CYTOLOGICAL STUDIES IN SOME WILD TUBER-BEARING SOLANUM

By

BENJAMIN GBEKELEOLUWA SANGOWAWA

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(with sixty eight tables and sixteen plates)

Department of Biological Sciences,
Faculty of Science,
Ahmadu Bello University, Zaria.

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DECLARATION

I hereby declare that this thesis has been written by me and that it is a record of my research work. It has not been presented in any previous application for a higher degree. All quotations are indicated by quotation marks and the sources of information are specifically acknowledged by means of references.



BENJAMIN GBEKELEOLUWA SANGOWAWA



DATE 23/6/83

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ABSTRACT

Cytological studies were carried out in eight tuber-bearing wild Solanum species namely, 1. S. mochicense Ochoa, 2. S. boliviense Dun., 3. S. raphanifolium Card et Hawkes, 4. S. pinnatisectum Dun., 5- S. stenotomum Juz. et Buk., 6. S. chacoense Bitt., 7. S. kuntzianum Bitt. et Wittm. and 8. S. polytrichon Rydb. The haploid number in six species (1-6) is found to be 12 (n= 12) and they are therefore diploids and the two species namely, S. kuntzianum Bitt. et Wittm and S. polytrichon Rydb. are found to have 24. haploid number of chromosomes (n= 24.) and are therefore, tetraploids.

Detailed meiotic studies have been made of the diploid and tetraploid species, and frequency of chiasmata in each species has been analysed both in diplotene and diakinesis and the terminalisation values of each of them have been estimated.

Association of chromosomes in three or four or more are seen in diploid species. The frequency of multivalents have been analysed. The occurrence of multivalents in diploids indicate the presence of translocation heterozygotes. In tetraploids the percentage of quadrivalents varies from 47.58 to 57.42 in S. kuntzianum and S. polytrichon respectively, and this high degree of association of four chromosomes to form

quadrivalents seem to indicate that these two species are autotetraploid in origin.

The incidence of pairing of homologues in diploids and tetraploids have been analysed and the frequency of failure of pairing have also been estimated.

The univalents which are formed due to failure of pairing among pairable chromosome mates behave in different ways in diploids and tetraploids. They either pass to the poles or lag between separating group of chromosomes or divide. The division and elimination of univalent causes unequal distribution of chromosomes in second metaphase and the frequency of these unequal distribution of chromosomes in diploids and tetraploids were analysed and the effects of these aberrations in the formation of morphologically good and deformed pollen have been studied.

The formation of dicentric chromosomes involving chromatid bridges and fragments is found to be a usual phenomenon in the diploids and tetraploid species and their significance on sterility has been analysed and discussed.

The secondary association of chromosomes occur in all species under consideration. There is preponderance of association of two over other groups of chromosomes in diploids and the significance of four groups of 2 and four free chromosomes has been discussed.

The cytological behaviour of chromosomes in diploid Solarium under consideration indicates that there is a good evidence of regarding them as of hybrid origin. It is also apparent that the main lines of evolution in Solarium species investigated is that of interspecific hybridization and occurrence of polyploidy.

CONTENTS

		Page
Declaration		ii
Acknowledgements		iii
Abstract		iv-vi
List of Contents		vii-viii
List of Tables		ix-xv
List of Plates		xvi
1.	INTRODUCTION	1-4
2.	MATERIALS AND METHODS	5-8
3.	RESULTS ON CYTOLOGICAL STUDIES	
	(i) Explanation of plates I and IA	9-11
	(ii) Chromosome number and Morphology in *S. mochicense* Ochoa	14-15
	(iii) Meiosis in wild tuber-bearing diploid *Solanum* species	15
	(iv) Meiosis in *S. mochicense* Ochoa	15-26
	(v) Explanation of plates II and IIA	27-28
	(vi) Meiosis in *S. boliviense* Dun	29-40
	(vii) Explanation of plates III and IIIA	41-42
	(viii) Meiosis in *S. raphanifolium* Cárd et Hawkes	43-54
	(ix) Explanation of plates IV abd IVA	55-56
	(x) Meiosis in *S. pinnatisectum* Dun	57-68
	(xi) Explanation of Plates V and VA	69-71
	(xii) Meiosis in *S. stenotomum* Juz. et Buk	72-84
	(xiii) Explanation of plates VI and VIA	85-86
	(xiv) Meiosis in *S. chacoense* Bitt	87-100
	(xv) Explanation of plates VII and VIIA	101-103
	(xvi) Meiosis in wild tuber-bearing tetraploid *Solanum* species	106

Page

(xvii) Meiosis in S. kuntzianum Bitt. et Wittm..... 104-117

(xviii) Explanation of plates VIII and VIIIA..... 118-120

(xix) Meiosis in S. polytrichon Rydb.... 121-133

4. DISCUSSIONS..... 134

(i) Pairing and asscciation of chromosomes in diploid and tetraploid Solanum species 134-139

(ii) Chiasma and terminalisation values. 140-143

(iii) Dicentric chromatid bridge..... 144-147

(iv) Secondary pairing or Association in Solanum species..... 148-150

(v) Failure of pairing in homologous chromosomes - cause and consequence. 151-154

(vi) Species formation and the Status of Diploid and Tetraploid Solanum..... 155-156

5. SUMMARY..... 157-165

6. REFERENCES..... 166-177

TABLE NO. LIST OF TABLES

Page

1. Diagnostic Morphological Characters of different species..... 5

2. Multivalent frequency at diakinesis in S. mochicense Ochoa..... 17

3. Frequency of chiasmata at diakinesis in S. mochicense Ochoa..... 18

4. Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. mochicense Ochoa..... 20

5. Frequency of different chromosomes distribution on second metaphase plates in S. mochicense Ochoa..... 21

6. Showing character and frequency of secondary association in second metaphase in S. mochicense Ochoa..... 22

7. Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at second anaphase in S. mochicense Ochoa..... 24

8. Frequency of micronuclei during pollen formation in S. mochicense Ochoa..... 26

9. Frequency of chiasmata at diplotene in S. boliviense Dun..... 31

10. Multivalent frequency at diakinesis in S. boliviense Dun..... 32

11. Frequency of chiasmata at diakinesis in S. boliviense Dun..... 33

Page

12. Frequency of chromatid bridges, fragments, lagging and eliminated chromosome at first anaphase in S. boliviense Dun..... 35

13. Frequency of different chromosome distribution on second metaphase plates in S. boliviense Dun..... 36

14. Showing character and frequency of secondary association in second metaphase in S. boliviense Dun..... 37

15. Showing frequency of chromatid bridges, fragment, lagging and eliminated chromosomes at second anaphase in S. boliviense Dun..... 38

16. Frequency of micronuclei during pollen formation in S. boliviense Dun..... 40

17. Multivalent frequency at diakinesis in S. raphanifolium Cárd et Hawkes..... 46

18. Frequency of chiasmata at diakinesis in S. raphanifolium Cárd et Hawkes..... 47

19. Frequency of bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. raphanifolium Cárd et Hawkes..... 49

20. Frequency of different chromosome distribution on second metaphase plates in S. raphanifolium Cárd et Hawkes..... 50

21. Showing character and frequency of secondary association in second metaphase in S. raphanifolium Cárd et Hawkes..... 51

22. Showing frequency of chromatid bridges, lagging, and eliminated chromosome at second anaphase in S. raphanifolium Cárd et Hawkes..... 52

Page

23. Frequency of micronuclei during pollen formation in S. raphanifolium Card et Hawkes.. 53

24. Multivalent frequency at diakinesis in S. pinnatisectum Dun..... 60

25. Frequency of chiasmata at diakinesis in S. pinnatisectum Dun..... 61

26. Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. pinnatisectum Dun..... 63

27. Frequency of different chromosomes distribution on second metaphase plates in S. pinnatisectum Dun..... 64

28. Showing character and frequency of secondary association in second metaphase in S. pinnatisectum Dun..... 65

29. Showing frequency of bridges, fragments and eliminated chromosomes at second anaphase in S. pinnatisectum Dun..... 66

30. Frequency of micronuclei during pollen formation in S. pinnatisectum Dun..... 67

31. Frequency of chiasmata at diplotene in S. stenotomum Juz. et Buk..... 75

32. Multivalent frequency at diakinesis in S. stenotomum Juz. et Buk..... 76

33. Frequency of chiasmata at diakinesis in S stenotomum Juz. et Buk..... 77

34. Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. stenotomum Juz. et Buk..... 79

Page

35. Frequency of different chromosome distribution on second metaphase plates in S. stenotomum Juz. et Buk..... 81

36. Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at second anaphase in S. stenotomum Juz. et Buk..... 82

37. Frequency of micronuclei during pollen formation in S. stenotomum Juz. et Buk..... 83

38. Frequency of chiasmata at diakinesis in S. chacoense Bitt..... 90

39. Multivalent frequency at diakinesis in S. chacoense Bitt..... 91

40. Frequency of chiasmata at diakinesis in S. chacoense Bitt..... 92

41. Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. chacoense Bitt..... 94

42. Frequency of different chromosome distribution on second metaphase plates in S. chacoense Bitt..... 96

43. Showing character and frequency of secondary association in second metaphase in S. chacoense Bitt..... 97

44. Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes, at second anaphase in S. chacoense Bitt..... 98

Page

45. Frequency of micronuclei during pollen formation in S. chacoense Bitt..... 99

46. Frequency of chiasmata at diplotene in S. kuntzianum Bitt. et Wittm..... 107

47. Quadrivalent and bivalent frequency at diakinesis in S. kuntzianum Bitt. et Wittm.. 108

48. Frequency of chiasmata at diakinesis in S. kuntzianum Bitt. et Wittm..... 109

49. Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. kuntzianum Bitt. et Wittm..... 112

50. Frequency of different chromosome distribution on second metaphase plates in S. kuntzianum Bitt. et Wittm..... 113

51. Showing character and frequency of secondary association in second metaphase plate in S. kuntzianum Bitt. et Wittm..... 114

52. Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at second anaphase in S. kuntzianum Bitt. et Wittm..... 115

53. Frequency of micronuclei during pollen formation in S. kuntzianum Bitt. et Wittm..... 116

54. Frequency of chiasmata at diplotene in S. polytrichon Rydb..... 123

55. Multivalent frequency at diakinesis in S. polytrichon Rydb..... 124

Page

56. Frequency of chiasmata at diakinesis in S. polytrichon Rydb..... 125

57. Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. polytrichon Rydb..... 127

58. Frequency of different chromosome distribution on second metaphase plates in S. polytrichon Rydb..... 128

59. Showing character and frequency of secondary association in second metaphase in S. polytrichon Rydb..... 129

60. Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at second anaphase in S. polytrichon Rydb..... 131

61. Frequency of micronuclei during pollen formation in S. polytrichon Rydb..... 132

62. Incidence of multivalents, bivalents and univalents in diploid species..... 136

63. Incidence of quadrivalents in tetraploid species..... 138

64. Frequency of chiasmata at diplotene and diakinesis in different Solanum species..... 142

Page

65. Showing percentage of chromatid bridges, along with percentages of morphologically good and deformed pollen in Solanum species. 145

