $3n = 33$. 10. *O. leptocaulis* (translocations, solid arrows), metaphase I, $2n = 3x = 33$. 11. *O. leptocaulis* × *O. spinosior*, diakinesis, $n = 11$. 12. *O.* aff. *lindheimeri*, prophase II, $n = 11$. 13. *O. littoralis* var. *littoralis*, metaphase I, $n = 33$. 14. *O. ramossissima*, anaphase I, $n = 22$. 15. *O.* aff. *robusta*, telophase I, $n = 22$. 16. *O. schottii* var. *schottii*, metaphase I, $n = 11$. 17. *O. spinosior* × *O. versicolor*, metaphase I, $n = 11$. 18. *O. stanlyi* var. *stanlyi*, metaphase I, $n = 22$. 19. *Pereskiopsis porteri*, mitosis metaphase, $2n = 110$. 20. *Lophocereus schottii* var. *tenuis*, diakinesis, $n = 11$.

FIGS. 21-35. Camera lucida drawings of meiotic chromosomes of cacti. Voucher specimens are cited in table 1. Spacing of chromosome groups adjusted in figs. 29 and 34. 21. *Echinocereus fasciculatus* var. *boyce-thompsonii*, telophase I, $n = 22$. 22. *E. pectinatus* var. *minor*, anaphase I, $n = 22$. 23. *E. triglochidiatus* var. *gurneyi*, metaphase I, $n = 22$. 24. *Neolloydia erectrocentra* var. *erectrocentra*, diakinesis, $n = 11$. 25. *N. intertexta* var. *dasyacantha*, diakinesis, $n = 11$. 26. *Coryphantha durangensis* var. nov., *ined.*, diakinesis, $n = 11$. 27. *C. organensis*, metaphase II, $n = 11$. 28. *C. sneedii* var. *sneedii*, metaphase I, $n = 11$. 29. *C. strobiliformis* var. *orcuttii*, telophase I, $n = 11$. 30. *Mammillaria armillata*, diakinesis, $n = 11$. 31. *M. dioica*, telophase I, $n = 22$. 32. *M. dioica*, metaphase I, $n = 33$. 33. *M. phitauiana*, metaphase I, $n = 11$. 34. *M. thornberi*, diakinesis, $n = 11$. 35. *M. viridiflora*, diakinesis, $n = 11$. 36. *M. yaquensis*, metaphase I, $n = 11$.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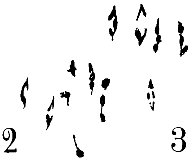
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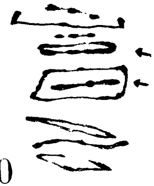
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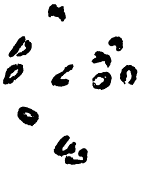
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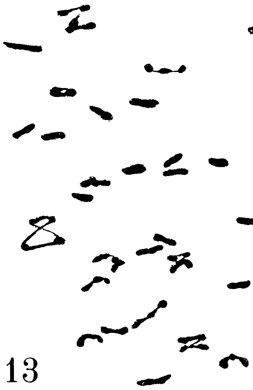
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14


15


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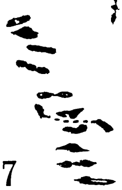
FIGS. 7, 12, 15 10u
OTHERS: 10u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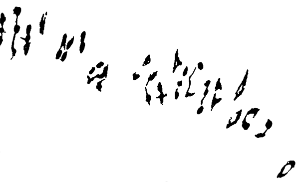
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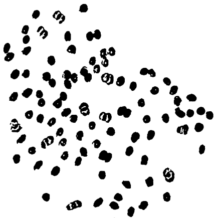
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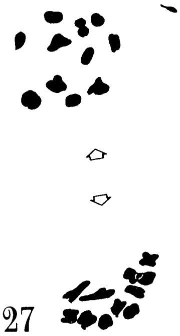
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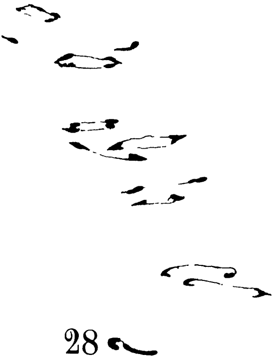
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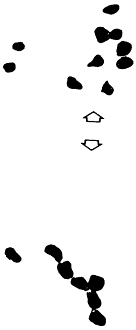
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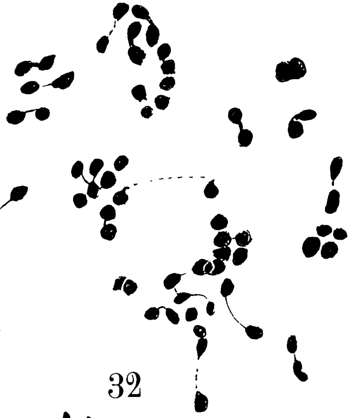
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36

