8027522

LEUCK, EDWIN E., II

BIOSYSTEMATIC STUDIES IN THE ECHINOCEREUS VIRIDIFLORUS COMPLEX

The University of Oklahoma PH.D. 1980

University
Microfilms
International 300 N. Zeeb Road, Ann Arbor, MI 48106 18 Bedford Row, London WC1R 4EJ, England

PLEASE NOTE:

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark ✓.

1. Glossy photographs ✓
2. Colored illustrations ____
3. Photographs with dark background ✓
4. Illustrations are poor copy ____
5. Print shows through as there is text on both sides of page ____
6. Indistinct, broken or small print on several pages ____
7. Tightly bound copy with print lost in spine ____
8. Computer printout pages with indistinct print ____
9. Page(s) ____ lacking when material received, and not available from school or author
10. Page(s) ____ seem to be missing in numbering only as text follows
11. Poor carbon copy ____
12. Not original copy, several pages with blurred type ____
13. Appendix pages are poor copy ____
14. Original copy with light type ____
15. Curling and wrinkled pages ____
16. Other ____

THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

BIOSYSTEMATIC STUDIES IN THE ECHINOCEREUS VIRIDIFLORUS COMPLEX

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

EDWIN E. LEUCK II

Norman, Oklahoma

1980

BIOSYSTEMATIC STUDIES IN THE *ECHINOCEREUS VIRIDIFLORUS* COMPLEX

APPROVED BY

DISSERTATION COMMITTEE

PREFACE

This dissertation is prepared in the form of a manuscript to be submitted to a refereed journal. The format is that of American Journal of Botany.

I wish to thank Robert Ross, Ross Sherwood, and Jim Weedin for their help in locating and collecting plants for this study and for valuable discussions concerning relationships within the complex. I am grateful to Drs Elroy Rice, John Skvarla, Harley Brown, Norman Boke, and Michael Huft for reviewing the manuscript, and especially to Dr. James Estes for his constructive comments, friendship, and guidance. I also thank Beth Leuck for her aid in field work and review and preparation of the manuscript. A Sigma Xi Grant-in-Aid of Research provided financial support for some collecting trips.

TABLE OF CONTENTS

	Page
LIST OF TABLES	v
LIST OF FIGURES	vi
ABSTRACT	1
INTRODUCTION	3
METHODS	4
RESULTS	7
TAXONOMY OF THE _ECHINOCEREUS_ _VIRIDIFLORUS_ COMPLEX	19
EVOLUTION IN THE COMPLEX	40
LITERATURE CITED	44
TABLES	47
FIGURES AND FIGURE LEGENDS	56
APPENDICES	78

LIST OF TABLES

TABLE | Page

1. List of Characters for Numerical Analysis 47
2. Seed-set in the Complex 49
3. Hybrid Potential of the Complex 50
4. Hybrid Potential among Complex Members 52
5. Collection Sites 53

LIST OF FIGURES

FIGURE Page

1-2. Pollen of E. viridiflorus 57

3-6. Floral Patterns in the Complex 59

7. Flowering Phenology of Greenhouse Grown Complex Members 61

8. Flowering Periods of Complex Members . . . 63

9. Correlation Phenogram of OTUs of Complex 65

10. Distance Phenogram of OTUs of Complex . . . 67

11. Projection of Principal Component Analysis 69

12. Distribution of Complex Members 71

13. Apparent Naturally Occurring Hybrids in the Complex 73

14-16. E. viridiflorus var. weedinii var. nov. . . 75

17. Central Spines of Two Complex Members . . . 77

BIOSYSTEMATIC STUDIES IN THE *ECHINOCEREUS VIRIDIFLORUS* COMPLEX

Edwin E. Leuck[1]

Department of Botany and Microbiology,

University of Oklahoma, Norman 73019

[1]Present address: Department of Biology, Centenary College, Shreveport, Louisiana 71104

ABSTRACT

Pollen of the Echinocereus viridiflorus complex is uniform throughout the group. The pollen is isopolar, radially symmetrical, prolate spheroidal, tricolpate, and 44 - 52 μ in diameter with a puncti-baculate exine. Chromosome number is n = 11. All taxa are allogamous. The complex occurs with five other species groups in the genus, and artificial hybridization studies reveal isolation barriers with these sympatric populations; crosses with allopatric populations are significantly more fertile. Differential flowering phenology further isolates the E. viridiflorus complex from congeners. Within the complex, intertaxon F_1 fruit and seed-set are reduced only in crosses of E. viridiflorus var. davisii with taxa in the same geographic region, E. chloranthus var. neocapillus and E. viridiflorus var. correllii. Greenhouse studies reveal that variation in flowering phenology results from climatic variables except for the earlier flowering period of E. viridiflorus var. davisii. Numerical analyses employing correlation and distance phenograms and a three-dimensional projection of principal component analysis show discrete groups of OTUs representing E. viridiflorus var. viridiflorus, var. correlli, and var. davisii, E. russanthus, E. chloranthus var. neocapillus, and an undescribed form Weedinii. No separation of E. viridiflorus var. cylindricus and E. chloranthus var. chloranthus is revealed. The lack of morphological discontinuity suggests that the latter two taxa are not distinct. Based on morphological discontinuity, partial sterility with complex members, and discrete flowering period, E. davisii is considered a separate species. All other taxa in the complex are considered varieties of E. viridiflorus because of

the lack of incompatibility barriers and apparent naturally-occurring hybrids connecting each taxon with at least one other. I recognize the varieties *E. viridiflorus* var. *viridiflorus*, var. *cylindricus*, var. *correllii*, var. *russanthus*, var. *neocapillus*, and var. *weedinii*.

The genus *Echinocereus* Engelmann (Cactaceae) is a geographically widespread and ecologically diverse assemblage of the western United States and Mexico north of Puebla (Benson, 1969a). Estimates of the number of species range from 20 to 30 (Benson, 1969a) to 73 (Backeberg, 1960), and new species have been described subsequent to these works. The only treatments of *Echinocereus* have been as parts of familial treatises, notably those of Britton and Rose (1922) and Backeberg (1960). These classifications were based largely on gross external morphology of a small number of specimens.

The members of the *E. viridiflorus* Engelmann complex form a distinct group, distinguished from the remaining members of the genus by their relatively small flowers borne only on areoles that are at least two years old and an early flowering season. The complex is distributed from southwestern South Dakota south along the eastern foothills of the Rocky Mountains and adjacent plains to the Rio Grande in the Texas Big Bend region. Backeberg (1960) considered the complex to consist of a single species, *E. viridiflorus*, composed of five varieties. However, Benson (1969a) recognized *E. viridiflorus* var. *viridiflorus*, var. *cylindricus* (Engelmann) Engelmann *ex* Rümpler, var. *correllii* Benson, var. *davisii* (Houghton) W.T. Marshall, and *E. chloranthus* (Engelmann) Engelmann *ex* Rümpler. Weniger (1969) described two additional taxa, *E. chloranthus* var. *neocapillus* Weniger and *E. russanthus* Weniger.

Geographical and morphological boundaries among the taxa appear indistinct; however systematic studies are largely lacking. One difficulty in ascertaining relationships has been the limited number of collections. This study was initiated to increase the distributional and ecological information on the _E. viridiflorus_ complex and to investigate the relationships among forms, leading to a revision based upon systematic evidence including field studies, artificial hybridization experiments, micromorphology, and numerical taxonomic analyses.

METHODS--Living plants of all taxa of the _E. viridiflorus_ complex were collected from 1975 to 1980. Other species of _Echinocereus_ sympatric with members of the complex were also collected. Collection sites (Leuck, 1980, Appendix A) were chosen to encompass as much morphological, ecological, and geographical diversity as possible without regard to taxonomic status. For each population, geographic location, substrate, rainfall, exposure, altitude, and vegetational associations were recorded and sympatry with other _Echinocereus_ species was noted. By observing flowering plants in natural habitat throughout the day and visiting many populations, flowering phenology and reproductive biology of the plants in the field were also determined. Four to 10 plants were gathered at each site. Plants were transferred to greenhouses at the Animal Behavior Laboratory and the Department of Botany and Microbiology, University of Oklahoma.

Plants were grown in a uniform greenhouse environment from the time of collection through the flowering season of 1980. Flowering was induced by a cold treatment for three months (1 November - 1 February) with natural photoperiod, and daily minimum temperatures were frequently below freezing. Greenhouse flowering phenology for each taxon was established in 1978-1979.

Individuals of each population were tested for self-compatibility by artificial transfer of pollen from anthers to receptive stigmas. Diallele hybridizations for all taxa and other sympatric Echinocereus were attempted by removing pollen-bearing anthers with forceps and brushing pollen onto the adaxial surface of the stigma. Flowers were taped shut after pollen transfer to exclude potential visitors. F_1 compatibility was tested at several stages: fruit-set; seed-set; seed germination; and seedling survival, vigor, and fertility. F_2 and backcross hybrids were evaluated by the same criteria. Intrapopulational crosses for each parental population served as standards against which hybrids could be evaluated.

Because of the slow growth and maturation of seedlings it would have been impossible to fully evaluate intertaxon crosses. Many hybrid seedlings were grafted onto mature stems of E. viridiflorus var. viridiflorus to increase growth rate, reduce time to maturity, and allow survival of albino seedlings of those lacking vigor. Grafted seedlings flowered one to two years earlier than seedlings on their own roots.

Floral buds were collected from field and greenhouse plants for meiotic observation. Buds were fixed in ethanol: glacial acetic acid (3:1, v:v) and stained with alcohol-carmine HCl (Snow, 1973). Observations of meiotic figures were made with a Leitz Labolux microscope with phase optics.

Pollen, seeds, and spines were also examined microscopically. Pollen samples from each population were collected and stored in glacial acetic acid prior to analysis. A representative pollen sample was acetolyzed following the method of Erdtman (1960), mounted on a plug, and sputter-coated for examination with a Super II-ISI scanning electron microscope (SEM). Seeds and spines were examined under a light microscope.

Flowers were photographed under natural light conditions and with yellow, blue, visible light, and ultraviolet light transmitting filters to record any floral patterns not apparent under daylight but possibly visible to bees.

I compared the plants collected from 62 populations using numerical taxonomic analysis. Sixty-five morphological and 17 ecological characters (Table 1) were recorded for individuals of each population. I calculated means for each population which was treated as an operational taxonomic unit (OTU). Multivariate analyses of the data were conducted on an IBM 370-158 computer using the NT-SYS package of Rohlf, Kispaugh, and Kirk (1974) at the University of Oklahoma. Pearson product-moment correlation and average taxonomic distance coefficients were used for comparison of the OTUs (Sneath and Sokal, 1973) using unweighted pair groups with arithmetic means for standardized data. Cophenetic correlation coefficients were generated to measure the agreement between each phenogram and its original similarity matrix. A product-moment correlation matrix of characters was also computed and used for principal component analysis (Sneath and Sokal, 1973). The OTUs were projected as a three-dimensional model. A minimum spanning tree and cophenetic correlation coefficients were also computed for the model (Sneath and Sokal, 1973).

Herbarium specimens were borrowed for examination of morphological variation and the determination of distribution of the taxa from the following institutions: Bebb Herbarium, University of Oklahoma (OKL), University of New Mexico Herbarium (UNM), New Mexico State University Herbarium (NMC), Gray Herbarium, Harvard University (GH), Pomona College Herbarium (POM), Rancho Santa Ana Botanic Garden Herbarium

(RSA), University of Kansas Herbarium (KAN), Kansas State University Herbarium (KSC), Texas A & M University Herbarium (TAES), New York Botanical Garden Herbarium (NY), US National Herbarium (US), Sul Ross State University Herbarium (SRSC), University of Colorado Herbarium (COLO), University of Texas Herbarium (UT), Rocky Mountain Herbarium, University of Wyoming (RM), Missouri Botanical Garden Herbarium (MO), and Texas Technological University Herbarium (TTC). Voucher specimens were deposited in the Robert Bebb Herbarium of the University of Oklahoma.

RESULTS--Palynology--Palynological surveys in the Cactaceae have demonstrated considerable diversity in cactus pollen that proved useful as a taxonomic tool (Kurtz, 1948, 1963; Tsukada, 1964; Leuenberger, 1975). Leuenberger (1975) provided a brief description of pollen diameter and number of colpi of an unspecified variety of E. viridiflorus and var. davisii (as E. davisii) from plants in cultivation. I examined 21 samples of pollen from all taxa within the E. viridiflorus complex and found all samples to be similar (Fig. 1, 2). The grains are isopolar, radially symmetrical, and prolate spheroidal as defined by Erdtman (1959). The exine is punctate with baculae or spinules. Cross-sections show a well-developed tectum, columellae, foot layer, and endexine. In the aperture regions the columellae are lacking, and the outer and inner walls are appressed to each other. Pollen of all taxa in the complex was found to be tricolpate and 44-52 μ in diameter. Occasional grains were syncolpate. Size range corresponds with that reported by Leuenberger (1975), but he noted that 1% of the grains were hexacolpate in E. viridiflorus. Pollen of all other congeners found within the range of the E. viridiflorus complex is similar in surface ornamentation and wall structure to that of the E. viridiflorus complex. These species, however, have 3 - 15 colpi and are 55-71 μ in diameter. The similarities in size and aperture number indicate that the taxa within the complex are more closely allied to one another than to other species of Echinocereus.

Chromosomal analysis--Several workers have reported chromosome counts for the E. viridiflorus complex (Pinkava et al., 1977; Weedin and Powell, 1978a, 1978b; Kolle, 1978). I observed meiosis in anther squashes from plants of 22 populations representing all taxa (Leuck, 1980, Appendix A). The chromosome number of all samples was n = 11 and in agreement with all previous counts. Chromosomes of the complex lack secondary associations, distinct heterochromatic regions, or other markers by which a detailed analysis could be made.

Floral biology and pollination--Flowers in the Echinocereus viridiflorus complex range from cylindrical through campanulate to rotate. Perianth parts are initiated centripetally and include transitions from rudimentary outer segments to longer petaloid inner parts. Stamens are initiated centrifugally, but develop synchronously (Ross, pers. comm.), and number from 20 to over 100. The style is elongate and erect and extends above the stamens. The stigma is erect to spreading and consists of five to nine lobes. Small nectaries are present at the base of the stamens.

In the field, plants flower from early February in the Big Bend region of Texas (E. viridiflorus var. davisii) through late June in the Black Hills of South Dakota (E. viridiflorus var. viridiflorus) (Fig. 2). Greenhouse studies reveal that in all taxa of the complex except E. viridiflorus var. davisii, most variation in time of anthesis in the field is due to climate and not to endogenous differences in periodicity (Fig. 3). The members of the E. viridiflorus complex flower before sympatric congeners. The flowering period in a population usually lasts 12 - 20 days, but this may be extended by late spring rainfall. From one to more than 10 flowers may occur on an individual in a season; normally the flowers on the south side of the plant mature first. Flowers open fully only on warm, sunny days. Cool or cloudy weather may delay the onset of flowering, retard full opening of flowers, or even inhibit opening completely.

Flowers are diurnal and open between 1000 and 1100 hr CDT. Full opening is achieved within 30 min, and flowers continue to open for three to four days and close at night. Time of anther dehiscence closely coincides with time of flower opening. Artificial pollen transfer and examination of excised stigmas for pollen tube growth demonstrate that the stigmas are receptive when the flowers open and remain so for at least three days. Flowers close when daily temperatures and light intensity decrease. Closure with sudden cool or cloudy conditions substantiates this inference.

Photographs taken of the taxa in sunlight with yellow, blue, and visible light transmitting filters revealed no differences in floral appearance. Photographs taken with a filter transmitting only UV light revealed two consistent floral patterns. In E. viridiflorus var. viridiflorus, var. correllii, and var. davisii the margins of the perianth segments reflect UV, whereas the inner segments, stamens, and pistil mostly absorb UV, giving the flowers a contrasting margin and center (target type blossom) (Fig. 3, 4). In E. russanthus, E. viridiflorus var. var. cylindricus, E. chloranthus var. chloranthus and var. neocapillus, and a previously undescribed form which I provisionally refer to as Weedinii, all floral parts absorb UV light, giving a uniform appearance (Fig. 5, 6). This phenomenon holds true regardless of whether the flowers are greenish-yellow, reddish, or reddish with a greenish-yellow center. The target pattern is correlated with a lemon odor not found in the latter floral pattern. These floral patterns are not altered as the flowers mature.

Pollination is by solitary halictid bees and usually occurs within the first two hours after anthesis. I failed to observe visitation by other potential pollinators, except in cultivated gardens where Apis mellifera Linnaeus frequently visited. The bees usually alight on the lobes of the stigma and crawl down the style into the yellow pollen mass presented on the dehisced anthers. They may either forage for pollen or move to the nectaries at the base of the stamens. Nectar is produced in minute quantities (less than 1 µl) and is available soon after anthesis only on the first day of flowering. As the bees emerge from the pollen mass, pollen completely covers their bodies. The bees shift some of the pollen load to the pollen baskets while they are positioned on the bases of the inner perianth segments or on the stigma lobes. Although a full pollen load could be easily collected from a single flower, the bees visit several flowers in close proximity, gathering small amounts of pollen in each, before departing. The small nectar reward may influence multiple flower visits, which in terms of pollen collection only are energetically wasteful. Flight nearly always takes place from the stigma in cylindrical flowers; in more open forms, flight may be initiated from the stigma or the expanded perianth parts. Visitation by bees within a population of cacti appears to be random. Bees do not appear to select any distinctive floral shape, color, or vegetative morphology when such variability occurs. The pollen is usually not depleted by the bees in a single day, and pollen-gathering flights may occur for as many days as the flowers remain open. Other anthophilous foragers are primarily small flower-eating beetles and early instar grasshoppers.

In drought years flowers of Echinocereus provide a valuable food resource for bees, perhaps permitting survival of populations when ephemeral and moisture-dependent flowers are unavailable or in limited number and scattered. However, when adequate rainfall promotes heavy flowering of other plants, bees apparently visit flowers with more substantial nectar rewards, and flowers of the E. viridiflorus complex are virtually ignored. Consequently fruit and seed-set should be lower in wet years than in times of water stress. The only test of this hypothesis occurred in 1979 when winter and early spring rains prior to flowering led to minimal bee visitation of E. russanthus and E. chloranthus var. neocapillus in the Big Bend region of Texas and subsequent reduction in fruit and seed-set compared to the drought season of 1978. This meteorological cycle presumably favors generalist foragers in the E. viridiflorus complex, as floral resources are consistently available each year.

No evidence of apomixis or autogamy was found since flowers in insect exclusion studies failed to set fruit. After cross-pollination, germination of the pollen and growth of the pollen tube occur within four to eight hours. Development of the fruit may be induced by as few as three or four pollen grains. The ovary consists of five to nine indistinct carpels forming a unilocular chamber with an indeterminate number of ovules ranging from as low as 40 (*E. viridiflorus* var. *davisii*) to over 400 (several varieties of *E. viridiflorus*) per ovary. Seed-set in the field varies from averages of 57-90% for each taxon in the *E. viridiflorus* complex (Table 2; Leuck, 1980, Appendix D).

Interspecific hybridization--The *E. viridiflorus* complex is sympatric with five other species groups in *Echinocereus* over parts of its range. All are presumed to be allogamous based on failure to set fruit in greenhouse self-compatibility experiments. *Echinocereus triglochidiatus* Engelmann may occur in close association with each taxon of the complex in rocky igneous habitats from the Rio Grande in Big Bend National Park north to the upper Arkansas River valley in south-central Colorado. *Echinocereus reichenbachii* (Terscheck) Haage var. *reichenbachii* is sympatric with *E. viridiflorus* var. *viridiflorus* on alluvial bluffs along major river courses in southern Colorado, eastern New Mexico, the western Texas Panhandle, and extreme southwestern Kansas. *Echinocereus fendleri* (Engelmann) Engelmann *ex* Rümpler var. *fendleri* occurs sympatrically with *E. viridiflorus* var. *viridiflorus* on the rocky high plains of north-central and northeastern New Mexico and with *E. chloranthus* var. *chloranthus* and *E. viridiflorus* var. *cylindricus* in the mountains of southern New Mexico and extreme western Texas. *Echinocereus enneacanthus* Engelmann var. *stramineus* (Engelmann) Benson is sympatric with *E. chloranthus* var. *chloranthus*, *E. russanthus*, and *E. viridiflorus* var. *cylindricus* in southern New Mexico and the Big Bend region of Texas. *Echinocereus pectinatus* (Scheidweiler) Engelmann var. *neomexicanus* (Coulter) Benson occurs with each taxon in the complex from central New Mexico south to the Rio Grande in Big Bend National Park. Despite the sympatric occurrence of these taxa with the *E. viridiflorus* complex no apparent hybrids have been found to occur in the field.

Equation 1,

$$HP = \frac{\text{number of fruits}}{\text{potential fruits}} \times \frac{\text{number of seeds}}{\text{potential seeds}} \times 100 \qquad (1)$$

was used as a first order approximation of hybrid potential (HP). I found that values of HP obtained in greenhouse crosses between the *E. viridiflorus* group and sympatric populations of other *Echinocereus* species were 1.0% or lower (Table 3). Incompatibility may be attributed to differences in ploidy level only in crosses with tetraploid *E. pectinatus* var. *neomexicanus*, southern forms of *E. triglochidiatus*, and possibly *E. enneacanthus* var. *stramineus*. Germination tests for F_1 seed from these crosses was 0-30%. The seedlings exhibited a high degree of albinism and weak growth; less than 30% achieved flowering size. Of these, approximately 50% exhibited total pollen sterility. The few F_2 and backcross hybrid seeds that were obtained germinated poorly (0-20%) and all lacked vigor or were albino. Thus, potential for gene flow between the *E. viridiflorus* complex and other sympatric *Echinocereus* species is almost nil.

In addition, the isolation barrier appears practically complete based on flowering phenology. In most years there is no overlap in the flowering period of the *E. viridiflorus* complex with sympatric congeners. However, in seasons when rainfall persists into early summer, a limited number of secondary buds may be initiated so the flowering season may overlap with the beginning of the flowering period of other sympatric *Echinocereus* species. This phenomenon is relatively uncommon. Therefore, this complex is genetically isolated, and I consider it to be a morphologically discontinuous and distinct unit within the genus

Echinocereus.

The low hybrid potential in crosses with sympatric noncomplex congeners is consistent with the view of Grant (1963) that strong incompatibility barriers generally exist between sympatric plant species thereby reducing genetic loss. However, within the *E. viridiflorus* complex, genetic barriers are less pronounced when the alien parent is allopatric than when sympatric (Table 3). For example, populations of *E. reichenbachii* var. *reichenbachii* that are sympatric with *E. viridiflorus* have a hybrid potential (HP) of 1.0% while populations that are allopatric have a HP of 11.4%. This relationship also holds when comparing crosses of the *E. viridiflorus* complex with sympatric and allopatric *Echinocereus* species. Crosses with allopatric taxa have hybrid potential values significantly greater than hybrids with sympatric taxa (Table 3). Seed germination of allopatric hybrids is 30-65% while that of sympatric hybrids is 10-42%, and is more rapid than in sympatric hybrids or field collected seed of the female parent. Allopatric hybrids are vigorous and lack the albinsim which is present in sympatric hybrids. It would thus appear that genetic barriers to hybridization are maintained more rigorously between the *E. viridiflorus* complex and sympatric populations of other *Echinocereus* species than with allopatric ones.

Intraspecific hybridization-- Greenhouse hybridization experiments were conducted among the eight previously described taxa in the complex and Weedinii (Table 4). These data indicate that reduction of hybridization potential at this level is slight, especially if compared to genetic barriers that exist between the *E. viridiflorus* complex and other *Echinocereus* species. The only exception to this generalization is *E. viridiflorus* var. *davisii*. This partial barrier to interbreeding involving E. viridiflorus var. davisii is greatest (HP = 43-54%) in the crosses with the taxa geographically and ecologically closest to E. viridiflorus var. davisii, namely E. chloranthus var. neocapillus and E. viridiflorus var. correllii. Reduction of hybrid potential below 75% is not found in crosses of E. viridiflorus var. davisii with geographically more distant taxa. This suggests that the maintenance of genetic barriers to interbreeding is favored only in areas of potential hybridization between E. viridiflorus var. davisii and other members of the E. viridiflorus complex. Crosses between all other taxa in the complex result in a hybrid potential of at least 71%, indicating the lack of strong isolation barriers at this level of genetic interaction among members of the E. viridiflorus complex.