66. Showing incidence of paired chromosomes and univalents in diploid Solanum species..... 151

67. Incidence of paired chromosomes and univalents in tetraploid Solanum species.... 152

68. Showing percentage of micronuclei during pollen formation in Solanum species..... 154

LIST OF PLATES

Page

Plates I and IA - showing meiotic division in pollen mother cells of S. mochicense Ochoa. 12-13

Plates II and IIA - showing meiotic division in pollen mother cells of S. boliviense Dun. 29-30

Plates III and IIIA - showing meiosis in pollen mother cells of S. raphanifolium Cárd. et Hawkes.. 43-44

Plates IV and IVA - showing meisis in pollen mother cells of S. pinnatisectum Dun. 57-58

Plates V and VA - showing meiosis in pollen mother cells of S. stenotomum Juz. et Buk. 72-73

Plates VI and VI^{A} - showing meiosis in pollen mother cells of S. chacoense Bitt. 87-88

Plates VII and VIIA - showing meiosis in pollen mother cells of S. kuntzianum Bitt. et Wittm. 104-105

Plates VIII and VIIIA - showing meiosis in pollen mother cells of S. polytrichon Rybd. 121-122

CYTOLOGICAL STUDIES IN SOME WILD TUBER-BEARING SOLANUM

1. INTRODUCTION

The common or Irish Potato (Solanum tuberosum L.) was introduced in Europe for about four centuries ago from its ancestral home in South America. Since that time it turned from a garden of curiosity into one of the staple food crops of mankind because of its capacity to give high outturns of food per acre. Possibly, it produces the heaviest weight of human food per acre with few exceptions. Unquestionably, potato now occupies a prominent position in the World's food economy and as a source of food energy it is not behind cereals. So it is no wonder that considerable attention is being paid all over the world to the amelioration of this crop, especially since the exploration expeditions in South America by the Russians in 1925 (Magoon, Ramanujam and Cooper 1962), which uncovered a vast store of genetic variability of wild forms of potatoes from which have descended the commercial potato varieties of today. If, however, the desirable genes present in this wild material is to be successfully incorporated into the cultivated varieties, an understanding of the interrelationships between the various groups as a whole as well as an adequate assessment of this nature of factors which may hinder or help such gene transfer is essential. The importance of such fundamental knowledge in crop improvement has, however, been fully realised and great progress has been made in utilization of wild resistant genes in development of disease - resistant and pest-resistant commercial varieties of potatoes in recent years.

The Solanums are divided into two groups namely, tuber-bearing and nontuber-bearing species. Though the genus is found in all parts of the world, the tuber-bearing forms are confined to the American continent. The wild potato species are found in Central and South America. In both sub-continents they are mainly plants of high altitudes, although in South America they are also found on the low plains. The indigenous cultivated potatoes of South America are most restricted in their range than the wild ones since except for a few exceptions they are only to be found in the temperate or cool temperate regions. It is then obvious that the wild potatoes occur over a wild range of latitudes and altitudes and flourish under conditions which other domestic potatoes could not withstand.

Despite the broad division of the genus Solanum into tuberiferous and non-tuberiferous types, only little attention has been paid on the taxonomy and cytogenetic studies of the latter group. Extensive data on the morphological characters and geographical distribution of wild and cultivated species have been carried out by several workers (Bitter 1911-1913), Hawkes (1958), elaborating the evolutionary trend in tuber-bearing Solanum of most wild and cultivated species. Intensive cytogenetic studies on wild and native cultivated diploid potatoes have been made by various workers (Rybin 1933, Ratera 1938). Choudhuri (1943, 1944) made comprehensive studies on the behaviour

of chromosomes of six wild diploid species and some of their hybrids. He also studied the inheritance of leaf form, stem wing and flower colour in some diploids and polyploids. On the basis of cross-fertility studies with 19 diploid species and varieties it was concluded that the Tuberosa and Commersoniana sections of the genus Solanum are closely related, the Pinnatisecta section is distinct from both (Choudhuri 1944, 1948a, 1948b). Despite all these contributions only few critical cytological studies of the diploid and polyploid species of potato were made. These may be due to relative small size of Solanum chromosomes and also due to difficulty of fixation in studying earlier stages of meiotic division. Thus the contributions were relatively few and less intensive.

The distribution and variability of wild and cultivated potatoes was not realised for sometime until recently when its affinity to the commercial potato (S. tuberosum) was known. They possess many valuable and desirable characteristic which include resistance to diseases and pests and also adaptation to different phyto-geographical regions.

In the early years there was a dispute concerning the number of chromosomes in the cultivated forms. Nemec (1899) was the first to count the somatic chromosome number of S, tuberosum in the meristems of stems and roots. He counted 2n= 36 but indicated that this was an underestimate. Several investigators after careful meiotic studies suggested gametic number in S. tuberosum as n = 24 i.e.,

2n= 48 (Salaman 1926, Fukuda 1927, Smith 1927 and Stow 1926 and 1927). Smith (1927) found n = 12 from some wild species and n = 24 for the semi-cultivated varieties of S. tuberosum. Thus the existence of polyploid series in the wild potatoes was established by Smith (1927) and Vilmorin and Simonet (1927a and 1927b). Longley and Clark (1930) confirmed the presence of polyploid series in the wild types. Although there exist considerable controversy regarding the basic number in the genus Solanum the present acceptance is that the basic number of chromosomes in potato is considered to be 12 (n = 12).

The present study is concerned primarily with behaviour of chromosomes in diploids and polyploids in some wild tuber-bearing Solanum with a view to ascertain the exact statue of these species.

2. MATERIALS AND METHODS

The potato-tubers used in the investigation were obtained from Inter-Regional Potato Introduction Project, Peninsular Experiment Station, Sturgeon Bay, Wisconsin, 54235 U.S.A. Genetically pure strands of different Solanum species shown were raised in the Botanical Garden of Ahmadu Bello University, Zaria. The diagnostic characters of the species were as follows (Table I):

TABLE I

Diagnostic morphological characters of different species of Solanum

Ref: No. PI 366334, S. mochicense Ochoa; Origin, Peru; Tuber, small, oval, white brownish skin, little eyes; Foliage, medium height leaves compound, stem round, red-purple; Flower, white; cropping quality moderate, produce natural berries.

Ref: No. PI 265861, S. boliviense Dun.,; Crigin Bolivia; Tuber, small, round, white brownish skin, small eyes with small eye brows; Foliage, medium height, leaves compound, stem square-shaped, greenish; Flower, white; cropping quality moderate.

Ref: No. PI HHC 5111, S. raphanifolium Cárd. et Hawkes; Origin, Peru; Tuber, oval, brownish skin, superficial small eyes with short eye brows; Foliage, medium height,

leaves compound, stem round, greenish-purple; Flower, blue-purple; cropping quality moderate.

Ref: No. PI 230489, S. pinnatisectum Dun.; Origin, Mexico; Tuber, fairly big, round, brownish skin, hollow eyes with long eye brows; Foliage, medium height, leaves compound, stem round, greenish; Flower, white; cropping quality moderate.

Ref: No. PI 234011, Solanum stenotomum Juz. et Buk.; Origin, Bolivia; Tuber, small, round, brownish skin, fairly deep eyes with short eye-brows; Foliage, Haulm of medium height, leaves compound, stem square-shaped and green; Flower, white, produce natural berries; cropping quality moderate.

Ref: No. PI Oka - 4956, S. chacoense Bitt.; Origin, Argentina; Tuber, small round, brownish, superficial eyes with short eye brows; Foliage, medium height, leaves compound, stem square-shaped, greenish-purple; Flower, white; produce natural berries; cropping quality moderate.

Ref: No. PI Oka - 4951, S. kuntzianum Bitt. et Wittm.; Origin, Mexico; Tuber, small, round, brownish, large eyes with long eye brows; Foliage, medium height, leaves compound,

stem square-shaped, purple green, hairy; Flower, purple; produce natural berries; cropping quality good.

Ref: No. PI 275240, S. polytrichon Rydb.; Origin, Mexico, Tuber, small, oval, brownish small eyes with short eyes brows; Foliage, medium height, leaves compound, stem round, greenish, hairy; Flower, purple; produce natural berries; cropping quality moderate.

For meiotic divisions, pollen-mother-cells were studied. Small flower buds were collected, anthers were dissected and fixed in Carnoy's fluid (6:3:1) for 24 hours washed for 3 hours in absolute alcohol and stored in 70% alcohol at 4°C until needed. The anthers were stained in basic fuschin (Fuelgen) after hydrolysis in NHCL at 60°C for 8 minutes (Choudhuri 1968). The anthers were smeared in the usual manner and temporary smears showing good dividing stages were sealed with Kerr's sticky wax (Choudhuri 1968), obtainable from (Kerr manufacturing Co., Michigan, U.S.A.). Occasionally, the anthers were squashed and mounted in 2% aceto-orcein.

Morphologically good pollen grains were determined on the basis of stainability in aceto-orcein or with aceto-carmine and glycerine (1:1) Matthew, Omana, Philip 1979). Well stained pollen grains with regular shape were considered good and viable while empty ones without any stain were considered as sterile.

Photomicrographs were taken from the temporary squash preparations with wild M-20 photomicroscope.

3. RESULTS ON CYTOLOGICAL STUDIES

(i) EXPLANATION OF FIGURES

Magnification 4500 x except those mentioned. All photomicrographs are from pollen mother cells except Fig. 1 of Plate I, which is from tapetum.

PLATES I and IA

Figs. 1-25, Showing meiotic divisions in pollen mother cells of S. mochicense Ochoa.

Fig. 1. A tetraploid tapetal cell with 48 chromosomes. Note the 4 satellite chromosomes.

Fig. 2. Pachytene with completely paired chromosomes along with an unpaired segment. Note the highly condensed regions in some chromosomes.

Fig. 3. Diakinesis showing 1 quadrivalent and 10 bivalents.

Fig. 4. First metaphase, side view with a non-orientated univalent.

Fig. 5. First anaphase showing a chromatid bridge along with a fragment.

Fig. 6. First anaphase showing 1 eliminated chromosome; its position indicate that it would eventually be included into one of the daughter nuclei.

Fig. 7. First anaphase with 1 eliminated chromosome.

Fig. 8. First anaphase showing 1 laggard and 1 eliminated chromosomes.

Fig. 9. First anaphase with 2 eliminated chromosomes.

Fig. 10. First anaphase showing presumably a broken bridge along with 1 eliminated chromosome.

Fig. 11. Second pro-metaphase showing distribution of 12 chromosomes in one of the poles.

Fig. 12. First anaphase showing 4 laggards of which 3 are dividing.

Fig. 13. Configurations of (a) trivalent and (b) quadrivalent taken from different cells at diakinesis.

