Some Chromosome Complements in the Cactaceae and a Study of Meiosis in Echinocereus papillosus
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SOME CHROMOSOME COMPLEMENTS IN THE CACTACEAE AND A STUDY OF MEIOSIS IN ECHINOCEREUS PAPILLOSUS[1]

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(WITH PLATES I, II AND TEXT FIGURES)

Introduction

The cytology of the Cactaceae is of particular interest because of the development in the family of certain morphological characters which sharply separate it from all others. As a whole, this family contains well over 1000 species in 124 genera. The material for this paper was taken entirely from the tribe Cereeae. Since the evidence indicates that this is the most highly evolved section, it seems reasonable to suppose that as wide a range of variation in chromosome numbers will be found here as in either of the other two tribes.

This paper reports briefly the results of a cytological study of forty-six species, including two forms and one species thought to be a hybrid. The chromosome complements of these species are described and their relationships to the taxonomy and phylogeny of the group are discussed. It is hoped that this contribution, supplemented by future work, may determine whether there are cytological peculiarities associated with taxonomic relationships already established on the basis of morphological characters. More particularly, series of polyploid and aneuploid chromosome numbers may be built up which may establish possible lines of evolution and points at which new species have arisen.

[1] Papers from the Department of Botany, University of Michigan, no. 614.

Since there was no account of meiosis in the Cactaceae, a careful study was made of microsporogenesis in *Echinocereus papillosus* Linke, a representative of one of the more complex genera.

TISCHLER (28) lists two counts of chromosomes in the *Neomammillaria*, one by JARETZKY (16) and the other by ISHII (14), both giving the haploid number as eleven. SUGIURA (25), in his list of chromosome numbers in the angiosperms, reports the diploid number of twenty-four in two species of *Neomammillaria* and one of *Zygocactus* (*Epiphyllum*). *Opuntia brasiliensis* is reported by JOHANSEN (17) as having a diploid number of twenty-two. STOCKWELL (24) gives haploid numbers of nine, eleven, twenty-two, and thirty-three from seventeen types. The brief paper by JOHANSEN and the longer one by STOCKWELL, both concerned with chromosomes as found in root tips, offer the first substantial contribution to the knowledge of the chromosomes of this group.

Material and methods

The material for this study was derived from a number of sources. Part of it has been under cultivation for some time at the University of Michigan Botanical Garden and came originally from the collections of the Missouri Botanical Garden. Most of the Central American species, with those from Tamaulipas, Mexico, were collected by Prof. H. H. BARTLETT. Those from the San Luis Potosi area were obtained by Dr. CYRUS LUNDELL. The remainder were collected by Dr. ELZADA CLOVER and the writer in the lower Rio Grande Valley, Texas.

Material was determined throughout from the monograph on the Cactaceae by BRITTON and ROSE (3).

The species which bloomed freely provided ample material for the study of the chromosomes of pollen mother cells during microsporogenesis. Counts were obtained in other species from root tips, particularly from certain species with characteristic aerial roots.

Neomammillaria and related genera were difficult to handle because the buds did not emerge at the bases of the papillae until almost mature. It was necessary to remove them as soon as the wool in which they were imbedded began to push out. At this time they

could be lifted out by inserting a small scalpel at the base of the papilla and prying gently.

To determine the stage of meiosis in buds, anthers were examined in aceto-carmine smears. It was found that meiotic divisions were most numerous from 10 A.M. until 2 P.M. Diakinesis stages were most frequently found just before noon. To obtain a successful smear, as many as ten anthers were required because various stages were often represented in the same bud.

Buds in good condition were split. One half was stripped of sepals, fixed at once in Navashin's fluid (Karpechenko formula), dehydrated through a long series of alcohols, and later imbedded. The other half was used to make permanent smears, after the method of TAYLOR (**26**). For smear preparations fixation in Navashin's fluid also proved most satisfactory.

The schedule used in staining smears was essentially SMITH'S (**23**) modification of the Gram stain. However, crystal violet in 0.5 of 1 per cent solution and the iodine-potassium-iodide similarly diluted proved easier to control. The picric acid wash was a saturated solution diluted four times. This method of staining gave a clear yellow cytoplasm and purple chromosomes.

Root tips were fixed in Allen's modification of Bouin's fluid, Zenker's fluid, modified Gilson's fluid, chrom-acetic, Navashin's fluid, and strong Flemming diluted about one-half. The last was most efficient. Mitoses went on rapidly from 10 A.M. until early afternoon. Tips from aerial roots were cut from the plant and allowed to stand for a few minutes in distilled water. This softened the mucilage that covered the root so that it could be largely removed by wiping with cotton. When the root tips were no longer slippery, they were slit up one side to aid penetration and cut back to within 5 mm. of the tip.

Iron-alum haematoxylin proved to be a more valuable stain for root tips than crystal violet, particularly when picric acid was used as a destaining agent (**29**).

Microsporogenesis in Echinocereus papillosus

Echinocereus papillosus Linke, selected for a study of meiosis, is native to southern Texas and is found over a large area. Both sec-

tioned and smeared material were used. Prophase smears were found to be of little value. The chromosomes in the Cactaceae are minute and not favorable for critical studies on chromosome structure.

The resting nucleus of the microsporocyte is less than 10 μ in thickness (fig. 1)[2] and presents the reticulum of fine threads characteristic of this stage. There is usually only one nucleolus. This body stains deeply during early prophase and does not begin to lose its chromaticity until late pachynema. It does not disappear until just before metaphase I, when it fades gradually but does not change from its spherical form.

With the beginning of prophase, the stage of leptonema (fig. 2) becomes clear. There is a definite thickening of the threads, and at the same time they show a tendency to run parallel to one another, which is sharply defined just before the stage of synizesis (fig. 3). At this time the nucleus begins to increase in size, and with this enlargement is possibly associated the condition of apparent contraction of the chromatic material, which may be due at least in part to imperfect fixation. The late stages of leptonema show a definite pairing of threads, which become closely associated. As has been pointed out by others, this association of threads (fig. 4) in a parasynaptic relation does not take place simultaneously all along the threads, but begins at random points.