Germination of seed generated within a given population is 30-65% in the first two years after planting; third year germination is minimal. Greenhouse studies show a similar germination record for several species groups in Echinocereus (Leuck, unpubl.; Ross, pers. comm.). Germination of seeds from the northern E. viridiflorus var. viridiflorus occurs primarily throughout the first season; in E. viridiflorus var. davisii germination occurs rapidly within one month of planting or early in spring of the second year; in all other taxa in the complex germination is relatively equally spaced across the first two years after planting and is not synchronous. Germination of inter- and intrataxon hybrid seed is also 30-65% in the first two years after planting. Survival of intertaxon F_1 and intrapopulational seedlings is 82-95%. No plants reaching flowering size were observed to be male or female sterile. F_2 and backcross hybridizations failed to reveal any further incompatibility barriers among the taxa in the complex.

Flowering phenology in the *E. viridiflorus* complex is also an important consideration in the delineation of those taxa. In the greenhouse most of the forms have a major portion of their flowering period in common with other taxa (Fig. 7). The exception is *E. viridiflorus* var. *davisii*. This taxon is the first to flower, and, under uniform environmental conditions, has little overlap in flowering period with other taxa in the complex, especially with the two forms with which it is most nearly sympatric. This difference is reflected in the field (Fig. 8), where *E. viridiflorus* var. *davisii* flowers from early February to mid-March. The two taxa geographically closest to it, *E. chloranthus* var. *neocapillus* and *E. viridiflorus* var. *correllii*, do not begin flowering until the end of the flowering period of *E. viridiflorus* var. *davisii*. In years when spring rains persist, there may be a small number of secondary flowers initiated in *E. viridiflorus* var. *davisii*. Despite the presence of apparently suitable habitat for F_1s, I found no hybrids between *E. viridiflorus* var. *davisii* and *E. viridiflorus* var. *correllii* or *E. chloranthus* var. *neocapillus*.

Cluster analysis-- Cluster analyses were undertaken to assist in detecting variational patterns and discontinuities within the complex and in formulating a taxonomic system. Sixty-two populations were sampled (Table 5). Inequality in the number of representative populations for each taxon is a reflection of the relative abundance of each taxon.

Correlation (Fig. 9) and distance phenograms (Fig. 10) constructed for 87 morphological and ecological characters of the 62 populations produced correlation coefficients of 0.914 and 0.931 respectively.

The correlation phenogram (Fig. 9) has three large, loosely linked clusters: (1) SODAKOTA-MATADOR, (2) SANMATEO-CHIN31, and (3) NINEPT-8MWMARTN. The first of these includes only and all populations of E. viridiflorus var. viridiflorus. The second group encompasses two major subsets, SANMATEO-ELGIN and LKVALLEY-CHIN31. The first subset encompasses most populations of E. viridiflorus var. cylindricus and E. chloranthus var. chloranthus. This subset has no highly correlated populations and subclusters do not correlate with either of the above two taxa alone. The second subset includes an E. chloranthus var. chloranthus population (LKVALLEY), three populations considered to be morphologically intermediate between E. viridiflorus var. cylindricus and Weedinii (TM5300, TM5600, TM5900), and the three highly correlated populations of Weedinii. In this large grouping the lack of correlations higher than 0.6 between any E. viridiflorus var. cylindricus and E. chloranthus var. chloranthus populations is an indication of the diversity of these taxa. The third large cluster of this phenogram inclues several taxa of limited distribution. A first coherent subunit with correlations about 0.6 or greater is NINEPT-LWRCATOK and represents E. russanthus. LRYNEOCP and BRLNEOCP are correlated at approximately the 0.8 level and represent E. chloranthus var. neocapillus. This unit is weakly linked to ROBRTLEE, a disjunct population that appears to have features of both E. chloranthus var. neocapillus and E. viridiflorus var. correllii. The single population of E. viridiflorus var. davisii (DAVISII) is not closely linked to any other. 1MEMARTN and FTPINACO are a tightly clustered unit representing E. viridiflorus var. correllii. 8MWMARTN is not closely linked to any other unit in the major group; its morphology is intermediate between E. viridiflorus var. correllii and var. cylindricus.

The distance phenogram (Fig. 10) has a large, tight cluster from SODAKOTA-MANZANO that includes only E. viridiflorus var. viridiflorus. This unit is loosely linked with E. viridiflorus var. viridiflorus from the Texas Panhandle (POTTERTX-MATADOR), ROBRTLEE and 8MWMARTN, the latter two populations having at least some of the characters of E. viridiflorus var. correllii. A second large grouping in this phenogram is SANMATEO-CHIN31. This grouping includes all populations of E. viridiflorus var. cylindricus and E. chloranthus var. chloranthus except ELGIN, which was obtained from a commercial source. The populations of these two taxa are apparently interspersed randomly with each other and with those populations which exhibit some characteristics of each taxon. The lower portion of the phenogram indicates moderately correlated small units and poor linkages of larger groups. NINEPT-MCKINNEY represents E. russanthus. The two OTUs of E. chloranthus var. neocapillus are clustered together (LRYNEOCP, BRLNEOCP) and are loosely linked to E. russanthus. The three populations of Weedinii (LIVRMORE-CATTAIL) are here highly correlated and not close to any other group. DAVISII (E. viridiflorus var. davisii) is the single taxon most distant from all other populations in the complex.

The cluster analyses would seem to indicate several coherent units that correlate well with existing taxa. Cohesive units include E. russanthus, E. chloranthus var. neocapillus, E. viridiflorus var. viridiflorus, var. davisii, and var. correllii, and Weedinii. Only Weedinii has not been taxonomically recognized. However, populations of E. chloranthus var. chloranthus and E. viridiflorus var. cylindricus cluster tightly, and the two could not be discriminated.

Principal component analysis--The first three components of principal component analysis of characters account for 42.9% of the variation in the data. High loadings for Component I include field and greenhouse plant height and shape, latitude, fruit dehiscence, and fleshiness. Component II is influenced largely by fruit width, radial and fruit spine diamter, radial spine color and substrate. Spine color, fruit length, seed-set, altitude, odor, and number of ovary areoles influenced Component III.

The three-dimensional projection of these first three axes of the principal component analysis displays seven discrete clusters of OTUs that roughly correspond to the taxa of previous authors (Fig. 11). The northern OTUs constitute a tight cluster corresponding to *E. viridiflorus* var. *viridiflorus*. *Echinocereus viridiflorus* var. *cylindricus* and *E. chloranthus* var. *chloranthus* again cluster closely and cannot be distinguished, and the single cluster includes OTUs that reflect mixed populations. Weniger's *E. chloranthus* var. *neocapillus* and *E. russanthus* form distinct clusters as do *E. viridiflorus* var. *correllii*, Weedinii, and *E. viridiflorus* var. *davisii*. Two OTUs representing hybrid populations are included in the analysis but are not considered as members of a single taxon.

TAXONOMY OF THE *ECHINOCEREUS VIRIDIFLORUS* COMPLEX

Description of the complex--STEMS usually solitary, depressed-globose to cylindrical, 1-25 cm long, 1-9 cm in diameter; ribs 6-17; areoles elliptical to round, 1.5-3.0 mm long and broad; SPINES acicular to subulate, white, golden-yellow or reddish-purple, if white then often with reddish-purple apices; spines often in alternating light and dark bands; central spines 0-10, porrect, deflexed or ascending, diameter at base 0.20-0.75 mm, longest 6-30 mm; radial spines 8-32, pectinate, appressed to slightly ascending, lowermost one longest, 4.2-14 mm long, diameter at base 0.20-0.45 mm; FLOWERS borne low on stem on growth at least two years old, 1.5-2.5 cm in diameter, cylindrical, campanulate or rotate, greenish-yellow to rust-red, sometimes with bases light and distal margins reddish; sepaloid perianth parts linear, midribs dark, apex acute, entire; petaloid perianth parts longer, 1.0-2.9 cm long, linear to oblanceolate, apex entire, acute or mucronate; filaments pale green, 4-8 mm long; anthers yellow, 0.5-1.5 mm long; stigma and style bright green to pale greenish-yellow, stigma lobes 5-9, spreading or erect; ovary areoles 10-30, usually shed at maturity of fruit, spines 10-25, white, diameter at base 0.07-0.21 mm, 4.0-11.5 mm long; FRUIT at maturity green to red, dry and dehiscent along longitudinal sutures or fleshy and indehiscent, round to twice as long as broad, 6.2-17.0 mm long, 4.0-12.0 mm in diameter; SEEDS 0.9-1.4 mm long, 0.8-0.9 mm broad, 0.7 mm thick, surface tuberculate with bold to indistinct reticulate pattern. Chromosome number *n* = 11.

KEY TO SPECIES

1 Stem largely subterranean, above ground portion 1-2 cm high, 1-2 cm broad; ribs 6-9, tubercles distinct; flowering early February to mid-March. . . . . *E. davisii*

1 Stems entirely aerial, 3-25 cm high, 3-9 cm in diameter; ribs 11-17, tubercles confluent; flowering late March to late June . . . . *E. viridiflorus*

Echinocereus davisii A.D. Houghton, Cact. Succ. J. Amer. 2: 466. 1931.

TYPE: Texas, Brewster Co., 4 m S Marathon, under *Selaginella*,

1931. A.D. Houghton 700 (holotype US1566585!; isotypes NY, not found, UC, GH!).

Echinocereus viridiflorus Engelmann var. davisii (A.D. Houghton) W.T. Marshall in Marshall and Bock, Cactaceae 119. 1941, nom. nud., validated by Backeberg, Cactaceae 4: 2017. 1960.

STEMS usually solitary, largely subterranean, obovoid, above ground portion depressed-globose, dark green, 1-2 cm long, 1-2 cm in diameter; ribs 6-9, weakly coalesced from prominently raised tubercles; areoles elliptical, 2 mm long, 1.5 mm broad; SPINES reddish-purple or white with reddish-purple apices, straight or curving upward, obscuring the surface of the plant; central spine lacking or occasionally one present in age, reddish-purple, 10-12 mm long; radial spines 8-14, pectinate, ascending, upper ones short, slender, lowermost ones longest, 5-13 mm long, diameter at base 0.35 mm; FLOWERS borne on lower 3/4 of aerial stem, greenish-yellow, campanulate or occasionally rotate, 1.5-2.0 cm in diameter, having a weak lemony scent; sepaloid perianth parts 1-1.5 cm long, linear to oblanceolate, apex entire, acute; filaments pale green, 5-8 mm long; anthers yellow, 0.5-1.2 mm long, stigma and style pale green, stigma lobes 5-7, erect or spreading; ovary areoles 10-14, shed at maturation of fruit, spines 10-12, white, diameter at base 0.15 mm, 5-6 mm long; FRUIT at maturity green, dry, dehiscent along longitudinal sutures, ca. twice as long as broad, 9-11 mm long, 4-5.5 mm in diameter; SEEDS 0.9-1.0 mm long, 0.8-0.9 mm broad, surface tuberculate; spines of seedlings pectinate, plumose, white, appressed to the stem.

Distribution and habitat: Caballos novaculite hills south of Marathon, Brewster County, Texas. Plants are seldom emergent from the mat of Selaginella in which they grow. This is the only known population, and plants have been heavily collected by cactus poachers. Possibly less than 100 individuals exist in nature. Only their diminutive nature has preserved the native stand. Because the fruits are dry and dehiscent at maturity, seed dispersal is extremely localized. The species has been declared Endangered (Fish and Wildlife Service, 1980).

Benson designated a neotype (POM317432!) that is here considered to be invalid, because isotype material examined (GH!) is adequate for identification. The holotype at US and isotype at NY were not found.

Echinocereus davisii Houghton has plumose, pectinate juvenile spines and produces a large underground stem, with as little as 10% of the stem projecting above the Selaginella mat. In times of water stress the stem shrinks, which pulls the plant totally beneath the Selaginella cover. The plants flower in early spring and set seed prior to the onset of high summer temperatures. Germination of seeds may occur within days if moisture is present, and usually occurs within one season.

The dwarf nature of the stems, large underground portion, and low rib number readily separate this taxon from any other taxon in the complex. The distance phenogram (Fig. 10) and principal component analysis (Fig. 11) further demonstrate that E. davisii is most dissimilar to all other OTUs in the complex. Echinocereus davisii is therefore morphologically discontinuous with E. viridiflorus. Echinocereus davisii is also genetically isolated from E. viridiflorus. It is partially intersterile, especially with E. viridiflorus var. correllii and E. viridiflorus var. neocapillus, which grow within six km of the E. davisii population on the novaculite. Flowering period is also discrete, further delineating this taxon. This view is supported by the apparent lack of natural hybrids. For these reasons I recognize E. davisii as a distinct species.

Echinocereus viridiflorus Engelmann in Wislizenus, Mem. Tour. N. Mex. 91. 1848.

TYPE: New Mexico, probably Santa Fe Co., near Wolf Creek on Santa Fe road, 1846. Dr. A. Wislizenus 514 (lectotype MO2016902!).

STEMS usually solitary, globose to cylindrical, 3-25 cm long, 3-9 cm in diameter; ribs 11-17, tubercles indistinct; areoles elliptical to round, 1.5-3.0 mm long and broad; SPINES acicular to subulate, white, golden-yellow or reddish-purple, if white then often with reddish-purple apices; spines often in alternating light and dark bands; central spines 0-10, porrect, deflexed or ascending, diameter at base 0.20-0.75 mm, 6-30 mm long; radial spines 12-36, pectinate, appressed or slightly ascending, lowermost ones longest, 4.2-14 mm long, diameter at base 0.20-0.45 mm; FLOWERS borne low on stem from areoles at least two years old, 1.5-2.5 cm in diameter, cylindrical, campanulate or rotate, greenish-yellow to rust-red, sometimes with basal portions light and distal margins reddish; sepaloid perianth parts linear, midribs darker, apex acute and entire; petaloid perianth parts longer, 1.0-2.0 cm long, linear to oblanceolate, apex entire, acute or mucronate; filaments pale green, 4-8 mm long; anthers yellow, 0.5-1.5 mm long; style and stigma bright green to pale greenish-yellow, stigma lobes 5-9, erect or spreading; ovary areoles 13-30, usually shed at maturation of fruit, spines 10-25, white, diameter at base 0.07-0.21 mm, 4.0-11.5 mm long; FRUIT at maturity green to red, dry and dehiscent along longitudinal sutures or fleshy and indehiscent, round to twice as long as broad, 6.2-17.0 mm long, 6.1-12.0 mm in diameter; SEEDS 0.9-1.4 mm long, 0.8-1.4 mm broad, 0.7 mm thick, surface tuberculate.

Field observations based on morphological evidence reveal possible hybridization among several of these taxa (Fig. 13). Intermediate states include number, size, and coloration of spines; flower color and shape; and fruit color, fleshiness, shape, and dehiscence. Hybrids of the above taxa generated in the greenhouse exhibit identical morphological traits as the presumed naturally-occurring hybrids when found.

Because of overlap in flowering periods (Fig. 8), lack of incompatibility barriers (Table 4), and apparent hybridization in the field linking all taxa except E. davisii (Fig. 13), I consider the remainder of the E. viridiflorus complex to consist of a single variable species, E. viridiflorus Engelmann.

Except in the case of E. viridiflorus var. cylindricus and E. chloranthus var. chloranthus, the areas of sympatry are few and restricted in size. The apparent hybrid swarms contain few individuals relative to the size of the contributing parental populations. However, several populations which include E. viridiflorus var. cylindricus and E. chloranthus var. chloranthus also include a full array of intermediate forms uniting the two taxa.

Principal component analysis provides a means to evaluate ecological and morphological variation within the species (Fig. 11). Distinct clusters are shown that correspond with each taxon recognized by either Benson (1969a) or Weniger (1969) with the exception of E. chloranthus var. chloranthus, the OTUs of which are inseparable from E. viridiflorus var. cylindricus. An additional cluster shown corresponds to Weedinii.

Within the species *Echinocereus viridiflorus* I recognize the following: var. *viridiflorus*, var. *cylindricus*, var. *correllii*, var. *russanthus*, var. *neocapillus*, and var. *weedinii* (Fig. 14-16).

Distribution and habitat: Granite soils and outcrops in southwestern South Dakota, southeastern Wyoming and the east slope of the Rocky Mountains through Colorado and northern New Mexico; granite, sandstone, alluvium, and (rarely) limestone derived soils and outcrops in the short-grass prairie of eastern Colorado, northeastern New Mexico, and extreme western Nebraska, Kansas, Oklahoma and the Texas Panhandle; granite and limestone mountains of southern New Mexico and western Texas south to the Rio Grande and adjacent Mexico; Caballos novaculite in Brewster Co., Texas.

KEY TO THE VARIETIES OF *ECHINOCEREUS VIRIDIFLORUS*

1 Radial spines 12-20

  2 Plants globose to short-cylindrical; flowers rotate with a lemon scent; mature fruits dry, green, dehiscent along longitudinal sutures. . . . . . var. *viridiflorus*

  2 Plants cylindrical; flowers mostly cylindrical to campanulate, lacking lemon scent; mature fruits fleshy, red, indehiscent, with sweet pulp . . . . var. *cylindricus*

1 Radial spines (20-)22-36

  3 Central spines 0-2; flowers with a lemon scent. . . . . var. *correllii*

  3 Central spines 6-10; flowers lacking lemon scent

    4 Juvenile spines flexuous, 2-5 cm long; radial

spines 6.0-7.5 mm long; mature fruits dry, green, dehiscent along longitudinal sutures, twice as long as broad . . . . .var. _neocapillus_

4 Juvenile spines rigid, less than 1 cm long; radial spines 7.0-18 mm long; fruits at maturity fleshy, green or red, indehiscent, mostly globose

5 Spines golden-yellow; perianth parts yellow to yellow-orange; seedling spines pectinate; fruits mostly red . . . var. _weedinii_

5 Spines red at tip; perianth parts red at apex; seedling spines divergent; fruits green. . . . . var. _russanthus_

Echinocereus viridiflorus Engelmann in Wislizenus, Mem. Tour. N. Mex. 91. 1848.

var. _viridiflorus_

Cereus viridiflorus Engelmann in A. Gray, Mem. Amer. Acad. 4: 49. 1849.

Cereus viridiflorus Engelmann var. _minor_ Engelmann, Proc. Amer. Acad. 3: 278. 1856.

Echinocereus viridiflorus Pritzel, Econ. Bot. Index 2: 113. 1866.

Echinocereus Labouretianus Lemaire, Cactées 57. 1868.

Echinocereus Labourettii Forster _ex_ Rümpler _in_ Forster, Handb. Cact., ed. 2, 811. 1885.

STEMS solitary or cespitose, globose to short-cylindrical, mostly broader than tall, 3-9 (-18) cm long; ribs 10-15; SPINES white or reddish-purple, frequently white with reddish-purple apices; spines often in alternating bands of color; central spines 0-1 (-3), porrect, stout, diameter at base 0.31-0.60 mm, 8-20 mm long; radial spines 12-18, pectinate and appressed to the stem, 4.2-8.0 mm long, diameter at base 0.19-0.32 mm; FLOWERS campanulate to rotate, greenish-yellow, having a strong lemony scent; ovary areoles 13-19, spines 10-14, 4.0-6.5 mm long, diameter at base 0.08-0.13 mm; FRUITS at maturity green, dry, dehiscent along longitudinal sutures, ca. 1.5 times longer than broad, 11.5-15.0 mm long, 8.1-11.5 mm in diameter; SEEDS 1.1-1.4 mm long, 1.0-1.4 mm broad; spines of seedlings short, pectinate, appressed to the stem.

Distribution and habitat: Granite soils and outcrops in southwestern South Dakota, southeastern Wyoming and the east slope of the Rocky Mountains through Colorado and northern New Mexico to about the latitude of Socorro; granite, sandstone, alluvium, and (rarely) limestone derived soils and outcrops in the short grass prairie of eastern Colorado, northeastern New Mexico, and extreme western Nebraska, Kansas, Oklahoma, and the Texas Panhandle.

The collection of Wislizenus in 1846 was the first collection of the genus Echinocereus in what then constituted the United States. Since Engelmann did not designate a type specimen, Benson designated this collection from the vicinity of Santa Fe, New Mexico, as the lectotype. Echinocereus viridiflorus var. viridiflorus is locally abundant across its range. Prior to extensive cultivation it was probably more evenly distributed. Although heavy grazing destroys habitat for seedling establishment, moderate grazing favors expansion of populations through decreased competition from palatable herbaceous vegetation. The dry dehiscent fruits often lead to small but dense populations.

Echinocereus viridiflorus var. viridiflorus is the most northern member of the genus. Within the E. viridiflorus complex, this taxon has the most marked response to winter conditions, dehydrating as the plant body shrinks, often below the ground line. This may be an adaptation to survival under snow. Southern forms of the complex can survive the low winter temperatures when transplanted to northern gardens, but the stems break under the weight of wet snow as the plants do not shrink appreciably (Taylor, pers. comm.).

Echinocereus viridiflorus Engelmann var. cylindricus (Engelmann) Engelmann ex Rümpler in Forster, Handb. Cact., ed. 2: 812. 1885.

TYPE: Texas, Jeff Davis Co., stony hills of the Limpia valleys among the mountain heads of the Limpia, Davis Mountains, 1851. Charles Wright s.n. (lectotype MO2016904!).

Cereus viridiflorus Engelmann var. cylindricus Engelmann, Proc. Amer. Acad. 3: 278. 1856.

Cereus chloranthus Engelmann, Proc. Amer. Acad. 3: 278. 1856.

TYPE: Texas, El Paso Co., stony hills near the Rio Grande at Frontera (El Paso), Franklin Mountains, 2 April 1852. Charles Wright 95 (lectotype MO2016809!; isolectotype POM!).

Echinocereus chloranthus (Engelmann) Engelmann ex Rümpler in Forster, Handb. Cact., ed. 2, 814. 1885.

Cereus viridiflorus Engelmann var. tubulosus Heller, Cat. N. Amer. Fl., ed. 2, 8. 1900.

Echinocereus standleyi Britton and Rose, Cactaceae 3: 24, Fig. 23. 1922.

Echinocereus viridiflorus Engelmann var. chloranthus (Engelmann)

Backeberg, Cactaceae 4: 2015. 1960.

Echinocereus viridiflorus Engelmann var. *intermedius* Backeberg, Cactaceae 4: 2015. 1960. *Nom. nud.*

Echinocereus viridiflorus Engelmann var. *standleyi* (Britton and Rose) Orcutt, cited by Weniger, Cact. Succ. J. Amer. 41: 37. 1960, with reference to Britton and Rose, 1922.

STEMS usually solitary, occasionally forming clumps of several heads, cylindrical, at least 1.5 times longer than broad, 7-25 cm long; ribs 12-17; SPINES white or reddish-purple, often white with reddish-purple tips; spines often in alternating bands of color; central spines 0-7 (-9), porrect, ascending or deflexed, diameter at base 0.30-0.63 mm, longest 10-35 mm long; radial spines 14-20, pectinate and appressed to the stem, longest 7.5-14 mm long, diameter at base 0.28-0.45 mm; FLOWERS green to yellow or reddish, or reddish with greenish-yellow centers, cylindrical or campanulate; ovary areoles 15-25, spines 12-17, 5.0-11.1 mm long, diameter at base 0.13-0.21 mm; FRUITS at maturity red, fleshy with sugary pulp, indehiscent, 9.2-17.5 mm long, 8.1-11.7 mm in diameter, ca. 1.5 times longer than broad; SEEDS 1.0-1.2 mm long and broad; spines of seedlings short, pectinate, appressed to the stem.

Distribution and habitat: Granite and limestone mountains and hills of southern New Mexico and western Texas south to the Rio Grande and adjacent Mexico.

Echinocereus viridiflorus var. *cylindricus* differs vegetatively from the type variety in its cylindrical shape and greater height, both in the field and from seed in the greenhouse. The flowers are cylindrical to campanulate and lack the lemon odor of *E. viridiflorus* var. *viridiflorus*.

Fruits are consistently red, fleshy with a sweet pulp and odor, and indehiscent. Spines are highly variable in number, diameter, length, and angle of projection from the areoles.