PLATE IA

Fig. 14. Second metaphase showing distribution of 12 - 8 chromosomes along with presumably 4 eliminated chromosomes. Note the secondary association of chromosomes in 2 groups of 3 on each metaphase plates.

Fig. 15. Second metaphase showing presumably distribution of 12 - 10 chromosomes with 2 eliminated chromosomes.

Fig. 16. Second metaphase showing distribution of 12-12 chromosomes. Note the secondary association of chromosomes in one of the plates.

Fig. 17. Second metaphase showing presumably distribution of 12 chromosomes on one of the metaphase plates. Note the secondary association of 6 chromosomes in 1 group along with 6 free chromosomes.

Fig. 18. Second metaphase showing presumably distribution of 11-11 chromosomes with 2 eliminated chromosomes.

Fig. 19. Second metaphase showing presumably distribution of 10-11 chromosomes with 3 eliminated chromosomes.

Fig. 20. Second metaphase showing equal distribution of 12-12 chromosomes. Note the secondary association of chromosomes in groups of 5.

Fig. 21. Second metaphase showing distribution of 11 chromosomes on one of the plates along with 1 eliminated chromosome, other plate presumably has 12 chromosomes.

Fig. 22. Second anaphase showing 1 eliminated chromosome along with a small fragment.

Fig. 23. Second telophase with an eliminated chromosome forming micronuclei.

Fig. 24. Showing morphologically deformed pollen grains x 1000.

Fig. 25. Morphologically good pollen grains x 1000.

PLATE I

Meiosis in S. mochicense Ochoa

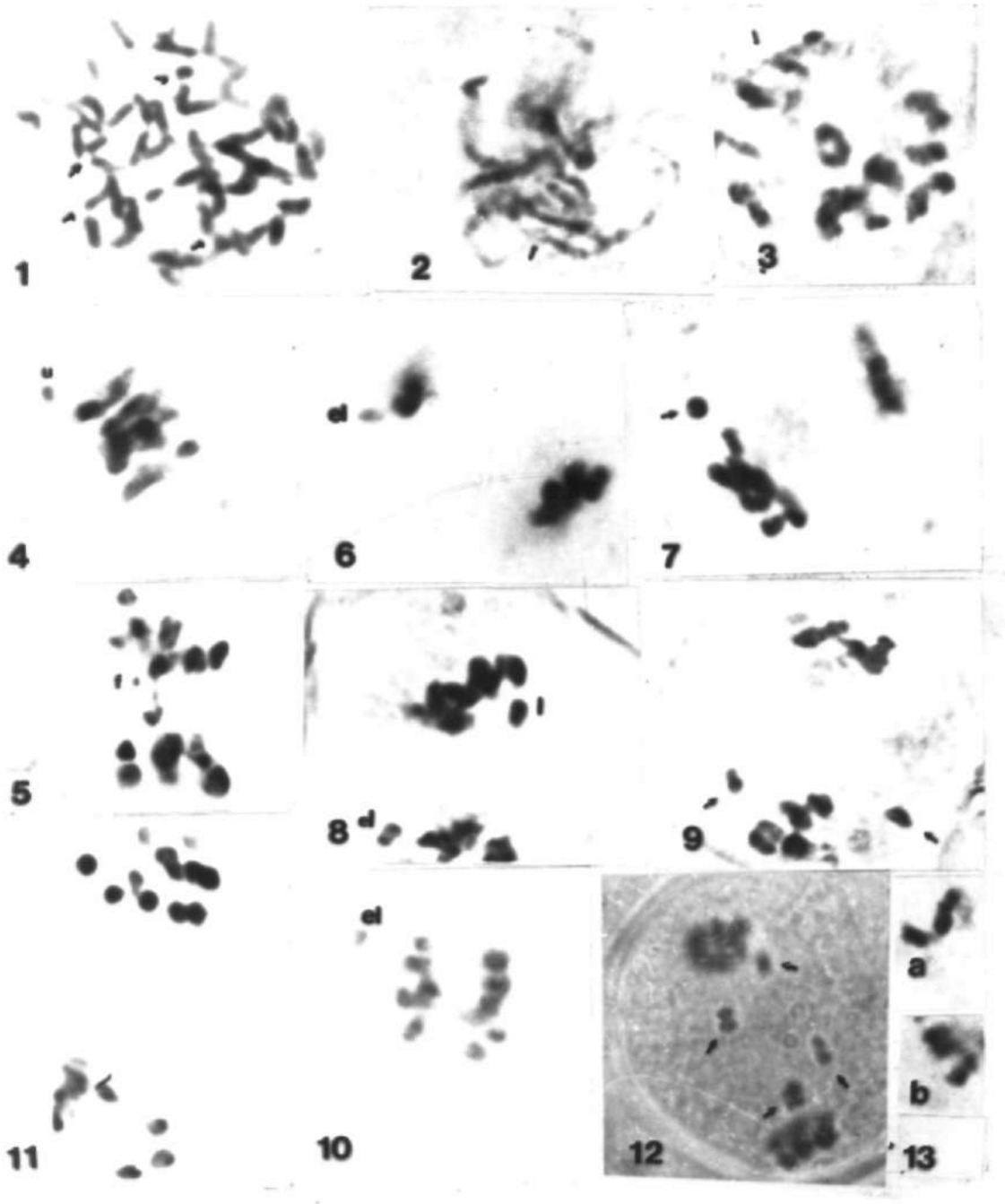
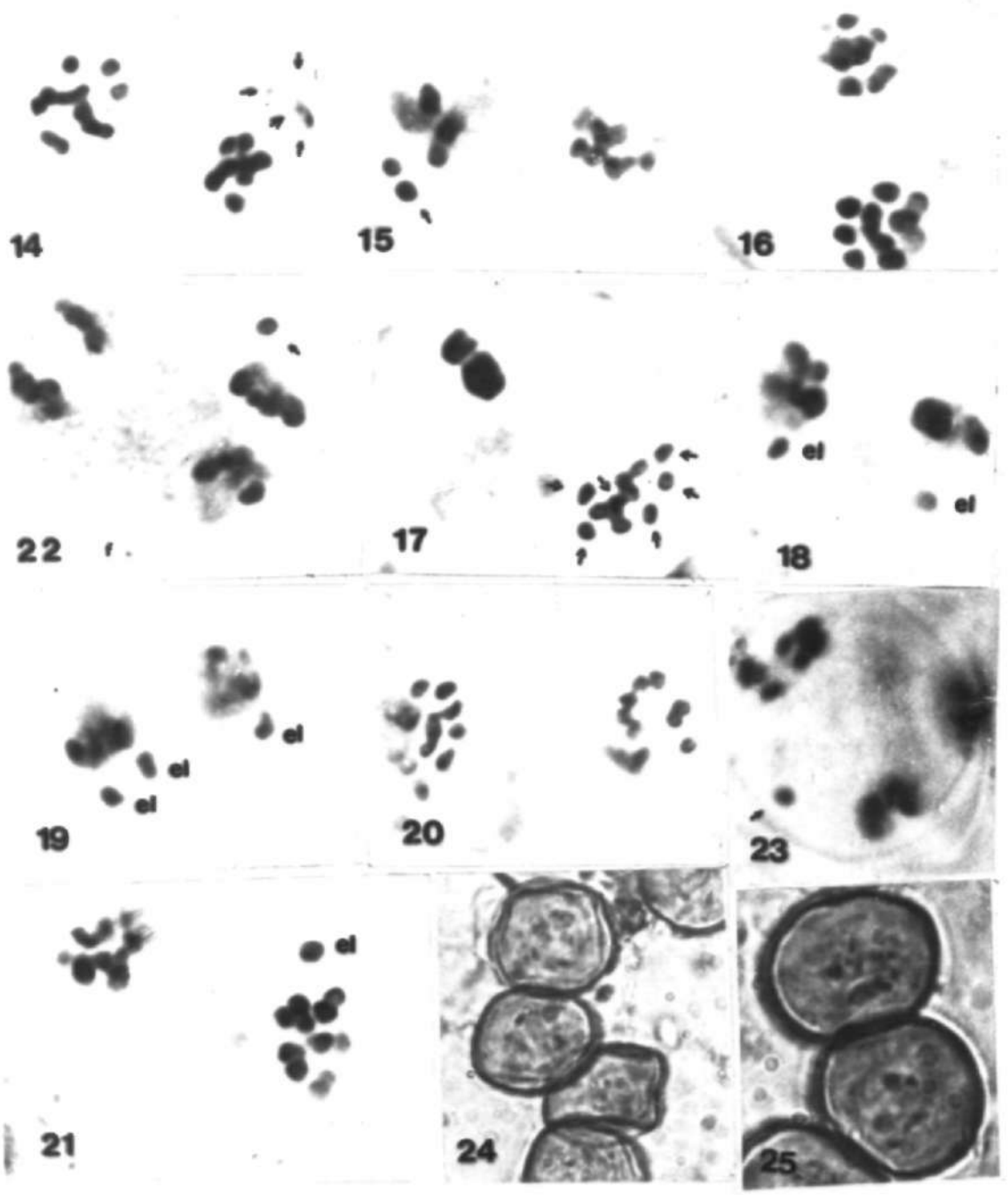


PLATE IA

Meiosis in S. mochicense Ochoa



(ii) Chromosome number and Morphology in S. mochicense Ochoa

In this investigation little attention was given to morphology of chromosomes, although the chromosome complements of the species, S. mochicense Ochoa were obtained from the tapetal cells (Pl. I, Fig. 1). There are 48 chromosomes all of which have either metacentric or sub-metacentric centromeres. There are also four satellite chromosomes which presumably were obtained by reduplication of chromosome complement since S. mochicense is a diploid species, 2n = 24, n= 12. Choudhuri (1943) reported the occurrence of such tetraploid tapetal cells with 48 chromosomes in the wild diploid potato species, S. infundibuliformePhil. High degree of ploidy was observed in tapetal cells of S. venturii Hawkes and Hjerting. Chromosome reduplication is so marked that normal diploid chromosome number 24 reached 96 (Choudhuri, 1971). Avanzi (1900) observed similar high polyploid cells in the development of tapetal cells of S. tuberosum.

Geitler (1937, 1939, 1941) discovered the phenomenon of chromosomal reduplication and subsequent separation without formation of spindle and without disappearance of nuclear membrance. He called this process endomitosis. Reduplication may be so marked that the diploid chromosome number normally 21 in Gerris lateralis may reach 1024 or 2048.

The existence of a ploypoid series in the wild relatives of the domestic potato was established by

Smith (1927) and Vilmorin and Simonet (1927a and 1927b). Rybin (1930, 1933) also published extensive monograph where he mentioned the chromosome number for 26 wild species and confirmed the existence of polyploid series in the cultivated potatoes.