FIG. 26: 10u

OTHERS: 10u

TABLE 1. Chromosome numbers determined for certain cacti of western North America. Voucher specimens are on deposit at ASU unless otherwise noted. * = first chromosome count for taxon; ** = new number for taxon; *** = count from mitotic material. Numbers in parentheses after collector numbers represent percent pollen stainability.

OPUNTIOIDEAE

Opuntia acanthocarpa Engelmann & Bigelow var. *coloradensis* Benson

n = 11 Arizona, Pima Co., Cabeza Prieta Game Refuge, 12.3 km E of Papago Well, *Daniel 2647.*

Opuntia acanthocarpa var. *ganderi* (C. B. Wolf) Benson

n = 11 Mexico, Baja California Norte, 19 km SW of Hwy 3, road to Rancho Mike, San Pedro Martir, *Baker et al. 3699.*

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

n = 11 Arizona, Maricopa Co., South Mtn. Park, ca. 13 km SW of Tempe, *Ruffner 2 & Baker*, Pinal Co., T1S R9E S11, 6 km N of US 60-89 on Peralta Rd., *Baker 4260, 4261;* Pinal Parkway SE of Florence, T6S R10E S32 SW¼, *Baker 4253, 4254,* 30 km SE, *Baker 4227, 4229, 4241;* ESE of Florence, T5S R11E S16, *Baker 4213,* S17, *Baker 4216, 4250, 4251, 4252,* S22, *Baker 4211;* T5S R12E S28 NE¼, *Baker 4263, 4264, 4308;* T6S R10E S32 SW¼ *Baker 4203, 4204;* TS R12E S11 C, *Baker 4267, 4268,* S3 NW¼, *Baker 4265;* 27.3 km SE, Pinkava et al. 14001.

Opuntia acanthocarpa var. *thornberi* (Thornber & Bonker) Benson

***n = 11** Arizona, Pinal Co., Oak Flat, T1S R13E S33 NE¼, *Baker 4679* (93.0) (fig. 1).

Opuntia acanthocarpa var. *major* × *O. leptocaulis* DeCandolle

***n = 11** Arizona, Pinal Co., 1 km SW of Dacite Cliffs, T1N R10E S31, *Baker 4584* (63.1): T1N R9E S31 SE¼, *Baker 4616* (43.3) (fig. 2).

Opuntia acanthocarpa var. *major* × *O. spinosior* (Engelmann) Toumey

***n = 11** Arizona, Pinal Co., SE of Florence, T6S R12E S11 C, *Baker 4300* (79.3), *4301* (91.7), S11 E, *Baker 4269* (72.1); 32.2 km ESE of Florence, *Pinkava 13810* (fig. 3), *McGill & Pinkava;* the following intermediate to *O. spinosior*: T7S R16E S4 SE¼, *Baker 4537* (96.5), *4538* (96.4) *& Trushell;* 1 km N of jct. Aravaipa Creek and San Pedro River, T7S R16E S4 SE¼, *Baker 4647* (81.6).

Opuntia arbuscula Engelmann

n = 33 Arizona, Maricopa Co., T5S R5W S31 NE¼, *Baker 4579;* Pima Co., Saguaro Nat'l. Mon. East, T14S R16E S20 NW¼, *Jenkins 2690;* Pinal Co., 38.1 km ESE of Florence, *Pinkava et al. 14011;* 40 km SE of Florence, T6S R13E S19 NW¼, *Baker 4315, 4330.*

Opuntia arbuscula × *O. spinosior* (Engelmann) Toumey or *O. kelvinensis* V. & K. Grant

n = 5*x Arizona, Pinal Co., SE of Florence,
= 55 T6S R13E S19, *Baker 4310* (65.3) (fig. 4), *4325* (58.4).

Opuntia arenaria Engelmann

n = 11 Texas, El Paso Co., I-10, 4.4 km N of jct. with N. Mesa Rd., dunes, *Worthington 8060* (fig. 5) (UTEP).