Engelmann failed to designate a type specimen for *E. viridiflorus* var. *cylindricus*. The oldest specimen is one collected by Charles Wright in 1846 but the locality was listed only as "western Texas." Benson designated the 1851 collection from the Davis Mountains as the lectotype. Unless noted, type specimens were not designated for other synonyms. *Echinocereus standleyi* Britton and Rose is not different from typical plants of *E. viridiflorus* var. *cylindricus* from southern New Mexico.

Both *E. viridiflorus* var. *cylindricus* and *E. chloranthus* were described by Engelmann (1856), although he expressed doubt as to their separate status. Subsequent authors have considered *E. chloranthus* a distinct species (Britton and Rose, 1922; Benson, 1969a; Weniger 1969), a variety of *E. viridiflorus* (Backeberg, 1960), or unworthy of formal taxonomic recognition (Wooton and Standley, 1915; Marshall and Bock, 1941). The principal distinctions between these two taxa as outlined by Engelmann are that *E. chloranthus* has narrower flowers which are borne lower on the plant than those of *E. viridiflorus* var. *cylindricus*, and five central spines compared to typically none or rarely one in *E. viridiflorus* var. *cylindricus*. As most recently circumscribed by Benson (1969a), *E. chloranthus* var. *chloranthus* has circular areoles, 5-6 stout central spines, and inner perianth segments 2-3 mm broad, whereas *E. viridiflorus* var. *cylindricus* has elliptical or elongate areoles, 0-1 or sometimes 2 or 3 slender central spines, and inner perianth segments 3-4 mm broad.

Throughout western Texas and southern New Mexico populations exhibiting morphology intermediate between the two taxa are common. Within individual populations forms having 0-6 slender to stout central spines, cylindrical to campanulate or nearly rotate corolla, and inner perianth parts of variable width are found. Flowers that are reddish with greenish-yellow centers are found in addition to the greenish-yellow noted by Engelmann for both taxa or the red color added to the descriptions by Benson. Each isolated population may exhibit a different range of variation in morphology.

Areole shape in the E. viridiflorus complex is largely an artifact of the number and basal diameter of the central spines. Thus, this cannot be considered as a separate character delineating taxa. There is no apparent correlation between central spine diameter and number and no discontinuity between central spine numbers of individual plants of E. chloranthus var. chloranthus and E. viridiflorus (Fig. 17). The third character used by Benson to distinguish E. chloranthus var. chloranthus from E. viridiflorus, width of petaloid perianth parts, is continuous; therefore there are no discontinuous variables which separate these taxa. It is apparent that these two taxa cannot be consistently distinguished; rather they represent the two ends of a continuum of morphological variation that may be found within some single populations, notably those in the Franklin, Chinati, Davis, and Guadalupe Mountains of Texas and the Guadalupe and Jarillo Mountains of New Mexico.

Field observations indicate that there are no apparent correlations of substrate or altitude with either morphotype. Plants representing either end of the morphological continuum may be found on limestone or granite and from 1000 to 2200 m of elevation. There are no greenhouse or field differences in flowering phenology (Fig. 7, 8). Observations of pollinator behavior in mixed populations of E. chloranthus var. chloranthus and E. viridiflorus var. cylindricus (Franklin Mountains, Texas; Guadalupe Mountains, New Mexico) failed to reveal species specificity by the visiting bees. Photographs with sunlight and ultraviolet light revealed the same pattern of the flowers within mixed populations and among populations of E. chloranthus var. chloranthus and E. viridiflorus var. cylindricus. Consequently it appears that external barriers to gene flow are lacking.

Subsequent greenhouse studies proved that incompatibility barriers are also absent between these morphotypes either within or between populations. In addition, crosses among specimens most closely fitting the descriptions of the two taxa result in hybrids that are intermediate in all measurable external characters and closely resemble apparent hybrids in the field.

Correlation and distance coefficients (Fig. 10, 11) failed to consistently group OTUs representing populations of E. chloranthus var. chloranthus and E. viridiflorus var. cylindricus. Principal component analysis (Fig. 12) also failed to discriminate between these two taxa.

Based on field and greenhouse observations and the results of cluster and principal component analysis, I consider E. chloranthus var. chloranthus and E. viridiflorus var. cylindricus to be equivalent with E. viridiflorus var. cylindricus, the name with priority at the varietal rank.

Echinocereus viridiflorus Engelmann var. correllii L. Benson, Cact. Succ. J. Amer. 41: 128. 1969.

TYPE: Texas, Brewster Co., hills above Fort Pina Colorada, 4 miles south of Marathon, 4400 ft., 4 April 1965, L. Benson and

D.S. Correll 16485 (holotype POM317079!).

STEMS cylindrical, 1.5-3 times longer than broad, 5-25 cm long; ribs 14-17; SPINES white or golden-yellow, in alternating bands of color; central spines 0-1 (-3), porrect, diameter at base 0.40-0.58 mm, longest 11-13 mm long; radial spines 20-27 (-29), diameter at base 0.33-0.48 mm, 7.0-9.6 mm long, pectinate and appressed to the stem; FLOWERS greenish-yellow, campanulate to rotate, having slight lemony scent; ovary areoles 19-25, spines 11-15, diameter at base 0.11-0.20 mm, 4.5-6.0 mm long; FRUITS at maturity green, dry, dehiscent along longitudinal sutures, 1.2-1.5 times longer than broad, 10.7-12.5 mm long, 7.1-9.4 mm in diameter; SEEDS 0.9-1.1 mm long and broad; spines of seedlings pectinate, plumose, appressed to the stem.

Distribution and habitat: Restricted to the Caballos novaculite outcrops in the vicinity of Marathon, Brewster Co., Texas.

This taxon is vegetatively indistinguishable from E. viridiflorus var. cylindricus except for its higher number of radial spines. The flower, however, is more like that of a northern E. viridiflorus in that it usually opens fully, is never red, and has a lemon odor. The fruits are dry, green, and dehiscent in contrast to E. viridiflorus var. cylindricus. The type locality has been repeatedly stripped of all adult plants and only the tendency of seeds to germinate over a several year period has maintained this population. At the north, east, and west edges of the novaculite the plants appear to intergrade with E. viridiflorus var. cylindricus.

A population north of Robert Lee in Coke Co., Texas, appears to have characteristics between E. viridiflorus var. correllii and var.

neocapillus. Seedling spines are hairy but much shorter than those of var. neocapillus. The flowers are identical to those of var. correllii, and the dry, green, dehiscent fruits are in common with both taxa. There appear to be no suitable habitats between this alluvial substrate and the novaculite, as the terrain in between is limestone, and no populations in the intervening 320 km have been found.

Echinocereus viridiflorus Engelmann var. russanthus (Weniger) Leuck, comb. et stat. nov.

Echinocereus russanthus Weniger, Cact. Succ. J. Amer. 41: 42, Fig. 6. 1969.

TYPE: D. Weniger 712 (holotype UNM, not found).

STEMS cylindrical, 2-3 times longer than broad, 5-25 cm long, 4-9 cm in diameter; ribs 12-17; SPINES evenly radiating and ascending, deflexed, slender, radial and central spines equal in thickness, diameter at base 0.27-0.35 mm, reddish-brown, white with reddish-brown apices or stripes, or rarely whitish-yellow; central spines 6-10, the lowermost ones longest, 9-25 mm long; radial spines (18-)20-36, 9-18 mm long; FLOWERS rust-red, often with greenish-yellow center, cylindrical to campanulate; ovary areoles 23-30, seldom shed at maturity, spines 11-23, diameter at base 0.10-0.17 mm, 9-12 mm long; FRUITS round to ovoid, green at maturity, fleshy but not sugary, indehiscent, 10.5-12.8 mm long, 8.9-10.5 mm broad; SEEDS 0.9-1.1 mm long and broad; spines of seedlings porrect or spreading, long, plumose.

Distribution and habitat: Igneous outcrops and mountains in the Texas Big Bend region, especially Big Bend National Park; rarely on novaculite; elevations from 750-2300 m, Brewster Co., Texas.

Despite the relative abundance of *E. viridiflorus* var. *russanthus* in Big Bend National Park on igneous hills and mountains, its brick red spines and flowers, and spine counts well above those reported for the *E. viridiflorus* complex, this taxon was submerged under *E. chloranthus* until Weniger's description (1969). The plants are uncommon outside the national park. Within the distribution there appears to be considerable variation in spination. The plants of lower elevations of the Chisos Mountains and in the McKinney Hills have very long deflexed radial and central spines. Those in the Chisos Basin and on the outwash slopes on the west side of the Chisos Mountains have short radials and centrals and parallel the vegetative appearance of the sympatric *E. pectinatus* var. *neomexicanus*. Further north and west near Terlingua the spines are again long and deflexed and are mostly purple and white, giving the plants a salt-and-pepper appearance. At the northern end of the range plants of *E. viridiflorus* var. *russanthus* with fewer radial spines occasionally grow on novaculite. Plants of *E. viridiflorus* var. *neocapillus* grow within 1 km and often have reddish coloration in the spines and flowers, perhaps resulting from occasional hybridization with var. *russanthus*. *Echinocereus viridiflorus* var. *russanthus* is sympatric with var. *cylindricus* just northwest of Big Bend National Park.

Seedlings of *E. viridiflorus* var. *russanthus* are small and lack vigor, with a mortality of 20-30% under greenhouse conditions. They produce numerous long, erect, plumose spines. These provide shade and some protection from herbivores, and may serve as absorptive organs when newly formed as they greatly increase area.

Echinocereus viridiflorus Engelmann var. *neocapillus* (Weniger) Leuck, comb. et stat. nov.

Echinocereus chloranthus (Engelmann) Engelmann ex Rümpler var. neocapillus Weniger, Cact. Succ. J. Amer. 41: 39, Fig. 4. 1969. TYPE: D. Weniger 711 (holotype UNM, not found).

STEMS cylindrical, 2-4 times longer than broad, 8-25 cm long, 3-7 cm in diameter; ribs 12-16; SPINES white or golden-yellow, or mixed white and red; spines in alternating light and dark bands; central spines 6-10, radiating evenly and ascending, lowermost ones sometimes longer, porrect or deflexed, diameter at base 0.28-0.33 mm, 12-16 mm long; radial spines 26-36, slender, diameter at base 0.18-0.23 mm, 6.0-7.5 mm long; FLOWERS greenish-yellow, occasionally with orange-red margins, cylindrical, campanulate or rarely rotate; ovary areoles 22-32, spines 20-25, diameter at base 0.08-0.09 mm, 8.5-10.5 mm long; FRUITS at maturity green, dry, dehiscent along longitudinal sutures, 12-14 mm long, 7.5-8.5 mm in diameter, 1.5-2 times longer than broad; SEEDS 1.0-1.2 mm long, 0.9-1.1 mm broad; spines of seedlings and juvenile plants long, white, flexuous, to 3 cm or more long, often persisting at the bases of mature plants.

Distribution and habitat: Restricted to the Caballos novaculite south of Marathon, Brewster Co., Texas.

This taxon was first discovered by Leding (1934), who noted the juvenile characteristic of long white hairs (spines). He remarked that if this characteristic is inheritable the plants deserved recognition as a species or variety, but they were not described until 1969. The long flexuous spines are maintained in greenhouse cultivation. They are produced for two years after germination in the greenhouse and apparently four to five years in the field before the numerous, golden-yellow, short, rigid spines of adult plants are produced apically. The plants are apparently incapable of flowering from juvenile areoles. Due to compression of the plant body, the juvenile spines are found only at the bases of mature plants. Death of the apical meristem results in the initiation of juvenile spines on new growth for about one year before mature spines are produced.

Plants occur in full sun where competition with herbaceous vegetation is presumably reduced; frequently they grow in a mat of *Selaginella*. The numerous long white flexuous spines are presumably an adaptation for seedling survival in the intense light and heat on the white novaculite outcrops. The spines provide shade and a dead air space that should lessen evaporation from the plant surface.

Adult plants are similar in color and general appearance to *E. viridiflorus* var. *correllii* except for the much greater numbers of radial and central spines in var. *neocapillus*; flowers lack the lemon odor of the former and are mostly cylindrical. There is possibly some gene exchange with *E. viridiflorus* var. *russanthus* at the south end of the var. *neocapillus* distribution. One herbarium specimen (*Pierce 4164*, UNM) appears to be a hybrid of *E. viridiflorus* var. *neocapillus* with var. *correllii*.

Benson (1969a) submerged this taxon under *E. chloranthus*, although his description of the species did not include mention of the unusual juvenile spination or allow a range in spine numbers adequate to encompass the 26-36 radial and 6-10 central spines found in *E. viridiflorus* var. *neocapillus*. The holotype (UNM) appears to be missing.

Echinocereus viridiflorus Engelmann var. *weedinii* Leuck, *var. nov.*

TYPE: Texas, Jeff Davis Co., Davis Mountains, top of Timber Mountain, 6400 ft. E.E. Leuck 193 and J.F. Weedin, 13 May 1978 (holotype OKL).

Caules vulgo solitarii, cylindrici, sensim contracti apicem versus, 1.5-3 plo longiores quam latiores, 6-20 cm longi, 3.5-6 cm lati; porcae 15-17; spinae translucentes, aureae, interdum spina unica longa porrecta centrali: centrales 6-9, 0.33-0.45 mm diametro basi, infimae longissimae, deflexae, 15-20 (-25) mm longae; radiales 20-34, graciles, aequaliter radiantes, 0.15-0.24 mm diametro basi, 7-11.2 mm longae; flores flavo-virentes, interdum flavo-aurantiaci, cylindrici vel campanulati; segmenta perianthii interiora 1-1.5 cm longa; areolae ovariorum 12-20, spinae 12-16, 0.08-0.12 mm diametro basi, 6-9 mm longae; fructus maturi rubri, raro virides, carnosi sed sine pulpa saccharata, indehiscentes, globosi vel ovoidei, 5.9-7.3 mm longi, 5.8-6.8 mm diametro; semina 1-1.2 mm longa et lata; spinae plantularum pectinatae, adpressae ad caulem.

STEMS usually solitary, cylindrical, tapering slightly at the apex, 1.5-3 times as long as broad, 6-20 cm long, 3.5-6 cm broad; ribs 15-17; SPINES translucent golden-yellow, occasionally with a single long white porrect central: central spines 6-9, diameter at base 0.33-0.43 mm, lowermost ones longest, deflexed, 15-20 (-25) mm long; radial spines 20-34, slender, evenly radiating, diameter at base 0.15-0.24 mm, 7.0-11.2 mm long; FLOWERS greenish-yellow, occasionally yellow-orange, cylindrical to campanulate; inner perianth parts 1.0-1.5 cm long; ovary areoles 12-20, spines 12-16, diameter at base 0.08-0.12 mm, 6-9 mm long; FRUITS at maturity red, rarely green, fleshy but not with sugary pulp, indehiscent, globose to ovoid, 5.9-7.3 mm long, 5.8-6.8 mm in diameter;

SEEDS 1.0-1.2 mm long and broad; spines of seedlings pectinate, appressed to the stem.

Distribution and habitat: Cracks in granite slabs at elevations of 1400-2700 m in the Big Bend region of Texas, especially the Chisos and Davis Mountains.

This variety is named after J.F. Weedin, a student of Chihuahuan Desert vegetation. Only three collections prior to his exist, and all were identified as *E. chloranthus*. Flowers, fruits, spines, and habitat all serve to distinguish this taxon from other members of the *E. viridiflorus* complex.

Both radial and central spines of *E. viridiflorus* var. *weedinii* are normally a translucent golden-yellow. The six to nine long deflexed central spines give the plant a shaggy appearance (Fig. 14) and provide considerable shading. Unlike *E. viridiflorus* var. *russanthus* and var. *neocapillus*, the central spines are not found in seedlings but are gradually increased in apical areoles in mature plants. Flowers are mostly cylindrical (Fig. 16) and are about 1/3 smaller than in other varieties in this species. They may be greenish-yellow to pale orange but never possess reddish perianth parts as in *E. viridiflorus* var. *russanthus*, the taxon most similar to it vegetatively. The indehiscent fruits differ from *E. viridiflorus* var. *russanthus* in their small size and red color and from var. *cylindricus* by their small size, round shape, and lack of sugary pulp.

Echinocereus viridiflorus var. *weedinii* may occur adjacent to var. *russanthus* on the west side of the Chisos Mountains in Big Bend National Park and near var. *cylindricus* at the top of Timber Mountain in the Davis Mountains. There is some overlap in flowering time with each of these taxa (Fig. 8) and there appear to be no incompatibility barriers (Table 4). However, the populations of _E_. _viridiflorus_ var. _weedinii_ appear discrete. There may be habitat selection for the _E_. _viridiflorus_ var. _weedinii_ morphology, as it grows only in small cracks in granitic slabs in south and west-facing locations. Despite the presence of intergrading forms at lower elevations, no _E_. _viridiflorus_ var. _cylindricus_ plants grow in the var. _weedinii_ population at the top of Timber Mountain, which is composed entirely of granite slabs. _Echinocereus viridiflorus_ var. _russanthus_ grows on outwash hills adjacent to the var. _weedinii_ population on a west-facing cliff in the Chisos Mountains. No plants of _E_. _viridiflorus_ var. _russanthus_ were found on the cliff face, nor were any var. _weedinii_ plants found on the outwash hills. Seed collected from _E_. _viridiflorus_ var. _weedinii_ plants on the cliff germinated to produce a few individuals that have the morphology of var. _russanthus_ from the outwash slopes. Thus, although there may be hybridization taking place, the two taxa appear to be separated by habitat selection.

Both correlation and distance phenograms (Fig. 10, 11) showed _E_. _viridiflorus_ var. _weedinii_ OTUs to be highly correlated but not closely related to other OTUs. Principal component analysis separated these OTUs as distinct from all other OTUs, including the _E_. _viridiflorus_ var. _russanthus_ population from the outwash hills below the Chisos Mountains and the apparent intergrade forms with var. _cylindricus_ from Timber Mountain. Therefore, based on its distinct morphology and habitat I recognize this form as _E_. _viridiflorus_ var. _weedinii_.

Evolution in the complex--Variation in the features of the spines undoubtedly reflects differing adaptations of populations to their respective environments. Longer and more numerous spines reduce evapotranspiration through the provision of shade and a boundary layer of air and would be expected in populations inhabiting high irradiation sites in deserts. Within the complex this prediction is confirmed, as the southern taxa in the Chihuahuan Desert possess spines that are longer and more numerous than those in the northern E. viridiflorus var. viridiflorus or var. cylindricus that are often associated with open evergreen woodlands.

Selection for greater spine length and number would seem to be especially important in seedlings. Seedlings of all taxa within the complex require open habitat for successful establishment. Presumably they do not compete well with herbaceous vegetation for sunlight and moisture. Seedlings of the taxa in the complex that do not occur in extreme desert habitats, E. viridiflorus var. viridiflorus, var. cylindricus, and var. weedinii have short, pectinate spines that provide scant deflection of sunlight from the stem. The acquisition of central spines in these taxa is a gradual process taking several years. Seedlings of all desert forms in the complex, however, have adaptations of the spines that reduce solar insolation reaching the plant body. Variation in the spines of seedlings is greatest on the Caballos novaculite south of Marathon, Texas. Echinocereus viridiflorus var. correllii spines are like those of var. cylindricus except that they are plumose, hence providing greater shading for the stem. Plants of E. viridiflorus var. russanthus produce long, plumose, erect spines providing shade and some protection from predators. Seedlings of E. viridiflorus var. neocapillus have extremely long, flexuous, white spines that should provide more protection from the sun than spines of any other taxon in the complex. Spines of E. davisii seedlings are short, pectinate and plumose, and the plants rapidly form an underground stem that pulls the entire plant below the Selaginella in times of water stress. Early spring flowering in E. davisii allows seed production and germination before the onset of high desert temperatures.

It is difficult to infer the most primitive form and possible evolutionary pathways in the E. viridiflorus complex because of the paucity of fossils of the complex. However, it appears that much of the variation in vegetative characters has occurred in recent times in response to changing environmental conditions in the Chihuahuan Desert, the center of diversity in the complex. As recently as 9000 years ago desert areas of the Texas Big Bend region above 1000 m in elevation were predominantly juniper woodlands (Wells and Hunziger, 1976). These woodlands are currently restricted mountain regions from 1300 to 2000 m in elevation. The juniper woodland today provides suitable habitat for E. viridiflorus var. cylindricus and some populations of var. weedinii, taxa with seedlings lacking highly modified spines. Echinocereus davisii and E. viridiflorus var. neocapillus, var. russanthus, and var. correllii all inhabit lower vegetation zones in short grasslands or low rocky mountains such as the Caballos novaculite outcrops. Even at the lowest elevations in the Big Bend region the juniper woodlands retreated no more than 12,000 years ago (Wells and Hunziger, 1976). It may be that as the juniper woodlands retreated to higher elevations, a formerly continuous distribution was divided into many island populations that evolved as separate units. In the southern distribution of the complex populations are largely discontinuous restricting gene flow. Thus, the taxa in the complex must have evolved in desert areas within 9000 to 12,000 years ago because they are not presently found in woodland habitats at greater elevations as is _E_. _viridiflorus_ var. _cylindricus_.

Echinocereus viridiflorus var. _cylindricus_ exists today in the same form as it did 2000 to 3000 years ago. Remains found in Ranger Cave near Alpine, Texas, and deposited in the Museum of the Big Bend, Sul Ross State University, Alpine, reveal the plant body and spination to be identical to plants found in the vicinity today.

Thus it appears that evolution of the species and varieties in the complex has been rapid. In the Chihuahuan Desert diversity is highest perhaps due to evolution of relatively small disjunct populations in response to the climatic changes in the Big Bend region in the last 9000 to 12,000 years. These morphological changes, although presumably adaptive, show random variation through drift.

LITERATURE CITED

Backeberg, C. 1960. Die Cactaceae, band IV. Gustav Fischer Verlag, Jena.

Benson, L. 1969a. Cactaceae. In Lundell, C.L., and coll., Flora of Texas, Vol. 2, part II. Texas Research Foundation, Renner.

__________. 1969b. The cacti of the United States and Canada- New names and nomenclature combinations- I. Cact. and Succ. J. Amer. 41: 124-128.

Britton, N.L. and J.N. Rose. 1922. The Cactaceae. Vol. III, Carnegie Inst., Washington, Publ. No. 248.

Engelmann, G. 1856. Synopsis of the Cactaceae of the territory of the United States and adjacent regions. Proc. Am. Acad. Arts and Sciences 3: 259-314.

Erdtman, G. 1959. Handbook of Palynology. Scandinavian University Books, Munksgaard.

__________, 1960. The acetolysis method: a revised description. Svensk. Bot. Tidskr. 54: 561-564.

Fish and Wildlife Service. 1980. Republication of lists of endangered and threatened species and correction of technical errors in final rules. Fed. Reg. 45, No. 99.

Houghton, A.D. 1931. Echinocereus davisii sp. nov. Cact. Succ. J. Amer. 2: 466.

Kolle, D.O. 1978. A populational study of Echinocereus chloranthus (Cactaceae) in trans-Pecos Texas. M.S. theses, Sul Ross State University, Alpine, Texas.

Kurtz, E.B., Jr. 1948. Pollen grain characters of certain Cactaceae.

Bull. Torrey Bot. Club 75: 516-522.

__________. 1963. Pollen morphology of the Cactaceae. Grana Palynol. 4: 367-372.

Leding, A.R. 1934. A new spine character in cactus. J. Hered. 25: 326-328.

Leuck, E.E. 1980. Biosystematic studies in the Echinocereus viridiflorus complex. Ph.D. dissertation, University of Oklahoma, Norman.

Leuenberger, B. 1975. Die Pollenmorphologie der Cactaceae und ihre Bedeutung für die Systematik. Ph.D. dissertation, Heidelberg.

Marshall, W.T. and T.M. Bock. 1941. Cactaceae. Abbey Garden Press, Pasedena.

Pinkava, D.J., L.A. McGill, T. Reeves, and M.G. McCleod. 1977. Chromosome numbers in some cacti of western North America- III. Bull. Torrey Bot. Club 104: 105-110.

Rohlf, F.J., J. Kispaugh, and D. Kirk. 1974. Numerical taxonomy system of multivariate statistical programs. State University of New York, Stony Brook.

Sneath, P.H.A. and R.R. Sokal. 1973. Numerical Taxonomy. W.H. Freeman and Co., San Francisco.