Keyn (1930) demonstrated the presence of satellite chromosomes in S. tuberosum. Meurman and Rancken (1932) in their studies of seventeen cultivated varieties of potato also found two satellited chromosomes in S. tuberosum and observed the presence of primary and secondary constrictions in certain other chromosomes. Lamm (1945) also investigated the somatic chromosomes of some potatoes and discovered four satellite chromosomes in the autotetraploid - S. rybinii and two satellited chromosomes in the diploids. In S. acaule he found four satellites. The presence of two satellited chromosomes in S. tuberosum might be due to amphidiploidy (Navashin 1928).

(iii) Meiosis in wild tuber-bearing diploid Solanum species

(iv) S. mochicense Ochoa

The early prophase stage of meiotic division were not suitable for critical studies although it was possible to follow the paired threads at pachytene. At pachytene stage most of the chromosomes showed a good degree of pairing. This indicates the high degree of homology of the chromosomes. The double nature of the chromosome threads is shown in certain regions (Fig. 2). The position of the centromere are conspicuous as these appeared as gap

in chromosome thread, and surrounded on both sides by intensely stained chromatic regions (Whelan 1969) as shown in (Fig. 2). The intensely stained region may presumably be due to the contraction of chromosome threads near the centromere.

Although by pachytene pairing is complete and when pairing ends, the pachytene chromosomes become thicker and shorter. However, some segments of the chromosomes remained unpaired (Fig. 2), presumably because these regions are non-homologous or due to the time available for pairing is short and the region lie farthest apart from the point of which pairing begins. Similar unpaired segments of pachytene have been demonstrated in diploid hybrids between Emilia sonchifolia and E. coccinea and Oryza by Olorode (1973) and Li et al. 1963), respectively. It often occurs that when pairing is delayed, it may never be completed since division of homologous threads interrupts pairing (Darlington 1965).

Diplotene is a stage of short duration so it was difficult to follow the bivalents at this stage. Although at diakinesis 12 bivalents are usually seen, multivalents in the form of quadrivalents were also seen (Fig. 13). The frequency of various multivalents observed are presented in Table 2. In Fig. 3 is shown a nucleus at diakinesis with a quadrivalent and 10 bivalents.

TABLE 2

Multivalent frequency at diakinesis in S. mochiçense Ochoa

Chromosome complements	No. of PMC observed	Percentage
12 bivalents	320	76.19
11 bivalents, 2 univalents	45	10.71
1 trivalent, 10 bivalents, 1 univalent	15	3.57
1 quadrivalent, 1 trivalent, 8 bivalents, 1 univalent	5	1.19
1 quadrivalent, 10 bivalents	25	5.95
2 quadrivalents, 8 bivalents	7	1.64
3 quadrivalents, 6 bivalents	3	0.75
	420	

At diakinesis the chromosomes are held either by a single chiasma or by two terminal chiasmata (Fig. 3). The frequency of chiasmata is low at diakinesis and varies from 0.9 to 1.2 per bivalent and the result of the analysis is shown in Table 3.

TABLE 3

Frequency of chiasmata at diakinesis in S. mochicense Ochoa

No. of PMC* observed	Total No. of chiasmata per nuclens	Average frequency of chiasmata per bivalent
20	18	1.5
18	17	1.4
16	16	1.3
15	14	1.2
12	13	1.1
10	12	1.0
8	11	0.9
Total 99		1.2

*PMC, Pollen-mother-cell

At first metaphase, as might be expected from diakinesis, usually 12 bivalents are seen. The multivalents could not be followed easily in metaphase owing to overcrowding of the bivalent chromosomes at the equatorial region of the spindle. Occasionally 13chromosomesare observed, owing presumably, to the presence of 11 bivalents and 2 univalents. The univalents are easy to trace at side view where they fail to orientate on the equatorial plate (Fig.4). In some nuclei only one univalent is observed without any corresponding increase of paired chromosomes (Fig. 4), so in all probability the other univalent is obscured by bivalents. Darlington (1965) considered non-orientation of bivalents

to increased distance between the centromere, with consequent decrease in repulsion, since he regarded repulsion as an effective agent in orientation.

At first anaphase the bivalents and polyvalents disjoin and move towards the poles while the univalents which failed to orientate on the metaphase plate, move slowly in between the poles. The behaviour of univalents varies, they lag, divide or are eliminated (Figs.7,8,12).

First anaphase figures were characterized by the presence of chromatid bridges and fragments (Fig. 5). The occasional existence of fragments at anaphase without any chromatid bridges seems to indicate that the bridge has either been disjoined early or carried to one of the poles, leaving the fragments between the separating groups of chromosomes. The occurrence of bridges and fragments had been explained on the basis of crossing over within an inversion and furnish a cytological method of detection of inversion (Smith 1935). The occurrence of chromatid bridges in the first anaphase is 3.60%.

The frequency of chromatid bridges, fragments, lagging and eliminated chromosomes have been analysed at anaphase and results are presented in Table 4.

TABLE 4

Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. mochicense Ochoa

No. of PMC showing clean separation	No. of chromatid bridges	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
350	-	-	-	-	350	84.33
-	1	1	-	-	10	2.40
-	-	-	1	1	15	3.62
-	1	-	-	1	5	1.20
-	-	-	-	1	15	3.62
-	-	-	-	2	12	2.89
-	-	-	4	-	6	1.45
-	-	-	1	-	2	0.49
					415	

As might be expected the distribution of chromosomes at second metaphase is often unequal owing to division and elimination of univalents. Plate IA, Fig. 14 shows a distribution of 12-8 chromosomes along with 4 eliminated chromosomes whereas Fig. 16, shows an equal distribution of 12 chromosomes on each of the second metaphase plates. In Table 5, is shown the extent of this unequal distribution of chromosomes on second metaphase plates.

TABLE 5

Frequency of different chromosomes distribution on second metaphase plates in S. mochicense Ochoa

No. of chromosomes on second metaphase plates	No. of eliminated chromosomes	No. of PMC observed	Percentage
12 - 12	-	307	91.65
12 - 8	4	2	0.59
11 - 11	2	10	2.98
10 - 11	3	12	3.59
11 - 12	1	4	1.19
		335	

Secondary association which involves the aggregation of chromosomes into groups at metaphase due to their affinity is conspicuous in this species. The extent of such secondary association in second metaphase are analysed and the results are shown in Table 6.

TABLE 6

Showing character and frequency of secondary association in second metaphase in S. mochicense Ochoa

No. of single chromosomes	No. of chromosomes in Groups of 2	3	4	5	6	Frequency
12	.	.	.	.	.	10
7	.	.	.	1	.	5
6	.	2	.	.	.	7
6	.	.	.	.	1	8
5	1	.	.	1	.	4
5	.	1	1	.	.	6
4	.	.	2	.	.	5
1	4	1	.	.	.	6
			Total PMC analysed			51

The most frequent combination is 2 groups of 3 in each metaphase plate. Secondary association of chromosomes at second metaphase is more conspicuous than in first and similar instance have been noted in Oryza (Nandi, 1936) in Brassica (Sikka, 1940) and also in S. polyadenium Greenman by (Choudhuri, 1943).

Second anaphase and telophase figures were characterized by the presence of lagging, eliminated chromosomes and fragments. In Fig. 22 is shown 1 eliminated chromosome with a fragment whereas Fig. 23 shows an eliminated chromosome forming a micronucleus. The frequency of lagging, eliminated chromosomes and fragments at second anaphase is analysed and the results are shown in Table 7.

TABLE 7

Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at second anaphase in S. mochicense Ochoa

No. of PMC showing clean separation	No. of chromatid bridge	No. of fragments	No. of laggards	No. of eliminated chromosome	Frequency	Percentage
285	-	-	-	-	285	81.42
-	-	1	-	-	12	3.43
-	-	1	-	-	8	2.29
-	-	-	1	-	11	3.14
-	-	1	1	-	6	1.72
-	-	-	-	1	24	6.86
-	-	-	-	2	4	1.14
					350	

The chromosomes and fragments which failed to be included in the daughter nuclei usually formed micronuclei (Fig. 23).

Pollen

Pollen formation in diploid S. mochicense Ochoa is not regular as one would expect in a diploid. The formation of micronuclei from eliminated chromosomes is not uncommon. Table 8 shows the frequency of micronuclei during pollen formation. As might be expected, certain amount of dwarf and morphologically deformed pollen grains occur (Fig. 24), resulting from irregularities during pollen formation. These are characterized by their small sizes compared with the good ones. Fig. 25 shows the morphologically good pollen grains, 88.46%.

An analysis of aberrations in the second division (c.f. Table 7) shows 18.58% irregularities along with 7.21% formation of micronuclei. The percentage of aberration (18.58) during the second division which is the final divisional phase in formation of pollen is nearly similar to the percentage of deformed pollen (11.54) and this seems to indicate that there is direct connection between cytological aberration and malformation of pollen.

TABLE 8

Frequency of micronuclei during pollen formation in *S. mochicense* Ochoa

No. of normal tetrads	No. of micronuclei	No. of PMC observed	Percentage
335	-	335	92.79
-	1	18	4.99
-	2	8	2.22
		361	

(V) PLATES II AND IIA

Figs.1-21, Showing meiotic divisions in pollen mother cells of S. boliviense Dun.

Fig. 1. Diplotene showing 12 bivalents. The number of chiasmata varies from 1 to 3 per bivalent.

Fig. 2. Diplotene with 12 bivalents. The number of chiasmata varies from 1 to 4 per bivalent.

Fig. 3. Diakinesis showing 2 quadrivalents and 8 bivalents.

Fig. 4. First metaphase showing 12 bivalents.

Fig. 5. First metaphase, side view with two non-orientated chromosomes.

Fig. 6. First anaphase showing delayed separation of bivalents.

Fig. 7. First anaphase showing two chromatid bridges which are broken along with 1 eliminated chromosome and two fragments.

Fig. 8. First anaphase with 2 lagging chromosomes one of which is dividing.

Fig. 9. Second prometaphase showing presumably equal distribution of chromosomes on each plate.

Fig. 10. First anaphase with chromosome which has failed to reach the pole with other chromosomes. This presumably is a laggard.

Fig. 11. Second metaphase showing distribution of 12 chromosomes in one of the plates. Note the secondary association of chromosomes in groups of 5 and 3.

Fig. 12. Configurations of (a) trivalent, (b and c) quadrivalents taken from different cells at diakinesis.

Fig. 13. Second metaphase showing distribution of 12-12 chromosomes. Note the secondary association of chromosomes in two groups of 4 on each plate.

Fig. 14. Second metaphase showing presumably distribution of 11-11 chromosomes along with 2 eliminated chromosomes.

Fig. 15. Second metaphase showing secondary association of chromosomes in three groups of 3 on each plate.

Fig. 16. Second anaphase with 1 chromosome which has reached the pole earlier than the rest of chromosomes, presumably due to elimination in earlier phase of division.

Fig. 17. Second anaphase showing 1 lagging chromosome along with 1 eliminated one.

Fig. 18. Second anaphase showing normal separation of chromosomes.

Fig. 19. Second anaphase with a chromatid bridge which is about to break.