With the increase in size of the nucleus, a marked thickening of the threads takes place which carries the nucleus into pachynema (figs. 5, 6). The parallel threads now become closely associated and apparently twisted. This is accompanied by a marked shortening of the elements. Coincident with this stage is the appearance of free ends at the periphery of the nucleus (fig. 7). In this species the tetrad structure of the chromosome is not obvious at metaphase of the first division. The lengthwise splitting of each chromosome may take place much earlier, but it is not apparent until early anaphase of the first division.

The close approximation of the synaptic mates continues through late pachynema, with further condensation of the threads (fig. 8). Finally during early diakinesis an apparent loosening of the association occurs which frees the members of the pairs except at one or

[2] See plate I, opposite page 20.

both ends (figs. 9, 10). The pairs of chromosomes condense still further and assume the forms characteristic of diakinesis (fig. 11). At this time the nucleus begins to decrease in size until it is again approximately 10 μ in thickness (fig. 12).

The chromosomes as they appear at metaphase I (fig. 13) are oval or round in outline, with an average width of from 1.7 to 2.0 μ and a length of from 2.0 to 2.5 μ. These dimensions represent an average for all the species studied. Throughout the tribe there is little difference in chromosome size at meiosis. The spindle establishes itself quickly following diakinesis, and the chromosomes become arranged at the plate. As seen from the pole, they are usually placed in a circle of eight with three in the center. The spindle fiber attachment for most of the chromosomes is median, but in some it is terminal. The chromosomes at anaphase I barely reach the poles before they show that they are split (fig. 14).

During interkinesis the sister chromatids tend to separate and to elongate (fig. 15), but again condense in preparation for the second division. The nucleolus which appeared at the beginning of interkinesis fades away soon after the disappearance of the nuclear membrane (fig. 16). Metaphase II is shown in figure 17 and anaphase in figure 18. The four daughter nuclei, after a long telophase, return to a resting condition (fig. 19). Furrows develop at the periphery of the sporocyte and proceeding inward apparently cut out the microspores (fig. 20).

In this species the pollen is almost wholly fertile, and there is no evidence of meiotic irregularity. The absence of lagging and nondisjunction indicates that the material is not of hybrid origin.

A matter of great interest was the appearance in this species, as well as in the majority of others studied, of certain bodies in the cytoplasm whose function and origin are obscure. They were first noticed in the material during interkinesis. They may be seen in early prophase and through diakinesis as two spherical or oval bodies at opposite ends of the cell (fig. 5). During metaphase I they arrange themselves on either side of the spindle. At anaphase I and through interkinesis and prophase II they lie close to the periphery of the cell, where they are conspicuous. At any time after metaphase I, four such bodies may be present. During interkinesis, two of the four

bodies are generally much more prominent (fig. 15) and remain so through prophase II (fig. 16). As the nuclei pass into metaphase II, the bodies become much less evident but are visible again in second anaphase (figs. 17, 18). When telophase II is initiated the four bodies come to lie one at the side of each nucleus, and shortly there are two by each nucleus. They fade away at this point.

The only reference to such structures noted in the literature is that of CASTETTER (5) in his paper on *Melilotus*. He figures similar bodies on either side of the metaphase I plate. In his discussion he refers to them as centrosome-like bodies, but states that he is unable to come to any conclusion as to their history or function.

The only further information which this study can offer is the reaction which these structures give to various stains and reagents. In general their staining reactions follow that of the chromatic material. It is necessary that the stain be left rather heavily in the nucleus, if these bodies are to show clearly. In prophase, when the nucleolus was prominent, they were more obscure. They are sharpest just before the formation of the metaphase II plate.

The bodies are not destroyed by fluids containing chromic acid, formaldehyde, or acetic acid. They also occur when material is fixed in a modification of Bouin's fluid in which anthroquinone replaces picric acid (1). They are partially or completely destroyed by a diluted Gilson's fluid. They show fairly well in sections or smears when stained with iron-alum haematoxylin. Crystal violet and safranin both bring them out brilliantly; the best results in the use of both stains are obtained when a counter wash of picric acid is employed. Alizarin will also stain them, but not sharply.

Chromosome configurations in other species

The results of the examinations of other species are given in the order in which the species are arranged by BRITTON and ROSE. The stages of meiosis best adapted for studies of chromosome configuration are diakinesis and late interkinesis. In root tips the metaphase plate is most useful.

The chromosomes in meiosis are compact and so small that peculiarities of size and form are difficult to recognize. Usually one pair is larger than the others, two to four pairs are medium sized,

and the remaining pairs consist of very small and almost spherical chromosomes.

Drawings of the chromosomes in the root tips were made from cells near the outermost layer, since these cells are larger and likely to be better fixed than those in the interior. They were never taken from further in than the sixth row and usually from the second or third.

In the following list, the numbers placed after the species names are accession numbers at the Botanical Garden of the University of Michigan.

1. *Wilcoxia poselgeri* (Lemaire) Br. & R. (15275): Diploid, twenty-two chromosomes; eleven pairs at metaphase I of meiosis (fig. 21); chromosomes all about the same size, ten pairs with median spindle fiber attachment, one with terminal attachment.

2. *Nyctocereus serpentinus* (Lagasca & Rod.) Br. & R. (13918): Diploid, twenty-two chromosomes; eleven pairs shown at metaphase I of meiosis (fig. 22); spindle fiber attachments seem to be terminal or slightly subterminal.