Snow, R. 1963. Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. Stain Tech. 38: 9-13.

Tsukada, M. 1969. Pollen morphology and identification. II. Cactaceae. Pollen Spores 6: 45-84.

Weedin, J.F. and A.M. Powell. 1978a. Chromosome numbers in Cactaceae, Trans-Pecos Texas. Amer. J. Bot. 65: 531-537.

__________ and __________. 1978b. In IOPB chromosome number reports. Taxon 27: 230-231.

Wells, P.V. and J.H. Hunziger. 1976. Origin of the creosote bush (Larrea) deserts of southwestern North America. Ann. Missouri Bot. Gard. 63: 843-861.

Weniger, D. 1969. The small-flowered echinocerei of Texas and New Mexico. Cact. and Succ. J. Amer. 41: 34-43.

Wooton, E.O. and P.C. Standley. 1915. Flora of New Mexico. Contrib. US Nat. Herb., Vol. 19.

Table 1. List of characters chosen for numerical analysis of *Echinocereus viridiflorus* complex. Characters 1 - 41 are two-state characters and 42 - 87 are continuous.

Character number	Character	Character number	Character
1	Fruit green	22	Central spines white
2	Fruit red	23	Central spines dark
3	Fruit not splitting	24	Central spines translucent
4	Fruit splitting	25	Basal clumping
5	No fruit abscission	26	Branching stems
6	Fruit abscission	27	Taproot
7	Fruit spines not shed	28	Novaculite
8	Fruit dry	29	Granite
9	Fruit juicy	30	Sandstone
10	Ovary spines white	31	Alluvium
11	Ovary spines dark	32	Limestone
12	Flowers yellow	33	North-facing slope
13	Flowers red	34	South-facing slope
14	Lemon floral odor	35	East-facing slope
15	Sweet floral odor	36	West-facing slope
16	Petals reflexed	37	Seedlings hairy
17	Petals erect	38	Seedling spines plumose
18	Annual bands of color	39	Seedling spines pectinate
19	Radial spines white	40	Seedling spines deflexed
20	Radial spines dark	41	Petals short
21	Radial spines translucent	42	Days to fruit maturity

Table 1. continued.

Character number	Character	Character number	Character
43	Ovary spine length	66	Third year germination
44	Fruit length	67	Total germination
45	Fruit width	68	Hilum diameter
46	Length of flowering season	69	Seedling survival
47	Average number of radial spines	70	Fruit spine diameter
48	Maximum length of radial spines	71	Fruit width/length
49	Maximum central spine length	72	Maximum radial spine diameter
50	Number of ribs	73	Maximum central spine diameter
51	Field plant width	74	Areole width/length
52	Height of two year plant	75	Number of central spines
53	Width of two year plant	76	Number of heads
54	Latitude	77	Areoles per ovary
55	Rainfall	78	Day of first flowering
56	Seed weight	79	Ovary spines per areole
57	Potential seed set	80	Maximum number of radial spines
58	Field seed set	81	Maximum number of central spines
59	Field plant height	82	Areole length
60	Longitude	83	Areole width
61	Seed width	84	Maximum number of ribs
62	Seed length	85	Altitude
63	Seed length/width	86	Second year width/length
64	First year germination	87	Field width/length
65	Second year germination		

Table 2. Seed set in the Echinocereus viridiflorus complex.

Taxon	Number of populations	Field		Greenhouse		% Field seed set / Greenhouse seed set
		Fruits	Seed set	Fruits	Seed set	
viridiflorus	23	275	119.5	415	153.9	77.8
cylindricus	19	187	110.8	204	182.6	60.7
chloranthus	7	95	102.5	115	165.0	62.1
correllii	2	29	118.9	32	189.5	62.7
russanthus	5	38	102.0	66	166.4	61.3
neocapillus	2	50	119.2	48	209.1	57.0
davisii	1	16	44.0	53	69.2	63.6
weedinii	3	34	83.5	42	93.2	89.6

Table 3. Hybrid potential (Eq. 1) of the Echinocereus viridiflorus complex with sympatric and allopatric populations of congeners. Taxa in parentheses indicate the E. viridiflorus complex members of the cross. HP values of sympatric and allopatric populations were compared using a one-way analysis of variance ($F = 8.70$; $p < 0.05$); HP values of sympatric and allopatric populations of E. reichenbachii var. reichenbachii were compared using a two-tailed Student's t-test ($t_s = 10.66$; $p < 0.05$).

Taxon	No. of crosses	HP
Sympatric populations		
E. reichenbachii var. reichenbachii (viridiflorus)	8	1.0%
E. fendleri var. fendleri (viridiflorus, cylindricus)	5	0.6%
E. pectinatus var. neomexicanus (neocapillus, cylindricus)	6	0.6%
E. triglochidiatus (viridiflorus, cylindricus, russanthus)	7	0.2%
E. enneacanthus var. stramineus (russanthus, chloranthus)	4	0.0%
Allopatric populations		
E. reichenbachii var. reichenbachii (viridiflorus)	10	11.4%
E. reichenbachii var. albertii (viridiflorus, cylindricus)	5	6.2%

Table 3. continued.

Taxon	No. of crosses	HP
E. pectinatus var. wenigeri (cylindricus)	4	5.7%
E. reichenbachii var. fitchii (viridiflorus, cylindricus)	6	4.6%
E. pectinatus var. pectinatus (cylindricus, davisii)	2	4.0%
E. reichenbachii var. chisoensis (russanthus, viridiflorus, cylindricus)	5	3.9%
E. poselgeri (Wilcoxia poselgeri) (viridiflorus, neocapillus)	7	3.3%
E. fendleri var. rectispinus (cylindricus)	4	2.1%
E. berlandieri var. angusticeps (viridiflorus, cylindricus)	4	1.6%
E. triglochidiatus var. inermis (viridiflorus, cylindricus)	6	1.5%

Table 4. Hybrid potential (Eq. 1) among members of the <u>Echinocereus</u> <u>viridiflorus</u> complex. Number in parentheses indicates the number of crosses.

	viridiflorus	cylindricus	chloranthus	correllii	neocapillus	russanthus	weedinii	davisii
viridiflorus	100(421)	100(57)	93(16)	82(14)	90(7)	75(9)	82(2)	83(10)
cylindricus	93(36)	100(105)	100(46)	94(14)	80(12)	79(10)	78(15)	80(7)
chloranthus	89(19)	99(53)	100(96)	89(7)	92(11)	84(20)	82(14)	81(4)
correllii	90(9)	89(19)	92(9)	100(48)	87(14)	94(9)	87(5)	47(17)
neocapillus	84(8)	79(9)	90(12)	80(12)	100(48)	76(24)	74(5)	52(14)
russanthus	87(7)	83(11)	90(13)	84(8)	81(21)	100(69)	72(7)	77(9)
weedinii	87(4)	73(13)	85(8)	--	97(4)	81(12)	100(42)	79(4)
davisii	84(11)	80(7)	75(11)	43(13)	54(21)	84(7)	--	100(93)

Table 5. Collection sites from which plants were collected for numerical analysis of the Echinocereus viridiflorus complex.

OTU code	Taxon	Collection site
SODAKOTA	viridiflorus	Custer Co., SD. Wind Cave.
WYOMING	viridiflorus	Platte Co., WY. Pleasanton.
LAPOUDRE	viridiflorus	Larimer Co., CO. La Poudre.
JULESBERG	viridiflorus	Sedgwick Co., CO. Julesburg.
BONNYRES	viridiflorus	Yuma Co., CO. Bonny Reservoir.
KITCRSON	viridiflorus	Cheyenne Co., CO. Kit Carson.
MORTONKS	viridiflorus	Morton Co., KS. Cimarron River
SHRMANKS	viridiflorus	Sherman Co., KS. SW Goodland.
PROWERS	viridiflorus	Prowers Co., CO. Two Buttes.
BALDMTN	viridiflorus	Boulder Co., CO. Bald Mountain.
BOULDER	viridiflorus	Boulder Co., CO. Boulder.
ROCKYFLT	viridiflorus	Jefferson Co., CO. Rocky Flats.
PENROSE	viridiflorus	Fremont Co., CO. N Penrose.
BRNTMILL	viridiflorus	Pueblo Co., CO. St. Charles River.
RATONPSS	viridiflorus	Colfax Co., CO. Raton Pass.
DIXONNM	viridiflorus	Rio Arriba Co., NM. Dixon.
MOSQUERO	viridiflorus	Harding Co., NM. Mosquero.
LCONCHAS	viridiflorus	San Miguel Co., NM. Lake Conchas.
CAPULIN	viridiflorus	Union Co., NM. Capulin Mountain.
MANZANO	viridiflorus	Valencia Co., NM. SE Belen.
POTTERTX	viridiflorus	Potter Co., TX. Canadian River.
SUMNERLK	viridiflorus	De Baca Co., NM. Lake Sumner.
BLKMESA	viridiflorus	Cimarron Co., OK. Black Mesa.

Table 5. continued.

OTU code	Taxon	Collection site
MATADOR	viridiflorus	Motley Co., TX. W Matador.
NEWMEXBM	viridiflorus	Union Co., NM. Clayton Lake.
SACRMNTO	cylindricus	Otero Co., NM. Sacramento Mountains.
ORGANMTN	cylindricus	Dona Ana Co., NM. Organ Mountains.
PINTO	cylindricus	Presidio Co., TX. Pinto Canyon.
VANHORN	cylindricus	Hudspeth Co., TX. W Van Horn.
DVSSTPK	cylindricus	Jeff Davis Co., TX. Davis Mountains.
SULROSS	cylindricus	Brewster Co., TX. Sul Ross Hill.
CHIN30	cylindricus	Presidio Co., TX. Chinati Peak.
CHIN31	cylindricus	Presidio Co., TX. Chinati Peak.
ELGIN	cylindricus	Unknown, commercial source.
TM5600	cylindricus	Jeff Davis Co., TX. Davis Mountains.
FLTPLCKE	cylindricus	Jeff Davis Co., TX. Davis Mountains.
CARLSBAD	chloranthus	Eddy Co., NM. Carlsbad Caverns.
LKVALLEY	chloranthus	Sierra Co., NM. Lake Valley.
LSCRUCES	chloranthus	Dona Ana Co., NM. Organ Mountains.
HUECOMTN	chloranthus	Hudspeth Co., TX. Hueco Mountains.
NINEPT	russanthus	Brewster Co., TX. Nine-point Mesa.
MCKINNEY	russanthus	Brewster Co., TX. McKinney Hills.
LRYRUSS	russanthus	Brewster Co., TX. Leary Ranch.
LWRCATOK	russanthus	Brewster Co., TX. Chisos Mountains.
RIVROAD	russanthus	Brewster Co., TX. River Road, BBNP.
LRYNEOCP	neocapillus	Brewster Co., TX. Leary Ranch.
BRLNEOCP	neocapillus	Brewster Co., TX. Bourland Mountains.

Table 5. continued.

OTU code	Taxon	Collection site
1MEMARTN	correllii	Brewster Co., TX. E Marathon.
FTPINACO	correllii	Brewster Co., TX. Fort Pina Colorada.
DAVISII	davisii	Brewster Co., TX. S Marathon. .
LIVRMORE	weedinii	Jeff Davis Co., TX. Mt. Livermore.
TIMBERTP	weedinii	Jeff Davis Co., TX. Timber Mountain.
CATTAIL	weedinii	Brewster Co., TX. Chisos Mountains.
SANMATEO	viridiflorus x cylindricus	Socorro Co., NM. San Mateo Mountains.
TM5300	cylindricus x weedinii	Jeff Davis Co., TX. Davis Mountains.
TM5900	cylindricus x weedinii	Jeff Davis Co., TX. Davis Mountains.
JARILLO	cylindricus x chloranthus	Otero Co., NM. Jarillo Mountains.
GUADLOUP	cylindricus x chloranthus	Culberson Co., TX; Eddy Co., NM. Guadalupe Mountains.
FRANKLIN	cylindricus x chloranthus	El Paso Co., TX. Franklin Mountains.
KENT	cylindricus x chloranthus	Culberson Co., TX. N Kent.
8MWMARTN	cylindricus x correllii	Brewster Co., TX. W Marathon.
ROBRTLEE	correllii x neocapillus	Coke Co., TX. Robert Lee.

Fig. 1, 2. Pollen of Echinocereus viridiflorus. Scanning electron micrographs. 1. Pollen grain of E. viridiflorus var. viridiflorus from Randall Co., TX. Polar view. x 1600. 2. Punctibaculate exine in colpus region of the same grain. x 7000.

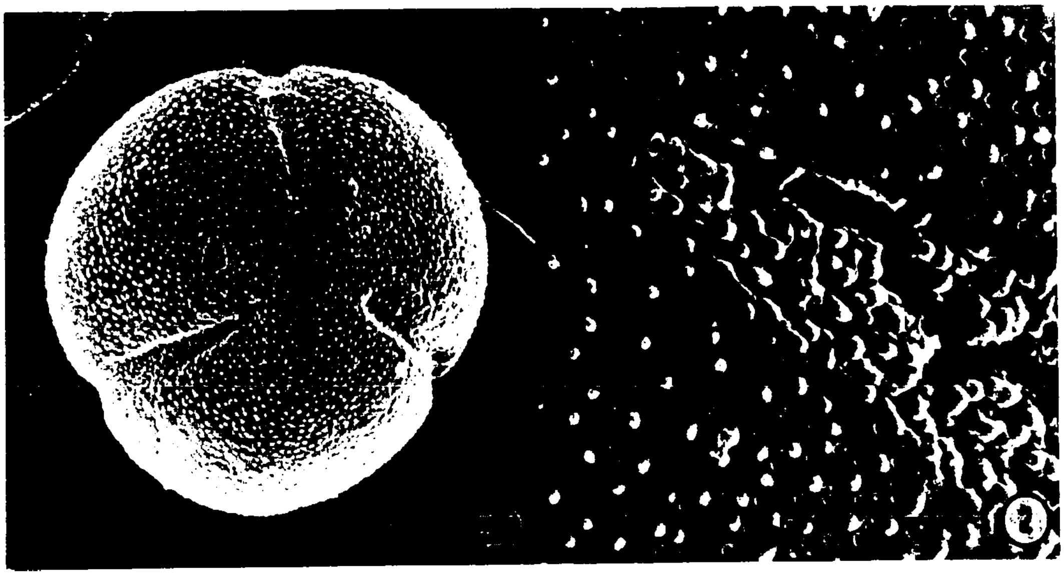


Fig. 3 - 6. Floral patterns in the Echinocereus viridiflorus complex. 3, 4. Flowering plants of E. viridiflorus var. viridiflorus from Cimarron Co., OK. 3. Photographed with sunlight. 4. Photographed with ultraviolet light only. 5 - 6. Flowering plant of E. russanthus from the McKinney Hills, Brewster Co., TX. 5. Photographed with sunlight. 6. Photographed with ultraviolet light only. All figures x 1.0.

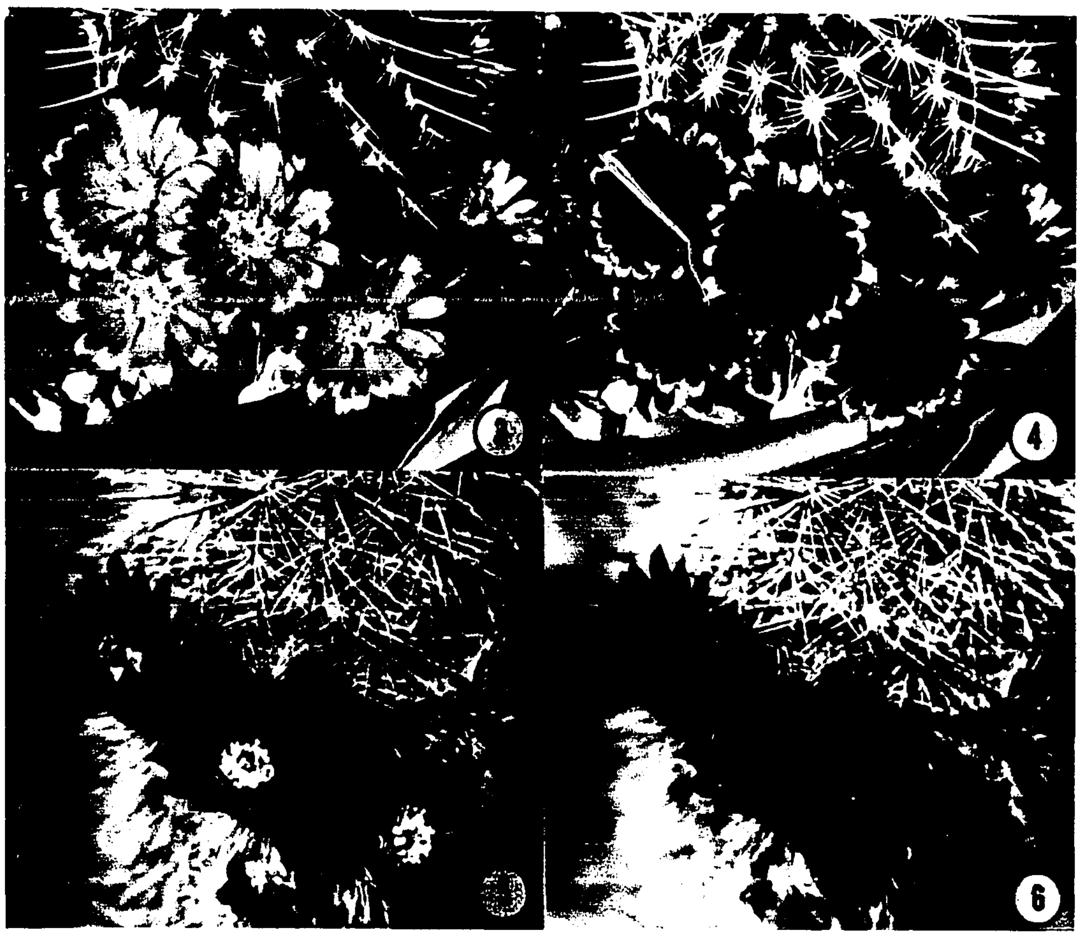

4
6

Fig. 7. Flowering phenology of greenhouse grown members of the *Echinocereus viridiflorus* complex.

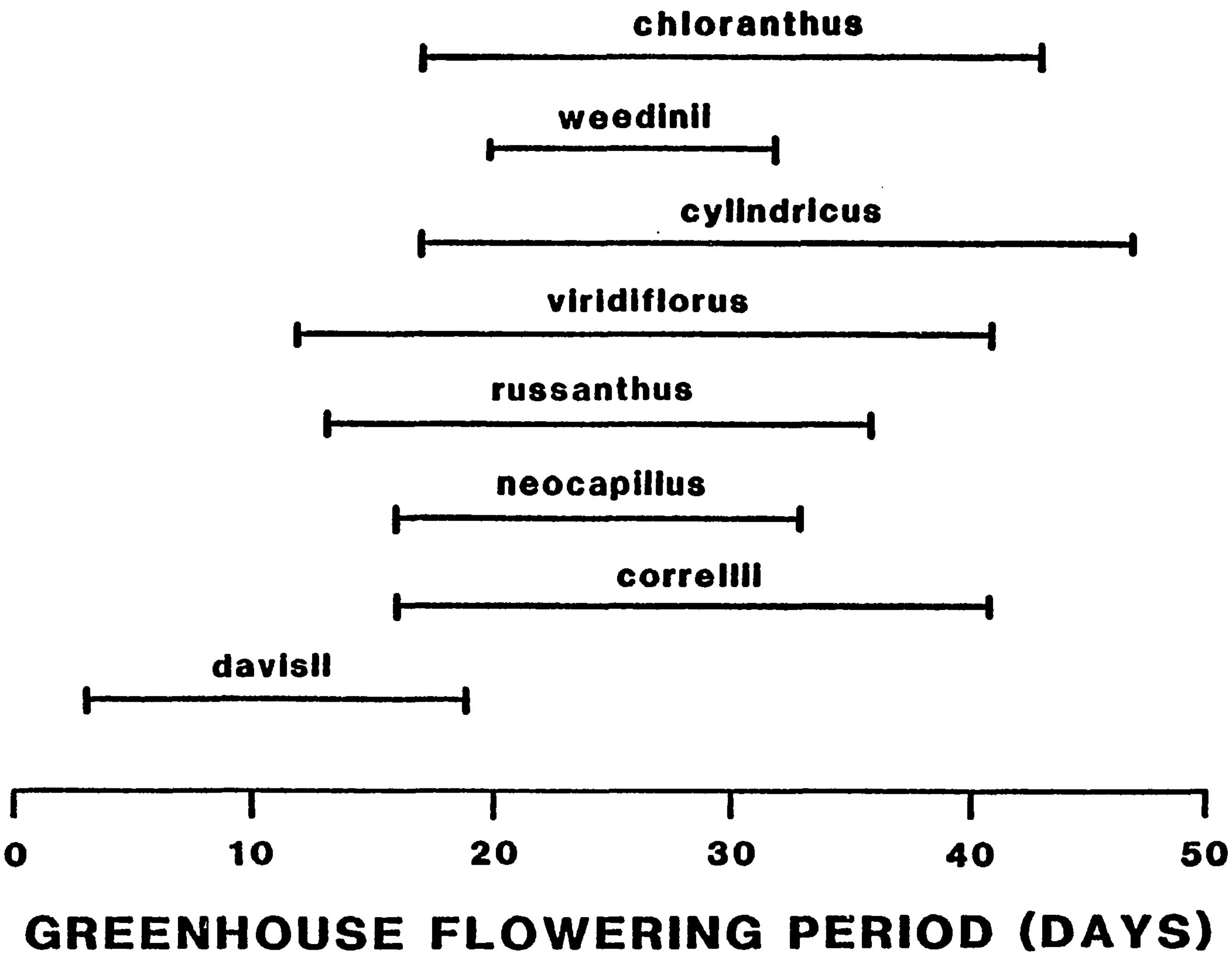
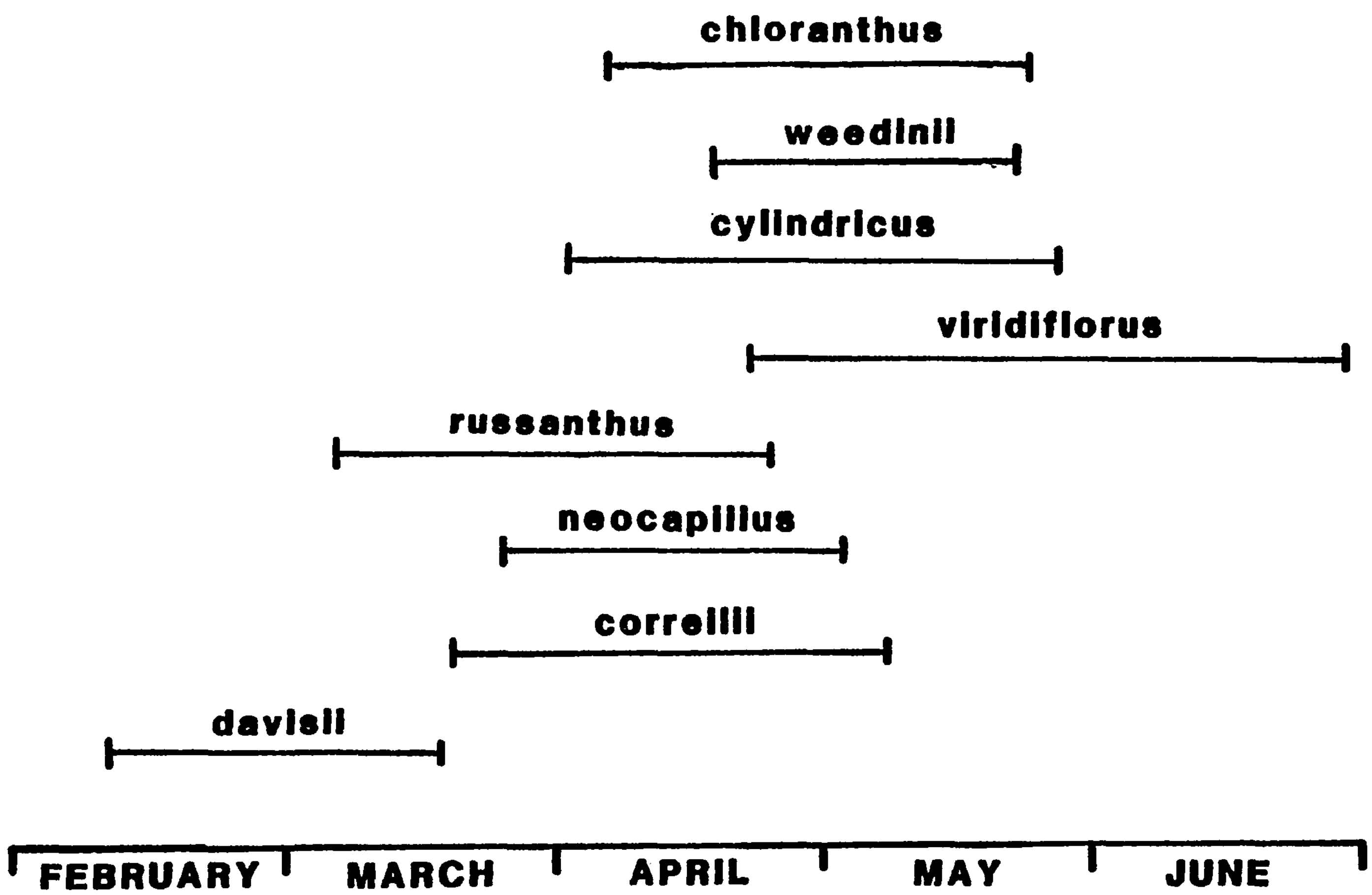

chloranthus
weedinii
cylindricus
viridiflorus
russanthus
neocapillus
correllii
davisii
0
10
20
30
40
50
GREENHOUSE FLOWERING PERIOD (DAYS)

Fig. 8. Flowering periods of members of the Echinocereus viridiflorus complex. Flowering times based on observations from 1976-1980.