Opuntia bigelovii Engelmann var. *bigelovii*

****n = 11** Arizona, Pinal Co.: Peralta Canyon, Superstition Mtns., T1N R10E S29, *Baker 4586, 4586A* (12.4) (fig. 6).

2n = 3*x* Arizona, Maricopa Co., Red Mtn.
= 33 Ranch, ca. 26 km NE of Tempe, *Parfitt 3009* (2.0), *3016* (12.3); T6N R2E S36 SE¼, *Baker et al. 4548* (5.0); T5N R4E S3 SW¼, *Baker 4525, 4527, 4531, 4533* (1.0), *4535,* T6N R4N S13, *Butterwick 8487;* Pinal Co., T1N R8E S36 SE¼, *Baker 4614* (17.2); T1N R9E S31 SE¼, *Baker 4615* (9.0); T1N R8E S11, *Baker 4540 & Pinkava.*

Opuntia aff. *chihuahuensis* Rose

***n = 11** Mexico, Chihuahua, Santa Cruz Microonadas Sta., Rte 45 S of Chihuahua City, *Pinkava et al. 13378* (fig. 7).

Opuntia echinocarpa Engelmann & Bigelow var. *echinocarpa*

n = 11 Nevada, Clark Co., 20 km W of Hwy 95, 15 km E of Charleston Peak, T19S R58E S29 *Baker 4398 & Trushell;* 10 km SE of Blue Diamond Hill, T19S R60E S21 NW¼, *Trushell 83-33 & Baker.*

Opuntia erinacea Engelmann & Bigelow var. *erinacea*

n = 22 Arizona, Navajo Co., ca. 16 km N of Snowflake, T15N R22E S32 NW¼, *Parfitt 3104, 3105 & Baker.*

TABLE 1. Continued.

Opuntia fulgida Engelmann var. *fugida*	
$n = 11$	Arizona, Gila Co., Hwy 77, 24.1 km S of Globe, T3S R15E, *Baker 3810* (78.2), *3811* (92.4), *3812*, *3813*; Pima Co., 7.1 km SE of Green Valley, T18S R14E, *Baker 3819*, *3820*, *3821* (39.2); Pinal Co., S of Dacite Cliffs, T1N R9E S12 NE¼, *Baker 4694*; T1S R9E S15 NW¼, Peralta Canyon Rd., *Baker 465* (67.7) *& Parfitt*.
**$2n = 3x$ $= 33$	Arizona, Pinal Co., 2 km ENE of Black Butte, T5S R7E S34 NW¼, *Baker 4654* (fig. 8); 12.9 km N of Oracle, T9S R13E S21, *Baker 3825* (both straw-colored spine forms).
Opuntia fulgida Engelmann var. *mammillata* (Schott) Coulter	
$n = 11$	Arizona, Gila Co., Hwy 77, 16.1 km N of Mammoth, T7S R16E, *Baker 3815*, *3818*.
Opuntia imbricata (Haworth) DeCandolle var. *imbricata*	
$n = 11$	Texas, Hudspeth Co., Hueco Mtns., 2.3 km ESE of Hueco Inn, US 62-180, *Worthington 8185*.
Opuntia kelvinensis V. & K. Grant (= *O. fulgida* Engelmann × *O. spinosior* (Engelmann) Toumey	
*$3n = 33$	Arizona, Pinal Co., 2 km E of Gila River, S of Cane Springs Canyon, T4S R14E S8, *Baker 4641* (15.0), *4642* (25.4), *4643* (38.7) (fig. 9) *& Pinkava* (type locality).
Opuntia kleiniae DeCandolle var. *tetracantha* (Toumey) Marshall	
$n = 11$	Arizona, Pima Co., Saguaro Nat'l. Mon. East, *Jenkins 1988* (ARIZ), *1989* (ARIZ), *2695*.
Opuntia leptocaulis DeCandolle	
$n = 11$	Arizona, Maricopa Co., Red Mtn. Ranch, ca. 26 km NE of Tempe, *Ruffner 27* (36.4; with translocations) (fig. 10), *28*; Pinal Co., SE of Florence, T6S R12E S11, *Baker 4321*, S19, *Baker 4328* (95.7); T6S R13E S34, *Baker 4338* (94.2).
Opuntia leptocaulis × *O. spinosior* (Engelmann) Toumey	
*$n = 11$	Arizona, Pinal Co., SE of Florence, T6S R13E S28 SE¼, *Baker 4311* (70.3) (fig. 11).
Opuntia aff. *lindheimeri* Engelmann	
*$n = 11$	Mexico, Chihuahua, Santa Cruz Microondas Sta., Rte 45 S of Chihuahua City, *Pinkava et al.* (21.1) (fig. 12).
Opuntia littoralis (Engelmann) Cockerell var. *littoralis*	
$n = 33$	Mexico, Baja California Norte, 8 km N of Colonet, Hwy 1, *Gallagher 82-30* (fig. 13).
Opuntia phaeacantha Engelmann var. *discata* (Griffiths) Benson & Walkington	
$n = 33$	Arizona, Pinal Co., Peralta Canyon Rd., Superstition Mtns., *Baker 4228 & Pinkava*; Yavapai Co.: road to Bloody Basin, 2 km W of Bishop Creek, *Baker 4285*, *Trushell & McGill*.
Opuntia phaeacantha var. *major* Engelmann	
$n = 33$	New Mexico, Dona Ana Co., Organ Mtns., mouth of Soledad Canyon, *Worthington 8096* (UTEP); Texas, Brewster Co., 1.6 km S of Terlingua, limestone hills, *Worthington 9694* (UTEP); El Paso Co., 0.5 air km from top of S. Franklin Mtn., *Worthington 10563* (UTEP). R17E S20 NW¼, *Jenkins 1905*; Pinal Co., Oak Flat, T1S R13E S28 SW¼, *Baker 4670* (96.8), *& Pinkava*; T7S R16E S4 SE¼, *Baker 4646* (97.7) *& Pinkava*; ca. 30 km SE of Florence, *Baker 4270* (94.1), *4271* (90.3), *4272* (97.7), *4273* (91.8), *4274*, *4275* (91.7), *4277* (92.8).
Opuntia phaeacentha Engelmann var. *phaeacantha*	
$n = 33$	Arizona, Coconino Co., Ranger Pass, T37N R1W S30, *Baker 4371*, *4379 & Trushell*; New Mexico, Dona Ana Co., 2.6 road km W of Rio Grande Bridge (Las Cruces), I-10, *Worthington 9993*.
Opuntia ramosissima Engelmann	
$n = 11$	Arizona, Maricopa Co., N of Agua Caliente Mtns., T4S R10W S32 SE¼, *Baker 4566*.
$n = 22$	Arizona, Maricopa Co., 3.9 km NW of I-8 on road to Sentinel, T6S R4W S30, *Baker 4557*, *4559* (fig. 14).
Opuntia aff. *robusta* (Wendlund) Pfeiffer	
*$n = 22$	Mexico, Sonora, 11 km SW of La Mesa de Compañero, road to Yecora, *Lehto 18675* 914.5) (fig. 15) *& Reeves* (meiosis irregular).
Opuntia schottii Engelmann var. *schottii*	
$n = 11$	Texas, Brewster Co., Lajitas, arroyo bottoms, *Worthington 9714* (fig. 16).
$n = 22$	Texas, El Paso Co., NW El Paso, andesite hills, *Worthington 6910.5* (cultivated; some intermediacy to var. *grahamii* (Engelmann) L. Benson.

TABLE 1. Continued.

Opuntia spinosior (Engelmann) Toumey	
$n = 11$	Arizona, Maricopa Co., T1S R7E S5 NE¼, *Baker 4649* (some intermediacy to *O. fulgida*), *4648* (89.7) *& Pinkava;* Pima Co., Saguaro Nat'l. Mon. East, T14S R17E S20 NW¼, *Jenkins 1905;* Pinal Co., Oak Flat, T1S R13E S28 SW¼, *Baker 4670* (96.8), *& Parfitt;* T7S R16E S4 SE¼, *Baker 4646* (97.7) *& Pinkava;* ca. 30 km SE of Florence, *Baker 4270* (94.1), *4271* (90.3), *4272* (97.7), *4273* (91.8), *4274*, *4275* (91.7), *4277* (92.8).
Opuntia spinosior introgressed by *O. imbricata* (Haworth) DeCandolle	
$n = 11$	Arizona, Gila Co., Rte 77, 3 km S of jct. Rte 30, T1S R16E S17, *Trushell 82-132* (79.7), *82-133* (94.7), *82-134* (69.6) *& Baker*, 7 km S, T1S R16E S29, *Trushell 82-138* (77.2), *82-139* (2.6), *82-140* (16.1) *& Baker;* Pinal Co., Oak Flat, T1S R13E S28 SW¼, *Baker 4686* (93.7) *& Parfitt.*
Opuntia spinosior × *O. versicolor* Engelmann	
*$n = 11$	Arizona, Pinal Co., ca. 30 km SE of Florence, *Baker 4221*, *4255* (30.3), *4256*, *4257* (57.7), *4258* (74.6), *4276* (21.0) (fig. 17), *4278* (24.9), *4279* (90.9), *4280* (55.7); (varying degrees of intermediacy).
Opuntia stanlyi Engelmann var. *stanlyi*	
$n = 22$	Arizona, Pinal Co., Aravaipa Rd., T7S R16E S2 NE¼, *Baker 4645* (fig. 18) *& Pinkava.*
Opuntia violacea Engelmann var. *macrocentra* (Engelmann) Benson	
$n = 11$	Texas, Presidio Co., 2.9 km NW of Lajitas, Hwy 170, *Worthington 8015* (UTEP).
Opuntia violacea var. *violacea*	
$n = 22$	New Mexico, Dona Ana Co., Organ Mtns., mouth of Soledad Canyon, *Worthington 8097* (UTEP); Hidalgo Co., Pyramid Mtns., 4.8 km S of Lordsburg, *Worthington 10201* (UTEP); Luna Co., Florida Mtns., T25S R8W S27 SE¼, *Worthington 19364* (atypical) (UTEP); Texas, El Paso Co.: Franklin Mtns., 31°52′04″N, 106°30′24″W, *Worthington 8093* (UTEP).
Pereskiopsis porteri (Brandegee) Britton & Rose	
***$2n = 110$	Mexico, Sonora, 66.6 km S of Navajoa and 12.9 km E on road to Alamos, *Mohlenbrock et al. 1990* (root tip cell) (fig. 19).
CACTOIDEAE	
Lophocereus schottii (Engelmann) Britton & Rose var. *tenuis* Lindsay	
*$n = 11$	Mexico, Sonora, 10.2 km W of Hwy 15 toward San Carlos, 7.1 km N toward Nacoupuli Canyon, *Parfitt 3037* (fig. 20), *Gallagher & Forbes.*
Stenocereus alamosensis (Coulter) Gibson & Horak (=*Rathbunia alamosensis* Coulter)	
$n = 11$	Arizona, Maricopa Co., cultivated on Arizona State Univ. campus, *Baker 3691.*
Stenocereus thurberi (Engelmann) Buxbaum var. *thurberi* (*Lemaireocereus thurberi* Engelmann)	
$n = 11$	Mexico, Sonora, 10.2 km W of Hwy 15 toward San Carlos, 7.1 km N toward Nacopuli Canyon, *Parfitt 3035, 3036 Gallagher & Forbes.*
Myrtillocactus cochal (Orcutt) Britton & Rose	
$n = 11$	Mexico, Baja California Norte, 8 km E of Hwy 1, along road to San Telmo, *Baker et al. 4023.*
Echinocereus engelmannii (Parry) Lemaire var. *acicularis* Benson	
$n = 22$	Arizona, Maricopa Co., South Mtn. Park, ca. 13 km SW of Tempe, *Ruffner 15.*
Echinocereus fasciculatus (Engelmann) Benson var. *bonkerae* (Thornber & Bonker) Benson	
$n = 22$	Arizona, Pima Co., 21.4 km S of Oracle, road to Mt. Lemmon, *Pinkava 11040, Lehto & Hensel.*
Echinocereus fasciculatus var. *boyce-thompsonii* (Orcutt) Benson	
*$n = 22$	Arizona, Maricopa Co., Red Mtn. Ranch, ca. 26 km NE of Tempe, *Parfitt 3013* (intermediate to *E. engelmannii* var. *acicularis*), *3010*, *3011* (fig. 21); Pinal Co., 30 km SE of Florence, *Baker 4224* (intermediate to var. *fasciculatus*), *4222 & Pinkava;* Yavapai Co., Bloody Basin Rd., 2 km W of Bishop Creek, T10N R3E S23, *Baker 4295, Trushell & McGill* (intermediate to var. *fasciculatus*).
Echinocereus fendleri (Engelmann) Engelmann ex Rümpler var. *rectispinus* (Peebles) L. Benson	
$n = 11$	New Mexico, Hidalgo Co., Pyramid Mtns., *Worthington 9929* (UTEP).

TABLE 1. Continued.

Echinocereus pectinatus (Scheidweiler) Engelmann var. *minor* (Engelmann) Benson

*n = 22 Texas, El Paso Co., Franklin Mtns., *Worthington 10290* (fig. 22) (UTEP).

Echinocereus triglochidatus Engelmann var. *gurneyi* L. Benson

n = 22 Mexico, Chihuahua, Sierra San Ignacio, 31°16′N, 106°00′W, *Worthington 9741 & Corral* (intermediate to var. *neomexicanus* (Standley) Standley ex Marshall) (fig. 23) (UTEP).

Echinocereus viridiflorus Engelmann var. *cylindricus* (Engelmann) Engelmann ex Rümpler

n = 11 Texas, El Paso Co., Franklin Mtns., 31°54′15″N, 106°23′30″W, *Worthington 8001* (UTEP).

Ancistrocactus uncinatus (Galeotti) Benson var. *wrightii* (Englemann) Benson

n = 11 Mexico, Chihuahua, Sierra San Ignacio, 31°16′N, 106°00′W, *Worthington 9761 & Corral* (UTEP).

Ferocactus gracilis Gates var. *gracilis*

n = 11 Mexico, Baja California Norte, Hwy 1, ca. 12.5 km N of Rosarito, *Reeves 443 & Pinkava* (counted by Tim Reeves).

Neolloydia erectrocentra (Coulter) Benson var. *erectrocentra*

n = 11 Arizona, Cochise Co., 9.7 km S of I-10, on AZ 80, *Clark 1491 & Parfitt* (fig. 24).

Neolloydia intertexta (Engelmann) Benson var. *dasyacantha* (Engelmann) Benson

n = 11 Texas, El Paso Co., Franklin Mtns., 31°54′15″N, 106°23′30″W, *Worthington 7990, 7991* (fig. 25) (both flowering juvenile forms) (UTEP).

Coryphantha durangensis Runge var. nov. A. Zimmerman *ined.*

*n = 11 Mexico, Coahuila, 16.5 km S of Rancho Los Charcos and 12.6 km N of jct. Coah. 2, *Keil 8169A* (fig. 26) *& McGill.*

Coryphantha organensis D. Zimmerman

*n = 11 New Mexico, Dona Ana Co., Organ Mtns., above Pine Tree Trail, T22S R4E S32, *Worthington 8083* (fig. 27) (UTEP).

Coryphantha sneedii (Britton & Rose) Berger var. *sneedii*

*n = 11 New Mexico, Dona Ana Co., Franklin Mtns., SE side of Anthony Gap, T26S R4E S36 C, *Worthington 8084* (=*7011*) (fig. 28) (UTEP); Texas, El Paso Co., Franklin Mtns. slopes at E end of Coronado Country Club, *Worthington 8164* (UTEP).

Coryphantha strobiliformis (Poselger) Moran var. *orcuttii* (Bödeker) Benson

n = 11 New Mexico, Grant Co., Little Hatchet Mtns., ca. 1.6 km SE of Old Hachita, *Worthington 9963* (very robust specimen) (fig. 29) (UTEP); Hidalgo Co., Peloncillo Mtns., Hwy 80 at Granite Gap, *Worthington 9781* (UTEP); Luna Co., Florida Mtns., Mahoney Park, *Worthington 8085, 8103* (UTEP).

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

n = 11 Arizona, Pinal Co., 8 km N of Falcon Ranch, S of Florence, T9S R13E S27, *Baker 4208*; Yavapai Co., Bloody Basin Rd., 2 km W of Bishop Creek, T10N R3E S23, *Trushell 82-104 & Baker.*

Mammillaria armillata K. Brandegee

n = 11 Mexico, Baja California Sur, Hwy 1, 11.3 km S of Los Barriles, then 3.2 km E on dirt road, *Mohlenbrock et al. 1980* (fig. 30).

Mammillaria dioica K. Brandegee

n = 22 Mexico, Baja California Sur, Rte 22, 25.6 km W of Ciudad Constitucion, *Mohlenbrock et al. 1962* (fig. 31).

n = 33 Mexico, Baja California Norte, 53.4 km S of El Rosario, *Baker et al. 4025* (fig. 32); Baja California Sur, Hwy 1, 15.3 km S of Santa Rosalia, *Mohlenbrock et al. 1953.* California, San Diego Co., Hwy S-2, 54 km NW of Ocotillo, *Parfitt 3006 & Jansen.*

Mammillaria heyderi Mühlenpfordt var. *macdougalii* (Rose) Benson

n = 11 Arizona, Pima Co., E of Box Canyon, N end of Santa Rita Mtns., *Parfitt 2977 & Knox.*

Mammillaria heyderi var. *meiacantha* (Engelmann) Benson

n = 11 New Mexico, Dona Ana Co., Organ Mtns., T23S R3E S23 NE¼, *Worthington 8056* (UTEP).

Mammillaria phitauiana (Baxter) Werdermann

*n = 11 Mexico, Baja California Sur, gravel

TABLE 1. Continued.

road to San Bartolo Microondas Sta., just W of Hwy 1, *Mohlenbrock et al. 1981* (fig. 33).

Mammillaria thornberi Orcutt
$n = 11$ Arizona, Pima Co., near Sells, *Knox 112* (fig. 34).

Mammillaria viridiflora (Britton & Rose) Bödeker
$n = 11$ Arizona, Gila Co., Hwy 60, 22.3 km E of jct. Hwy 177 (Superior), *Parfitt 3106 & Baker*; Maricopa Co., 0.8 km SSW of Seven Springs Campground, *Mohlenbrock 2015* (fig. 35) *& Baker* (robust specimen).

Mammillaria yaquensis Craig
$^*n = 11$ Mexico, Sonora, Rte 15, 66.6 km S of Navajoa, then 12.9 km E on road to Alamos, *Mohlenbrock et al. 1989* (fig. 36).

CORRECTIONS

Opuntia bigelovii Engelmann var. *bigelovii*
$2n = 3x = 33$ Arizona, Maricopa Co., 0.5 km N or Morning Star, *Dodge s.n.* (17.0). Originally reported by Pinkava and McLeod (1971) as $n = 11$, misinterpreting fig. 4 as $11_{\rm II}$ instead of correctly as $11_{\rm III}$.

Opuntia littoralis (Engelmann) Cockerell var. *littoralis*
$n = 33$ Mexico, Baja California Norte, Rte 1, 30 km S of San Vincente, *McGill & Pinkava P8773*; ca. 9.7 km W of Rosario toward Punta Baja, *McGill, Nash & Pinkava P9161*. Originally published as *O. oricola* Philbrick intermediate to *O. phaeacantha* complex (Pinkava et al. 1977).

Opuntia phaeacantha Engelmann var. *major* Engelmann
$n = 33$ Mexico, Coahuila, Sierra de la Madera, *Pinkava 13658, 13659, McGill, Reeves & Nash*. Originally published as aff. var. *nigricans* Engelmann (Pinkava and Parfitt 1982).

as polyploid. Pereskioideae consists of two genera, amphitropical *Pereskia* and South American *Maihuenia*. Only in five of the perhaps 20 species of *Pereskia* are chromosome numbers known; all are diploid.

In Opuntioideae, however, most taxa (63.3%) are polyploid: 75 of 125 taxa (60%) in North America and 32 of 44 taxa (72.7%) in South America. In its largest genus, *Opuntia*, the frequency of polyploidy in morphological counterparts in the two hemispheres is higher in South America than in North America: chollas (87.5% in *Austrocylindropuntia* versus 44.1% in *Cylindropuntia*); club chollas (64.3% in *Tephrocactus* versus 42.9% in *Corynopuntia*); and prickly-pears of subgenus *Opuntia* (73.7% versus 67.5%). Also, the highest levels of polyploidy occur in South American taxa.

In Cactoideae, the largest and most advanced subfamily, only 47 of 377 reported taxa (12.5%) are polyploid. Except for *Mammillaria* and *Echinocereus*, polyploids occur in one or two taxa per genus and mostly at the tetraploid level.

The differences in frequency of polyploidy among the subfamilies may be partly explained by the theory of Stebbins (1950) that polyploidy is more likely to be established in self-fertile or apomictic taxa than in self-sterile or panmictic taxa. Ross (1981) found polyploidy to be correlated with self-fertility, adventive embryony, profuse branching, and vegetative reproduction in his study of 55 taxa of Cactaceae. *Opuntia*, which has a high frequency of vegetative propagation, apomixis, and self-fertility (Philbrick 1963; Ross 1981), has extensive polyploidy (table 2). Pereskioideae and Cactoideae apparently have few of the reproductive characters favoring polyploids (Craig 1945; Ross 1981).

Polyploidy, particularly at the triploid and tetraploid levels, is believed to originate most often from the fertilization of unreduced gametes (Lewis 1980; deWet 1980). We postulated that fertilization of unreduced gametes accounts for several interspecific and intraspecific, polyploid *Opuntia* hybrids (Pinkava et al. 1977; Pinkava and Parfitt 1982). Ross (1981) proposed that polyploidy in Cactaceae might originate through such premeiotic abnormalities as he found in *Pereskia diaz-romeriana* or by somatic doubling in meristems as hypothesized by Remski (1954). Since mitotic euploid counts at different ploidal levels have been reported from the same root tip (e.g., Remski 1954; Weedin and Powell 1978), we have preferred to work with meiotic materials.

Aneuploidy plays no role in the modern evolution of cacti. Of the 11 aneuploid counts pub-

TABLE 2. Taxonomic and geographic distribution of polyploid taxa in the Cactaceae. Data tabulated from published reports compiled and edited by Pinkava (unpubl.). Generic delimitation according to Hunt (1967) excepting for our inclusion of *Escobaria* in *Coryphantha*. Genera of Cactoideae with only diploid members are excluded from the table. Symbols: Px = polyploid state at any level ($>2x$), including taxa with diploid and polyploid individuals; N = North American; S = South American; T = North and South American; * = monotypic taxa.

Taxon	Geographic distribution	Total taxa	Species (Px)	Infraspecific taxa + hybrids (Px)	Percent Px	Levels Px
PERESKIOIDEAE	T	5	0	0	0.0	
Pereskia	T	5	0	0	0.0	—
OPUNTIOIDEAE	T	169	83	24	63.3	
Opuntia	T	163	78	24	62.6	
Austrocylindropuntia	S	8	7	0	87.5	6, 10–11, ca. 20
Corynopuntia	N	7	3	0	42.9	4, 6
Cylindropuntia	N	34	15	0	44.1	3–6
*Grusonia**	N	1	0	0	0.0	—
Opuntia	T	99	44	24	63.7	
	(N)	(80)	(31)	(23)	(67.5)	3–8
	(S)	(19)	(13)	(1)	(73.7)	3–4, 6, 8
Tephrocactus	S	14	9	0	64.3	3–6, 8, 13 ca. 19, ca. 30
Pereskiopsis	N	3	3	0	100.00	10
Pterocactus	S	1	1	0	100.00	4
Quiabentia	S	1	1	0	100.00	10
*Tacinga**	S	1	0	0	0.0	—
CACTOIDEAE	T	377	35	12	12.5	
Ariacarpus	N	3	1	0	33.3	ca. 4
*Blossfeldia**	S	1	1	0	100.00	6
Cephalocereus	T	3	2	0	66.7	4
Coryphantha	N	24	2	0	8.3	4
Echinocereus	N	43	7	8	37.2	4
Gymnocalycium	S	7	1	0	14.4	4
Lobivia	S	2	1	0	50.0	4
Mammillaria	N	110	10	3	11.8	4, 6, 8, 24
Melocactus	T	2	1	0	50.0	4
× *Myrtgerocactus**	N	1	0	1	100.00	3
Notocactus	S	3	2	0	66.7	4
Pachycereus	N	3	1	0	33.3	4
Rebutia	S	5	2	0	40.0	4
Rhipsalis	T	42	1	0	2.4	4, 8
Selenicereus	T	8	1	0	12.5	4
Thelocactus	N	0	1	0	11.1	4
Trichocereus	S	3	1	0	33.3	4
CACTACEAE	T	551	118	36	27.9	

lished, ten were made before 1939 and nine of these have been recounted at euploid levels. The one exception that cannot be discounted as yet is a count of $n = 12$ for *Deamia testudo* (Karw.) Britt. and Rose by Bhattacharyya (1970). There are also reports of non-disjunction in certain meiotic cells in *Mammillaria* by Beard (1937) and in *Opuntia* by Pinkava and McLeod (1971) and Pinkava et al. (1973).

Numerous reports of hybridization at intergeneric, interspecific, and infraspecific levels have been published for the Cactaceae (Hawkes 1982–1983). Hybridization, often coupled with polyploidization and/or apomixis, forms important evolutionary mechanism in the Cactaceae, particularly in *Opuntia* and certain cactoid genera such as *Mammillaria* and *Echinocereus.*

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