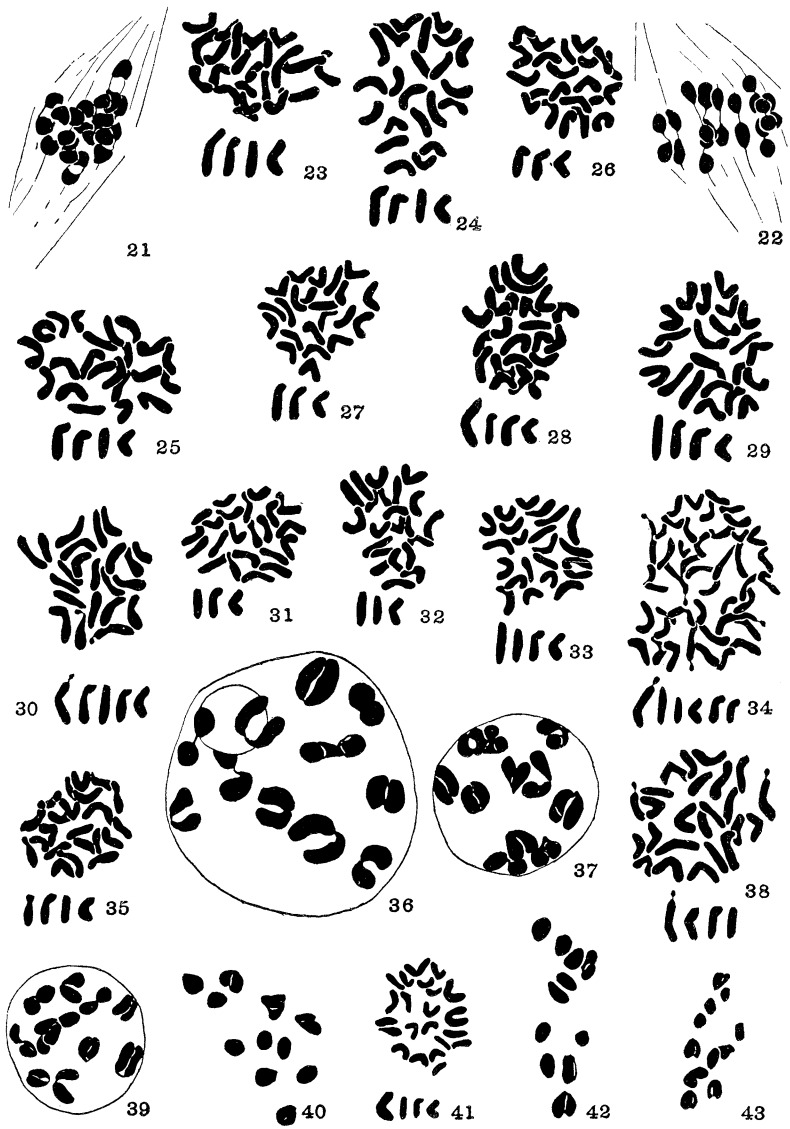
3. *Acanthocereus pentagonus* (Linnaeus) Br. & R. (15277): Diploid, twenty-two chromosomes; root tip metaphase (fig. 23); two chromosomes large with submedian attachments, four subterminal, six terminal, ten median or nearly median.

4. *Hylocereus guatemalensis* (Eichlam) Br. & R. (13941): Diploid, twenty-two; four groups of chromosomes in root tip metaphase (fig. 24); two largest chromosomes have spindle fiber attachments subterminal, two submedian, six terminal, twelve median varying considerably in size.

5. *Hylocereus purpusii* (Weingart) Br. & R. (13900): Diploid, twenty-two; root tip metaphase (fig. 25); chromosomes fall into the same groups as do those of the preceding species, to which it is closely related.

6. *Hylocereus undatus* (Haworth) Br. & R. (1526): Diploid, twenty-two; root tip metaphase (fig. 26); four chromosomes with subterminal attachments, six with submedian, twelve median; chromosomes more uniform in size and shape than those in the preceding two species.

7. *Hylocereus cubensis* Br. & R. (13997): Diploid, twenty-two; root tip metaphase (fig. 27); since this species is closely related to



FIGS. 21–43.—Fig. 21, *Wilcoxia poselgeri*, metaphase I. Fig. 22, *Nyctocereus serpentinus*, metaphase 1. Root tip metaphase of: fig. 23, *Acanthocereus pentagonus;* fig. 24, *Hylocereus guatemalensis;* fig. 25, *Hylocereus purpusii;* fig. 26, *H. undatus;* fig. 27, *H. cubensis;* fig. 28, *H. monacanthus;* fig. 29, *H. triangularis;* fig. 30, *Selenicereus hondurensis;* fig. 31, S. *pteranthus;* fig. 32, *S. kunthianus;* fig. 33, *S. spinulosus;* fig. 34, *Mediocactus coccineus* (with 44 chromosomes); fig. 35, *Werkleocereus glaber.* Fig. 36, *Echinocereus angusticeps*, diakinesis. Fig. 37, *E. pentalophus*, diakinesis. Fig. 38, *E. blanckii*, root tip metaphase, diploid 24 chromosomes. Fig. 39, *E. reichenbachii*, diakinesis. Fig. 40, *E. fitchii*, prophase II. Fig. 41, *Lophophora williamsii*, root tip metaphase. Fig. 42, *Hamatocactus setispinus* var. *hamatus*, prophase II. Fig. 43, *H. setispinus* var. *setaceous*, prophase II.

H. undatus, it would be expected to have similar chromosome complements, which is the case.

8. *Hylocereus monacanthus* (Lemaire) Br. & R. (14067): Diploid, twenty-two; root tip metaphase (fig. 28) shows chromosomes of this species distinctly different from others in the genus; two chromosomes half again as long as the next largest appear to have median attachments, two subterminal, eight submedian, ten median.

9. *Hylocereus triangularis* (Linnaeus) Br. & R. (1569): Diploid, twenty-two; root tip metaphase (fig. 29); two chromosomes longer than the rest, with terminal attachments, four subterminal, six submedian, ten median.

10. *Selenicereus hondurensis* (Schumann) Br. & R. (14688): Diploid, twenty-two; root tip metaphase (fig. 30); two chromosomes of the set with spindle fiber attachments submedian have satellites on the shorter arm, four have attachments subterminal, ten terminal, four submedian, two median.

11. *Selenicereus pteranthus* (Linke & Otto) Br. & R. (1547): Diploid, twenty-two; root tip metaphase (fig. 31) presents chromosomes similar in size and form; six short with terminal attachments, six subterminal, ten median.

12. *Selenicereus kunthianus* (Otto) Br. & R. (1360): Diploid, twenty-two; root tip metaphase (fig. 32); eight chromosomes with terminal attachments, remainder with median or near median attachments and similar in size.

13. *Selenicereus spinulosus* (DeCandolle) Br. & R. (13697): Diploid, twenty-two; root tip metaphase (fig. 33); six chromosomes terminally attached, four have subterminal attachments, remaining twelve attachments are all nearly median.