Fig. 20. Second anaphase with 4 eliminated chromosomes.

Fig. 21. A morphologically good and a deformed pollen grains x 1000.

PLATE II

Meiosis in S. boliviense Dun.

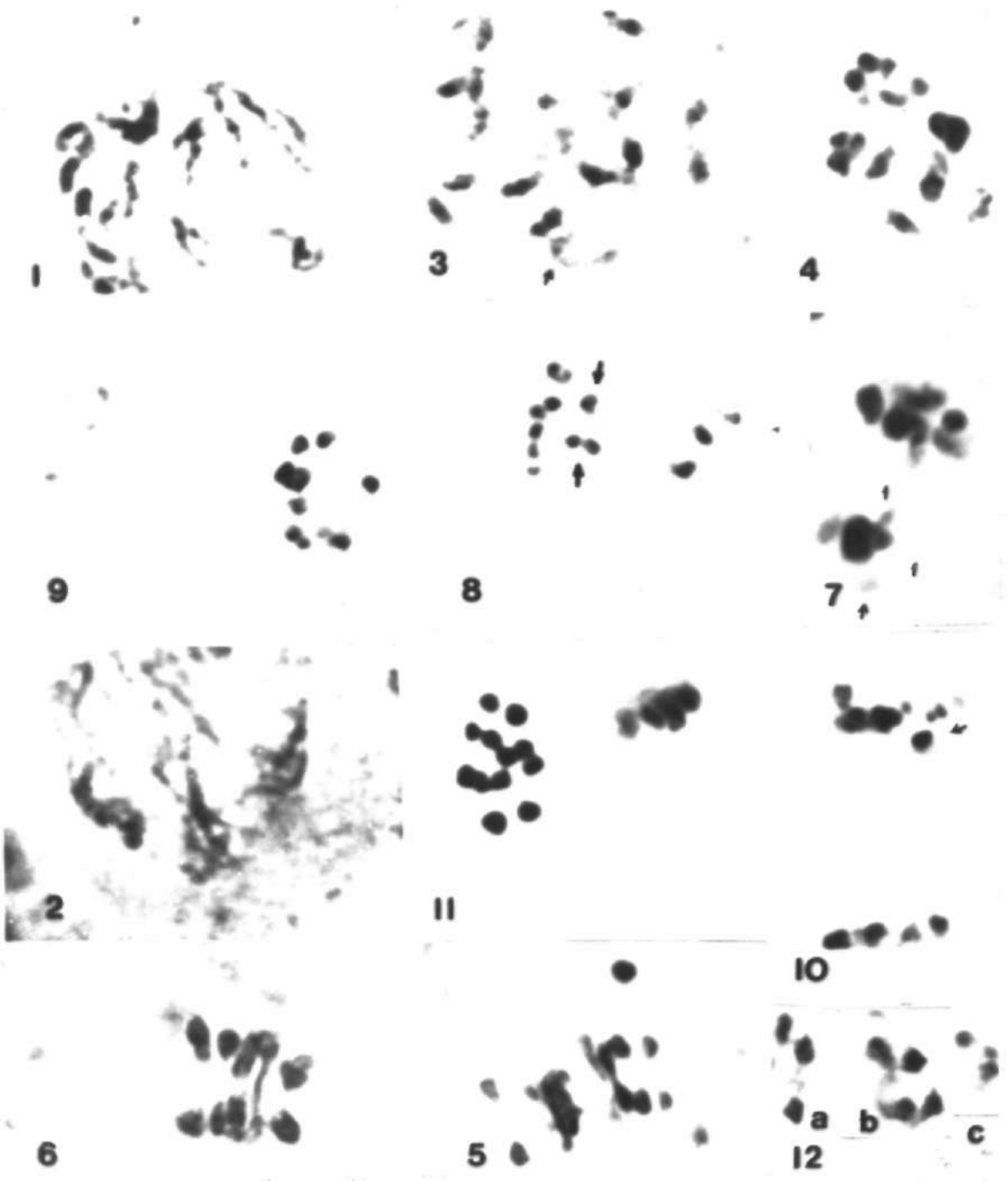
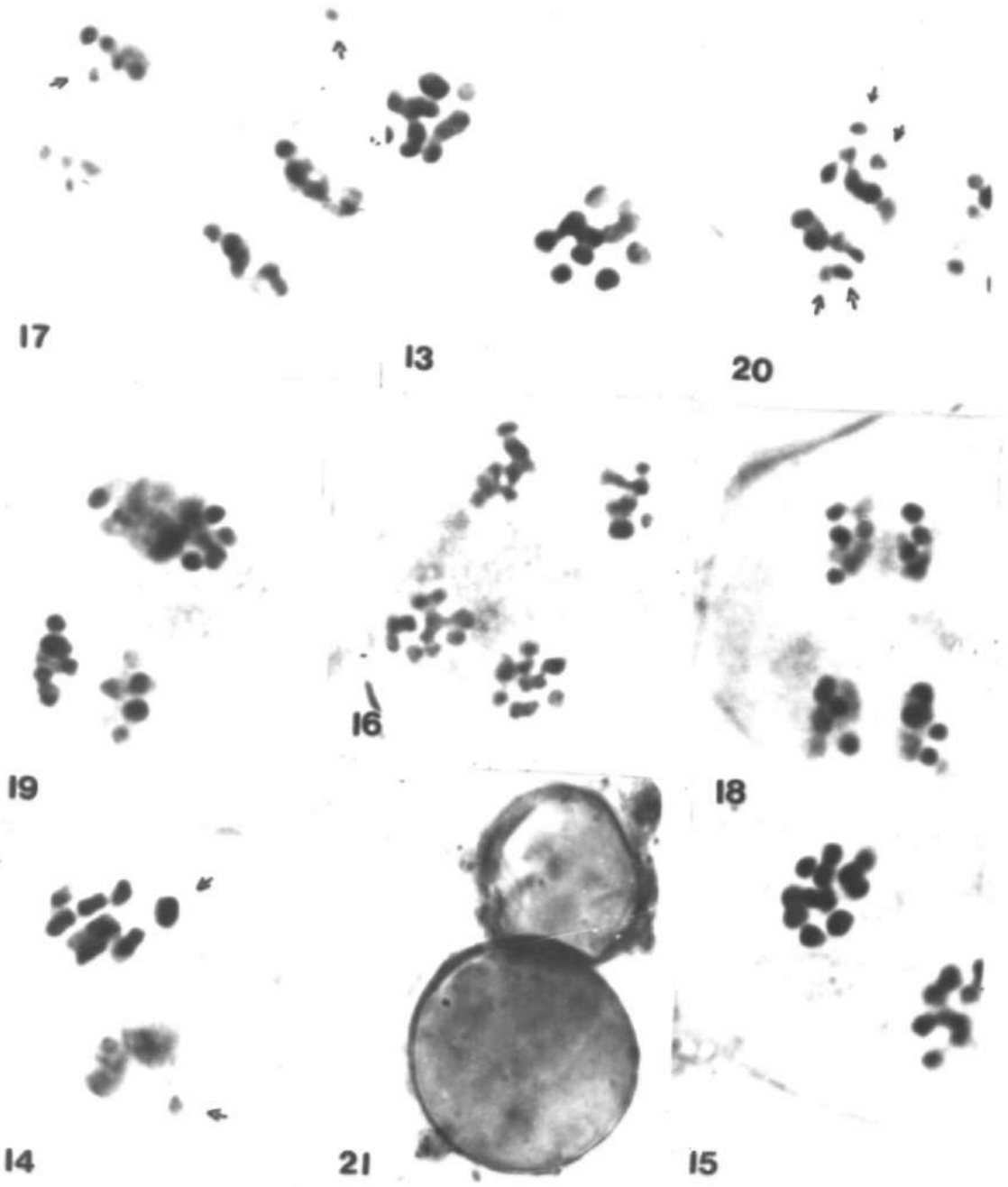


PLATE IIA

Meiosis in *S. boliviense* Dun.



(vi) S. boliviense Dun.

Early prohase stages in this material was also found unsuitable for critical studies, although at diplotene it was possible to follow 12 bivalents in the nuclei. In diplotene the paired chromosomes separate completely and are joined only at points of chiasmata (Plate II, Figs.1,2). In Fig. 2 is shown a diplotene with as many as 27 chiasmata in the nucleus. The frequency of chiasmata varies from 1.5 to 1.9 per bivalent as shown in Table 9.

TABLE 9

Frequency of chiasmata at diplotene in S. boliviense Dun.

No. of PMC observed	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
10	27	2.3
15	26	2.2
14	25	2.1
13	24	2.0
9	22	1.8
8	21	1.7
7	20	1.6
7	19	1.5
Total 83	Average frequency	1.9

At diakinesis, 12 bivalents were usually seen although multivalents in form of quadrivalents and trivalent were not infrequent. The frequency of such multivalents seen at diakinesis are presented in Table 10. In Fig. 3 is shown as many as 2 quadrivalents and 8 bivalents. Pattern of different configuration of multivalents observed in different pollen-mother-cells are shown in Fig. 12a, b, c.

TABLE 10

Multivalent frequency at diakinesis in S. boliviense Dun.

Chromosome complements	No. of PMC observed	Percentage
12 bivalents	210	71.67
11 bivalents, 2 univalents	22	7.51
10 bivalents, 4 univalents	18	6.14
1 quadrivalent, 10 bivalents	20	6.82
1 quadrivalent, 1 trivalent, 8 bivalents, 1 univalent	8	2.74
2 quadrivalents, 8 bivalents	15	5.12
	293	

At diakinesis the bivalents are either ring or rod-shaped being held together by either two terminal chiasmata in case of the former or by one chiasma in case of the latter. The average frequency of chiasmata was reduced at this stage and varied from 0.9 to 1.1 per bivalent.

The frequency of chiasmata observed at diakinesis is presented in Table 11.

TABLE 11

Frequency of chiasmata at diakinesis in S. boliviense Dun.

No. of PMC observed	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
19	17	1.4
15	16	1.3
18	15	1.2
11	14	1.1
10	12	1.0
8	11	0.9
Total 81	Average frequency	1.1

As might be expected, first metaphase was characterized by the presence of 12 bivalents (Fig. 4). The behaviour of univalents was easily noticeable, since they failed to orientate at the equatorial region of spindle (Fig. 5). Association of chromosomes in form of multivalents could not be followed at metaphase because of overcrowding of bivalent chromosomes.

At first anaphase, the bivalents and multivalents disjoin and moved towards the poles while the univalents which fail to orientate at equatorial region lie in between

the two poles (Fig. 8) or are eliminated (Fig. 7). First anaphase figures are often characterized by delayed separation of bivalents (Fig. 6). The configuration of such separation of chromosomes of bivalents is quite different from chromatid bridges formed due to inversion (c.f. Figs. 6 and 7). It may be that delayed separation of chromosomes is due to difficulty in movement of chiasmata. Such instances of delayed separation of chromosomes of a bivalent owing to arrest of terminalisation has been noted in Lachenalia glaucina (Moffett, 1936) and Brassica oleracea (Richharia, 1937) and Solanum melongena var. Bassawa (Choudhuri, 1975). It has been suggested that the arrest of movement of chiasmata may be due to change in homology of chromosomes (Lawrence, 1931). The occurrence of this phenomenon in S. boliviense Dun. suggests that structural change has taken place in the chromosome complement of this species.