FIELD FLOWERING PERIOD

Fig. 9. Correlation phenogram of *Echinocereus viridiflorus* complex OTUs. Based on the unweighted pair group method with arithmetic means over 87 characters for 62 OTUs. Cophenetic correlation coefficient is 0.914.

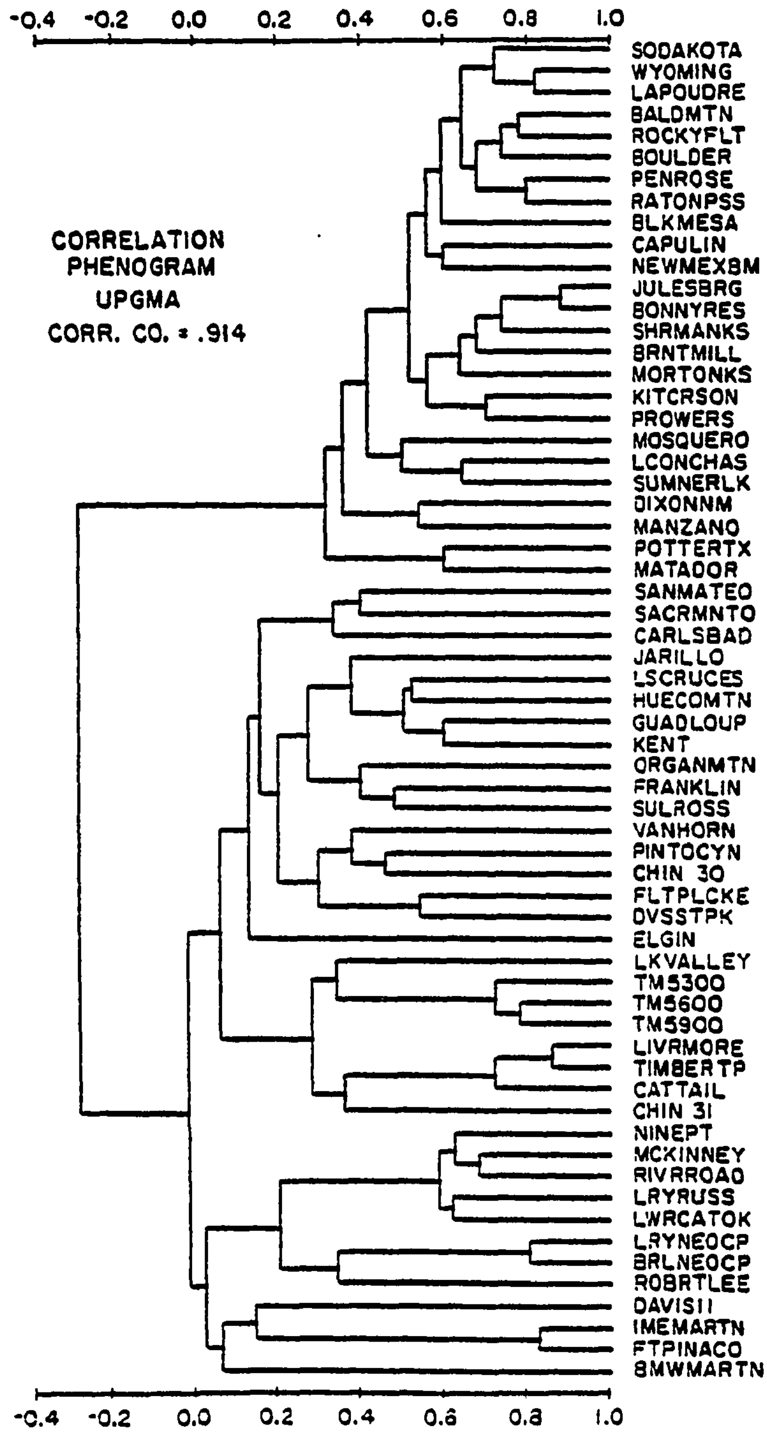

-0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0
CORRELATION
PHENOGRAM
UPGMA
CORR. CO. = .914
SODAKOTA
WYOMING
LAPOUDRE
BALDMTN
ROCKYFLT
BOULDER
PENROSE
RATONPSS
BLKMESA
CAPULIN
NEWMEXBM
JULESBRG
BONNYRES
SHRMANKS
BRNTMILL
MORTONKS
KITCRSON
PROWERS
MOSQUERO
LCONCHAS
SUMNERLK
DIXONNM
MANZANO
POTTERTX
MATADOR
SANMATEO
SACRMNTO
CARLSBAD
JARILLO
LSCRUCES
HUECOMTN
GUADLOUP
KENT
ORGANMTN
FRANKLIN
SULROSS
VANHORN
PINTOCYN
CHIN 30
FLTPLCKE
DVSSTPK
ELGIN
LKVALLEY
TM5300
TM5600
TM5900
LIVRMORE
TIMBERTP
CATTAIL
CHIN 31
NINEPT
MCKINNEY
RIVRROAD
LRYRUSS
LWRCATOK
LRYNEOCP
BRLNEOCP
ROBRTLEE
DAVIS11
IMEMARTN
FTPINACO
BMWMARTN

Fig. 10. Distance phenogram of Echinocereus viridiflorus complex OTUs. Based on the unweighted pair group method with arithmetic means over 87 characters for 62 OTUs. Cophenetic correlation coefficient is 0.931.

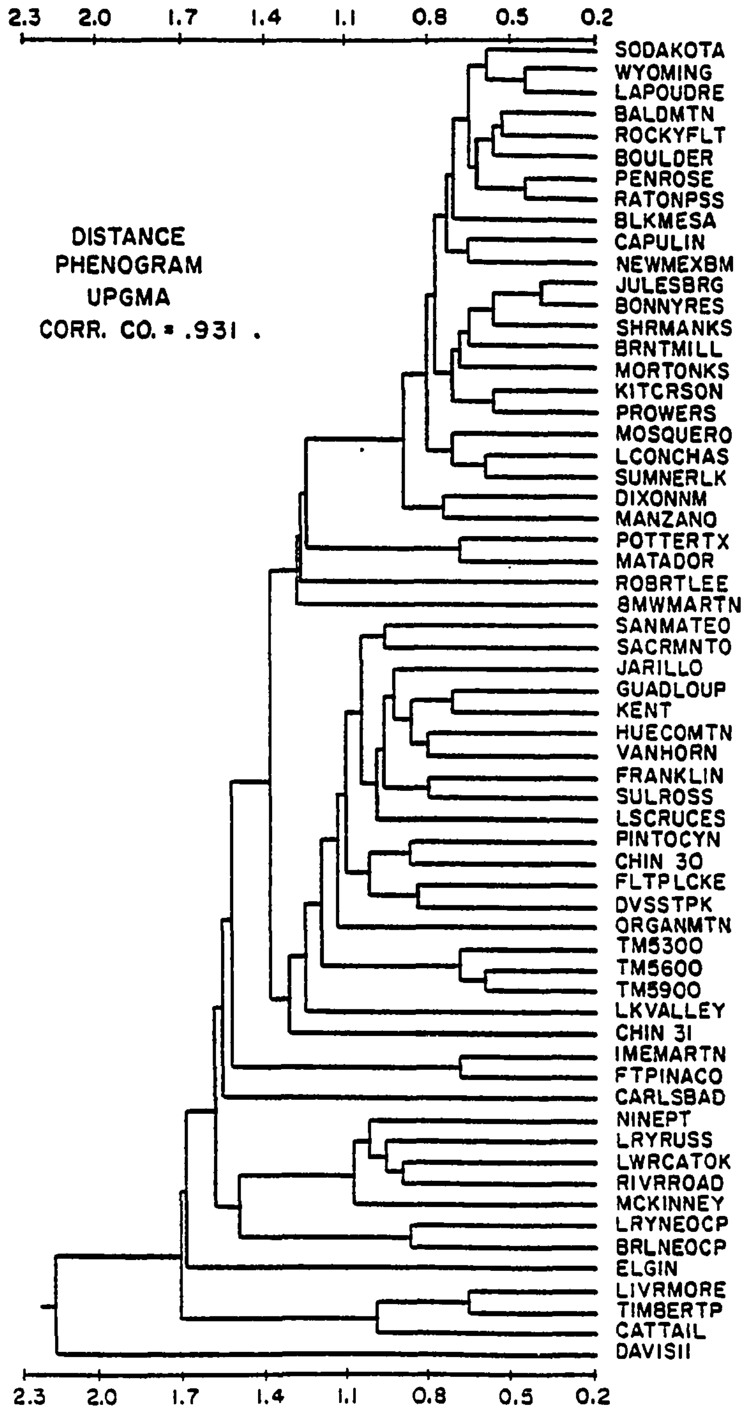

2.3 2.0 1.7 1.4 1.1 0.8 0.5 0.2
DISTANCE
PHENOGRAM
UPGMA
CORR. CO. = .931 .
SODAKOTA
WYOMING
LAPOUDRE
BALDMTN
ROCKYFLT
BOULDER
PENROSE
RATONPSS
BLKMESA
CAPULIN
NEWMEXBM
JULESBRG
BONNYRES
SHRMANKS
BRNTMILL
MORTONKS
KITCRSON
PROWERS
MOSQUERO
LCONCHAS
SUMNERLK
DIXONNM
MANZANO
POTTERTX
MATADOR
ROBRTLEE
BMWMARTN
SANMATEO
SACRMNTO
JARILLO
GUADLOUP
KENT
HUECOMTN
VANHORN
FRANKLIN
SULROSS
LSCRUCES
PINTOCYN
CHIN 30
FLTPLCKE
DVSSTPK
ORGANMTN
TM5300
TM5600
TM5900
LKVALLEY
CHIN 31
IMEMARTN
FTPINACO
CARLSBAD
NINEPT
LRYRUSS
LWRCATOK
RIVRROAD
MCKINNEY
LRYNEOCP
BRLNEOCP
ELGIN
LIVRMORE
TIMBERTP
CATTAIL
DAVISII
2.3 2.0 1.7 1.4 1.1 0.8 0.5 0.2

Fig. 11. Projection of the principal component analysis of *Echinocereus viridiflorus* complex OTUs. Three-dimensional projection of total variation of the 62 OTUs over 87 characters as explained by the first three principal component axes. Arrows indicate *E. chloranthus* var. *chloranthus* OTUs.

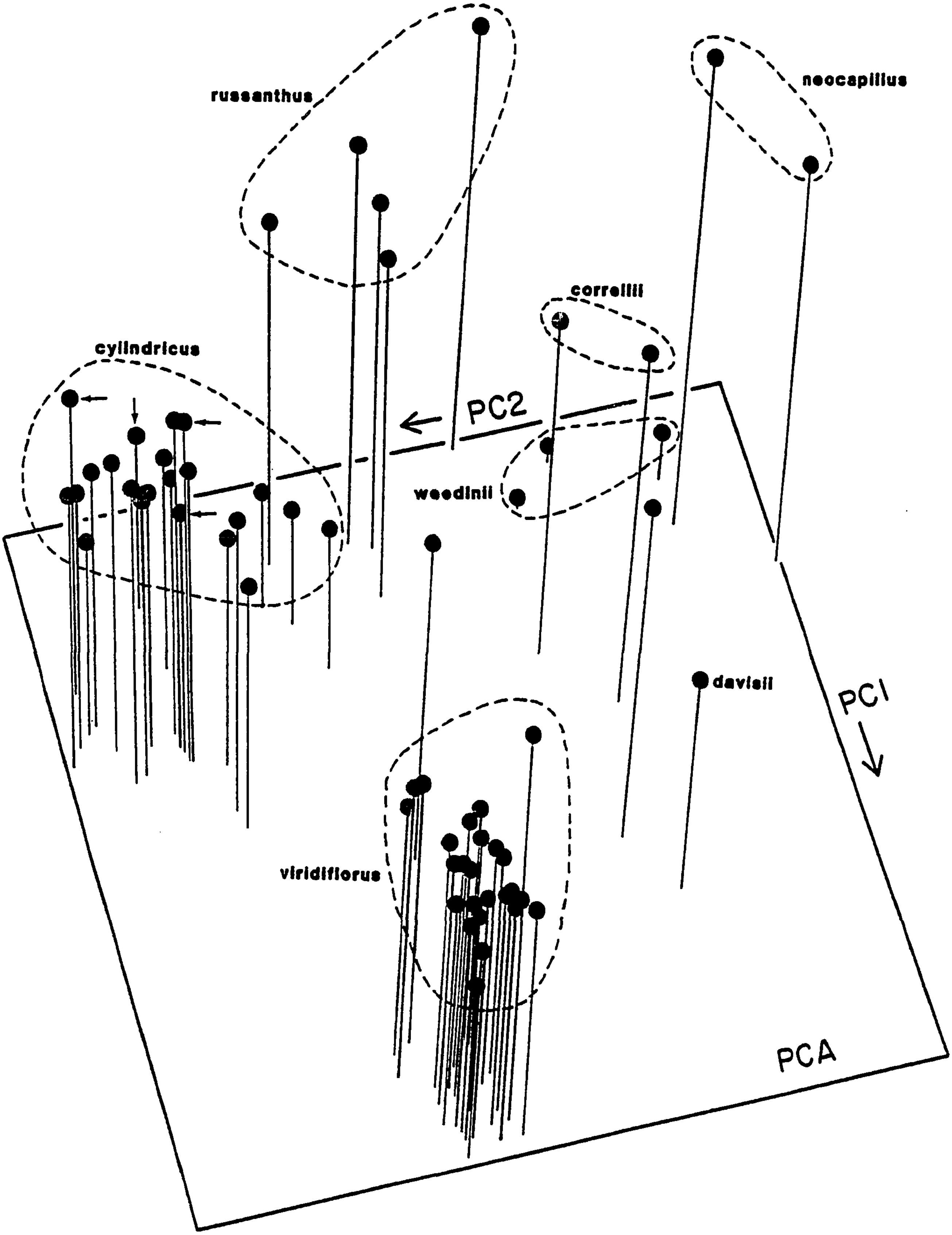

russanthus
neocapillus
correllii
cylindricus
PC2
weedinii
daviesii
PCI
viridiflorus
PCA

Fig. 12. Distribution of the *Echinocereus viridiflorus* complex. Based on herbarium records.

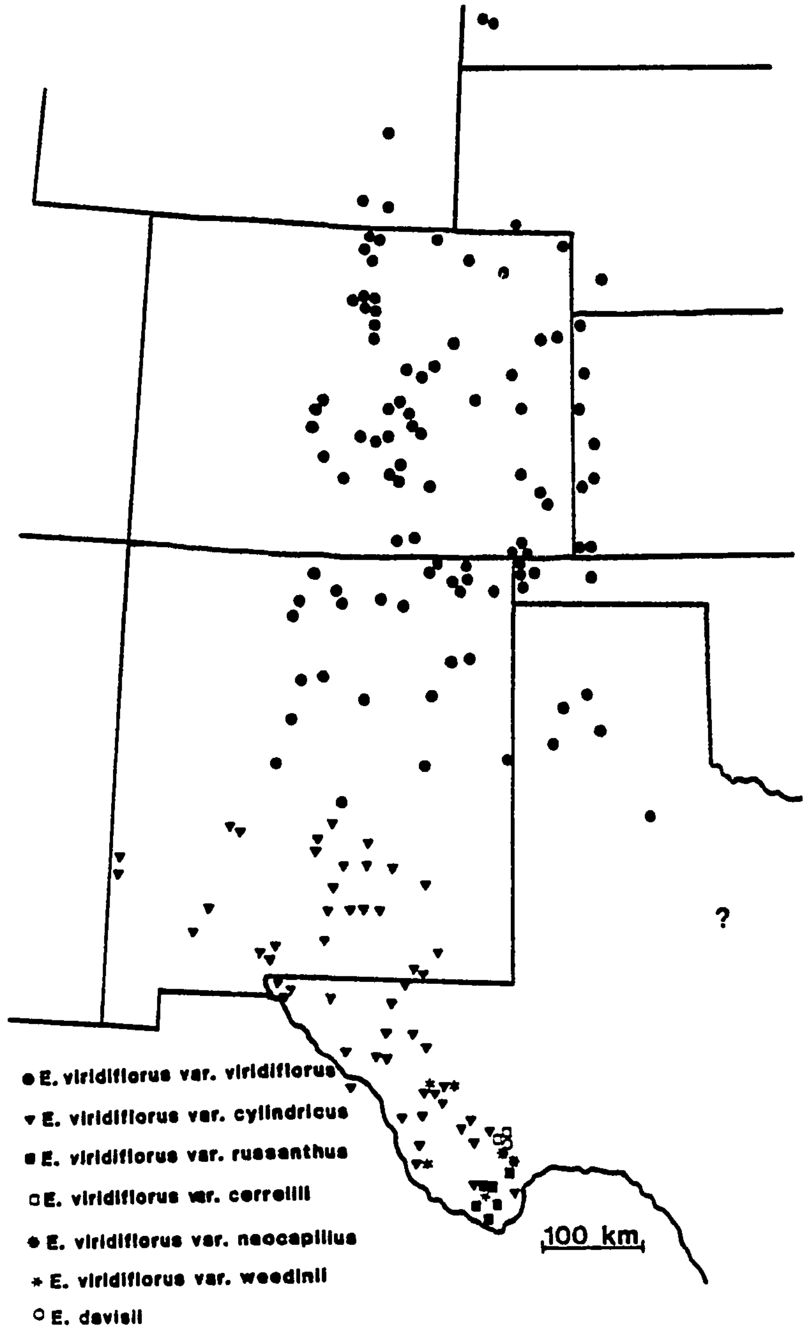

E. viridiflorus var. viridiflorus
E. viridiflorus var. cylindricus
E. viridiflorus var. russanthus
E. viridiflorus var. correllii
E. viridiflorus var. neocapillus
E. viridiflorus var. weedinii
E. davisii
100 km
?

Fig. 13. Apparent naturally occurring hybrids within the *Echinocereus viridiflorus* complex. Lines connect taxa that hybridize in the field.

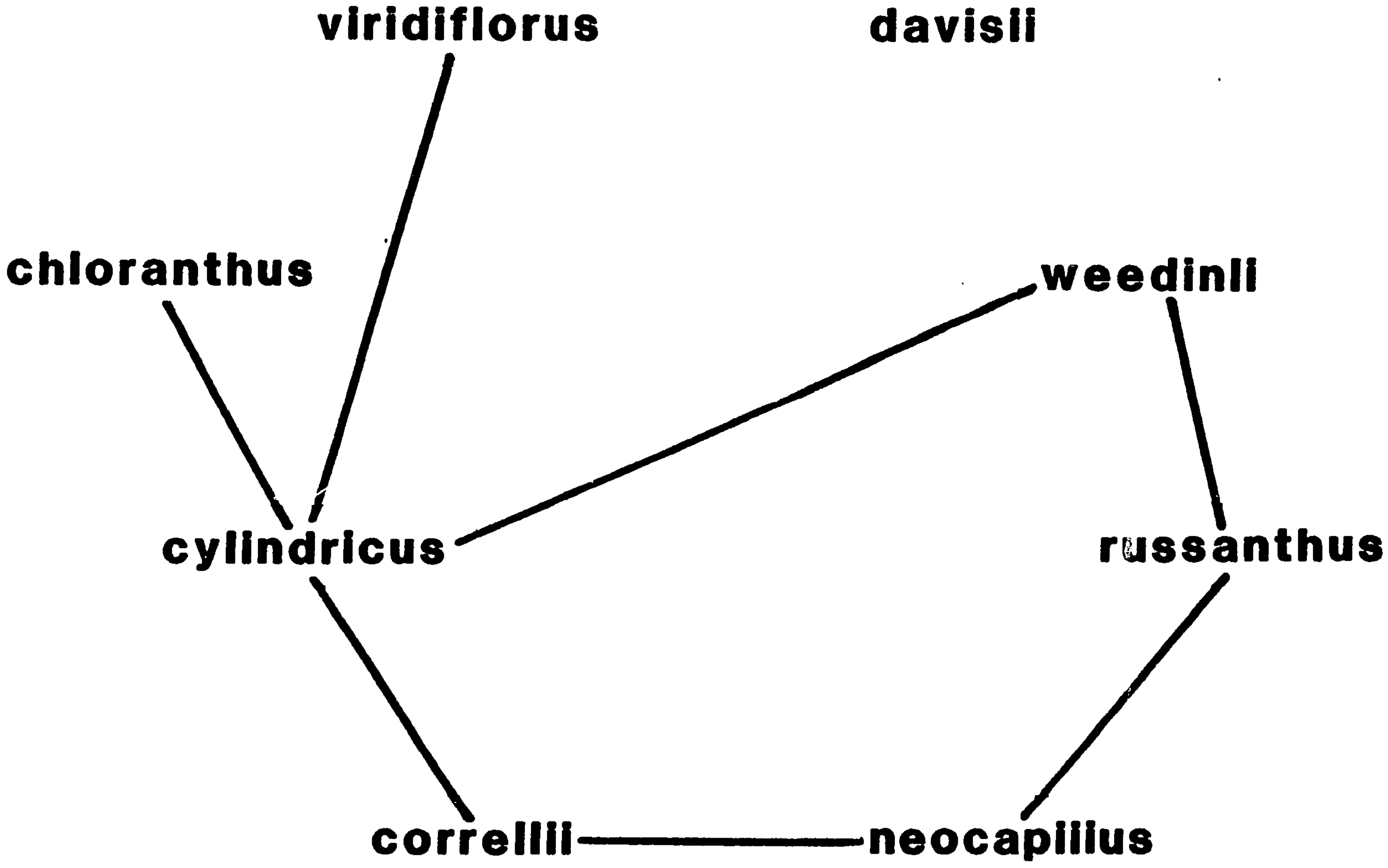
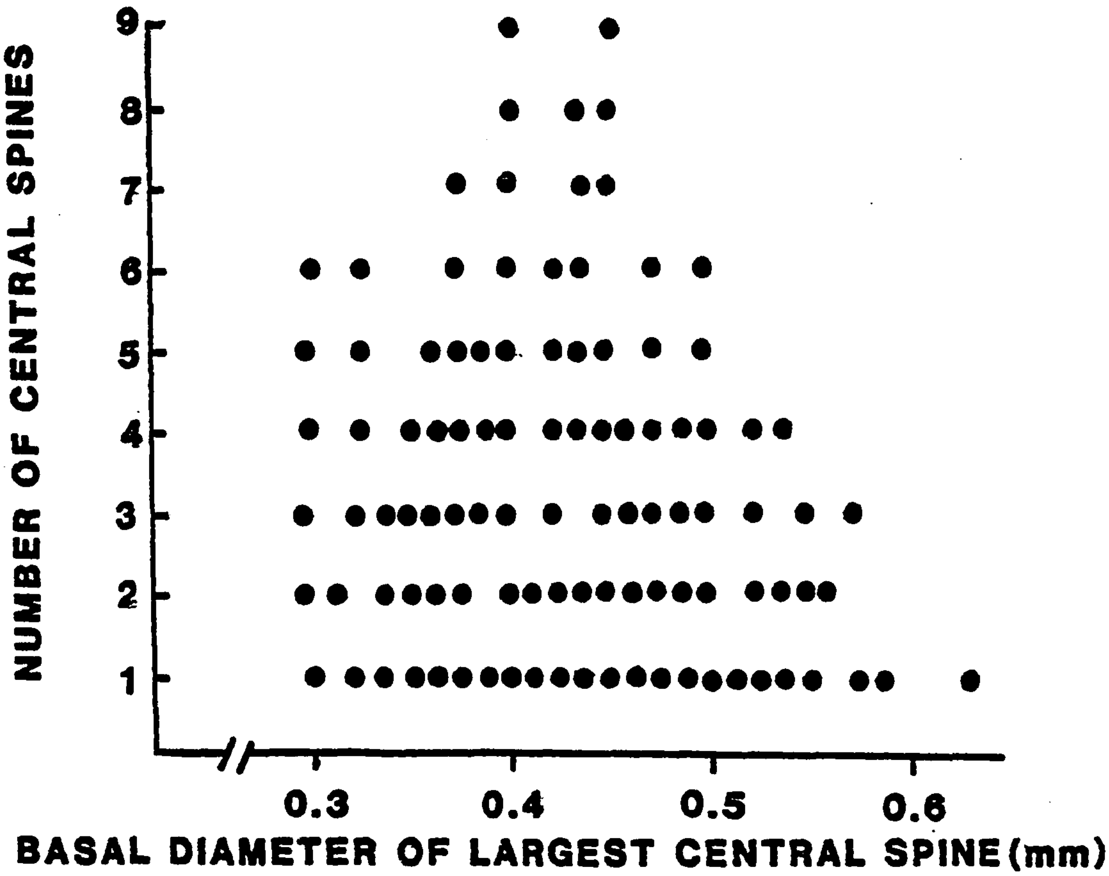

viridiflorus
davisii
chloranthus
weedinii
cylindricus
russanthus
correllii
neocapillus

Fig. 14 - 16. *Echinocereus viridiflorus* var. *weedinii var. nov.*

14. Flowering plant from the Davis Mountains, Jeff Davis Co., TX. x 0.4. 15. Top of thick-spined open-flowered form from the Davis Mountains. x 0.9. 16. Top of thin-spined, cylindrical-flowered form from the Chisos Mountains, Brewster Co., TX. x 0.9.

Fig. 17. Analysis of central spines of _Echinocereus viridiflorus_ var. _cylindricus_ and _E. chloranthus_ var. _chloranthus_. Dots represent individual plants from across the ranges of the taxa.


9
8
7
6
5
4
3
2
1
NUMBER OF CENTRAL SPINES
0.3
0.4
0.5
0.6
BASAL DIAMETER OF LARGEST CENTRAL SPINE (mm)

Appendix A. Collection sites. Live specimens used in numerical taxonomic and hybridization studies. Representatives of each collection are deposited in the Bebb Herbarium of the University of Oklahoma (OKL). OTU codes are given for those populations used in numerical analysis.

Echinocereus viridiflorus var. *viridiflorus*

COLORADO:

Baca Co.: N of Carriso River and Black Mesa, volcanic outcrops. E.E. Leuck 227, 11 August 1976; occasional. Boulder Co.: Lower end of Sunshine Canyon, City of Boulder greenbelt land; south-facing slope; E.E. Leuck 153, 14 August 1977; occasional; BOULDER. Left Hand Canyon, hillside across from Buckingham Park; E.E. Leuck 210, 19 August 1978; abundant. 7th St. and Aurora Ave., Boulder; rocky vacant lot; E.E. Leuck 142; 2 June 1977; formerly common but now extinct; *n* = 11. Top of Bald Mtn, 7500 ft; City of Boulder Park, Sunshine Canyon approximately 8 m NW Boulder; E.E. Leuck 226, 2 June 1977; common; BALDMTN. Cheyenne Co.: 11 m N Kit Carson; roadside right-of-way, east side; E.E. Leuck 205, 6 July 1978; occasional; KITCRSON. Fremont Co.: 7.5 m N Penrose along Co Hwy 115; road cut on W side of road, south-facing; 5800 ft; E.E. Leuck 139, 1 June 1977; infrequent; PENROSE. Fremont Co. Sanitary Landfill, 2 m SE Florence; open sandy hillside, pinyon-juniper; E.E. Leuck 151, 14 August 1977; rare. Jefferson Co.: Junction of Co Hwy 93 and 72, Rocky Flats; stony pasture; E.E. Leuck 141, 2 June 1977; occasional;

Appendix A. cont.

ROCKYFLT. Larimer Co.: 0.5 m S Wyoming state line along W side of US 287; granitic outcrops in ponderosa pine; E.E. Leuck 137, 30 May 1977; rare. W edge La Poudre, La Poudre Canyon; grassy south-facing slope; E.E. Leuck 138, 30 May 1977; abundant; n = 11; LAPOUDRE. Prowers Co.: 3 m N Two Buttes, midway between Lamar and Springfield along E side of US 287-385; E.E. Leuck 152, 15 August 1977; infrequent; PROWERS. Pueblo Co.: 4.5 m SW on Burnt Mill Rd from I-25 S of Pueblo; tops of south-facing alluvial hills on N side of St. Charles R; 5500 ft; E.E. Leuck 140, 1 June 1977; E.E. Leuck 155, July 1976; occasional; n = 11; BRNTMILL. Red Top Ranch, 0.5 m N junction with Co Hwy 10; sandstone hills with scattered junipers; E.E. Leuck 209, 21 August 1978; rare. Saquache Co.: 5 m E Crestone, 8200 ft; P.E. Nighswonger s.n., 1977. Sedgewick Co.: 3 m SE Julesburg, alluvial hills on E side of US 385; E.E. Leuck 207, 7 July 1978; abundant; JULESBERG. Yuma Co.: Prairie hilltop 0.5 m SW Bonny Reservoir dam; E.E. Leuck 206, 6 July 1978; infrequent; BONNYRES.

KANSAS:

Morton Co.: 8 m N Elkhart on Kansas Hwy 51, then 7 m SW on first road N Cimarron R into National Grassland; N side and top of alluvial hills N of oil rigging 0.5 m N of river; E.E. Leuck 203, 6 July 1978; common; MORTONKS. Sherman Co.: Short grass prairie hilltops near Sherman Co. State Fishing Lake, 10 m S and 2 m W Goodland; E.E. Leuck 208, 7 July 1978; common; n = 11; SHRMANKS.

Appendix A. cont.

NEW MEXICO:

Colfax Co.: S approach to Raton Pass; Alan Taylor s.n., 1977; RATON. Curry Co.: 1.5 m N Pleasant Hill; open pasture, southeast-facing slope above playa lake; B.E. Leuck 1, 30 May 1978; occasional. De Baca Co.: SE corner of Lake Sumner, sandstone outcrop, 4500 ft; E.E. Leuck 202, 20 May 1978; rare; SUMNERLK. Harding Co.: 9.5 m E Mosquero, half of distance up mesa along Hwy 39; 4500 ft; E.E. Leuck 145, 18 June 1977; rare. 2 m E Mosquero Hwy 39; sandstone above wash, 5450 ft; E.E. Leuck 146, 18 June 1977; rare; MOSQUERO. Rio Arriba Co.: Near Dixon; H. Kuenzler s.n., April 1978; common; DIXON. San Miguel Co.: Conchas Lake State Park, 2 m N of dam near Bell Ranch entrance, open juniper, sandstone, 4300 ft; E.E. Leuck 143, 17 June 1977; rare; LCONCHAS. Union Co.: Capulin Mtn National Monument; volcanic soil; R.T.B. Sherwood s.n., 1977; F. Forcella s.n., 1978; CAPULIN. Along Hwy 370 on volcanic outcrops near Clayton Lake; R.G. Ross and K. Pierce 182, May 1976; NEWMEXBM. Valencia Co.: 17 m SE Belen, gravel prairie outwash plains below Manzano Mtns; E.E. Leuck 201, 18 May 1978; occasional; MANZANO.

OKLAHOMA:

Cimarron Co.: 7 m N Boise City, E side of US 287-385; west-facing slope of small mesa; E.E. Leuck 154, July 1977; occasional. S side Black Mesa, one third to one half of distance up mesa; E.E. Leuck 156, 157, 158, 10 August 1976;

common. Regnier Ranch, Tesequite Canyon near Kenton; E.E. Leuck s.n., 9 August 1976; common; BLKMESA.

SOUTH DAKOTA:

Custer Co.: Ranch bordering Wind Cave National Park on W, 1 m toward Pringle on road leaving park; E slope, rocky grassland with ponderosa pine; D. Buitron s.n., 2 July 1978; common; n = 11; SODAKOTA.

TEXAS:

Deaf Smith Co.: 1 m SW Hereford; grassy slope leading to playa lake; K. Miller s.n., no date; formerly common, now extinct following plowing. Motley Co.: 8 m W Matador along US 62-70; S side of road in grassland sloping to south; E.E. Leuck 228, May 1979; E.E. Leuck 230, 17 April 1980 (both sides of road); infrequent. Potter Co.: E side of US 87-287, sandstone caps on limestone hills on S side of Canadian R floodplain; R.G. Ross and K. Pierce 181, May 1976; common, but restricted; POTTERTX. Randall Co.: On rim of Palo Duro Canyon, 0.25 m from edge along state park road leading into canyon; sandstone; R.G. Ross and K. Pierce 180, May 1976; rare.

WYOMING:

Platte Co.: 17 m N Wheatland on I-25, then 15 m W from El Rancho exit; igneous soil; J.F. and T.J. Weedin 500, 22 May 1977; common; n = 11; WYOMING.

Echinocereus viridiflorus var. cylindricus

NEW MEXICO:

Chaves Co.: 8 m W junction Hwy 13 on US 82; limestone; S side of road with Agave; E.E. Leuck 232, 30 April 1980. Dona Ana Co.: Granitic NE foothills of Organ Mtns, 5100 ft in outwash flats along BLM road; E.E. Leuck 198, 16 May 1978; rare; ORGANMTN. Limestone hills E New Mexico State University campus, Las Cruces; steep E and north-facing slopes, 4000 ft; E.E. Leuck 117, 18 May 1977; rare; n = 11; LSCRUCES. Eddy Co.: At entrance to Carlsbad Caverns National Park from US 62-180, on steep limestone south-facing slope, 3850 ft; E.E. Leuck 128, 24 May 1977; occasional; n = 11; CARLSBAD. 1 m W of US 62-180 at rest area just N Texas state line; 1 m SW Pine Springs, 5650 ft, open limestone hills; E.E. Leuck 127, 24 May 1977; occasional; GUADLOUP. Otero Co.: 0.25 m W High Rolls at 6700 ft, W side of Sacramento Mtns; N side US 82, south-facing pinyon-ponderosa pine hillside, limestone; E.E. Leuck 131, 25 May 1977; occasional; SACRMNTO. Jarillo Mtns NW Orogrande; N-facing slopes near summits of limestone mountains; E.E. Leuck 196, 15 May 1978; infrequent; n = 11; JARILLO. Edge of national forest land between Elk and Mayhill, US 62, Sacramento Mtns; E.E. Leuck 231, 17 April 1980; occasional. Sierra Co.: N-facing steep talus slope, granitic, Lake Valley, 4550 ft; E.E. Leuck 198, 16 May 1978; occasional; LKVALLEY. Sierra Co.: S side of San Mateo Peak, San Mateo Mtns, 7300 ft; open steep rocky slope, some pinyon-juniper; E.E. Leuck 199, 17 May 1978; infrequent; n = 11; SANMATEO.

TEXAS:

Brewster Co.: Sul Ross Hill, Alpine; steep igneous slope, 4500

Appendix A. cont.

ft; E.E. Leuck 114, 19 May 1977; occasional; SULROSS. Culberson Co.: 4 m N Kent, on overgrazed limestone benches and outwash flats, 4150 ft; E.E. Leuck 179, 180, 13 March 1978; KENT. 5 m SW Pine Springs along US 67-385 just north of junction with US 62-180; limestone benches on W-facing slope above rest area, 1600 m; E.E. Leuck 126, 24 May 1977; occasional. El Paso Co.: Fusselman Canyon, south side of Intermountain Hwy, Franklin Mtns; scattered on low rocky hills; E.E. Leuck 118a, 18 May 1977; infrequent. Low outwash hills, E foothills of Franklin Mtns along Intermountain Hwy; granitic grassland; E.E. Leuck 118b, 18 May 1977; abundant; n = 11; FRANKLIN. Hudspeth Co.: Limestone benches at S edge Hueco Mtns along US 62-180, W of turnoff to state park, 5000 ft; E.E. Leuck 194, 15 May 1978; infrequent; n = 11; HUECOMTN. Igneous road cut on S side of US 80 - I-10, 5 m W Van Horn just W Culberson Co. line; E.E. Leuck 183, 13 May 1978; occasional; VANHORN. Jeff Davis Co.: Grassy slope with ponderosa pine below McDonald Observatory; S-facing igneous slope, 6450 ft; E.E. Leuck 106, 22 May 1977; occasional; n = 11; FLTPICKE. Lower Madera Canyon, N Timber Mtn, Davis Mtns; near Epsy Ranch property line 5200 ft; J.F. Weedin 847, 848, 29 June 1977. Lower Madera Canyon, near old Hunsaker Resort N of Timber Mtn; rocky slopes; J.F. Weedin and M.B. Crabtree 590, 20 June 1977; infrequent. Top of loop drive in Davis Mtns State Park N Fort Davis, Davis Mtns; E.E. Leuck 181, 13 March 1978; infrequent; DVSSTPK. Presidio Co.: Chilicote Ranch, 20 m W Marfa; B.H. Warnock s.n.,

Appendix A. cont.

15 October 1977. Head of Pinto Canyon, overgrazed steep igneous slopes near cattle guard, 34 m SW Marfa; E.E. Leuck 172, 9 January 1978; infrequent; n = 11; PINTOCYN. Chinati Mtns, among granitic boulders on NE slopes of Chinati Peak; upper half of Indian Cave Canyon; E.J. Lott and M. Butterwick 31 (CHIN31); Tigna Canyon; Lott and Butterwick 29; upper slopes leading to saddle E of Chinati Peak; Lott and Butterwick 30 (CHIN30); 15 October 1977; infrequent.

Echinocereus viridiflorus var. weedinii

TEXAS:

Brewster Co.: Cattail Falls, W side Chisos Mtns, Big Bend National Park; cracks in vertical igneous cliff, W-facing, 4250 ft; E.E. Leuck 110 and J.F. Weedin, 20 May 1977; n = 11; CATTAIL. Jeff Davis Co.: Top of Timber Mtn, 6400 ft; cracks in igneous rock, Davis Mtns; E.E. Leuck 193, 13 May 1978; J.F. Weedin 1100, June 1977; C.L. Peterson and M.B. Crabtree s.n., 24 September 1977; common; n = 11; TIMBERTP. Mt. Livermore, Davis Mtns, 7500 ft; D.O. Kolle 135. 8250 ft; upper SE slope, J.F. Weedin 913, 19 September 1977; LIVRMORE.

Echinocereus viridiflorus var. correllii

TEXAS:

Brewster Co.: 5 m S Marathon at Fort Pina Colorada; W side, Caballos novaculite, 4000 ft; E.E. Leuck 113, 19 May 1977; E.E. Leuck 184, 12 March 1978; common; FTPINACO. 3 m NE Marathon at NW corner of junction US 90 and Hwy 385; 4150 ft; Caballos novaculite grassland; E.E. Leuck 124, 13 May 1977; common;

Appendix A. cont.

1MMARTN.

Echinocereus viridiflorus var. neocapillus

TEXAS:

Brewster Co.: 10 m S Marathon US 385, 0.5 m W rest stop; E Bourland Mtn; novaculite; E.E. Leuck 119, 14 May 1977; common; n = 11; BRLNEOCP. 12 m S Marathon, novaculite, W side of road cut; E.E. Leuck 182, 12 March 1978; rare. 15 m S Marathon, US 385; Tom Leary Ranch, E side; novaculite outcrops and hills, S-facing; E.E. Leuck 173, 10 January 1978; E.E. Leuck 188, 15 March 1978; common; n = 11; LRYNEOCP.

Echinocereus viridiflorus var. russanthus

TEXAS:

Brewster Co.: NW flank of Chilocotal Mtn, Big Bend National Park; E.E. Leuck 187 and J.F. Weedin, 14 March 1978; common. Leary Ranch, 16 m S Marathon E of US 385; steep novaculite hills; E.E. Leuck 174, 10 January 1978; occasional. Leary Ranch 18 m S Marathon E of US 385; steep novaculite hills; E.E. Leuck 175, 176, 10 January 1978; rare; LRYRUSS. SE slope Nine-point Mesa, 55 m S Alpine, Hwy 118, 4200 ft; D.O. Kolle 69A; NINEPT. 2 m E Terlingua, black igneous low hills; R.T.B. Sherwood s.n., 7 March 1979. Trail to Cattail Falls on W mesas below Chisos Mtns, Big Bend National Park; gravelly igneous soil, 3850-4450 ft; E.E. Leuck 111 and J.F. Weedin, 20 May 1977; common; n = 11; LWRCATOK. McKinney Hills, Big Bend National Park, 15-18 m N of south entrance to Old Ore Road, 3000-3150 ft; igneous soil among boulders; E.E. Leuck 123 and J.F. Weedin, 14 May 1977; n = 11; MCKINNEY. Big Bend National Park, between Smokey Creek and Buenos Aires along River Road; J.F. and T.J. Weedin 435, 22 March 1977; RIVROAD.

Echinocereus davisii

TEXAS:

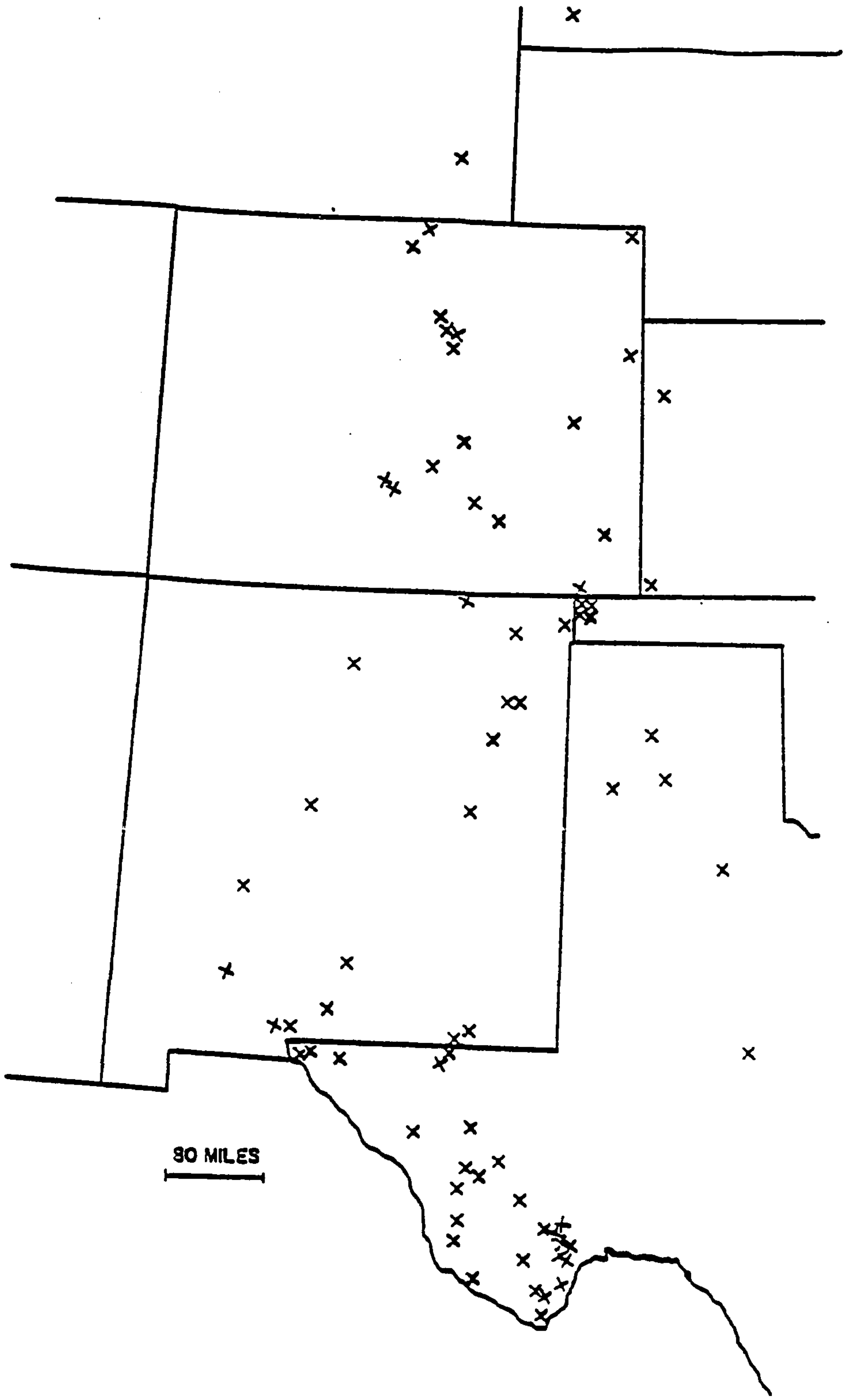
Brewster Co.: 3.5 m S Marathon along Hwy 385; Caballos novaculite outcrops, with Selaginella, 4000 ft; E.E. Leuck 120, 14 May 1977. E.E. Leuck 108, 20 May 1977; rare; n = 11; DAVISII.

Possible hybrids:

Talus slope W of Cattail Falls, 4450 ft; Chisos Mtns, Big Bend National Park, Brewster Co., TX; E.E. Leuck 189 and J.F. Weedin, March 1978 (hybrid of E. viridiflorus var. russanthus and var. weedinii). Ridge above Pigpen Canyon, 1800 m, Davis Mtns, Jeff Davis Co., TX; E.E. Leuck 191, 192, 13 May 1978; TM5900 (hybrid of E. viridiflorus var. cylindricus and var. weedinii). Sul Ross Research Station, Pigpen Canyon, 1640 m, Davis Mtns, Jeff Davis Co., TX; E.E. Leuck 190, 13 March 1978; TM5300 (hybrid of E. viridiflorus var. cylindricus and var. weedinii). Old Madera Springs Resort, E rim of Timber Mtn, 1950 m, Davis Mtns, Jeff Davis Co., TX; J.F. Weedin 672, 674, 22 June 1977 (hybrid of E. viridiflorus var. cylindricus and var. weedinii). 8 m W Marathon, US 90; railroad access on S side of road, alluvial grassland, Brewster Co., TX; E.E. Leuck 119, 14 May 1977; 8MWMARTN (hybrid of E. viridiflorus var. cylindricus and var.

correllii). 10 m NW Robert Lee, alluvial hills along Texas 228, Coke Co., TX; *E.E. Leuck 229*, August 1978; *R.T.B. Sherwood s.n.*, March 1978; ROBRTLEE (hybrid similar to *E. viridiflorus* var. *correllii*, var. *neocapillus*).

Appendix A. cont. Collection sites for the *E. viridiflorus* complex.


80 MILES

Appendix B. Herbarium sheets examined.

Echinocereus viridiflorus var. viridiflorus

COLORADO:

Arapahoe Co.: 5 m N Deertrail; S. Stephens 22572 and R. Brooks, 13 June 1968 (KU). Baca Co.: Sections 4, 9 E Sandy Creek Canyon; W.A. Weber 4630, 6 May 1949 (CU). 20 m S, 3 m W Pritchett; S. Stephens 21855 and R. Brooks, 5 June 1968 (KU). 1 m S Mt. Carrizo; G. Arp 828, 16 August 1969 (CU). 5 m W, 18 m S Pritchett; S. Stephens 54233, 5 June 1972 (KU). 4 m W, 20 m S Pritchett; S. Stephens 57309, 19 July 1972 (KU). 1 m N Carriso River, Black Mesa area; E.E. Leuck 227, 11 August 1976 (OKL). Bent Co.: Rule Creek; G.E. Osterhout 6904, 9 June 1910 (RM). 3 m S Hasty, John Martin Reservoir; S. Stephens 64757, 26 May 1973 (KU). Boulder Co.: Plains and foothills near Boulder; F. Tweedy 5009, 5010, July 1902 (RM, NY). Junction Foothills Hwy and Left Hand Canyon Rd 8 m N Boulder; W.A. Weber s.n., 15 April 1949 (CU). 1.5 m S junction Co 7 and 66, N Boulder; L. and R. Benson 16215, 22 August 1962 (RSA). 7th St and Aurora Ave, Boulder; E.E. Leuck 159, June 1973; 142, 2 June 1977 (OKL). Top of Bald Mtn 8 m NW Boulder; E.E. Leuck 226, 2 June 1977 (OKL). Left Hand Canyon, near Buckingham Park; E.E. Leuck 210, 19 August 1978 (OKL). Chaffee Co.: 10 m W Salida, E approach to Monarch Pass; L. and R. Benson 14738, 29 October 1950 (RSA). 2 m W summit of Trout Creek Pass; G.K. Arp 1428, 15 August 1970 (CU). 2 m W Buena Vista; G.K. Arp 1435, 15 August 1970 (CU). Cheyenne Co.: 11 m N Kit Carson;

S. Stephens 54749, 12 June 1972 (KU). E.E. Leuck 205, 6 July 1978 (OKL). Douglas Co.: Plains at Franktown; W.A. Weber s.n., 13 May 1951 (CU). Elbert Co.: Pine grove 14 m E Elbert; W.A. Weber 6000, 13 May 1951 (CU). 4 m NE Elbert; S. Stephens 22507 and R. Brooks, 12 June 1968 (KU). El Paso Co.: Pike's Peak region; G. Engelmann s.n., May 1861 (MO). Mountains of Colorado, N Pike's Peak; W.M. Canby s.n., August 1871 (NY). Plains, Colorado Springs; M.F. Jones 103, 23 May 1878 (MO, US, RSA). Colorado Springs; 1-392, 26 June 1896 (US, NY). Mountains, Manitou; C.I. Shear 3685, 2 July 1896 (NY). Colorado Springs; F.W. Homace 12-83, 20 May 1912 (US). US 85-87 22 m SE Colorado Springs; L. and R. Benson 15696, 8 August 1956 (RSA). 8 m S Fountain; R.O. Albert 64, 24 July 1960 (RSA). Colorado Springs; R.O. Albert 66, 24 July 1960 (RSA). Fremont Co.: Canyon of the Arkansas; J.S. Brandage 542, 19 May 1873 (MO, US). 7 m E Canon City; L. and R. Benson 14734, 28 October 1950 (RSA). 14 m NW Canon City; S. Stephens 26941 and R. Brooks, 4 August 1968 (KU). 7.5 m N Penrose along Co 115; E.E. Leuck 139, 1 June 1977 (OKL). Fremont Co. Sanitary Landfill, 2 m SE Florence; E.E. Leuck 151, 14 August 1977 (OKL). Jefferson Co.: Mesa top junction Coal Creek Canyon and Rocky Flats Roads, 9 m S Boulder; W.A. Weber 13200, 27 June 1967 (CU). Junction Co 72 and 93; G. Arp 954, 27 October 1969 (CU). 0.25 m NW N Table Mesa, E Co 93; G.K. Arp 870, 29 May 1970 (CU). 7 m S Boulder, Rocky Flats Pediment; G. Kunkel and L. Schultz 132, 13 June 1973 (CU). Junction Co 72 and 93, Rocky Flats; E.E. Leuck 141, 2 June 1977

(OKL). Kit Carson Co.: 1.5 m E Flagler; S. Stephens 54726, 11 June 1972 (KU). Larimer Co.: Roadside between Trail's End and Livermore; E.B. and L.B. Payson 4241, 31 May 1925 (MO, GH, RM). Between Cherokee Park and Virginia Dale; E.B. and L.B. Payson 4241, 31 May 1925 (US). Near Dale Creek, below Virginia Dale; G.J. Goodman 100, 28 May 1927 (OKL). Loveland, mouth of Big Thompson Canyon; S.L. Heacock s.n., June 1964 (RSA). 10 m S Virginia Dale; W.A. Weber and G.N. Jones 12384, 9 June 1965 (CU). 2 m N entrance to Owl Creek Canyon along US 187; G.K. Arp 1384, 2 August 1970 (CU). 0.5 m S Wyoming state line along W side US 287; E.E. Leuck 137, 30 May 1977 (OKL). W edge La Poudre, La Poudre Canyon; E.E. Leuck 138, 30 May 1977 (OKL). Las Animas Co.: Trinidad; A. Eastwood 3293, June 1891 (CU). Vicinity of Trinidad; J.N. Rose and W.R. Fitch 17517, 26 September 1913 (US, NY). 5 m W Westen near Trinidad; G. Arp 829, 16 August 1969 (CU). Lincoln Co.: Rush Creek, 17 m S Limon; T.P. Maslin 6002, 28 April 1951 (CU). Logan Co.: 10 m S Sterling; S. Stephens 5088, 19 June 1966 (KU). Prowers Co.: 23 m S Lamar; S. Stephens 54498, 9 June 1972 (KU). 22 m S Lamar; S. Stephens 64832, 26 May 1973 (KU). 3 m N Two Buttes along US 287-395; E.E. Leuck 152, 15 August 1977 (OKL). Pueblo Co.: Near Beulah; W.W. Robbins 4945, 5-9 June 1908 (CU). 24 m S Pueblo, US 85-87; L. and R. Benson 14730, 28 October 1950 (RSA). 4.5 m SW I-25 on Burnt Mill Rd S Pueblo; E.E. Leuck 140, 1 June 1977; E.E. Leuck 155, July 1976 (OKL). Red Top Ranch, 0.5 m N junction Co 10 E I-25 near Huerfano-Las Animas line; E.E. Leuck

209, 21 August 1978 (OKL). Saguache Co.: Villa Grove; F. Ramaley and K.R. Johnson 14622, 17 June 1935 (CU). 5 m E Crestone; P.E. Nighswonger s.n., 1977 (OKL). Sedgwick Co.: 3 m SE Julesburg; R.L. McGregor 23818, 20 June 1971 (KU). E.E. Leuck 207, 7 July 1978 (OKL). Weld Co.: 3 m N Stoneham; S. Stephens 11695 and R. Brooks, 15 June 1967 (KU). Pawnee Buttes National Grassland 13 m NW Keota; G.K. Arp 1612, 20 May 1971 (CU). Yuma Co.: 10 m E Joes; S. Stephens 11750 and R. Brooks, 15 June 1967 (KU). 0.5 m SW Bonny Reservoir dam; E.E. Leuck 206, 6 July 1978 (OKL). County unknown: Rocky Mountain Flora, lat 39° - 41°; E. Hall and J.P. Harbour 69, 1862 (GH). Colorado; Dr. Scoville s.n., 1869 (US). Golden City; E.L. Greene 132, 23 May 1870 (GH). Colorado; J.W. Toumey 1 May-15 September 1895 (RSA, MO, US, NY). Veta Mtn, southern Colorado; P.A. Rydberg and F.K. Vreeland 5868, 24 May 1900 (NY). Colorado; E. Hall s.n., no date (NY).

KANSAS:

Cheyenne Co.: 9 m W, 13.5 m N St. Francis; S. Stephens 48020, 7 June 1971 (KU). Greeley Co.: 15 m N, 7.5 m E Tribune; S. Stephens 57294, 18 July 1972 (KU). Hamilton Co.: Vicinity of Syracuse; J.N. Rose and W.R. Fitch 17048, 15 September 1912 (US, NY). 4 m N, 0.5 m E Syracuse; S. Stephens 50296, 1 August 1971 (KU). 3 m W, 2 m N Syracuse; S. Stephens 52950, 18 May 1972 (KU). Morton Co.: A.S. Hitchcock s.n., August 1895 (KSU). 7 m N, 1 m E Elkhart; S. Stephens 52054, 12 Sepetember 1971 (KU). 8 m N Elkhart Kansas 51, then 7 m SW along Cimarron R; E.E. Leuck

203, 6 July 1978 (OKL). R.C. McGregor 30790, 21 July 1978 (KU). Sherman Co.: 10 m S, 2.5 m W Goodland, Sherman Co. State Lake; S. Stephens 57263, 18 July 1972 (KU). E.E. Leuck 208, 7 July 1978 (OKL). Stanton Co.: Plains; A.S. Hitchcock 184, 5 August 1895 (KSU, RM, MO, US, NY). Stevens Co.: A.S. Hitchcock s.n., August 1895 (KSU). Wallace Co.: 1.5 m N Weskan; S. Stephens 47984, 6 June 1971 (KU). 13 m S, 1 m E Sharon Springs; S. Stephens 64672, 24 May 1973 (KU).

NEBRASKA:

Chase Co.: 3 m SE Enders; R.L. McGregor 23896, 23 June 1971 (KU). Cheyenne Co.: 2 m S Colton; S. Stephens 5310, 21 June 1966 (KU).

NEW MEXICO:

Bernalillo Co.: E slope Sandia Mtns; P. Pierce 1100, 29 July 1962 (NM). Above Sandia Park, Sandia Mtns; E.F. Castetter 3055, 14 June 1965 (NM). Colfax Co.: Vermejo Park; E.O. Wooton 13-391; 2 September 1913 (US). Vicinity of Raton; J.N. Rose and W.R. Fitch 17531, 27 September 1913 (US, NY). Vicinity of Ute Park; P.C. Standley 14189, 1 September 1916 (US). Near Cimarron; R.O. Albert 59, 23 July 1960 (RSA). S edge of Raton Airport; P. Pierce 719, 720, 5 December 1961 (NM). NE of Raton along State 72; P. Pierce 1214, 27 September 1962 (NM). Cimarron Creek, 0.5 m W Palisades; P. Pierce 2111, 6 August 1963 (NM). Bartlett Mesa N Raton; P. Pierce 2083, 2084, 8 August 1963 (NM). Philmont Scout Ranch near Cimarron; R.L. Hartman 1711, 12 April 1968 (RM). Hilltop with Gambell's oak; G.K. Arp 1804, 11 September

1971 (CU). S approach to Raton Pass; A. Taylor s.n., 1977 (OKL). Near Ute Park; P. Pierce 1204, no date (NM). Curry Co.: 1.5 m N Pleasant Hill; P. Pierce 2195, 19 October 1963 (NM). B.E. Leuck 1, 30 May 1979 (OKL). De Baca Co.: SE corner Lake Sumner; E.E. Leuck 202, 20 May 1978 (OKL). Harding Co.: 9.5 m E Mosquero, Hwy 39; E.E. Leuck 146, 18 June 1977 (OKL). Lincoln Co.: Along US 380 in W foothills Capitan Mtns; P. Pierce 2280, 11 November 1963 (NM). Several m S Corona, just W US 54; P. Pierce and E.F. Castetter 2213, 25 October 1963 (NM). Rio Arriba Co.: Hills E Rio Vallicitos about 3 m N La Madera; E.F. Castetter 1021, 4 June 1962 (NM). SE face San Antonio Peak; P. Pierce 1061, 1062, 1063, 1064, 1065, 27 June 1962 (NM). 1 m N Ghost Ranch Headquarters N Albiquiu; P. Pierce 1166A and B, 14 August 1962 (NM). Near Dixon; H. Kuenzler s.n., April 1978 (OKL). San Antonio Peak; D. and J. Cowper s.n., no date (RSA). Santa Fe Co.: Near Wolf Creek on Santa Fe Rd; Dr. Wizlizenus 514, 1846 (MO). Vicinity of Santa Fe; J.N. Rose and W.R. Fitch 17772, 4 October 1913 (US, NY). San Miguel Co.: Ridge 13 m S Las Vegas along US 84; L. and R. Benson 14698, 26 October 1950 (RSA). Conchas Lake State Park; E.E. Leuck 143, 17 June 1977 (OKL). Taos Co.: E rim Rio Grande Box Canyon; E.F. Castetter 2153, 2154, 4 September 1963 (NM). 18 m SW Taos along Hwy 64; W. Reid 101, November 1970 (CU). Rio Grande Gorge; R. and M. Spellenberg 4972, 29 May 1978 (TAM). Union Co.: Cimarron R several m S Folsom; E.F. Castetter 221, August 1952 (NM). Williams Canyon, dry Cimarron R; E.F. Castetter 220, 9 August

1953 (NM). N slope Sierra Grande S of Des Moines; E.F. Castetter 2176, 2177, 6 September 1963 (NM). N slope Sierra Grande near Des Moines; E.F. Castetter 2178, 2179, 5 September 1963 (NM). 5 m S Folsom; S. Stephens 75581, 13 May 1974 (KU). Along Hwy 370 near Clayton Lake; R.G. Ross and K. Pearce s.n., 1978 (OKL). Capulin Mtn National Monument; R.T.B. Sherwood s. n., 1977 (OKL). F. Forcella s.n., 1978 (OKL). Valencia Co.: 17 m SE Belen; E.E. Leuck 201, 30 May 1978 (OKL). Santa Fe; A. Fendler 278, 6 September 1847 (MO, GH). 15 m W Santa Fe; A.A. Heller and E.G. Heller 3580, 22 May 1897 (MO, US, NY). Mara Visa; G.L. Fisher 102, 21 April 1911 (US). Santa Fe; C. Wright s.n., no date (GH).

OKLAHOMA:

Cimarron Co.: 20 m W Boise City; F. Barkley s.n., 8 July 1928 (OKL). Top of Black Mesa; G.J. Goodman 5300, 5 June 1959 (OKL). 1.5 m N Lake Etling State Park; S. Stephens 73742, 15 September 1973 (KU). Regnier Ranch, Tesequite Canyon near Kenton; E.E. Leuck s.n., 9 August 1976 (OKL). S side Black Mesa; E.E. Leuck 156, 157, 158, 10 August 1976 (OKL). 7 m N Boise City, E side US 287-385; E.E. Leuck 154, July 1977 (OKL). Texas Co.: High level prairie near Camp; G.W. Stevens s.n., 11 May 1913 (OKL, GH, MO, NY).

SOUTH DAKOTA:

Custer Co.: Hot Springs; P.A. Rydberg 715, 15 June 1892 (NY). 6 m N Hot Springs; S. Stephens 6009, 26 June 1966 (KU). 1 m W Wind Cave National Park; D. Buitron s.n., 2 July 1978 (OKL).

Appendix B. cont.

TEXAS:

Armstrong Co.: 15 m SSW Claude; C.M. Rowell 11013, 21 May 1966 (TTC). Deaf Smith Co.: 1 m SW Hereford; K. Miller s.n., no date (OKL). Motley Co.: 8 m W Matador, US 62-70; E.E. Leuck 228, May 1979. 230, 17 April 1980. Oldham Co.: 10 m E Vega, US 66; L. and R. Benson 14711, 27 October 1950 (RSA). Potter Co.: E side US 87-287 on S side Canadian R; R.G. Ross and K. Pearce 181, May 1976 (OKL). Randall Co.: Rim of Palo Duro Canyon; R.G. Ross and K. Pearce 188, May 1976 (OKL). County unknown: Plains near Canadian; J.M. Bigelow 726, 12 September 1853 (MO).

WYOMING:

Albany Co.: Base of Laramie Mtn; F.V. Hayden s.n., 1856 (MO). Pole Creek; A. Nelson 113, 2 June 1894 (RM). Laramie Co.: Foothills W of Isley; M. Carey 311, 25 June 1909 (US). Platte Co.: Sybille Creek; C.L. Porter 6702, 27 June 1955 (RM). 17 m N Wheatland on I-25, 15 m W El Rancho exit; J.F. and T.J. Weedin 500, 22 May 1977 (SR, OKL).

UNKNOWN:

NY #15598, photograph of flowering plant in 1904. F.W. Kas, MO #2240082. MO #2016895.

Echinocereus viridiflorus var. cylindricus

MEXICO:

Chihuahua: 20 m S Rio Grande, 18 m out from El Porvenir; M.B. Gurney s.n., 27 February 1958 (RSA).

NEW MEXICO:

Catron Co.: On Holliman Ranch near Pleasanton; P. Pierce 3521, 3523, 3524, 11 October 1967 (NM). Chaves Co.: 51 m W Artesia; L. and R. Benson 15562, 20 July 1955 (RSA). Hills W Roswell along US 380; R. Villard 615, 616, 617, 1959 (NM). Border Hills 23 m W Roswell; E.F. Castetter and P. Pierce 629, 631, 634, 635, 3 December 1961 (NM). Pecos R bottom, Dexter; P. Pierce and E.F. Castetter 626, 1962 (NM). 8 m W junction Hwy 13 on US 62, S side with agave; E.E. Leuck 232, 30 April 1980 (OKL). Dona Ana Co.: Organ Mtns; E.O. Wooton 263, May 1892 (US). Mesa, Las Cruces; E.O. Wooton s.n., June 1892 (GH). Tortugas Mtn SE Las Cruces; E.O. Wooton s.n., 22 April 1896 (US). Organ Mtns; E.O. Wooton 3079, 20 October 1904 (NM, NMS). Tortugas Mtn; E.O. Wooton and P.C. Standley 3082, January 1905 (GH, NMS, US). Organ Mtns; E.O. Wooton s.n., 11 June 1906 (RM, KSU). Organ Mtns; P.C. Standley s.n., 11 June 1906 (MO, US). Tortugas Mtn; J.N. Rose, P.C. Standley, P.G. Russell 12255, 28 February 1910 (US, NY). Cactus Garden at the Agriculture College; J.N. Rose, P.C. Standley, P.G. Russell 15195, 30 April 1910 (US). Boyd Ranch, mouth of Dripping Springs Canyon in the W face of the Organ Mtns, 3 m SE Huevos Rocks, 14 m E Las Cruces; D.B. Dunn 7936, 24 May 1952 (NMS). Tortugas Mtn E of NM State Univ; P. Pierce 668, 17 November 1961 (NM). E slope San Andreas Mtns; G. Sandborg 1043, 26 June 1962 (NM). SW base Bishop's Cap, Organ Mtns; E.F. Castetter 2325, 17 October 1963 (NM). Soledad Canyon, W slope Organ Mtns; P. Pierce 2430, 13 February 1964 (NM). Base W slope central part Organ Mtns; G. Wiens 2891, 29

November 1964 (NM). N base Tortugas Mtn Organ Mtns; L. Benson 16475, 2 April 1965 (RSA). Just below Dripping Springs, Organ Mtns; L. Benson 16469, 16471, 12 April 1965 (RSA). N end E ridge Dona Ana Mtns; G. Wiens 3337, 22 June 1966 (NM). Bishop's Cap; T. Corbett 3996, March 1972 (NM). Limestone hills E NMSU Campus, Las Cruces; E.E. Leuck 117, 18 May 1977 (OKL). Limestone "A" mountain, Las Cruces; D. Kolle 1341, 1342, 7 September 1977 (SR). NE foothills Organ Mtns; E.E. Leuck 198, 16 May 1978 (OKL). Organs; no name, date (NM #18931). Eddy Co.: Queen (Guadalupe Mtns); E.O. Wooton s.n., 3 August 1909 (NMS). Near Carlsbad; R.T. Craig G, 22 December 1951 (RSA). SW Carlsbad; E. and J. Nadolny 4A, 4B, 2 September 1961 (NM). Along Pecos R, Carlsbad; J. Blea 1144, August 1962 (NM). Along canal E side Pecos R N Carlsbad along US 285; J. Blea 1143, 1145, 19 August 1962 (NM). Rattlesnake Canyon, Carlsbad Caverns National Park; E.F. Castetter 1471, 1472, 14 November 1962 (NM). N end Carlsbad on terrace Pecos R; E.F. Castetter 2248, 2249, 2250, 2251, 27 October 1963 (NM). Rattlesnake Ridge 4 m W Headquarters Carlsbad Caverns National Park; P. Pierce and E.F. Castetter 2252, 28 October 1963 (NM). Rattlesnake Canyon, Carlsbad Caverns National Park; E.F. Castetter 1471, 1472, 14 November 1962 (NM). Middle Walnut Canyon, Carlsbad Caverns National Park; E.F. Castetter 2494, 15 April 1964 (NM). Old Bat Cave, Carlsbad Caverns; L. and R. Benson 15542, 19 July 1965 (RSA). 1 m SW Pine Springs, 1 m W US 62-180 at rest area; E.E. Leuck 127, 24 May 1977 (OKL). Entrance to Carlsbad Caverns National Park; E.

E. Leuck 128, 24 May 1977 (OKL). Grant Co.: Holliman Ranch, 8 m W Pleasanton, foothills Brushy Mtn; P. Pierce 3526, 11 October 1967 (NM). Lincoln Co.: Little Creek, White Mtn Peak; E.O. Wooton s.n., 29 July 1901 (US). Just N US 380 and just W Sunset, Hondo Valley; E.F. Castetter and P. Pierce 622, 3 December 1961 (NM). 2.5 m N Tinnie, Hondo Valley, along State Route 386, E foothills Capitan Mtns; P. Pierce 803, 804, 805, 15 February 1962 (NM). 4 m N Tinnie, E foothills Capitan Mtns, State Route 386 from Tinnie to Arabela; P. Pierce 808, 15 February 1962 (NM). 12 m S road intersecting US 380 2 m W Picacho; P. Pierce 815, 816, 20 February 1962 (NM). Near Arabela; P. Pierce 823, 7 March 1962 (NM). 10 m N Border Hill from US 380 on Clyde Morley Ranch; P. Pierce 851, 21 March 1962 (NM). Top of limestone hill T8S, R19E; P. Pierce 1907, 28 February 1963 (NM). Just W Carizozo (sic) lava bed, 5 m S US 380; G. Wiens 1945, 28 March 1965 (NM). 5 m SE Fort Stanton Guard Station at base Capitan Mtns; J. French 2751, 11 October 1964 (NM). 12 m S Carrizozo; B. Huychins 3915, 25 October 1971 (NM). Jacarilla Mtns, 6 m SSE Jack's Peak; K. Schwerin 4115, 21 August 1972 (NM). Luna Co.: Cooks Peak; Adhman s.n., no date (US). Otero Co.: White Mtn Peak; E.O. Wooton s.n., 6 July 1895 (US). Sacramento Mtns (standley); P.C. Standley s.n., 1 May 1910 (US, NY). NE slope Deer Mtn; E.F. Castetter 2513, 11 May 1962 (NM). Jarilla (sic) Mtns, NW Orogrande; E.F. Castetter and P. Pierce 1703, 6 April 1963 (NM). White Mtns, SE Mescalera; P. Pierce and E.F. Castetter 2258, 2259, 26 October 1963 (NM).

Appendix B. cont.

ENE slope Deer Mtn, Cornudas Mtn group; E.F. Castetter 2510, 2511, 2512, 4 April 1964 (NM). Dog Canyon, Sacramento Mtns; G. Wiens 3512, 3513, September 1967 (NM). Brokeoff Mtns on escarpments; G. Wiens 3828, April 1971 (NM). Jarilla (sic) Mtns near Orogrande; T. Corbett 3993, March 1972 (NM). No location; G. Wiens 4028 Part B, late May 1972 (NM). 0.25 m W High Rolls, W side Sacramento Mtns, US 82; E.E. Leuck 131, 25 May 1977 (OKL). Jarillo Mtns NW Orogrande; E.E. Leuck 196, 15 May 1978 (OKL). Lincoln National Forest boundary between Elk and Mayhill, US 82; E.E. Leuck 231, 17 April 1980. Sierra Co.: Lake Valley; P. Pierce 110, 4 October 1961 (NM). H. Hicks 3987, March 1972 (NM). D.A. and A.D. Zimmerman 1507, 20 May 1970 (NM). E.E. Leuck 198, 16 May 1978 (OKL). Socorro Co.: S side San Mateo Peak, San Mateo Mtns; E.E. Leuck 199, 17 May 1978 (OKL). 5 m SW San Mateo Peak, San Mateo Mtns; E.E. Leuck 200, 17 May 1978 (OKL). County unknown: V. Blake, from her garden, 3 July 1962 (NM #36226). C. Wright 41, 1852 (GH).

TEXAS:

Brewster Co.: Alpine; B. Mackensen 09-294, September 1901 (US). 10 m up the Rio Grande from Reagan Canyon; B.H. Warnock 47-443, 4 April 1947 (SR). Paradise Canyon 4 m W Alpine; B.H. Warnock 47-444, 47-454, 10 April 1947 (SR). Sul Ross Hill, Alpine; B.H. Warnock 47-447, 10 April 1947 (SR). 20 m S Alpine, Texas 118; L. and R. Benson 15478, 15 July 1955 (SR). Sul Ross Hill; W.D. McBryde 341, 346, 29 March 1957 (SR). 15 m N Study Butte along Hwy 118; D. Weniger 157, 158, 6 May 1963 (NM). Simpson

Spring, halfway between Marathon and Big Bend; P. Pierce 4229, 18 March 1973 (NM). Sul Ross Hill; J.F. Weedin 424, 15 March 1977 (SR). E.E. Leuck 114, 19 May 1977 (OKL). D. Kolle 137, 4 October 1977 (SR). 8 m W Marathon, US 90; E.E. Leuck 119, 19 May 1977 (OKL). Coke Co.: 10 m NW Robert Lee, Texas 208; R.T. B. Sherwood s.n., March 1978 (OKL). E.E. Leuck 229, August 1978 (OKL). Culberson Co.: Hills about 5 m W Van Horn; B.H. Warnock 47-476, 30 May 1947 (SR). Limestone hills E Salt Basin, 20-25 m NE Van Horn; L.C. Hinckley 4025, 29 August 1947 (US). Near Hwys 69 and 160 (180?) within sight of Signal Peak of Guadalupe Mtns; D. Weniger 346, 14 October 1963 (NM). Top of Guadalupe Mtns; B.H. Warnock 21210, 10 August 1966 (SR). 3.3 m N Kent; D. Kolle 91, 2 April 1977 (SR). 5 m SW Pine Springs along US 67-385 just N junction US 62-180; E.E. Leuck 126, 24 May 1977 (OKL). Guadalupe Springs, Guadalupe Mtns; D. Kolle 120, 13 July 1977 (SR). 4 m N Kent; E.E. Leuck 179, 180, 13 March 1978 (OKL). Deadman Canyon, Apache Mtns; J.F. Weedin 1175, 3 July 1978 (SR). El Paso Co.: Stony hills near the Rio Grande at Frontera; C. Wright 95, 2 April 1852 (MO, RSA, NY). El Paso; J.M. Bigelow s.n., April 1852 (MO). Rocky gravelly hills, Frontera; C.C. Parry, J.M. Bigelow, C. Wright, A. Schott s.n., April 1852 (US). G. Engelman s.n., 1873 (US). El Paso; G.R. Vasey s.n., 1881 (US, NY). M.E. Jones 3746, 21 April 1884 (US, RSA, NY). M.E. Jones s.n., 25 April 1884 (RSA). J.W. Toumey s.n., 12 May 1896 (US, NY). J.W. Toumey s.n., 20 May 1896 (US). Franklin Mtns; J.N. Rose, P.C. Standley, P.G. Russell 12275, 26

Appendix B. cont.

February 1910 (US, NY). El Paso; P.C. Standley and P.G. Russell s.n., 1910 (NY). Franklin Mtns; J.N. Rose 13854, 1913 (NY). Canutillo; C.R. Orcutt 239, 6 April 1924 (US). Canyon E side Franklin Mtns, 5 m from the S end; L. Benson 15461, 15463, 12 July 1955, mixed pectinatus-cylindricus (RSA). Mundy Canyon, E side Franklin Mtns; M.B. Gurney s.n., 10 October 1957 (RSA). Trans Mtn Road, Franklin Mtns; D. Kolle and B.H. Warnock 76, 25 March 1977 (SR). Canyon E side Franklin Mtns on El Paso by-pass; D. Kolle and B.H. Warnock 82, 2 April 1977 (SR). Fusselman Canyon, Franklin Mtns; E.E. Leuck 118A, 18 May 1977 (OKL). Outwash hills E side Franklin Mtns; E.E. Leuck 118B, 18 May 1977 (OKL). Franklin Mtns, Trans Mtn Hwy; D. Kolle 121, 17 July 1977 (SR). Tom May Park, Franklin Mtns; D. Kolle 138, 5 October 1977 (SR). Hudspeth Co.: 6 m W Sierra Blanca; B.H. Warnock 13988, 5 September 1955 (SR). Sierra Blanca Mtn; K. Wilson, D.O. Kolle, B.H. Warnock 101, 1976 (SR). US 80 - I-10 5 m W Van Horn; E.E. Leuck 183, 13 May 1978 (OKL). S edge Hueco Mtns along US 62-180; E.E. Leuck 194, 15 May 1978 (OKL). Jeff Davis Co.: Stony hills of the Limpia; valleys among the mountain heads of the Limpia; C. Wright s.n. 1851 (MO). Davis Mtns; L.C. Hinckley 1175, 14 August 1939 (NY). Tricky Gap, Buffalo Train Scout Ranch, Davis Mtns; B.L. Turner 8056, 8 August 1948 (SR). 12 m S Kent; L. and R. Benson 15470A, 14 July 1955 (RSA). Limpia Creek Canyon, 10 m NE Fort Davis; along Hwy 118; D. Weniger 372, October 1963 (NM). 12 m NW Alpine along Hwy 118; D. Weniger 380, October 1963 (NM). Above

Appendix B. cont.

pool at head of Fern Canyon, Mitre Peak Girl Scout Ranch; E. Keough 239, 30 September 1964 (SR). 5 m W Toyahvale; R. Reach 35, 2 April 1966 (TTC). Near E water well at roadside park, Davis Mtns State Park; B.H. Warnock 22075, 15 April 1967 (SR). Slopes above lodge Davis Mtns State Park; B.H. Warnock 22681, 7 July 1967 (SR). S-facing slope below McDonald Observatory, Davis Mtns; E.E. Leuck 106, 22 May 1977 (OKL). Lower Madera Canyon, near old Hunsaker Resort, N side of Timber Mtn; J.F. Weedin and M.B. Crabtree 590, 20 June 1977 (OKL). Old Madera Springs Resort, E rim Timber Mtn, Davis Mtns; J.F. Weedin 672, 674, 22 June 1977 (OKL). Lower Madera Canyon, N Timber Mtn, Davis Mtns, near Epsy property line; J.F. Weedin 848, 874, 29 June 1977 (OKL). E side Mt. Livermore; D. Kolle, Blackenship, J. Martin, R. Martin 135, 14 September 1977 (SR). Trail to Madera Canyon Overlook, old Nations Estate; J.F. Weedin 905A-H, 906A-D, 8 October 1977 (SR). Ridge tops, Davis Mtns State Park; E.E. Leuck 181, 13 March 1978 (OKL). Sul Ross research station, Pigpen Canyon, Davis Mtns; E.E. Leuck 190, 13 May 1978 (OKL). Ridge above Pigpen Canyon toward Timber Mtn; E.E. Leuck 191, 192; 13 May 1978 (OKL). Presidio Co.: Musgrove Canyon, Sierra Tierra Vieja; L.C. Hinckley 2764, 13 June 1943 (NY). Love Ranch S Marfa near Pinto Canyon; J.F. Weedin and M. Lockhart 119, 25 August 1975 (SR). Chilocote Ranch 20 m W Marfa; B.H. Warnock s.n., 15 October 1977 (OKL). Head of Pinto Canyon, 34 m SW Marfa; E.E. Leuck 172, 9 January 1978 (OKL). Chinati Mtns, NE slope Chinati Peak; upper half Indian Cave Canyon; E.J. Lott and

Butterwick 31; Tigna Canyon, Lott and Butterwick 29; upper slopes leading to saddle E Chinati Peak; Lott and Butterwick 30, 15 October 1977 (OKL). County unknown: C. Wright s.n., 1851 (GH). C. Wright s.n., 1851, var. major (GH). Western Texas; C. Wright s.n., 1849 (NY). From L.A. cactus garden; W.T. Swingle 236, 4 January 1905 (US).

Echinocereus viridiflorus var. russanthus

TEXAS:

Brewster Co.: Chisos Mtns; J. Ashman s.n., 1923 (US). Blue Creek Canyon; J.H. Ferriss 526, March 1925 (US). J.H. Ferriss 528 (US). J.H. Ferriss s.n., 1925 (US). 14 m E Castalon; H. Cutler 667, 25 February 1937 (MO, TAM). 3 m W junction to Panther Pass, BBNP; L. and R. Benson 15502, 16 July 1955 (RSA). 15 m N Study Butte along Hwy 118; D. Weniger 156, 6 May 1963 (NM). Panther Pass, Chisos Mtns, BBNP; L. Benson 18513, 12 April 1965 (RSA). BBNP, 5 m E ranger headquarters; J.E. Hodgkins 3, 1965 (UT). N side Castalon Peak; B.H. Warnock 21079, 5 March 1967 (SR). Panther Canyon in Chisos Mtns, BBNP; B.H. Warnock 21207, 20 March 1967 (SR). Panther Canyon (Mouse Canyon), BBNP; B.H. Warnock 21174, 22 March 1967 (SR). Rocky fan W Oak Creek; R.H. Waner BI, 18 February 1968 (RSA). Chilocotal Mtn, BBNP; D. Smith 2201, 2 July 1972 (SR). Talley Mtn, BBNP; D. Smith 2206, 2 July 1972 (SR). 7 m N Terlingua; P. Pierce 4206, 20 March 1973 (NM). 3 m N McKinney Ranch House, Old Ore Road, BBNP; J.F. Weedin 20, 29 February 1975 (SR). Black Hill near Nine Point Mesa; J.F. Weedin and D.O. Kolle 409, 25 February 1977 (SR). Green Gulch; D. Kolle and J.F. Weedin 46, 4 March 1977 (SR). S of Castalon, 2 m N Smokey Creek; D. Kolle 64, 12 March 1977 (SR). BBNP, along River Road between Smokey Creek and Buenos Aires; J.F. and T.J. Weedin 435, 22 March 1977 (OKL). McKinney Springs ranch house; D. Kolle 70, 23 March 1977 (SR). Government Spring; D.O. Kolle 73, 24 March 1977 (SR). Laguna Meadows, Ward Mtn, BBNP; D. Kolle 97, 8 April 1977 (SR). McKinney Hills, 15-18 m N south entrance to Old Ore Road, BBNP; E.E. Leuck 123 and J.F. Weedin, 14 May 1977 (OKL). Oak Springs Road, W side Chisos Mtns, BBNP; E.E. Leuck 111 and J.F. Weedin, 20 May 1977 (OKL). 68 m S Alpine; D. Kolle 116, 27 June 1977 (SR). Green Gulch; Kolle and Kolle 119, 30 June 1977 (SR). 17.6 m S Marathon; D. Kolle 130, 1 September 1977 (SR). 17.2 m S Marathon; D. Kolle 141, 13 October 1977 (SR). 55 m S Alpine, Hwy 118, Nine Point Mesa; D. Kolle 142, 25 October 1977 (SR). SE slope Nine Point Mesa, 55 m S Alpine; D.O. Kolle 69A, 1977 (OKL). Leary Ranch 16 m S Marathon; E.E. Leuck 174, 10 January 1978 (OKL). Leary Ranch, 18 m S Marathon; E.E. Leuck 175, 176, 10 January 1978 (OKL). NW flank Chilocotal Mtn, BBNP; E.E. Leuck 187 and J.F. Weedin, 14 March 1978 (OKL). 2 m E Terlingua; R.T.B. Sherwood s.n., 7 March 1979 (OKL). R.O. Albert 36, no date or collection site (RSA).

Echinocereus viridiflorus var. neocapillus

TEXAS:

Brewster Co.: Simpson Spring Rest Area, 10 m SW Marathon; P. Pierce 4163, 4164, 18 March 1973 (NM). W side East Bourland Mtn;

J.F. and T.J. Weedin 191, 30 January 1976 (SR). Tom Leary Ranch, Marathon; D. Kolle and B.H. Warnock 92A, 92B, 5 April 1977 (SR). 10 m S Marathon, East Bourland Mtn; E.E. Leuck 119, 14 May 1977 (OKL). D. Kolle s.n., 8 June 1977 (SR). D. Kolle, Blackenship, Martin and Martin 136, 15 September 1977 (SR). D. Kolle 140, 13 October 1977 (SR). 12 m S Marathon; E.E. Leuck 182, 12 March 1978 (OKL). 15 m S Marathon, Leary Ranch; E.E. Leuck 173, 10 January 1978 (OKL). E.E. Leuck 188, 15 March 1978 (OKL).

Echinocereus viridiflorus var. correllii

TEXAS:

Brewster Co.: 3 m S Marathon; L. Vortman 2807, 2808, 2809, 10 October 1964 (NM). Hills above Fort Pena, 4 m S Marathon (type); L. Benson and D.S. Correll 16485, 14 April 1965 (RSA). Hess Ranch, 6 m from gate at ranch house, Glass Mtns; J.F. Weedin 156, 18 October 1975 (SR). Near Hess Canyon, Glass Mtns; J.F. Weedin 188, 18 October 1975 (SR). 3 m NE Marathon, US 90; E.E. Leuck 124, 13 May 1977 (OKL). 5 m S Marathon, Fort Pena Colorada; E.E. Leuck 113, 19 May 1977 (OKL). E.E. Leuck 184, 12 March 1978 (OKL). 3 m SE Marathon; B.H. Warnock s.n., 20 May 1977 (SR). 3 m E Marathon, US 90; D.O. Kolle 139, 13 October 1977 (SR). Pecos Co.: Hills N Fort Stockton; B.H. Warnock 11031, 12 March 1953 (SR).

Echinocereus viridiflorus var. weedinii

TEXAS:

Appendix B. cont.

Brewster Co.: Ward Mtns, BBNP; B.H. Warnock 21209, 25 September 1967 (SR). Cattail Falls, Chisos Mtns, BBNP; E.E. Leuck 110 and J.F. Weedin, 20 May 1977 (CKL). D. Kolle 127, 31 August 1977 (SR). Jeff Davis Co.: Mt. Livermore; L.C. Hinckley s.n., 19 August 1939 (NY). E slope Timber Mtn; L.C. Hinckley 7773, 20 July 1947 (SR). Top of Timber Mtn; J.F. Weedin 1100, June 1977 (OKL). C.L. Peterson and M.B. Crabtree s.n., 24 September 1977 (OKL). E.E. Leuck 193, 13 May 1978 (OKL). Mt. Livermore, Davis Mtns; D.O. Kolle 135 (OKL). J.F. Weedin 913, 19 September 1977 (OKL).

Echinocereus davisii

TEXAS:

Brewster Co.: 4 m S Marathon; P. Pierce 4201, 18 March 1973 (NM). Under Selaginella; A.D. Houghton 700, 1931 (GH, US). 4 m S Marathon; G. Lazas and A. Klar s.n., no date (SR). 5 m S Marathon; B.H. Warnock 22849, 28 March 1969 (SR). S Marathon, BBNP; D. Smith 2225, 4 July 1972 (SR). 3.5 m S US 90 E Marathon; L. Benson 16499, 6 April 1965 (RSA). E.E. Leuck 120, 14 May 1977 (OKL). E.E. Leuck 108, 20 May 1977 (OKL).

Appendix C. Loadings for the first three principal components of the members of the *Echinocereus viridiflorus* complex based on all characters.

Character	Components I	II	III
Fruit green	0.505	-0.495	0.299
Fruit red	-0.613	0.356	-0.214
Fruit not splitting	-0.922	0.083	0.014
Fruit splitting	0.817	-0.383	0.206
No fruit abscission	-0.409	0.007	0.293
Fruit abscission	0.121	-0.111	0.069
Fruit spines not shed	-0.302	-0.517	0.189
Dry fruit	0.825	0.415	0.167
Fruit juicy	-0.910	0.257	0.010
Ovary spines white	-0.056	0.218	0.075
Ovary spines dark	-0.154	0.041	0.024
Flowers yellow	0.658	-0.324	-0.203
Flowers red	-0.776	0.465	0.110
Lemon floral odor	0.684	-0.421	-0.235
Sweet floral odor	-0.313	-0.297	-0.553
Petals reflexed	0.326	-0.235	0.203
Petals erect	-0.675	0.388	-0.315
Annual bands of color	-0.309	-0.098	0.397
Radial spines white	0.323	0.364	0.648
Radial spines dark	0.377	0.547	0.375
Radial spines translucent	-0.549	-0.511	-0.288

Appendix C. cont.

Character	Components I	II	III
Central spines white	0.344	0.292	0.487
Central spines dark	0.377	0.547	0.375
Central spines translucent	-0.532	-0.525	-0.238
Basal clumping	0.475	0.356	-0.360
Branching stems	0.513	0.162	-0.223
Taproot	0.056	-0.218	-0.075
Novaculite	-0.134	-0.551	0.343
Granite	-0.029	-0.025	-0.136
Sandstone	0.606	-0.034	0.077
Alluvium	0.316	-0.055	0.093
Limestone	-0.284	0.475	-0.037
North-facing slope	-0.200	0.159	0.123
South-facing slope	0.007	-0.226	0.138
East-facing slope	-0.306	-0.126	0.220
West-facing slope	-0.043	-0.016	0.027
Seedlings hairy	-0.135	-0.496	0.363
Seedling spines plumose	-0.044	-0.356	0.118
Seedling spines pectinate	0.493	0.665	-0.082
Seedling spines deflexed	-0.577	-0.286	-0.263
Petals short	-0.568	0.358	-0.451
Days to fruit maturity	-0.416	0.264	0.319
Ovary spine length	-0.718	-0.097	0.131
Fruit length	0.429	0.412	0.543

Appendix C. cont.

Character	Components I	II	III
Fruit width	0.154	0.556	0.367
Length of flowering season	0.073	-0.099	0.232
Average number of radial spines	-0.691	-0.498	0.179
Maximum length of radial spines	-0.723	0.264	0.123
Maximum central spine length	-0.483	0.182	-0.167
Number of ribs	-0.560	0.055	-0.213
Field plant width	-0.618	0.424	0.159
Height of two year plant	-0.803	-0.068	0.200
Width of two year plant	0.135	0.084	0.311
Latitude	0.894	0.088	-0.148
Rainfall	0.215	-0.348	-0.331
Seed weight	0.047	0.238	-0.056
Potential seed set	-0.142	0.218	0.726
Field seed set	0.276	0.207	0.522
Field plant height	-0.835	0.229	0.106
Longitude	-0.165	0.513	-0.223
Seed width	-0.115	0.321	-0.335
Seed length	0.677	0.080	-0.006
Seed width/length	0.585	0.222	-0.199
First year germination	-0.378	-0.076	-0.406
Second year germination	0.391	0.123	0.393
Third year germination	-0.040	-0.330	0.229
Total germination	-0.104	-0.132	0.179

Appendix C. cont.

Character	Components I	II	III
Hilum diameter	0.645	0.062	-0.038
Seedling survival	0.314	0.165	-0.289
Fruit spine diameter	-0.351	0.515	-0.070
Fruit width/length	-0.466	-0.001	-0.451
Maximum radial spine diameter	-0.340	0.515	0.158
Maximum central spine diameter	-0.115	0.398	-0.142
Areole width/length	-0.322	-0.145	-0.176
Number of central spines	-0.696	-0.342	0.050
Number of heads	0.410	0.312	-0.226
Areoles per ovary	-0.618	0.011	0.519
Day of first flowering	0.023	0.521	-0.282
Ovary spines per areole	-0.549	-0.338	0.414
Maximum number of radial spines	-0.673	-0.513	0.198
Maximum number of central spines	-0.683	-0.376	0.079
Areole length	-0.468	0.244	0.346
Areole width	-0.642	0.105	0.208
Maximum number of ribs	-0.557	0.101	-0.116
Altitude	-0.017	0.243	-0.521
Second year width/length	0.850	-0.025	-0.084
Field width/length	0.858	-0.023	-0.081

Appenidix D. Field and greenhouse seed set of fruits in populations of the <u>Echinocereus</u> <u>viridiflorus</u> complex.

Population	Field No. of fruits	Field Seed set	Greenhouse No. of fruits	Greenhouse Seed set	% Field / Greenhouse
<u>E</u>. <u>viridiflorus</u> var. <u>viridiflorus</u>					
Custer Co., SD	10	131.0	26	160.4	81.7
Platte Co., WY	11	129.0	20	155.5	83.0
Larimer Co., CO	31	117.1	39	139.4	84.0
Julesburg, CO	8	106.4	12	145.0	73.4
Bonny Reservoir, CO	--	--	6	155.0	--
Kit Carson, CO	--	--	10	162.0	--
Morton Co., KS	8	96.8	12	174.3	55.5
Sherman Co., KS	--	--	9	149.0	--
Prowers Co., CO	17	120.3	7	173.5	69.3
Bald Mtn, CO	21	98.6	23	150.0	65.7
Boulder, CO	26	134.8	41	167.1	80.7
Rocky Flats, CO	6	120.0	7	161.0	74.5
Penrose, CO	--	--	13	154.2	--
Burnt Mill Rd, CO	14	111.4	25	162.2	68.7
Raton, NM	4	102.5	8	136.0	75.4
Dixon, NM	3	118.3	14	139.0	85.1
Mosquero, NM	13	139.0	19	172.0	80.8
Lake Conchas, NM	38	114.6	37	209.8	54.6
Capulin, NM	21	99.1	17	126.6	78.3
Manzano Mtns, NM	16	155.3	9	174.3	87.2

Appendix D. cont.

Population	Field No. of fruits	Field Seed set	Greenhouse No. of fruits	Greenhouse Seed set	% Field / Greenhouse
Potter Co., TX	--	--	11	142.9	--
Sumner Lake, NM	8	115.9	13	180.9	64.1
Black Mesa, OK	24	141.1	37	188.0	75.0
Robert Lee, TX	17	125.2	20	181.0	69.2
<u>E</u>. <u>viridiflorus</u> var. <u>cylindricus</u>					
San Mateo Mtns, NM	12	155.3	8	174.3	89.1
Sacramento Mtns, NM	16	141.1	14	188.0	75.1
Carlsbad, NM	21	51.8	16	119.6	43.3
Jarillo Mtns, NM	14	132.4	13	180.4	73.4
Lake Valley, NM	12	68.7	23	121.6	56.5
Las Cruces, NM	9	146.6	12	190.5	76.9
Organ Mtns, NM	16	128.2	10	178.2	71.9
Guadalupe Mtns, TX	23	137.2	17	169.1	81.1
Franklin Mtns, TX	15	98.2	23	152.3	64.5
Hueco Mtns, TX	8	138.2	8	194.1	71.2
Van Horn, TX	--	--	15	238.5	--
Kent, TX	14	160.0	14	199.2	80.3
Pinto Canyon, TX	--	--	9	168.2	--
Sul Ross Hill, TX	9	109.0	16	173.5	62.8
Flat Top, TX	7	142.4	9	233.4	61.0
Davis Mtns State Park, TX	--	--	14	202.3	--

Appendix D. cont.

Population	Field No. of fruits	Field Seed set	Greenhouse No. of fruits	Greenhouse Seed set	% Field / Greenhouse
TM 5300, TX	14	69.6	11	145.4	47.9
TM 5600, TX	6	80.0	6	164.0	48.8
TM 5900, TX	13	78.0	13	133.7	58.4
E. viridiflorus var. *weedinii*					
Mt Livermore, TX	--	--	7	98.7	--
Timber Mtn, TX	23	80.9	21	87.7	92.2
Cattail Falls, TX	11	89.0	14	99.2	89.7
E. viridiflorus var. *russanthus*					
Nine-point Mesa, TX	--	--	5	239.8	--
McKinney Hills, TX	16	78.0	31	133.7	58.3
Oak Springs, TX	14	120.3	13	166.2	72.4
Leary Ranch, TX	8	118.0	17	204.6	57.7
E. viridiflorus var. *neocapillus*					
Leary Ranch, TX	24	131.6	21	217.8	60.4
Bourland Mtns, TX	26	107.2	27	202.0	53.1
E. viridiflorus var. *correllii*					
1 m E Marathon, TX	17	124.2	21	211.9	58.6
Fort Pena Colorada, TX	12	111.5	27	172.0	64.8
E. davisii					
S Marathon, TX	16	44.0	53	69.2	63.6