14. *Mediocactus coccineus* (Salm-Dyck) Br. & R. (7520): Diploid, forty-four chromosomes; root tip metaphase (fig. 34); four chromosomes, among the largest in the complement, have subterminal attachments and appear to bear satellites on the longer arm, four other long chromosomes with terminal attachments, four short chromosomes with terminal attachments, sixteen with median attachments, eight subterminal and eight submedian. This species is the only tetraploid so far known in this subtribe. The material was obtained from a plant in the greenhouses of the Botanical Garden of the Uni-

versity. It has not flowered since the writer began work on the material, so there has been no opportunity for studies of meiosis. The cells of the root are noticeably larger than those of related diploid species, but the chromosomes are smaller and more slender than those found in normal diploid cells.

15. *Werkleocereus glaber* (Eichlam) Br. & R. (7553): Diploid, twenty-two; root tip metaphase (fig. 35); two chromosomes with subterminal attachments, two with attachments more markedly subterminal, two with terminal attachments, sixteen median or nearly so.

16. *Echinocereus papillosus* Linke (15255): Diploid, twenty-two; diakinesis figure shows eleven pairs of chromosomes (fig. 11).

17. *Echinocereus angusticeps* Clover (15261): Diploid, twenty-two; eleven pairs are evident at diakinesis (fig. 36); in about 20 per cent of the cells examined there is non-disjunction at metaphase I, ten and twelve chromosomes passing to either pole. This species is most closely allied to *E. papillosus* and is possibly derived from it. Morphologically it resembles that species but is much smaller. Its habitat is different from that of *E. papillosus* in that it grows in sandy loam in open woods, while the other species is found on gravel or limestone hills. The two species are found within a few miles of each other, but their ranges apparently do not overlap.

18. *Echinocereus pentalophus* (DeCandolle) Rümpler (15253): Diploid, twenty-two; eleven pairs evident at diakinesis (fig. 37); this species differs from the two in the same genus previously discussed in being a slender procumbent plant whereas the others are erect. The spines are borne on ridges rather than on papillae, and the flowers are rich mallow purple with white centers as compared with the pale yellow and maroon red of the foregoing two species.

19. *Echinocereus blanckii* (Poselger) Palmer (15268): Diploid, twenty-four; root tip metaphase (fig. 38); two chromosomes having the spindle fiber attachments subterminal bear satellites on the longer arm, twelve chromosomes have median attachments, four subterminal, six terminal. This species is morphologically different from the preceding species in the increase in the number of ribs, the presence of definite papillae bearing the spine areoles, and the appearance of flowers which are entirely mallow purple. Cytologically this spe-

cies is interesting because the haploid number of chromosomes is twelve. In cultivation the plants bloom poorly, and a large percentage of the buds abort. Such buds as mature do not show complete pollen fertility. No fruit has been reported for this species by BRITTON and ROSE. All evidence yet available suggests that *E. blanckii* came out of *E. pentalophus* by the addition of an extra chromosome through non-disjunction.

20. *Echinocereus reichenbachii* (Terschek) Haage Jr. (15262): Diploid, twenty-two; diakinesis figure presents the usual eleven pairs of chromosomes (fig. 39); the plant is one of wide range and adaptability.

21. *Echinocereus fitchii* Br. & R. (15267): Diploid, twenty-two; haploid number of eleven shown at metaphase II (fig. 40).

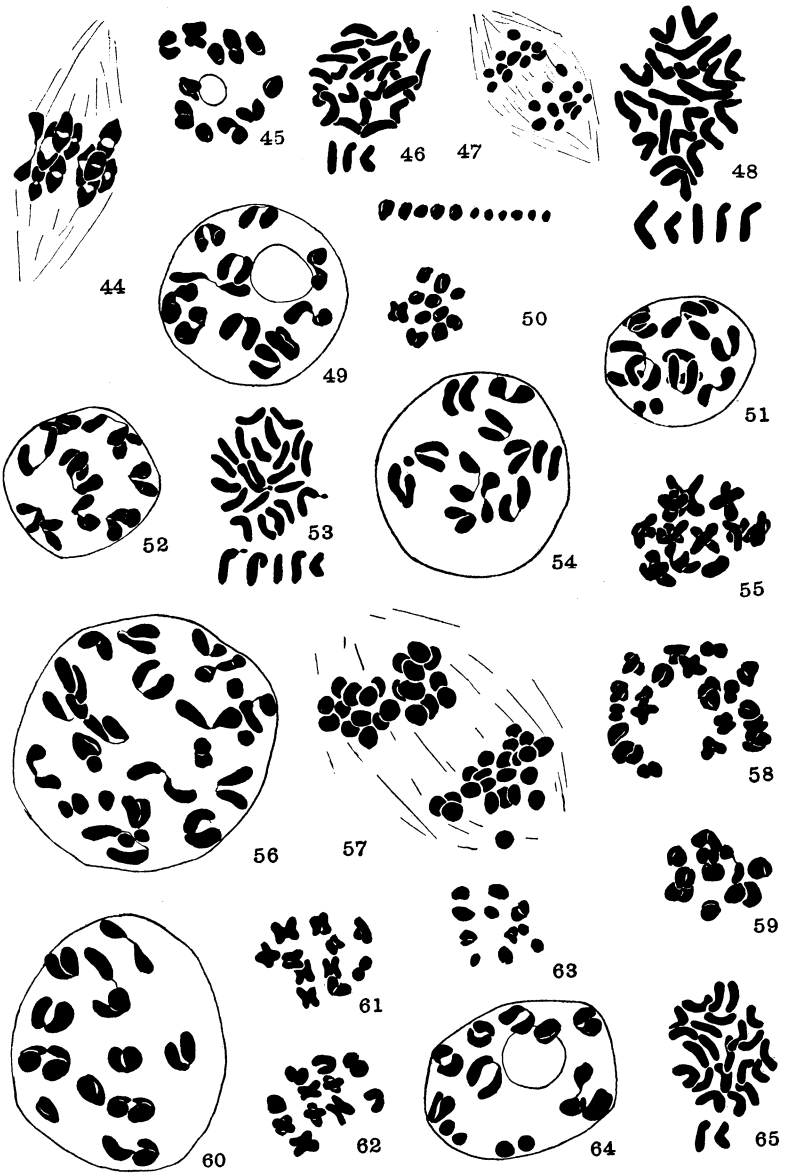
22. *Echinocereus enneacanthus* Engelmann (15256): Diploid, twenty-two (?); chromosomes were studied in root tips, all found to be nearly the same size.