First anaphase figures were also characterized by the presence of chromatid bridges and fragments (Fig. 7). The frequency of chromatid bridges, fragments, laggards and eliminated chromosomes have been analysed at anaphase and results are shown in Table 12.

TABLE 12

Frequency of chromatid bridges, fragments, lagging and eliminated chromosome at first anaphase in S. boliviense Dun.

No. of PMC showing clean separation	No. of chromatid bridge	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
264	-	-	-	-	264	76.74
-	2	2	-	1	8	2.33
-	-	1	-	-	5	1.46
-	-	1	1	-	7	2.03
-	-	1	2	-	10	2.90
-	-	-	2	-	25	7.26
-	-	1	1	-	5	1.46
-	-	-	1	-	15	4.36
-	-	-	-	2	5	1.46
					344	

Usually 12 chromosomes were seen on the second metaphase plates. (Plate IIA, Fig. 13), but as might be expected the distribution of chromosomes in some cases was unequal. Fig. 14 shows a distribution of 11-11 crhomosomes along with 2 eliminated chromosomes. The frequency of distribution of chromosomes observed in second metaphase plates is shown in Table 13.

TABLE 13

Frequency of different chromosome distribution on second metaphase plates in S. boliviense Dun.

No. of chromosomes on second metaphase plates	No. of eliminated chromosomes	No. of PMC observed	Percentage
12 - 12	-	323	90.73
12 - 11	1	11	3.09
11 - 11	2	15	4.22
12 - 10	2	4	1.12
11 - 10	3	3	0.84
		356	

At second metaphase the secondary association of chromosomes is conspicuous. Table 14 shows the extent of this secondary association. The most frequent combination is 2 groups of 4 on each plate.

TABLE 14

Showing character and frequency of secondary association in second metaphase in S. boliviense Dun.

No. of single chromosomes	No. of chromosomes in Groups of 2	3	4	5	6	Frequency
12	.	.	.	.	.	20
10	1	.	.	.	.	6
9	.	1	.	.	.	7
7	1	1	.	.	.	6
5	2	1	.	.	.	8
4	.	1	.	1	.	22
4	.	.	2	.	.	18
3	.	3	.	.	.	15
			Total PMC analysed			103

Second anaphase is as irregular as the first. The figures were chracterized by the presence of chromatid bridges, lagging and eliminated chromosome. In Fig. 17 is shown a lagging along with an eliminated chromosome while in Fig. 19 is shown the presence of chromatid bridge. Fig. 20 shows as many as 4 eliminated chromosomes. The frequency of chromatid bridges, fragments, lagging and eliminated chromosomes have been analysed at second anaphase and results are shown in Table 15.

TABLE 15

Showing frequency of chromatid bridges, fragment, lagging and eliminated chromosomes at second anaphase in S. boliviense Dun.

No. of PMC showing clean separation	No. of chromatid bridge	No. of fragments	No. of laggards	No. of eliminated chromosome	Frequency	Percentage
329	-	-	-	-	329	79.85
-	1	-	-	-	10	2.43
-	-	1	-	-	4	0.97
-	-	-	1	-	8	1.95
-	-	-	1	1	12	2.91
-	-	-	-	1	11	2.66
-	-	-	-	2	15	3.64
-	-	-	-	3	8	1.95
-	-	-	-	4	15	3.64
					412	

The chromosome forming bridges have been observed in various plants and animals. The presence of these bridges and fragments had been explained on the basis of crossing over within an inversion and furnish a cytological method of detection of inversion (Smith, 1935). The occurrence of chromatid bridges varied from 2.33 to 2.43 in the first and second anaphases respectively. The chromosomes and fragments which failed to be included in the daughter nuclei usually formed micronuclei.

Pollen:

Pollen formation in the diploid S. boliviense Dun. is not so regular as one would expect. The formation of micronuclei from eliminated chromosomes and fragments was not unusual (Fig. 20). Table 16 shows frequency of micronuclei during pollen formation. As might be expected there were certain amount of dwarf and morphologically deformed pollen grains which occurred as a result of irregularities during pollen formation.

TABLE 16

Frequency of micronuclei during pollen formation in *S. boliviense* Dun.

No. of normal tetrad	No. of micronucleus	No. of PMC observed	Percentage
450	-	450	96.56
-	1	11	2.37
-	2	4	0.86
-	3	1	0.21
		466	

Analysis of aberration during second division shows 20.15% irregularities along with 3.44% formation of micronuclei. The percentage of morphologically good pollen was 88.42 and 11.58 being percentage of deformed pollen. The percentage of aberration (20.15) during second division indicate that there is some connection between cytological aberration and deformity of pollen (11.58). It may be emphasised in this connection that apparent morphologically good pollen may be misleading since Becker (1939) demonstrated that nearly half of the morphologically good pollen was non-viable.

(vii) PLATES III and IIA

Figs. 1-21, showing meiosis in pollen mother cells of S. raphanifolium Cárd. et Hawkes

Fig. 1. Pachytene showing completely paired chromosomes along with unpaired segments.

Fig. 2. Diakinesis showing 12 bivalents.

Fig. 3. First metaphase showing 12 bivalents.

Fig. 4. First metaphase, side view, with a non-orientated univalents.

Fig. 5. An unreduced nucleus at metaphase with 24 chromosomes.

Fig. 6. First anaphase showing delayed separation of a bivalent.

Fig. 7. First anaphase showing 2 lagging chromosomes.

Fig. 8. First anaphase showing a chromatid bridge.

Fig. 9. First anaphase with normal separation of 12 chromosomes in each pole.

Fig. 10. Configurations of (a) trivalent and (b) quadrivalent from different cells at diakinesis.

PLATE IIIA

Fig. 11. First anaphase showing normal separation of chromosomes. 3 chromosomes seem to have reached the poles earlier than the rest of the chromosomes.

Fig. 12. First anaphase with 2 eliminated chromosomes.

Fig. 13. Second metaphase showing presumably distribution of 12-10 chromosomes along with 2 eliminated chromosomes. Note secondary association of chromosomes in 2 groups of 3 chromosomes.

Fig. 14. Second metaphase showing presumably distribution of 12-11 chromosomes along with 1 eliminated chromosome.

Fig. 15. Second metaphase showing equal distribution of 12-12 chromosomes on each plates. Note the secondary association of chromosomes in a group of 5 and a group of 6 chromosomes.

Fig. 16. Second metaphase showing distribution of 12-10 chromosomes along with 2 eliminated chromosomes. Note the secondary association in 3 groups of 3 chromosomes in one of the plates.

Fig. 17. Second anaphase showing a chromatid bridge.

Fig. 18. Second anaphase showing 1 lagging chromosome.

Fig. 19. Second telophase with 2 eliminated chromosomes forming micronuclei.

Fig. 20. Second telophase with 2 eliminated chromosomes forming a micronucleus.

Fig. 21. Morphologically good and deformed pollen grains x 1000.

PLATE III

Meiosis in S. raphanifolium Cárd. et Hawkes

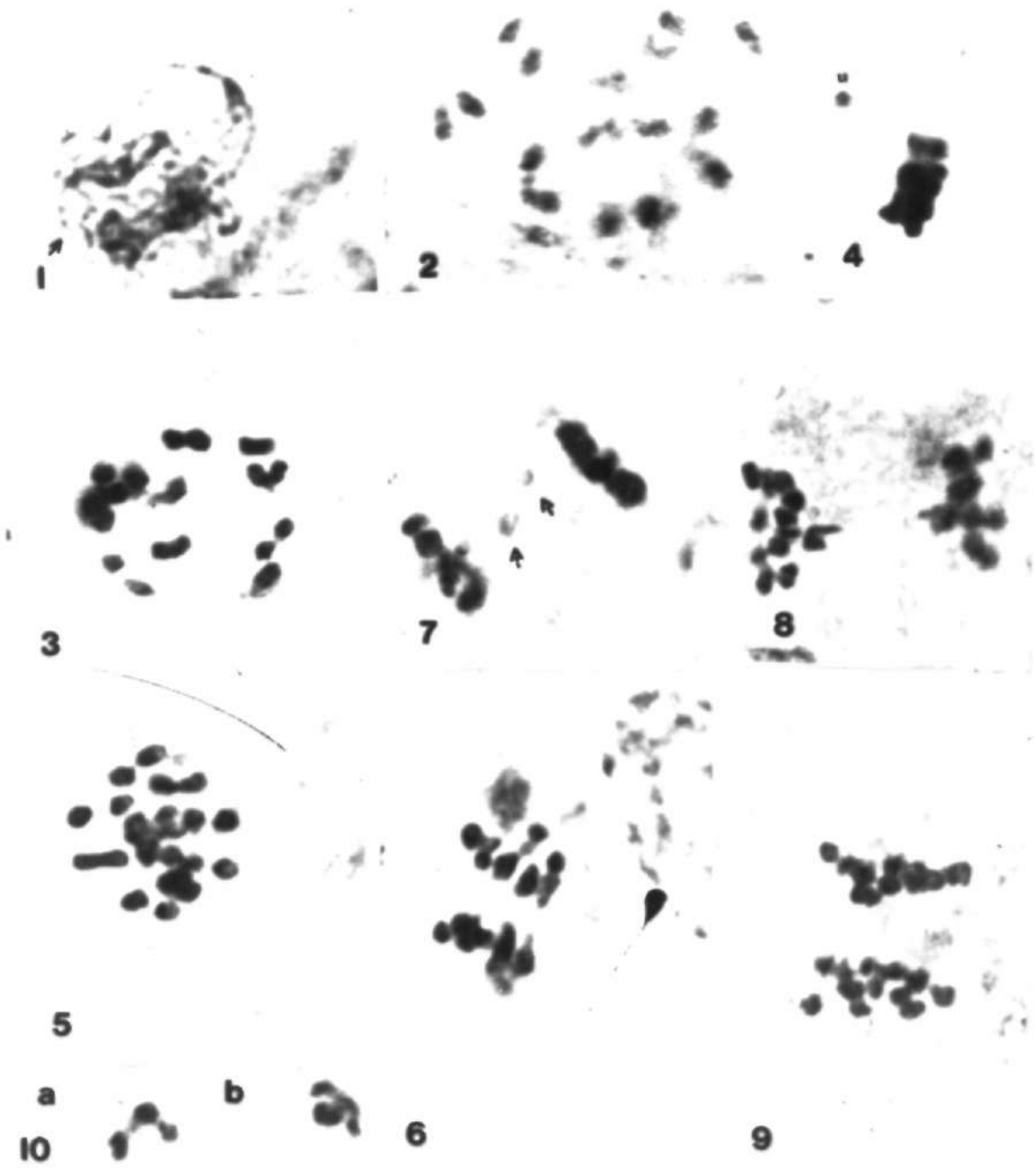
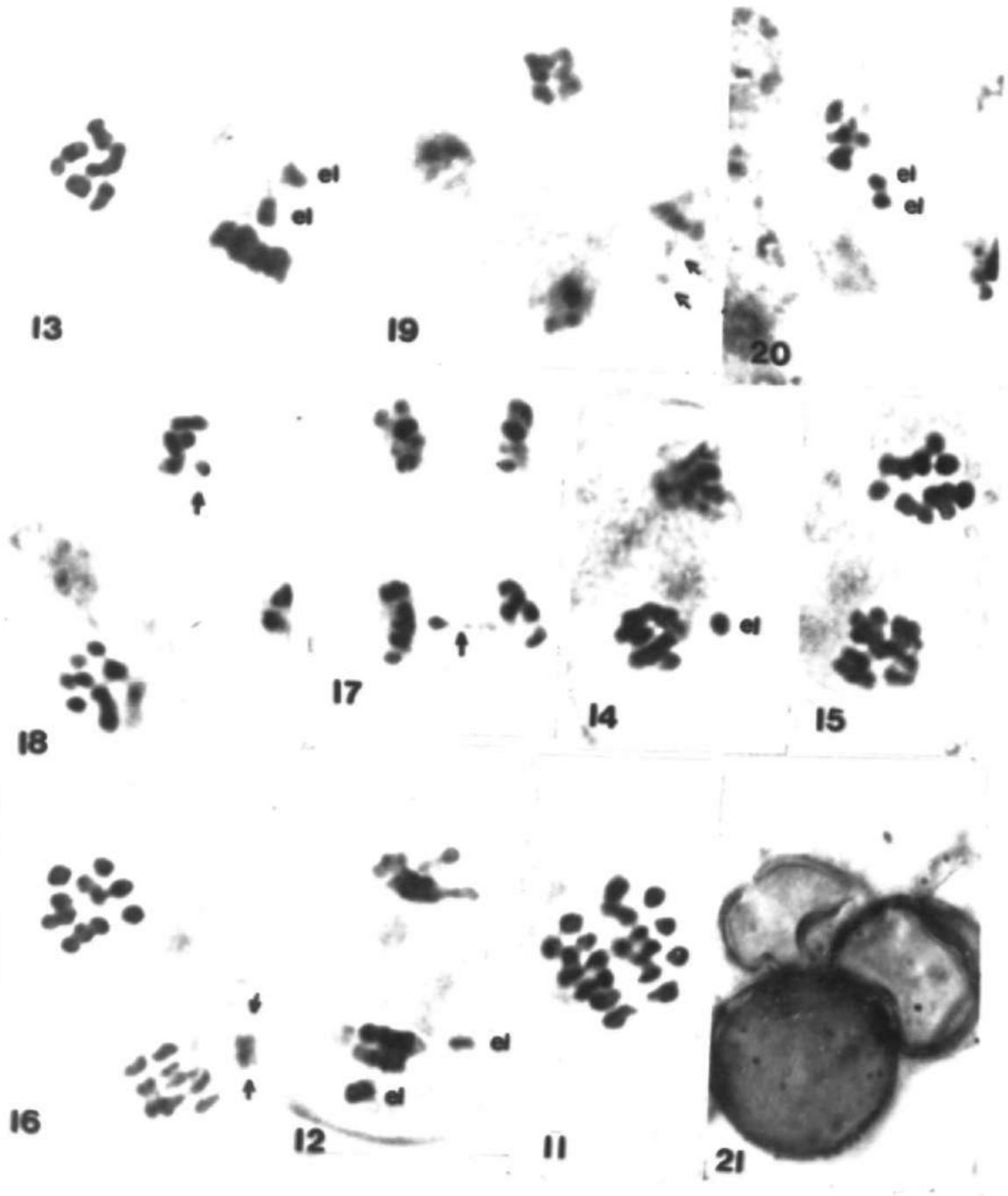


PLATE IIIA

Meiosis in S. raphanifolium Cárd. et Hawkes



(viii) S. raphanifolium Cárd et Hawkes

In this material early prophase stages of meiotic division was found not suitable for critical studies although at pachytene, the pairing of chromosome threads could be followed. At the end of pairing, the chromosomes become shorter and thicker and the double nature of the chromosomes is shown in certain regions (Plate III, Fig. 1). Pairing is not complete in certain segments of the chromosomes which may be due to segments being not homologous or the time available for pairing is short. It may so happen that when pairing is delayed it may never be completed as division of homologous threads interrupts pairing as suggested by Darlington (1965).

The diplotene stage was found not very favourable for critical analysis, although 12 bivalents could be followed at diakinesis stage in the nuclei (Fig. 2). Multivalents in form of quadrivalents and trivalents were not infrequent. The frequency of such multivalents at diakinesis is presented in Table 17.

TABLE 17

Multivalent frequency at diakinesis in S. raphanifolium Cárd et Hawkes

Chromosome complements	No. of PMC observed	Percentage
12 bivalents	208	77.04
11 bivalents, 2 univalents	16	5.92
1 trivalent, 10 bivalents, 1 univalent	15	5.56
2 trivalents, 9 bivalents	18	6.67
1 quadrivalent, 10 bivalents	7	2.59
2 quadrivalents, 8 bivalents	6	2.22
	270	

The chromosomes at diakinesis are held together by single or two chiasmata. The frequency of chiasmata varies from 1.0 to 1.3 per bivalent, analysis of which is shown in Table 18.

TABLE 18

Frequency of chiasmata at diakinesis in S. raphanifolium Cárd et Hawkes

No. of PMC observed	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
15	18	1.5
13	17	1.4
14	16	1.3
9	15	1.2
11	14	1.1
8	12	1.0
Total 70	Average frequency	1.3

At first metaphase 12 bivalents are easily followed (Fig. 3) and it was not possible to follow multivalents clearly owing to overcrowding of chromosomes at equatorial region of spindle. The univalents could be easily followed at side view where they fail to orientate on the equatorial region of the spindle (Fig. 4). Occassionally, first metaphase plates with unreduced 24 chromosomes are seen (Fig. 5). The occurrence of such restitution nuclei with 2n chromosomes is known in hybrids and arises presumably through failure of nucleus to complete division after splitting of chromosomes (Karpechenko, 1928).

At first anaphase the bivalents and multivalents disjoin and move towards the poles while the univalents which failed to orientate at the equatorial region of the spindle move slowly in between the poles, where they lag, divide or are eliminated (Fig. 7, plate IIIA, Fig. 12). First anaphase figures were also characterized by the presence of chromatid bridges (Fig. 8). The frequency of bridges, fragments, lagging and eliminated chromosomes have been analysed at first anaphase and results of which are shown in Table 19.

TABLE 19

Frequency of bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. raphanifolium Cárd et Hawkes

No. of PMC showing clean separation	No. of chromatid bridges	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
380	-	-	-	-	380	82.60
-	1	-	-	-	10	2.17
-	1	1	-	-	7	1.53
-	-	-	1	-	20	4.34
-	-	-	2	-	15	3.26
-	-	-	1	1	5	1.09
-	-	-	-	1	15	3.27
-	-	-	-	2	8	1.74
-	-	-	-		460	

The distribution of chromosomes on the second metaphase plates is irregular. In plate IIIA, Fig. 13 is shown a distribution of 12-10 chromosomes along with 2 eliminated chromosomes while in Fig. 15 is shown an equal distribution of 12-12 chromosomes. The frequency of distribution of chromosomes on second metaphase plates is shown in Table 20.

TABLE 20

Frequency of different chromosomes distribution on second metaphase plates in S. raphanifolium Card et Hawkes

No. of chromosomes on second metaphase plate	No. of eliminated chromosome	No. of PMC observed	Percentage
12 - 12	-	286	92.87
12 - 11	1	8	2.59
12 - 10	2	10	3.25
11 - 13	-	4	1.29
		308	

Secondary association of chromosomes of various types are seen at second metaphase. These are presented in Table 21.

TABLE 21

Showing character and frequency of secondary association in second metaphase in S. raphanifolium Card et Hawkes

No. of single chromosomes	No. of chromosomes in Groups of 2	3	4	5	6	Frequency
12	.	.	.	.	.	7
10	1	.	.	.	.	3
7	1	1	.	.	.	4
6	.	2	.	.	.	10
6	1	.	1	.	.	3
3	.	3	.	.	.	5
3	.	1	.	.	1	2
1	.	.	.	1	1	3
			Total PMC analysed			37

Second anaphase-telophase figures were characterized by the presence of chromatid bridges along with lagging and eliminated chromosomes. In Fig. 17 is shown a chromatid bridge at second anaphase while in Fig. 19 is shown a second telophase with 2 eliminated chromosomes. The frequency of chromatid bridges, fragments, lagging and eliminated chromosomes observed at second anaphase have been analysed and results are presented in Table 22.

TABLE 22

Showing frequency of chromatid bridges, lagging and eliminated chromosomes at second anaphase in S. raphanifolium Cárd et Hawkes

No. of PMC showing clean separation	No. of chromatid bridges	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
230	-	-	-	-	230	79.03
-	1	-	-	-	6	2.07
-	1	1	-	-	8	2.75
-	-	1	-	-	4	1.37
-	-	-	1	1	8	2.75
-	-	-	1	-	15	5.15
-	-	-	-	1	10	3.44
-	-	-	-	2	10	3.44
					291	

The chromosomes which failed to be included in the daughter nuclei from micronuclei (Fig. 20).

Pollen

Pollen formation in diploid S. raphanifolium Card et Hawkes is not so regular as has been imagined. The formation of micronuclei from an eliminated chromosome is not an unusual feature. Table 23 shows the frequency of micronuclei during pollen formation.

TABLE 23

Frequency of micronuclei during pollen formation in S. raphanifolium Card et Hawkes

No. of normal tetrads	No. of micronuclei	No. of PMC observed	Percentage
404	-	404	95.05
-	1	9	2.12
-	2	12	2.83
		425	

As expected there are some deformed pollen grains along with morphologically good pollen (Fig. 21). An analysis of aberration during second division (c.f. Table 22) shows 20.97% irregularities along with 4.95% of micronuclei. The percentage of morphologically good

pollen was 56.74 while the percentage of deformed pollen was 43.26. The percentage of aberration during second division (20.97), the final stage of pollen formation seems to indicate that there is no direct relationship between cytological aberration and deformity of pollen (43.26). The deformity of pollen far exceeds the percentage of aberration during second division. It seems then that pollen deformity is likely due to gene mutation (Beadle, 1932). Choudhuri (1943, 1944) demonstrated the presence of similar gene controlled deformity of pollen grains in diploid wild Solanums. Similar gene controlled mutants were induced by X-irradiation in Pisum sativum by Gottschalk and Baquar (1971, 1972).

(ix) PLATES IV and IVA

Figs. 1-25, showing meiosis in pollen mother cells of S. pinnatisectum Dun.

Fig. 1. Zygotene showing pairing of homologous chromosomes.

Fig. 2. Pachytene with completely paired chromosome along with unpaired segments.

Fig. 3. Diakinesis showing 1 hexavalent, 2 quadrivalents along with 5 bivalents.

Fig. 4. Configurations of (a) hexavalent (b) quadrivalent (c) trivalent taken from different cells at diakinesis.

Fig. 5. First metaphase, side view, with 1 non-orientated univalent.

Fig. 6. First metaphase, with 1 non-orientated rod bivalent along with 2 univalents.

Fig. 7. First anaphase showing 2 lagging along with 1 eliminated chromosomes.

Fig. 8. First anaphase showing a chromatid bridge.

Fig. 9. First anaphase with a lagging chromosome which is dividing.

Fig. 10. First anaphase showing 2 lagging chromosomes which are dividing.

Fig. 11. First anaphase showing 4 lagging chromosomes, 2 of which are dividing.

Fig. 12. First anaphase showing 2 eliminated chromosomes.

Fig. 13. First anaphase showing 3 lagging chromosomes.

PLATE IVA

Fig. 14. First anaphase showing 3 lagging chromosomes along with 1 eliminated chromosome.

Fig. 15. First anaphase showing 2 lagging chromosomes.

Fig. 16. Second metaphase showing equal distribution of 12 chromosomes on each plates.

Fig. 17. Second metaphase showing distribution of 12-10 chromosomes along with 2 eliminated chromosomes. Note secondary association of chromosomes in groups of 3 and 4.

Fig. 18. Second metaphase showing distribution of 12-11 chromosomes along with 1 eliminated chromosome. Note the secondary association of 4 chromosomes in one of the plates.

Fig. 19. Second metaphase showing distribution of 12-10 chromosomes along with 2 eliminated chromosomes. Note secondary association of chromosomes in 3 groups of 3 chromosomes.

Fig. 20 Second metaphase showing presumably distributions of 12-10 chromosomes with 2 eliminated ones.

Fig. 21. Second anaphase with 1 eliminated chromosome.

Fig. 22. Second anaphase showing 1 lagging chromosome along with 1 eliminated chromosome.

Fig. 23. Second telophase showing 2 eliminated chromosomes forming micronuclei.

Fig. 24. Tetrads showing 2 eliminated chromosomes forming micronuclei.

Fig. 25. Morphologically good and deformed pollen grains x 1000.

PLATE IV

Meiosis in *S. pinnatisectum* Dun.

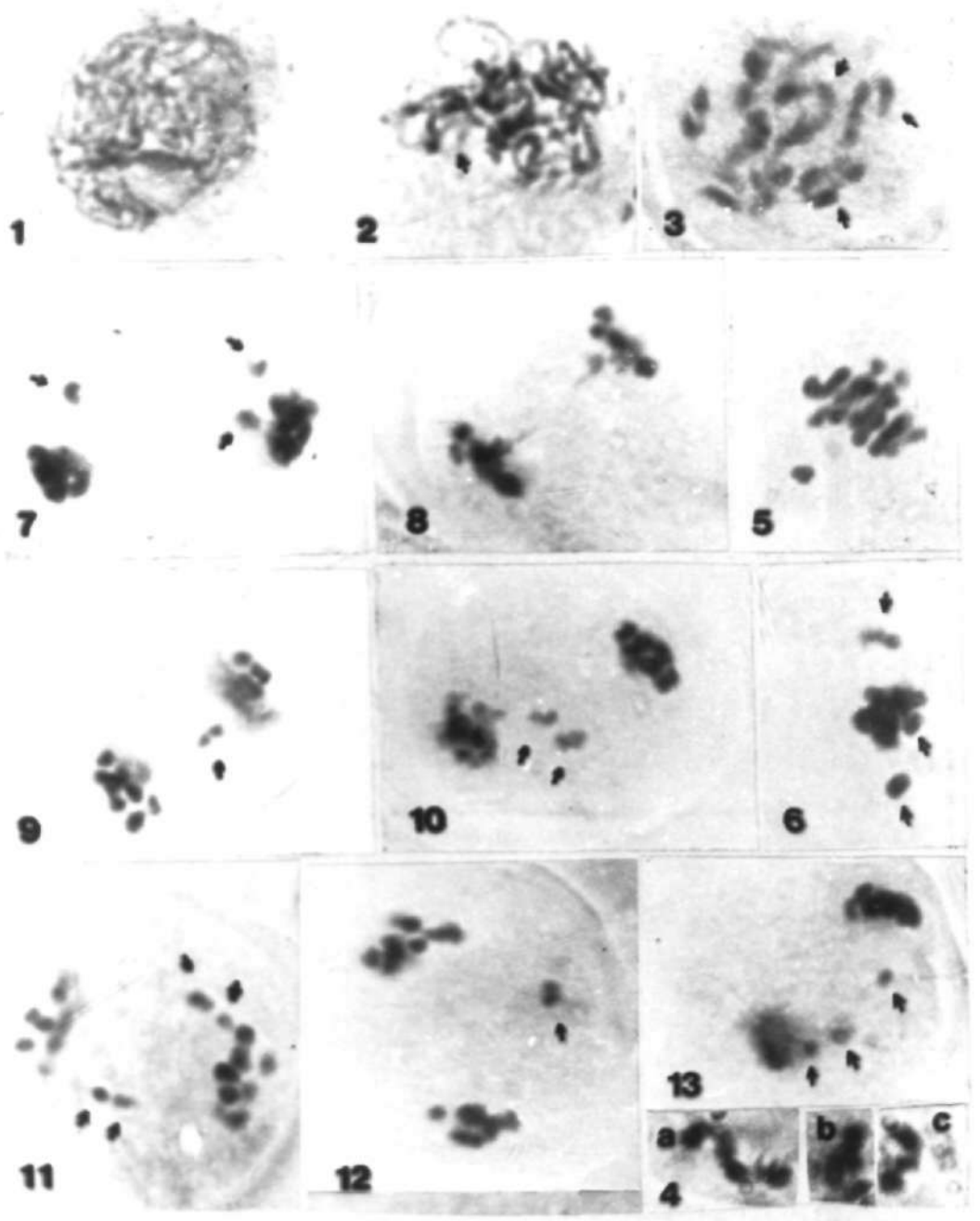
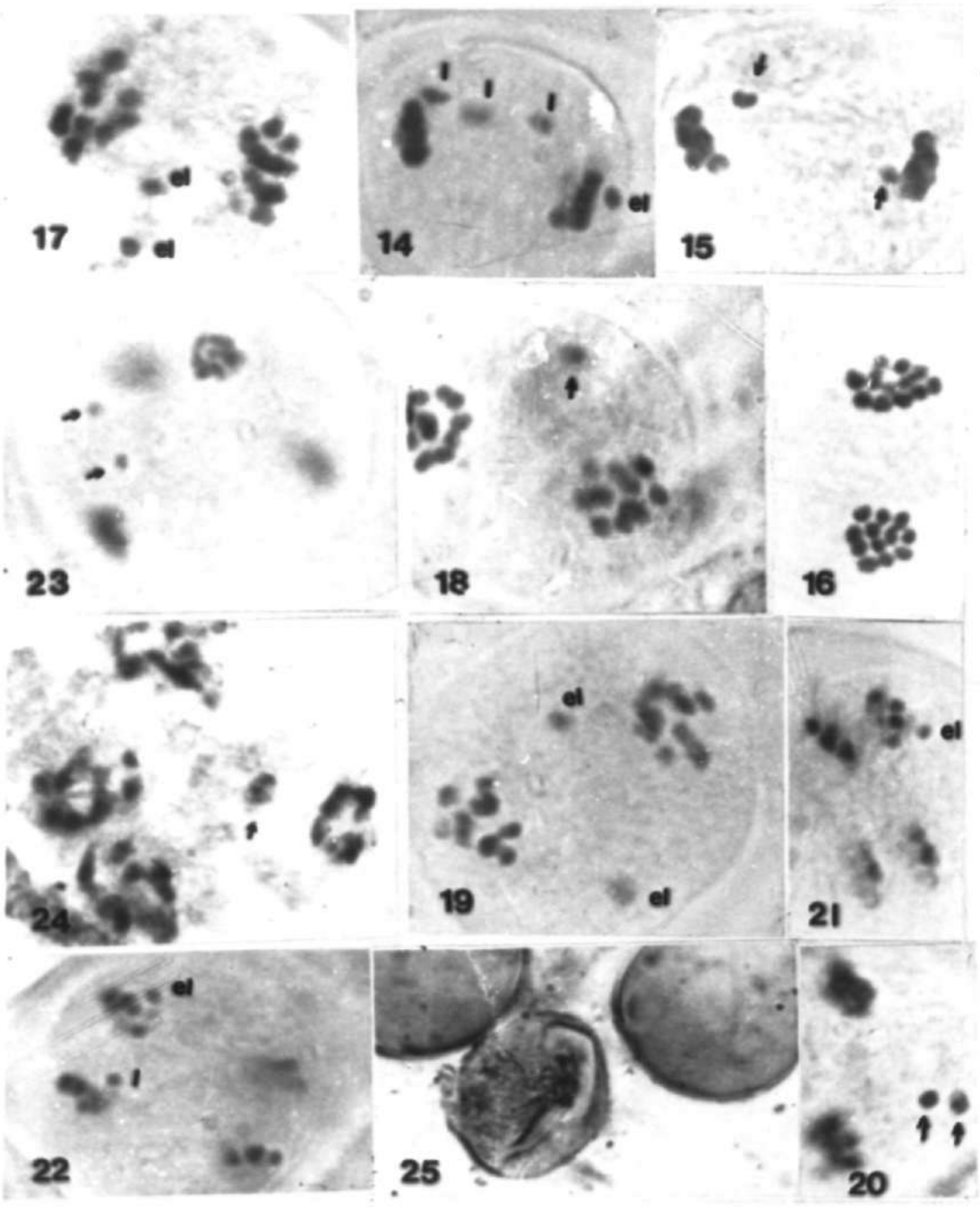


PLATE IVA

Meiosis in S.pinnatisectum Dun.



(x) S. pinnatisectum Dun.

The material was found to be favourable for the study of chromosome behaviour in the early stages of meiosis.

Prophase of meiotic division begins with the appearance of slender threads, which cannot be followed continuously for any considerable length. The occasional free ends indicate that there is no continuous thread.

Chromosome pairing begins at a point during zygotene, when the homologous chromosomes lie side by side. The points at which pairing begin are more deeply stained than the other parts of the chromosomes and are probably the centromere region (Plate IV, Fig. 1) which are more contracted than other parts of the chromosomes. