Chromosome Number Variation and Polyploidy in the Genus Echinocereus (Cactaceae)

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CHROMOSOME NUMBER VARIATION AND POLYPLOIDY IN THE GENUS *ECHINOCEREUS* (CACTACEAE)[1]

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Analyses of meiotic and mitotic chromosomes were undertaken in 16 taxa of *Echinocereus* belonging to 12 species and all seven taxonomic sections (sensu Taylor). Chromosome numbers are reported for the first time for eight taxa, and previously published chromosome counts are confirmed for the remaining eight. Both diploid and polyploid counts were obtained. Eleven (69%) of the taxa surveyed were diploid ($2n = 22$); the five varieties of *E. engelmannii* were polyploid ($2n = 44$). Overall, chromosome counts are available for 23 of the 48 proposed species (sensu Taylor). Of these, 19 (82%) are diploid, and four (18%) are polyploid. Polyploid cytotypes are most common in the primitive sections, e.g., sections *Erecti* and *Triglochidiatus*, which suggests that polyploidy is probably a derived condition in *Echinocereus*. Polyploid taxa range from medium to high latitudes and elevations relative to the overall distribution of the genus. Polyploidy, hybridization, and cryptic chromosomal rearrangements are thought to be the major causes of the speciation events of the genus.

The genus *Echinocereus* is widely distributed in the deserts and semideserts of central and northwestern Mexico and the southwestern United States (Taylor, 1985). According to Barthlott (1988), the genus belongs to the subfamily Cactoideae within the tribe Echinocereeae. Morphological variation in the genus is extreme, resulting in disagreement in number of species according to various author's taxonomic treatments, e.g., from 47 (Bravo, 1937) to 60 (Britton and Rose, 1922), to 73 (Backeberg, 1960). More recently, Taylor (1985, 1988, 1989) proposed a classification recognizing 48 species. It seems that in *Echinocereus* the lack of extensive field research and the production of taxonomies that are based on the analysis of few morphological characters have yielded taxonomic confusion. In addition, frequent cases of convergent evolution in both vegetative and floral features have made the understanding of infraspecific relationships difficult. Since the purpose of this study is not a taxonomic treatment of the genus, and the discussion of species boundaries is beyond its objectives, the reader is advised to consult these references for detailed taxonomic information of the treatment. However, some aspects regarding Taylor's (1985) treatment will be briefly discussed in this section because the taxa selected in this study were circumscribed using such a treatment. This information will provide a better understanding of the concepts used in the following sections.

Taylor's taxonomic treatment of *Echinocereus* considers a detailed analysis of floral morphology (in addition to vegetative characters) for the first time. In this treatment, the genus is divided into seven sections and several species groups based on patterns of geographic distribution and degree of specialization. The degree of specialization is referred to by Taylor in terms of water conservation efficiency. Some of the characters considered to be unspecialized are: 1) exposed, branched stems with high ribs; 2) not very dense spines; and 3) large flowers and fruits. Conversely, examples of specialized characters are: 1) solitary stems with many low ribs; 2) dense spine distribution on stems; and 3) small flowers and fruits. Sections are arranged according to such patterns of specialization. However, as in many groups of angiosperms, some taxa in *Echinocereus* have a mixture of both primitive and advanced features, due perhaps to mosaic evolution. This treatment considers the degree of morphological specialization to delineate taxonomic sections but it does not assess phylogenetic relationships. Taylor's taxonomic treatment based on primitiveness or specialization of morphological features is thus not a direct application of cladistic analysis, but instead a statement of relationships based primarily upon morphological and geographic characters. Therefore, primitive or advanced characters as referred to herein should not be interpreted as plesiomorphies or synapomorphies in the cladistic sense.

Chromosome number variation, especially polyploidy, is believed to be one of the major phylogenetic processes that has affected angiosperm evolution (Stebbins, 1971). In addition, polyploidy usually leads to different and/or new evolutionary lines and promotes new gene combinations in organisms (DeWet, 1980). Polyploidy is also believed to have played a fundamental role in the evolution of the Cactaceae, since different levels of polyploidy are known. Pinkava et al. (1985) found that 154 (27.9%) of the 551 taxa of Cactaceae cytologically analyzed thus far were polyploids. The same study indicated that polyploid cytotypes are more common in the subfamilies Opuntioideae (e.g., *Opuntia*) and Cactoideae (e.g., *Echinocereus* and *Mammillaria dioica*). Triploids, tetraploids,

TABLE 1. Species of *Echinocereus* investigated. List includes chromosome numbers, localities, collector, and collection number (complete label data is available, and will be provided upon request). Abbreviations indicate the acronyms of the herbaria in which the cytovouchers were deposited.[a]

Species	Chromosome number[b]	County, Locality, Collector, Herbaria
Section *Morangaya* (G. Rowley) N. P. Taylor		
E. pensilis (Brandegee) Purpus	$2n = 22$*	MEXICO. Baja California Sur. *R. Moran, 7448* (RSA, SD, and living collection of HNT, 48731).
Section *Erecti* (Schumann) Bravo-H.		
E. engelmannii (Engelm.) Lem.		
var. acicularis Benson	$2n = 44$	U.S.A. CA. *D. Benadom, s.n.* (RSA).
var. chrysocentrus (Engelm. & Bigelow) Ruempler	$2n = 44$	U.S.A. CA. *D. Benadom, 468* (RSA).
var. engelmannii	$n = 22$	MEXICO. Baja California Norte. *H. Cota, 7520* (RSA).
	$2n = 44$	MEXICO. Baja California Norte. *H. Cota, 7513, 7518* (ENCB, RSA). *H. Cota, 7509* (RSA). U.S.A. CA. *W. Wisura & J. Dice, s.n.* (Living collection RSA, 4918).
var. munzii (Parish) Pierce & Fosb	$n = 22$*	MEXICO. Baja California Norte. *H. Cota, 7523* (RSA).
	$2n = 44$	U.S.A. CA. *H. Cota, 7535, 7536* (RSA). *D. Michener & W. Wisura, s.n.* (Living collection RSA, 15208).
var. variegatus (Engelm. & Bigelow) Ruempler	$2n = 44$	U.S.A. CA. *D. Benadom, 467* (RSA).
E. maritimus (M. E. Jones) Schumann	$2n = 22$	MEXICO. Baja California Norte. *H. Cota, 7939, 7940* (ENCB, RSA)
E. nicholii (Benson) Parfitt	$2n = 22$	U.S.A. AZ. *H. Cota and R. Felger, s.n.* (ARIZ).
Section *Triglochidiatus* Bravo-H.		
E. scheeri (Salm-Dyck) Scheer	$2n = 22$*	MEXICO. Chihuahua. *M. Kimnach & Brandt, 982* (Living collection of HNT, 20780).
E. triglochidiatus Engelm.		
var. mojavensis (Engelm. & Bigelow) Benson	$2n = 22$*	U.S.A. CA. *P. A. Munz & P. C. Everett, 17453* (Living collection of RSA, 7811). *L. Arnseth, 10* (RSA).
Section *Echinocereus* Engelm.		
E. cinerascens (DC) Lem.	$2n = 22$	MEXICO. Hidalgo. *E. F. Anderson, 4981* (Living collection of HNT, 58598). Querétaro. *R. Fernández, 1601* (ENCB).
E. knippelianus Liebner	$2n = 22$*	MEXICO. Nuevo León. *C. Glass & R. Foster, 3902* (Living collection of HNT, 42153).
E. pentalophus (DC) Lem.	$2n = 22$	MEXICO. Tamaulipas. *J. Folsom et al., 1105* (Living collection HNT, 53249).
Section *Reichenbachii* N. P. Taylor		
E. stoloniferus W. T. Marshall	$2n = 22$*	MEXICO. Sonora. *Boutin & M. Kimnach, 3654* (Living collection of HNT, 30307).
Section *Wilcoxia* (Br. & Rose) N. P. Taylor		
E. leucanthus N. P. Taylor	$2n = 22$*	MEXICO. Sonora. *Koutnik and J. Trager, s.n.* (Living collection of HNT, 30018).
Section *Pulchellus* N. P. Taylor		
E. laui G. R. W. Frank	$2n = 22$*	MEXICO. Sonora. *A. Lau, 780.* (ZSS)

[a] ARIZ: University of Arizona, ENCB: Escuela Nacional de Ciencias Biológicas (México), HNT: Huntington Botanic Garden, RSA: Rancho Santa Ana Botanic Garden, SD: San Diego Natural History Museum, and ZSS: Stadische Sukkulentensammlung (Switzerland).

[b] * = new chromosome count for the taxon; n = count obtained from meiotic material; $2n$ = count obtained from mitotic material.

and hexaploids have been documented in the family (Pinkava and Parfitt, 1982, 1988; Pinkava et al., 1985). In addition, a high frequency of infraspecific polyploidy has been indicated in *Opuntia* (20%), corresponding to 19 species (Lewis, 1980). Moreover, decaploid ($2n = 132$) individuals occur in *Opuntia rubescens* (Katagiri, 1953; Cota, unpublished data). Overall, polyploidy has been reported in approximately 20 genera of the Cactaceae, and is slightly more common in the southern hemisphere (Pinkava et al., 1985). However, for this family no detailed analysis regarding the pattern of distribution of polyploids in terms of latitude and altitude is available.

Surveys of chromosome variation, both numerical and structural, have also been successfully applied in systematic studies in several groups of the Cactaceae (e.g., Pin-

kava, McGill, and McLeod, 1977; Pinkava and Parfitt, 1982; Pinkava et al., 1985; Mazzola, Romano, and Fici, 1988). For instance, taxonomic problems in the opuntias of the Chihuahuan Desert have been clarified by analyses of chromosome behavior during meiosis, as well as chromosome number variation (polyploidy). Also, by using chromosome counts Pinkava and Parfitt (1988) established the hybrid status of *Opuntia × spinosibacca*. Cytological investigation has also revealed the first evidence of chromosomal structural rearrangements in the Cactaceae, e.g., translocations in *O. leptocaulis* (Pinkava et al., 1985) and inversions in *O. curvospina* (Pinkava et al., 1973).

Although somewhat limited in scope, cytological studies have also been valuable in understanding the system-
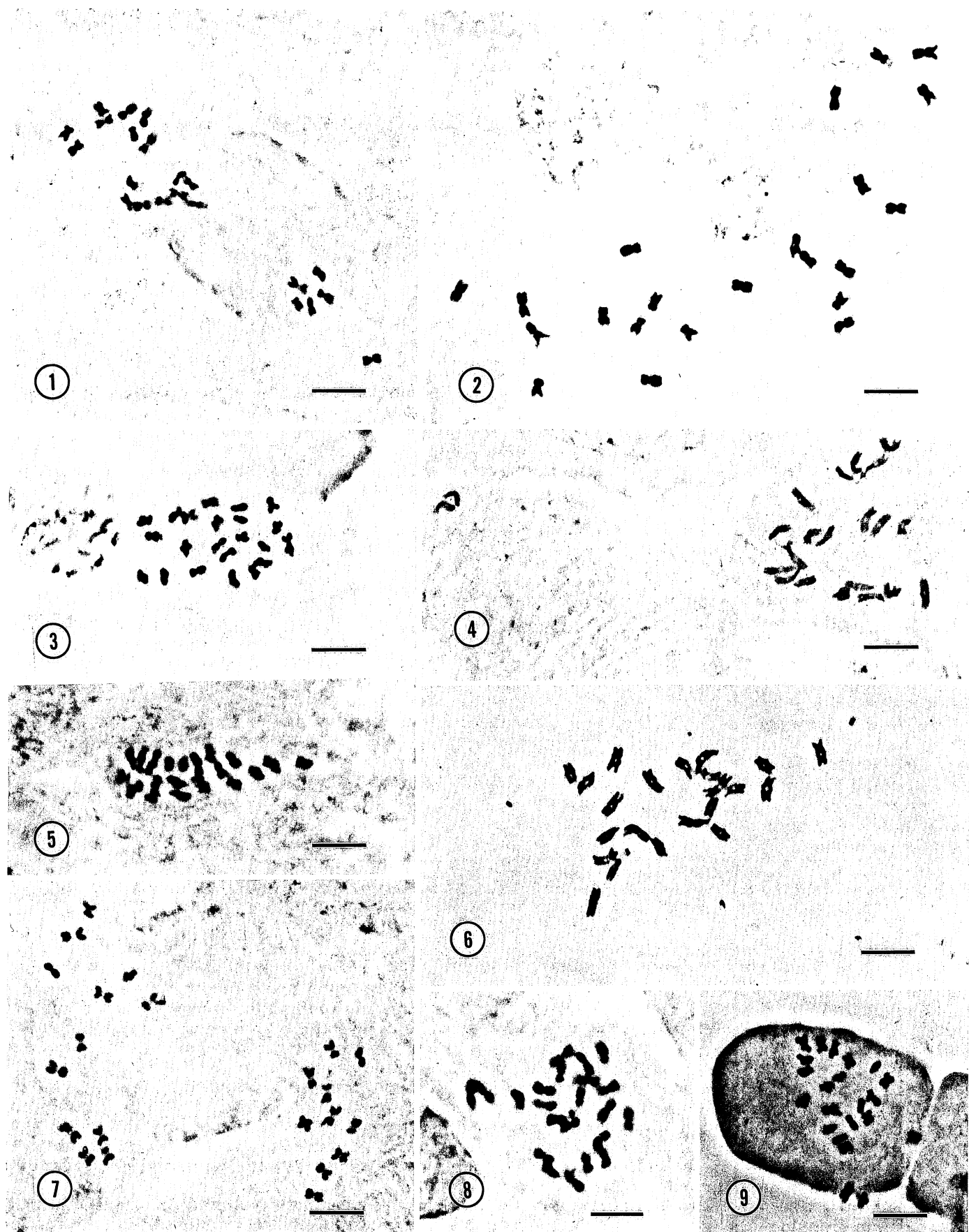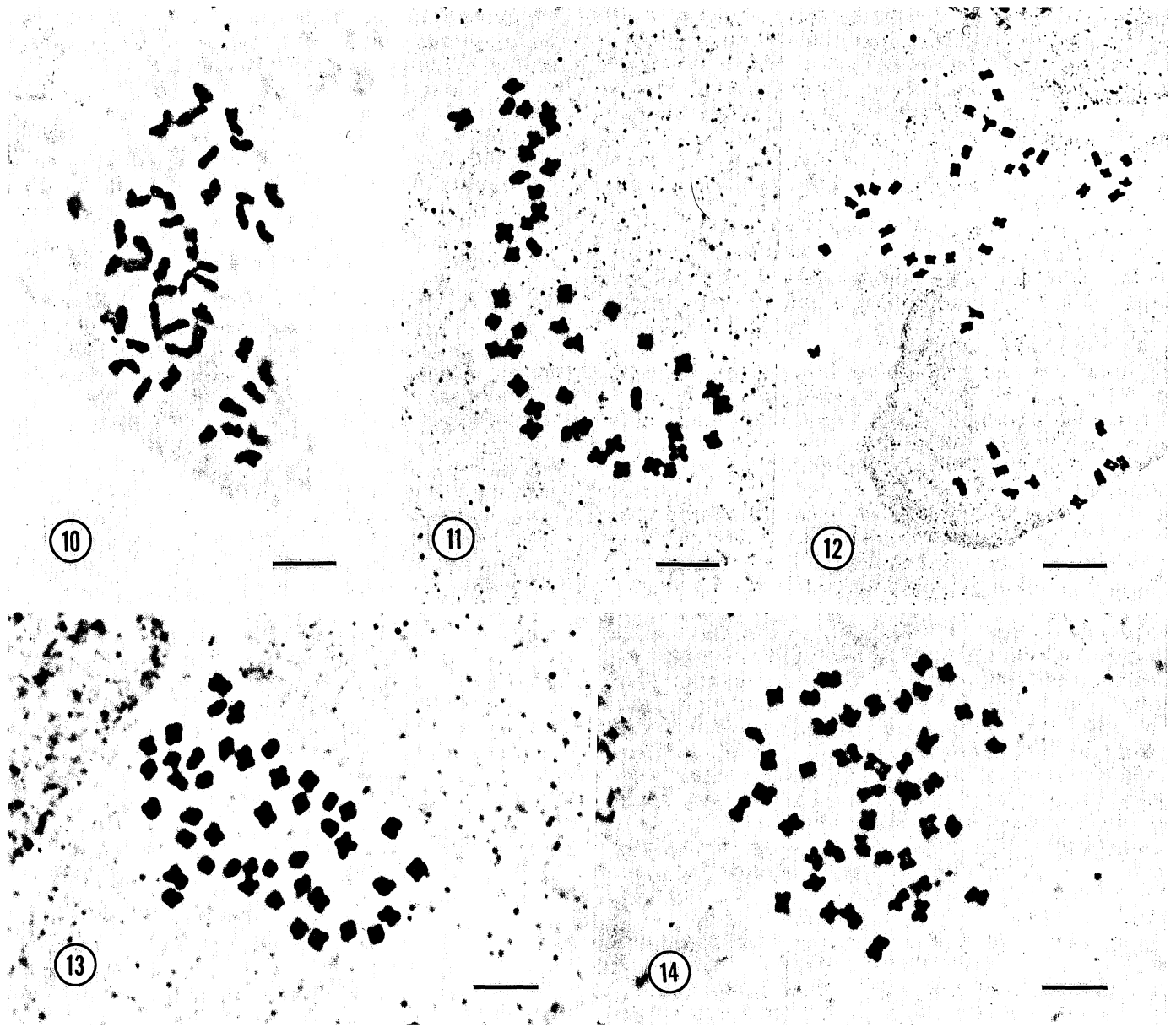
Figs. 10–14. Photomicrographs of mitotic chromosomes of representative polyploid *Echinocereus engelmannii* varieties. **10.** var. *acicularis* (D. Benadom, s.n.). **11.** var. *chrysocentrus* (D. Benadom, 468). **12.** var. *engelmannii* (H. Cota, 7518). **13.** var. *munzii* (H. Cota, 7535). **14.** var. *variegatus* (D. Benadom, 467). Bars = 10 μm for Figs. 10, 11, 13, 14, and 15 μm in Fig. 12.

atics of *Echinocereus*. In this genus, as well as in the family, the basic chromosome number is $x = 11$ (Pinkava et al., 1985). Both diploid and polyploid cytotypes have been documented (e.g., Stockwell, 1935; Beard, 1937; Katagiri, 1953; Remski, 1954; Pinkava and McLeod, 1971; Pinkava, McGill, and McLeod, 1977; Pinkava and Parfitt, 1982; Pinkava et al., 1973, 1985, 1992). In addition, Parfitt (1987) removed *E. nicholii* from *E. engelmannii* based in part on differences in ploidy level.

In spite of the relatively large number of references in which chromosome counts for *Echinocereus* are provided, the proportion of species analyzed thus far is less than 50%. Therefore, additional cytological work is needed to better understand the diversity, distributional patterns, and evolution of the genus. The purpose of this study is to address the following questions: 1) What are the chromosome numbers for the species of *Echinocereus* included in this study? 2) How does the incidence of polyploidy in

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Figs. 1–9. Photomicrographs of mitotic chromosomes of representative diploid *Echinocereus* species. **1.** *E. pentalophus* (HNT, 53249). **2.** *E. triglochidiatus* var. *mojavensis* (L. Arnseth, 10). **3.** *E. laui* (A. Lau, 780). **4.** *E. nicholii* (H. Cota & R. Felger, s.n.). **5.** *E. scheeri* (HNT, 20780). **6.** *E. maritimus* (H. Cota, 7940). **7.** *E. knippelianus* (HNT, 42153). **8.** *E. stoloniferus* (HNT, 30307). **9.** *E. leucanthus* (HNT, 30018). Bars = 10 μm.

Echinocereus compare with the rest of the family? 3) What are the relationships between polyploidy and geography (latitude and elevation) as well as the relative degree of morphological specialization in the genus? 4) Is there a phylogenetic-taxonomic correlation in the occurrence of polyploidy in the genus?

MATERIALS AND METHODS

The taxa examined in this study were selected because they exhibit a wide range of variation in terms of morphology, floral attributes, pollination syndromes, ecology, distribution, and altitudinal and latitudinal range. In addition, these taxa represent each of the sections in Taylor's (1985) taxonomic treatment.

Counts were made from both field-collected material and the living collections at the Rancho Santa Ana Botanic Garden and Huntington Botanic Garden. Voucher specimens are listed in Table 1.

Both mitotic and meiotic chromosome counts were conducted when possible. For mitotic counts, root tips from either seedling radicles or adventitious roots from stems were used. Seeds were germinated on moist filter paper in petri dishes at 32 C. Prior to germination, seeds were disinfected in commercial bleach (1:10 with tap water) for 10 minutes, rinsed with distilled water, and transferred to a solution of 70% EtOH for 5 minutes. After germination, root tips were pretreated in a saturated solution of paradichlorobenzene (PDB) for 5 hours at room temperature. Cell division was observed to be most active from 7:00 to 9:00 a.m. After pretreatment, root tips were rinsed at least three times with distilled water and transferred to a 3:1 solution of 95% EtOH-acetic acid for 24 to 48 hours at room temperature. Then they were rinsed with distilled water and hydrolyzed in 1 N HCl at 60 C for 11 minutes. After hydrolysis, root tip meristems were isolated and stained with iron-aceto-carmine for 1 to 2 minutes. The squashing routine used is modified from Parfitt (1979).

For meiotic analysis flower buds were preserved in a 3:1 solution of 95% EtOH-acetic acid for 24 hours, and transferred to 70% EtOH until used. Staining procedure followed the same routine as for mitotic material. Smears and semipermanent slides for both mitotic and meiotic figures were made using Hoyer's fluid (Beeks, 1955). Microscopic observations of chromosomes were made with a Leitz phase-contrast microscope at ×100 (oil).

RESULTS

Chromosome numbers are reported for the first time for eight taxa: *Echinocereus engelmannii* var. *munzii*, *E. knippelianus*, *E. laui*, *E. leucanthus*, *E. pensilis*, *E. scheeri*, *E. stoloniferus*, and *E. triglochidiatus* var. *mojavensis* (Table 1). Additional chromosome counts that confirm previous reports were obtained for *E. cinerascens*, *E. maritimus*, *E. nicholii*, *E. pentalophus*, and four varieties of *E. engelmannii*: var. *acicularis*, var. *chrysocentrus*, var. *engelmannii*, and var. *variegatus* (Table 1).

Relative to the base number of $x = 11$, both diploid and tetraploid numbers were revealed. Eleven (69%) of the 16 taxa surveyed in this study were diploid ($2n = 22$):

Echinocereus cinerascens, *E. knippelianus*, *E. laui*, *E. leucanthus*, *E. maritimus*, *E. nicholii*, *E. pensilis*, *E. pentalophus*, *E. scheeri*, *E. stoloniferus*, and *E. triglochidiatus* var. *mojavensis* (Figs. 1–9). The five varieties of *E. engelmannii* were tetraploid ($2n = 44$) (Figs. 10–14).

Chromosomes in both diploid and polyploid species were relatively small (2–5 μm), and morphologically uniform (mostly metacentric) with few secondary constrictions (Figs. 1–14).

DISCUSSION

In *Echinocereus*, chromosome counts are available for 23 of the 48 proposed species (Tables 1, 2). Of these, 19 (82%) are diploid, and four (18%) are polyploid. Eighteen percent polyploidy in *Echinocereus* is higher than that cited by Pinkava et al. (1985) for the subfamily Cactoideae (12.5%), in which *Echinocereus* belongs. However, the frequency of polyploidy in *Echinocereus* is similar to that reported by Lewis (1980) for *Opuntia* (20%), a genus in which the highest frequency of polyploidy has been reported for the family.

Chromosome counts for the varieties of *Echinocereus engelmannii* correspond to those reported for the species by Pinkava and McLeod (1971), Pinkava, McGill, and McLeod (1977), and Pinkava et al. (1985, 1992), in which tetraploidy ($n = 22$) is the usual condition. Although aneuploidy ($2n = 24$) has been reported for *E. blanckii* (Beard, 1937), subsequent euploid counts ($2n = 22$) have not confirmed it (Table 2), (Katagiri, 1953; Remski, 1954).

In plants, polyploidy occurs most commonly through the production of unreduced gametes (DeWet, 1980) caused perhaps by environmental factors (Jackson, 1976). Although little research has been done in the Cactaceae regarding the origin of polyploids, it is likely that the same basic premise applies here (Ross, 1981; Pinkava et al., 1985). Ross (1981) hypothesized that polyploidy originated in the family through premeiotic abnormalities analogous to those observed in *Pereskia diaz-romeroana*. In *Opuntia*, both autotetraploids and autoallotetraploids have been documented (Pinkava et al., 1985). Both processes are thought to have occurred through the fusion of reduced and unreduced gametes. In *Echinocereus* there is little evidence to indicate whether polyploid taxa are of autopolyploid or allopolyploid origin. The overall similarity in karyotypes of *Echinocereus* (Cota, 1991) has failed to reveal karyotypic markers that indicate allo- or autopolyploidy.

Polyploid taxa occur in two of the seven sections of *Echinocereus*: *Erecti* and *Triglochidiatus*. The frequency of polyploids is higher in those two sections that have more primitive morphological characters, for instance, in section *Erecti* they are represented by some of the varieties of *E. engelmannii*, *E. fendleri*, and *E. pectinatus* (Tables 1, 2). In contrast, only one taxon in section *Triglochidiatus* is polyploid: *E. triglochidiatus*.

Although polyploid taxa tend to be more common in the putatively primitive sections, some polyploids exhibit a combination of primitive, intermediate, and derived morphological character states. For example, the members of the *Echinocereus engelmannii* group (section *Erecti*) have flowers, growth habit, and flower bud develop-

TABLE 2. Chromosome counts from species of *Echinocereus*. List includes meiotic (*n*) and mitotic (2*n*) counts as reported in the literature. Taxa are listed following Taylor (1985, 1988, 1989). The "reported as" column refers to synonyms relative to Taylor's treatment under which the numbers were reported.[a]

Taxon	Reported as	Count	Reference
Section *Erecti*			
E. engelmannii (Engelm.) Lem.			
var. *acicularis* Benson	*E. engelmannii* var. *acicularis*	$n = 22$	4, 6, 10
var. *chrysocentrus* (Engelm. & Bigelow) Ruempler	*E. engelmannii* var. *chrysocentus*	$2n = 44$	11
var. *engelmannii*	*E. engelmannii* var. *engelmannii*	$2n = 44$	11
var. *howei* Benson	*E. engelmannii* var. *howei*	$2n = 44$	11
var. *variegatus* (Engelm. & Bigelow) Ruempler	*E. engelmannii* var. *variegatus*	$n = 22$	9
		$2n = 44$	11
E. maritimus (M. E. Jones) Schumann	*E. maritimus*	$n = 11$	6
E. nicholii (Benson) Parfitt	*E. nicholii*	$n = 11$	11, 12
E. fendleri (Engelm.) Ruempler			
var. *bonkerae* (Thornber & Bonker) Benson	*E. bonkerae* Thornber & Bonker	$n = 11$	11
	E. fasciculatus (Engelm.) Benson var. *bonkerae* (Thornber & Bonker) Benson	$n = 22$	9, 10
var. *boyce-thompsonii* (Orc.) Benson	*E. fasciculatus* (B. D. Jackson) var. *boyce-thompsonii* (Orc.) Benson	$n = 22$	10
		$2n = 44$	11
var. *fasciculatus*	*E. fasciculatus* var. *fasciculatus*	$n = 22$	9
		$2n = 44$	11
var. *fendleri* (Engelm.) Ruempler	*E. fendleri* var. *fendleri*	$n = 11$	7, 11
var. *ledingii* (Peebles) N. P. Taylor	*E. ledingii* Peebles	$n = 11$	11
var. *rectispinus* (Peebles) Benson	*E. fendleri* var. *rectispinus*	$n = 11$	4, 10, 11
E. pectinatus (Scheidw.) Engelm.			
var. *dasyacanthus* (Engelm.) N. P. Taylor	*E. pectinatus* var. *minor* (Engelm.) Benson	$n = 22$	10
	E. pectinatus var. *neomexicanus* (J. Coulter) Benson	$n = 22$	7
var. *pectinatus*	*E. pectinatus* var. *pectinatus*	$n = 11$	8, 9
var. *wenigeri* Benson	*E. pectinatus* var. *wenigeri*	$n = 11$	8
Section *Triglochidiatus*			
E. triglochidiatus Engelm.			
var. *gonacanthus* (Engelm. & Bigelow) Boissev.	*E. triglochidiatus* var. *gonacanthus*	$n = 11$	6
var. *gurneyi* Benson	*E. triglochidiatus* var. *gurneyi*	$n = 22$	10
		$2n = 44$	7
var. *melanacanthus* (Engelm.) Benson	*E. triglochidiatus* var. *melanacanthus*	$n = 22$	5, 6
		$2n = 44$	7
var. *neomexicanus* (Standley) Benson	*E. triglochidiatus* var. *neomexicanus*	$n = 22$	9
		$2n = 44$	7
var. *paucispinus* (Engelm.) W. T. Marshall	*E. triglochidiatus* var. *paucispinus*	$2n = 44$	7
Section *Echinocereus*			
E. berlandieri (Engelm.) Haage	*E. blanckii* (Poselger) Ruempler	$2n = 22$	2, 3
		$2n = 24$	1
E. chloranthus (Engelm.) Haage	*E. chloranthus*	$2n = 22$	7
var. *cylindricus* (Engelm.) N. P. Taylor	*E. viridiflorus* Engelm. var. *cylindricus* (Engelm.) Ruempler	$n = 11$	6, 7, 10
E. cinerascens (DC) Lem.	*E. cinerascens*	$n = 11$	9
E. enneacanthus Engelm.	*E. enneacanthus*	$n = 11$	1
		$2n = 22$	13
var. *enneacanthus*	*E. enneacanthus* var. *dubius* (Engelm.) Benson	$n = 11$	7
		$2n = 22$	13
var. *brevispinus* (W. O. Moore) Benson	*E. enneacanthus* var. *brevispinus*	$2n = 22$	7
E. papillosus Ruempler			
var. *angusticeps* (Clover) W. T. Marshall	*E. angusticeps* Clover	$n = 11$	1
	E. blanckii var. *angusticeps*	$n = 11$	8
var. *papillosus*	*E. papillosus*	$n = 11$	1

TABLE 2. Continued.

Taxon	Reported as	Count	Reference
E. pentalophus (DC) Lem.	E. pentalophus	$n = 11$	1
		$2n = 22$	2
E. stramineus (Engelm.) Ruempler	E. stramineus	$2n = 22$	13
E. viridiflorus Engelm.			
var. davisii (A. D. Houghton) W. T. Marshall	E. viridiflorus var. davisii	$2n = 22$	7
var. viridiflorus	E. viridiflorus var. viridiflorus	$n = 11$	6, 8
Section Reichenbachii			
E. chisoensis W. T. Marshall	E. reichenbachii (Walp.)	$n = 11$	8
var. chisoensis	Haage var. chisoensis (W. T. Marshall) Benson	$2n = 22$	7
E. reichenbachii (Walp.) Haage var. baileyi N. P. Taylor	E. reichenbachii var. albispinus (Lahman) Benson	$n = 11$	8
E. reichenbachii			
var. fitchii (Br. & Rose) Benson	E. fitchii Br. & Rose	$n = 11$	1
	E. reichenbachii var. fitchii	$n = 11$	8
	E. reichenbachii var. albertii Benson	$n = 11$	8
var. perbellus (Br. & Rose) Benson	E. reichenbachii var. perbellus	$n = 11$	8
var. reichenbachii	E. reichenbachii var. reichenbachii	$n = 11$	8
E. rigidissimus (Engelm.) Haage	E. pectinatus var. rigidissimus (Engelm.) Ruempler	$n = 11$	8

[a] References: 1. Beard, 1937; 2. Katagiri, 1953; 3. Remski, 1954; 4. Pinkava and McLeod, 1971; 5. Pinkava et al., 1973; 6. Pinkava, McGill, and McLeod, 1977; 7. Weedin and Powell, 1978; 8. Ross, 1981; 9. Pinkava and Parfitt, 1982; 10. Pinkava et al., 1985; 11. Pinkava et al., 1992; 12. Parfitt, 1987; 13. Moore, 1967.

ment that are considered to be the primitive condition in the genus (Taylor, 1985). Conversely, the tetraploid *E. triglochidiatus* var. *mojavensis* in section *Triglochidiatus* is rather unspecialized in its growth habit (Taylor, 1985), although its bird pollination syndrome is specialized (Taylor, 1985; Cota, 1993). The distribution of both primitive and advanced character states in some species of *Echinocereus* is not well known. However, it is possible that some of these characters have converged in those species having similar ecological requirements in geographically separated areas.

Polyploid taxa of *Echinocereus* are generally distributed from medium elevations (400 m) to elevations above 1,500 m, and from relatively low to high latitudes (approximately from 22° to 38°N latitude), compared to the overall distribution of the genus (Fig. 15). However, the majority of known localities of polyploid cytotypes are located at latitudes near 33°N (Fig. 15). Polyploids in *Echinocereus* seem to follow the same distributional pattern proposed for polyploids in other flowering plants, e.g., Stebbins (1971): the incidence of polyploidy in *Echinocereus* evidently increases with increasing latitude and elevation. In *Echinocereus* it is still unclear whether polyploidy characterizes the entire range of a species or only certain populations. Nonetheless, the above distributional pattern of polyploid cytotypes for the genus is predicted herein based on chromosome counts obtained in this study as well as on documented polyploid taxa reported in other bibliographic sources (Table 2).

Tetraploidy is considered to be the most successful condition among polyploids (DeWet, 1980). Indeed, tetraploidy is the most frequent form of polyploidy in the

Cactaceae (Pinkava et al., 1985). In *Echinocereus* all polyploids are tetraploids ($2n = 44$). Thus, it is not surprising that the success of polyploids in this genus might be reflected in their wide geographical distribution, e.g., apparently greater capacities to colonize new environments as has been suggested by Stebbins (1985) for polyploids in general. In the genus, polyploid cytotypes occupy areas where climatic changes are more extreme (lower temperatures and water availability). This finding supports Stebbins's (1971) and DeWet's (1980) arguments for the ability of polyploids to colonize new areas and persist in habitats with different environmental conditions than their diploid precursors.

Much of the controversy in phylogenetic and evolutionary issues in the Cactaceae is related to the lack of appropriate paleobotanical information. The available fossil material is not sufficient to assess relatedness or to reconstruct phylogeny. Thus, few phylogenetic hypotheses have been proposed. For *Echinocereus*, little insight into the evolutionary history of the genus is available; the existence of fossil record is limited to seeds of Holocene pack rat middens (Miller, 1988). Miller's cladistic analysis of 14 species of *Echinocereus* using floral flavonoids is the first detailed phylogenetic study in the genus, and concurs in part with that of Taylor's (1985) classification. Taylor suggested that *Echinocereus* originated in northwestern Mexico, from which the primitive species in sections *Morangaya*, *Erecti*, and *Triglochidiatus* arose. The genus then evolved and radiated into new areas in central and northern Mexico. Similarly, Miller's findings indicate that species of *Echinocereus* with ancestral flavonoid characters occur at the suggested center of origin in western
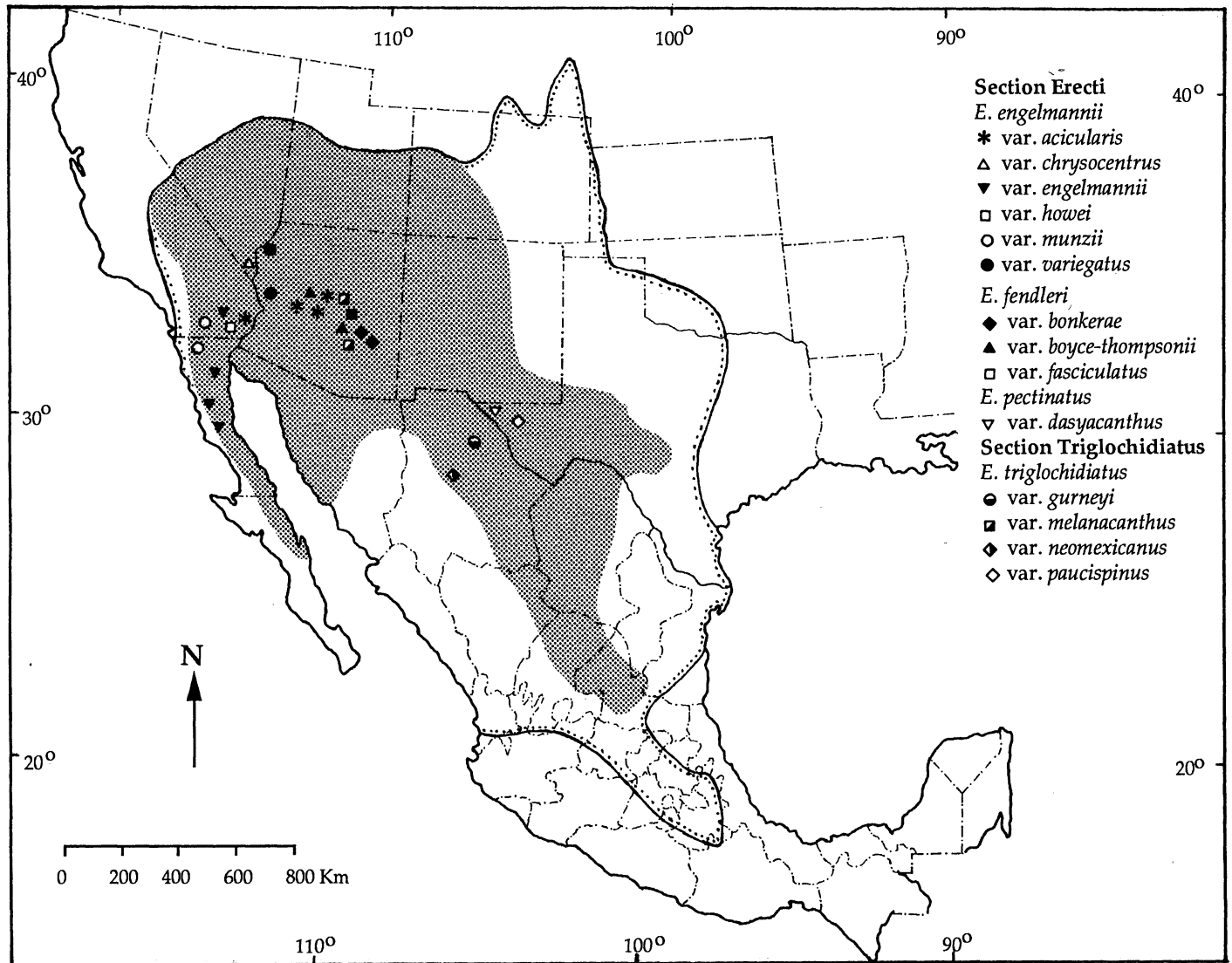
Fig. 15. Geographic distribution of polyploids in the genus *Echinocereus*. Symbols represent known localities of polyploid cytotypes. Solid/dotted line represents the overall distribution of the genus, and includes Baja California peninsula. The shaded area represents the predicted distribution of polyploids.

Mexico. Although polyploid cytotypes of *Echinocereus* are restricted to the primitive sections *Erecti* and *Triglochidiatus,* the occurrence of the basic number $x = 11$ in most of the Cactaceae, and especially in some sister genera of *Echinocereus,* e.g., *Nyctocereus* (Palomino, Zuleta, and Scheinvar, 1988), and *Hylocereus,* and *Peniocereus* (Cota, unpublished data) indicates that polyploidy is probably a derived condition in the genus. Indeed, in *Echinocereus* most polyploids have diploid relatives near the suggested center of origin. Whether polyploids in the genus are of neo- or ancient origin is unresolved. Isozyme and pale-obotanical information related to the origin of the genus would certainly be useful in clarifying this issue.

In *Echinocereus* the highest proportion of polyploid cytotypes is located in central Arizona and southern California (Fig. 15). The relatively high incidence of polyploids in these areas may simply reflect the fact that most individuals thus far investigated are distributed in these regions. However, considering Taylor's and Miller's phy-

logenetic ideas for the primitiveness of the genus, it is possible that polyploids in *Echinocereus* originated in central Arizona in members of the oldest sections of the genus. Indeed, many polyploid cytotypes from the primitive sections *Erecti* and *Triglochidiatus* occur there. From this area, polyploidy possibly radiated into new areas and evolved in other taxa of these sections, e.g., in Baja California within the *E. engelmannii* complex, and in northern Mexico and eastern Texas within section *Triglochidiatus.* By contrast, taxa in sections with intermediate and advanced characters, in particular sections *Wilcoxia* and *Pulchellus* (which are distributed further south), have not been studied cytologically. Thus the lack of documented cytotypes limits our understanding of the overall distribution of polyploid species of *Echinocereus.*

In the Cactaceae, polyploidy and hybridization have been suggested as important processes leading to speciation (Remski, 1954; Pinkava et al., 1985). It is evident that evolution in the genus *Echinocereus* is also related

to numerical changes in chromosomes (polyploidy). The existence of diploid and tetraploid phenotypically similar cytotypes in *E. fendleri* var. *bonkerae, E. chisoensis* var. *chisoensis, E. chloranthus* var. *cylindricus,* and the varieties of *E. pectinatus* and *E. triglochidiatus* suggests that polyploidy is playing a major role in the evolution of the genus. Moreover, hybridization is suspected to occur in nature in *Echinocereus* (D. J. Pinkava and B. D. Parfitt, ASU, personal communication). Additionally, the existence of populations with individuals exhibiting intermediate morphology relative to their putative progenitors (*E. englemannii* var. *engelmannii* and *E. engelmannii* var. *munzii* [Cota, personal observation]) may be a manifestation of natural hybridization or clinal variation of these varieties through an altitudinal range. These populations are located at an intermediate altitudinal range in which the plant communities are a mixture of xerophytic and woodland species. Also, these areas correspond to the geographic boundaries between the two taxa. The probable incidence of hybridization in the genus might be related to the geographical proximity of taxa allowing them to interbreed as has been proposed by Remski (1954) for the Cactaceae as a whole. Data derived from further studies regarding the patterns of variation in morphology and interspecific compatibility may provide insight into examples of intermediacy that are associated with hybridization and polyploidy in *Echinocereus.*

Because of the physical homogeneity of chromosomes within and between species of *Echinocereus* no structural differences (inversions, translocations) were detected, and if chromosomal rearrangements occur they remain cryptic. The use of techniques that allow higher resolution would be useful in detecting such rearrangements. Finally, molecular data derived from isozyme and cpDNA variation stand as powerful techniques to clarify the origin of hybrid species and polyploid complexes leading to the understanding of the evolutionary history of the genus.

LITERATURE CITED

BACKEBERG, C. 1960. Die Cactaceae. Band IV. Gustav Fisher Verlag, Jena.

BARTHLOTT, W. 1988. Uber die Systematischen Gliederungen der Cactaceae. *Beitrage zur Biologie der Planzen* 63: 17–40.

BEARD, E. C. 1937. Some chromosome complements in the Cactaceae and a study of meiosis in *Echinocereus papillosus. Botanical Gazette* 99: 1–20.

BEEKS, R. M. 1955. Improvements in squash technique for plant chromosomes. *Aliso* 3: 131–134.

BRAVO, H. 1937. Las Cactáceas de México. Universidad Nacional Autónoma de México, México.

BRITTON, N. L., AND J. N. ROSE. 1922. *Echinocereus.* 3–44. *In* The Cactaceae, vol. 3. Dover, New York, NY.

COTA, J. H. 1991. Karyotype evolution in the genus *Echinocereus.* Masters thesis, The Claremont Graduate School, Claremont, CA.

———. 1993. Pollination syndromes in the genus *Echinocereus:* a review. *Cactus and Succulent Journal* (Los Angeles) 65:19–26.

DEWET, J. M. J. 1980. Origin of polyploids. *In* W. H. Lewis [ed.], Polyploidy: biological relevance, 3–15. Plenum, New York, NY.

JACKSON, R. C. 1976. Evolution and systematic significance of polyploidy. *Annual Review of Ecology and Systematics* 7: 209–234.

KATAGIRI, S. 1953. Chromosome numbers and polyploidy in certain Cactaceae. *Cactus and Succulent Journal* (Los Angeles) 25: 141–143.

LEWIS, W. H. 1980. Polyploidy in angiosperms: dycotyledons. *In* W. H. Lewis [ed.], Polyploidy: biological relevance, 241–268. Plenum, New York, NY.

MAZZOLA, P., S. ROMANO, AND S. FICI. 1988. Contributo a la conoscenza del genere *Opuntia* Miller. Dati cariologici e distributivi delle specie spontaneizzate e coltivate in Sicilia. *Naturalista Siciliana* 12: 159–168.

MILLER, J. M. 1988. Floral pigments and phylogeny in *Echinocereus* (Cactaceae). *Systematic Botany* 13: 173–183.

MOORE, W. O. 1967. The *Echinocereus enneacanthus-dubius-stramineus* complex (Cactaceae). *Brittonia* 19: 77–94.

PALOMINO, H. G., S. ZULETA, AND L. SCHEINVAR. 1988. Estudios citogenéticos de dos especies y una variedad del género *Nyctocereus* (Cactaceae). *Boletín Sociedad Botánica de México* 40: 75–80.

PARFITT, B. D. 1979. *Acacia glanduligera* (Leguminosae): distribution and chromosome number. *Madroño* 26: 103.

———. 1987. *Echinocereus nicholii* (L. Benson) Parfitt, stat. nov. (Cactaceae). *Phytologia* 63: 157–158.

PINKAVA, D. J., M. A. BAKER, B. D. PARFITT, M. W. MOHLENBROCK, AND R. D. WORTHINGTON. 1985. Chromosome numbers in some cacti of western North America—V. *Systematic Botany* 10: 471–483.

———, L. A. MCGILL, AND M. G. MCLEOD. 1977. Chromosome numbers in some cacti of western North America—III. *Bulletin of the Torrey Botanical Club* 104: 105–110.

———, AND G. MCLEOD. 1971. Chromosome numbers in some cacti of western North America. *Brittonia* 23: 171–176.

———, ———, L. A. MCGILL, AND R. C. BROWN. 1973. Chromosome numbers in some cacti of western North America—II. *Brittonia* 25: 2–9.

———, AND B. D. PARFITT. 1982. Chromosome numbers in some cacti of western North America—IV. *Bulletin of the Torrey Botanical Club* 109: 121–128.

———, AND ———. 1988. Nomenclatural changes in Chihuahuan Desert *Opuntia* (Cactaceae). *Sida* 13: 125–130.

———, ———, M. A. BAKER, AND R. D. WORTHINGTON. 1992. Chromosome numbers in some cacti of western North America—VI, with nomenclatural changes. *Madroño* 39: 98–113.

REMSKI, M. F. 1954. Cytological investigations in *Mammillaria* and some associated genera. *Botanical Gazette* 116: 163–171.

Ross, R. 1981. Chromosome counts, cytology, and reproduction in the Cactaceae. *American Journal of Botany* 68: 463–470.

STEBBINS, G. L. 1971. Chromosomal evolution in higher plants. E. Arnold, London.

———. 1985. Polyploidy, hybridization, and the invasion of new habitats. *Annals of the Missouri Botanical Garden* 72: 824–832.

STOCKWELL, P. 1935. Chromosome counts in some Cactaceae. *Botanical Gazette* 96: 565–570.

TAYLOR, N. P. 1985. The genus *Echinocereus.* Timber Press, Portland, OR.

———. 1988. Supplementary notes on Mexican *Echinocereus* (1). *Bradleya* 6: 65–84.

———. 1989. Supplementary notes on Mexican *Echinocereus* (2). *Bradleya* 7: 73–77.

WEEDIN, J. F., AND M. POWELL. 1978. Chromosome numbers in Chihuahuan Desert Cactaceae. Trans-Pecos Texas. *American Journal of Botany* 65: 531–537.