23. *Lophophora williamsii* (Lemaire) Coulter (15269): Diploid, twenty-two; root tip metaphase interesting in that all but one pair of chromosomes are very small (fig. 41); two largest chromosomes have median attachments, two subterminal, four terminal, and fourteen median or nearly so.

24. *Hamatocactus setispinus* (Engelmann) Br. & R. (15295, 15297): Diploid, twenty-two; prophase II figures show eleven split chromosomes (figs. 42, 43); in the species there are two distinct forms which have been investigated. Morphological variations involving number of ribs, presence or absence of papillae on the ribs, and number and shape of the spines are found. ENGELMANN went so far as to give varietal names to the forms, but these are not recognized by BRITTON and ROSE. Observations in the field have led the writer to believe that these types should be recognized as distinct. Both have a haploid number of eleven, but there is a marked difference in chromosome size.

25. *Echinofossulocactus grandicornis* (Lemaire) Br. & R. (16142): Diploid, twenty-two (?); root tip material too scant to permit positive statement.

26. *Ferocactus hamatacanthus* (Muhlenpfordt) Br. & R. (15271):



FIGS. 44–65.—Fig. 44, *Ferocactus hamatacanthus*, metaphase I. Fig. 45, *Homalocephala texensis*, prophase II. Fig. 46, *Astrophytum asterias*, root tip metaphase. Fig. 47, *Thelocactus bicolor*, anaphase II. Fig. 48, *Coryphantha runyonii*, diakinesis. Fig. 49, *Escobaria runyonii*, diakinesis. Fig. 50, *Dolicothele longimamma*, prophase II. Fig. 51, *Neomammillaria heyderi*, diakinesis. Fig. 52, *N. hemisphaerica*, diakinesis. Fig. 53, *N. magnimamma*, root tip metaphase. Fig. 54, *N. chinocephala*, diakinesis. Fig. 55, *N. aureiceps*, prophase II, characteristic H shaped split chromosomes. Fig. 56, *N. multiceps*, tetraploid, 44 chromosomes showing pairing. Fig. 57, *N. multiceps*, anaphase I. Fig. 58, *N. multiceps*, prophase II. Fig. 59, *N. decipiens*, prophase II. Fig. 60, *N. longicoma*, diakinesis. Fig. 61, *N. tenampensis*, prophase II. Fig. 62, *N. minuta*, prophase II. Fig. 63, *Epiphyllum strictum*, anaphase I. Fig. 64, *E. ackermannii*, diakinesis Fig. 65, *Rhipsalis mesembrianthemoides*, root tip metaphase.

Diploid, twenty-two; figure of metaphase I shows eleven pairs of chromosomes (fig. 44).

27. *Homalocephala texensis* (Hopffer) Br. & R. (15272): Diploid, twenty-two; prophase II shows haploid number of eleven (fig. 45); this species is representative of a small genus closely related to *Echinocactus*.

28. *Astrophytum asterias* (Zuccarini) Lemaire (15274): Diploid, twenty-two; root tip metaphase (fig. 46); ten chromosomes straight with no evident constrictions, suggesting terminal attachments; two attachments subterminal, and ten with attachments median.

29. *Thelocactus bicolor* (Galeotti) Br. & R. (15294): Diploid, twenty-two; eleven chromosomes shown in anaphase II (fig. 47).

30. *Coryphantha runyonii* Br. & R. (15270): Diploid, twenty-two; root tip metaphase, with chromosomes distinctly larger than those in preceding genera (fig. 48); fourteen chromosomes with median spindle fiber attachments, two with terminal attachments, four subterminal, and two submedian; three pairs of chromosomes were pointed at the tips, suggesting the presence of satellites.

31. *Escobaria runyonii* Br. & R. (15303): Diploid, twenty-two; eleven pairs of chromosomes clear at diakinesis (fig. 49).

32. *Dolicothele longimamma* (DeCandolle) Br. & R. (1540): Diploid, twenty-two; the usual eleven split chromosomes at metaphase II (fig. 50); chromosomes show wide range in size, one pair large, four medium, six small.

33. *Neomammillaria heyderi* (Muhlenpfordt) Br. & R. (15286): Diploid, twenty-two; diakinesis shows eleven pairs of chromosomes (fig. 51).

34. *Neomammillaria hemisphaerica* (Engelmann) Br. & R. (15287): Diploid, twenty-two; diakinesis, eleven pairs of chromosomes (fig. 52); this species is closely related to *N. heyderi*.

35. *Neomammillaria magnimamma* (Haworth) Br. & R. (16164): Diploid, twenty-two; root tip metaphase (fig. 53); two chromosomes have attachments submedian and appear to carry a satellite.

36. *Neomammillaria compressa* (DeCandolle) Br. & R. (1520): Diploid, forty-four; pollen mother cells at interkinesis show twenty-two pairs of chromosomes; chromosomes give evidence of lagging and non-disjunction; material in greenhouse failed to set fruit.

37. *Neomammillaria chinocephala* (Purpus) Br. & R. (16172): Diploid, twenty-two; eleven pairs of chromosomes at diakinesis (fig. 54); a fragment appeared at diakinesis in addition to the normal set; material scant, complete history not available.

38. *Neomammillaria aureiceps* (Lemaire) Br. & R. (1541): Diploid, twenty-two; prophase II shows eleven split chromosomes in characteristic H shapes (fig. 55).

39. *Neomammillaria multiceps* (Salm-Dyck) Br. & R. (1538 and 15201): Diploid, forty-four; diakinesis shows twenty-two pairs of chromosomes (fig. 56). Two distinct forms of this species are under cultivation at the University of Michigan Botanical Garden. The larger of them, which is fully three times the size of the other and which has certain definite peculiarities of spine color and arrangement, was collected in the lower Rio Grande Valley and was also present in the collection from the Missouri Botanical Garden. The smaller form was also collected in the lower Rio Grande Valley. Both of them are tetraploid with identical behavior in meiosis. Diakinesis (fig. 56) shows a close association of the chromosomes in pairs with no evidence of groupings in fours. In several hundred cells examined, only one showed four homologues together. Separation after metaphase I is prompt and complete (fig. 57). The split preparatory to second division is not so well defined in early anaphase I as it is in normal diploids. The prophase of the second division is entirely normal. The chromosomes are so small that no distinguishing characteristics can be noted in either set.

40. *Neomammillaria decipiens* (Scheidw.) Br. & R. (7546): Diploid, twenty-two; metaphase II shows eleven split chromosomes (fig. 59).

41. *Neomammillaria longicoma* Br. & R. (16161): Diploid, twenty-two; eleven pairs of chromosomes at diakinesis (fig. 60).

42. *Neomammillaria tenampensis* Br. & R. (16151): Diploid, twenty-two; prophase II, eleven split chromosomes (fig. 61); interesting because of similarity to *N. aureiceps*.

43. *Neomammillaria minuta* Bartlett unpub. man. (13756): Diploid, twenty-two; prophase II shows eleven split chromosomes (fig. 62); pollen mother cells smaller than average.

44. *Epiphyllum strictum* (Lemaire) Br. & R. (13901): Diploid,

twenty-two; metaphase II (fig. 63); chromosomes much smaller than average.

45. *Epiphyllum ackermanni* Haworth (12737): Diploid, twenty-two; diakinesis, eleven pairs of chromosomes (fig. 64); the form is interesting because it is generally supposed to be a hybrid.

46. *Rhipsalis mesembrianthemoides* Haworth (7539): Diploid, twenty-two; root tip metaphase (fig. 65); chromosome complement very simple; short chromosomes with either terminal or median attachments.

Discussion

In the past decade much has been written on the relation of chromosome complements to taxonomy. TISCHLER (**27**) discusses the conditions which have been reported and classifies them as follows:

1. The *Pinus* type, in which all species studied in a given family have a uniform chromosome count.

2. The *Chrysanthemum* type, in which species within a genus present a straightforward polyploid series.

3. The *Carex* type, genera with species presenting chromosome numbers or series of numbers apparently unrelated.

4. The *Antirrhinum* type, in which each genus has a basic number which is strictly followed but in which each genus is separated from those closely related to it by the difference of one chromosome.

JÖRGENSEN (**18**) arranges types to include (a) genera in which all species studied have the same number; (b) genera with aneuploid numbers; (c) genera with numbers in multiple relations. It has become increasingly evident as more material is handled that many exceptions will be found to such classifications.

The cacti seem likely to fall chiefly into the first group of both JÖRGENSEN and TISCHLER, in that all of the twenty-one genera here considered contain the basic number of eleven, as do those reported elsewhere. One genus, *Mediocactus*, is represented so far only by a tetraploid, but the evidence indicates that in this case eleven is also the basic number. At the same time there is evidence (**24**) of a well developed polyploid line in *Opuntia*. SUGIURA (**25**) reports a haploid count of twelve for two species in two genera. STOCKWELL records a haploid number of nine for *Neomammillaria applanata* (Engelmann) Br. & R. The writer finds one aneuploid (*Echinocereus*

blanckii) and three tetraploids (*Neomammillaria multiceps*, *N. compressa*, *Mediocactus coccineus*). Briefly, these constitute the exceptions to the general classification.

As has been suggested, the tribe Opuntieae may be considered more primitive than the Cereeae. It is interesting to note in this connection that so far no basic number other than eleven has been found in the former tribe, and that the only aneuploids reported fall in the Cereeae.

The Cereeae, with which this paper is primarily concerned, contains several scattered tetraploids as well as certain aneuploids. The information available does not permit more than conjecture as to their origin, but certain observations can be made concerning their behavior and position.

Mediocactus coccineus, which is the only tetraploid reported from the subtribe Hylocereaneae, is a relatively primitive type. It is a climbing form found in Brazil and Argentina. There are four chromosomes which are alike in shape and size and which appear to bear satellites. This suggests that the plant is a possible autotetraploid (fig. 34).

Neomammillaria multiceps is a tetraploid (fig. 56) in which the chromosomes at meiosis are so nearly alike that it has not been possible to differentiate them. As has been stated, the chromosomes are present in pairs at diakinesis. Only rarely do they appear in fours. The view has been generally held that the chromosomes of autotetraploids associate in fours with a fair degree of regularity, and such behavior has been reported in *Aucuba* (**21**), *Datura* (**2**), *Hyacinthus* (**8**), *Solanum* (**19, 20**), *Primula* (**9**), and *Prunus* (**7**). On the other hand, DAVIS (**10**), in describing an *Oenothera* known to be autotetraploid, reports that the chromosomes do not form groups of four but are in pairs at diakinesis. It has been suggested that autotetraploid plants may in time undergo sufficient stabilization through differentiation of homologous chromosomes so that they become digenomic. The behavior suggests that this may have occurred here, since there is only one species to which *Neomammillaria multiceps* is obviously closely allied (*N. prolifera*), and there is no evident way by which it could have arisen through hybridization. Dr. ELZADA CLOVER of the University of Michigan Botanical Garden has secured

germination of 90 per cent or more from seeds of different plants of this species. The range of *N. multiceps* is not great. It is found from the coast to approximately 100 miles up the Rio Grande River valley and a short distance south into Mexico.

The third tetraploid, *N. compressa*, shows pairing to a large extent at diakinesis, but metaphase I is often disturbed and a few univalents occur. It flowers freely but has not set fruit in the greenhouses of the University. This species is common in Mexico, and has a number of well recognized varieties which suggest a series of forms similar to that reported for *Opuntia polyacantha* (24).

The only aneuploid discovered in the present material is *Echinocereus blanckii*, with a haploid number of twelve. As was pointed out, this species is very similar to *E. pentalophus*, except that (a) the flower is a uniform mallow purple, lacking the white center of *E. pentalophus;* (b) the plant is characteristically 5–6 ribbed rather than 4–5; (c) the ribs have more prominent papillae; (d) the plants have heavy tuberous roots which are not found in the other species. Both species are found in the region of the lower Rio Grande River valley, although *E. blanckii* is distinctly more limited in range. It is possible that this species arose from *E. pentalophus* through the addition of one chromosome by non-disjunction. There are many cases of aneuploidy on record, among them members of *Primula* (4), *Viola* (6), *Crepis* (22), *Antirrhinum* (13), *Lactuca* (15), and *Carex* (11, 12). Aneuploidy may be expected in a group as large as the Cactaceae.

Satellites have been reported in the Cactaceae by JOHANSEN (17) and STOCKWELL (24). The writer found satellites in *Selenicereus hondurensis*, *Mediocactus coccineus*, *Echinocereus blanckii*, and *Neomammillaria magnimamma*.

Primary constrictions appear with varying degrees of clarity in somatic chromosomes. Usually they are clearly indicated by a bend in the chromosome. An attempt has been made to group the chromosomes on the basis of primary constrictions. The random sampling here reported is not sufficient to present an accurate picture of chromosome morphology in the Cereeae, but it does suggest some possibilities of relationships in chromosome configuration.

The facts that the basic number eleven is so consistently present

in all of the genera studied, and that it is the haploid number for the majority, suggest strongly that evolution in this family has been accomplished largely through gene mutations. The two factors which appear to rank next in importance in the development of the family are polyploidy and hybridization.

From the available information, the Cereeae do not seem to show as strong an inclination toward polyploidy as do the Opuntieae. Such polyploids as do occur in the Cereeae may arise through somatic doubling. There appears to be a stronger tendency in this tribe to develop aneuploids, possibly owing to the fact that the genera are more divergent than in the Opuntieae.

The evidence seems to show that the family is still relatively young, in that it is known to be giving rise to numerous new types.

Summary

1. The cytological work on record is briefly surveyed. There are reports on only nineteen species. Work has been confined to members of the tribe Cereeae, which is the most highly evolved tribe in the family and contains the greatest number of genera.

2. The chromosome numbers are given for forty-six species, including two forms and one hybrid. The basic number, eleven, is present in every genus here reported, and is the haploid number in the majority of species.

3. Three tetraploids are recorded and discussed as to origin. Of these, *Mediocactus coccineus* is one of the simpler Cereeae and the others, *Neomammillaria compressa* and *N. multiceps*, are both members of the largest genus in the tribe.

4. One aneuploid species, *Echinocereus blanckii*, is described. It is suggested that it arose out of *E. pentalophus* by reduplication of one chromosome through non-disjunction.

5. Meiosis of *Echinocereus papillosus* was studied. The behavior is reported as entirely normal. The prophase threads associate by parasynapsis.

6. Certain bodies in the cytoplasm are described as they occur in *E. papillosus* and a majority of the other species studied. They can commonly be seen in early pachynema as two oval structures lying at either end of the cell. Their staining reactions become more in-

tense as prophase advances and is greatest just before telophase I. At this time or shortly after, two other such bodies appear which come to lie between the two nuclei. At the end of second division there is one body beside each nucleus. Often eight bodies are found at the end of telophase II.

7. The relation of the chromosome numbers to taxonomy is discussed, and it is pointed out that the rather simple chromosome situation is in keeping with the morphological evidence that the tribe Cereeae is young.

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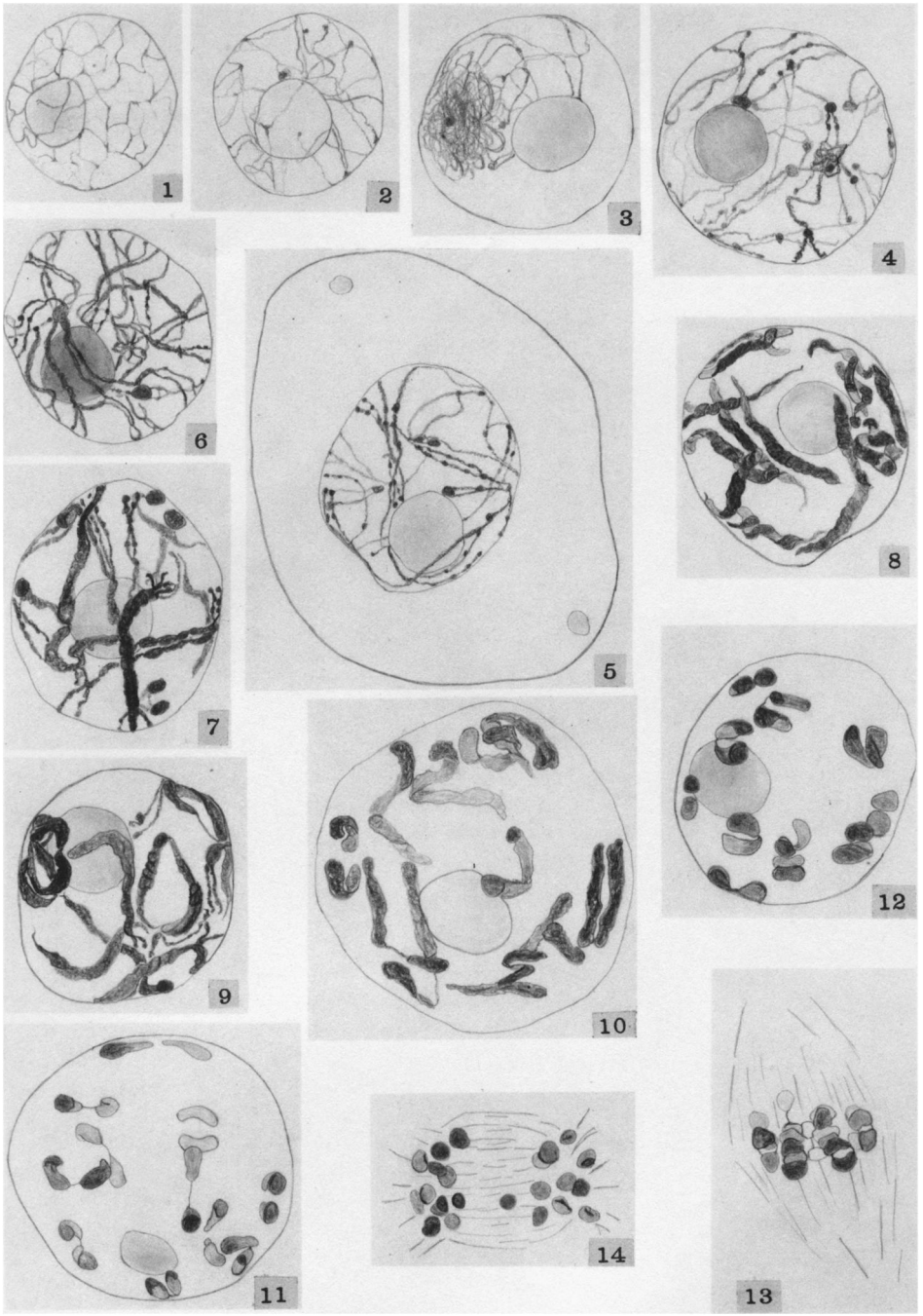
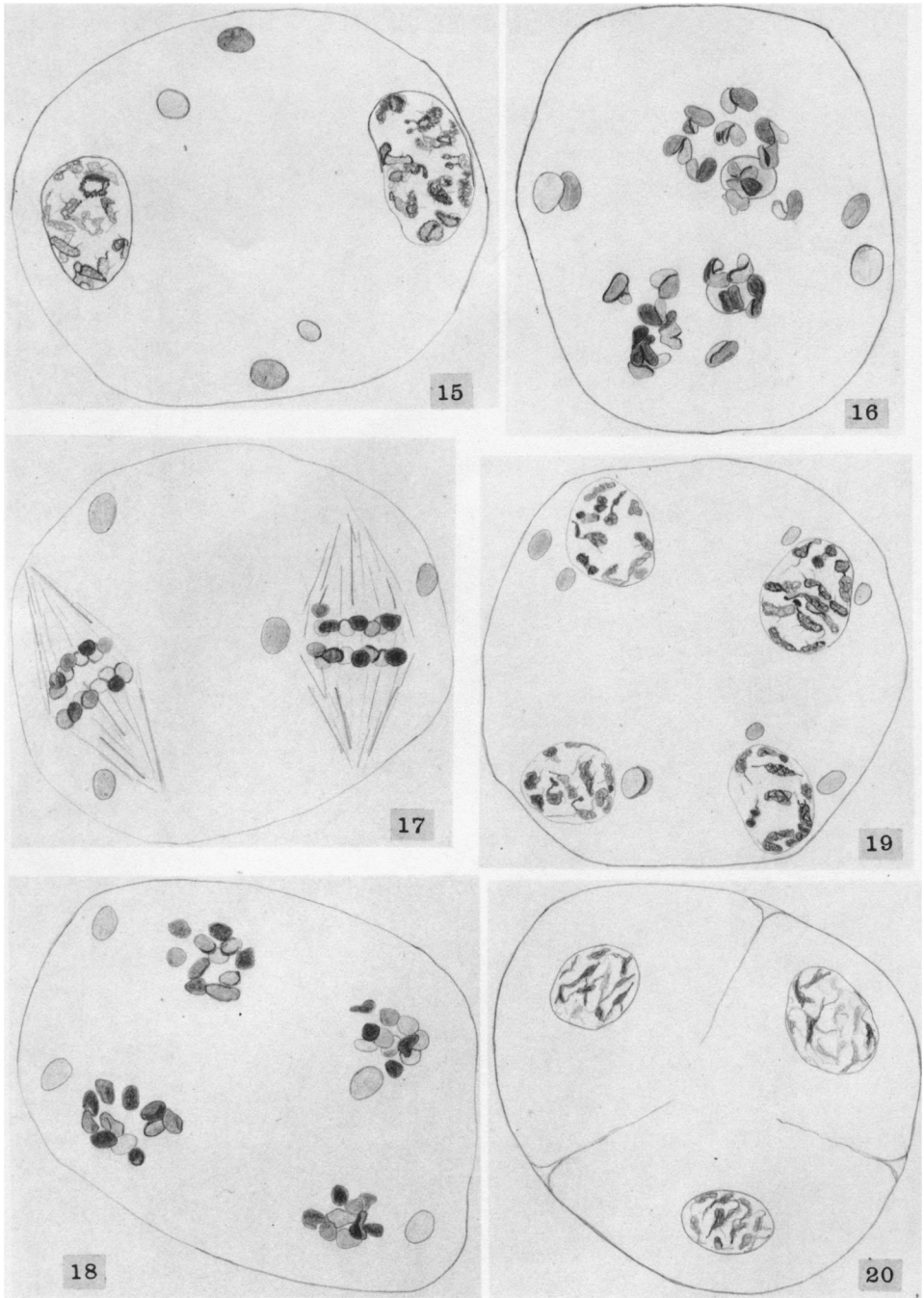


BEARD on CACTACEAE



BEARD on CACTACEAE

EXPLANATION OF PLATES I, II

All figures were drawn with the aid of a camera lucida under Zeiss apochromatic objective 1.5 (120×) in combination with the ocular K 20×. Measurements were made with an eyepiece micrometer in the Zeiss K 10× ocular.

Echinocereus papillosus Linke

PLATE I

FIG. 1.—Resting nucleus from archesporium.
FIG. 2.—Late leptonema.
FIG. 3.—Synizesis.
FIG. 4.—Early pachynema, parallel threads evident.
FIG. 5.—Middle pachynema, appearance of cytoplasmic bodies.
FIG. 6.—Zygonema conspicuous.
FIG. 7.—Late pachynema, appearance of four closely associated threads.
FIG. 8.—Chromosome segments defined.
FIG. 9.—Diakinesis, two chromonemata visible.
FIG. 10.—Diakinesis.
FIG. 11.—Late diakinesis.
FIG. 12.—Diakinesis, condensation practically complete.
FIG. 13.—Metaphase I.
FIG. 14.—Anaphase I, chromosomes beginning to show split preparatory to second division.

PLATE II

FIG. 15.—Interkinesis, four bodies present in cytoplasm.
FIG. 16.—Prophase II, four bodies in cytoplasm, nucleolus also present.
FIG. 17.—Metaphase II.
FIG. 18.—Anaphase II.
FIG. 19.—Telophase II, eight bodies in cytoplasm.
FIG. 20.—Tetrad showing cleavage by furrowing.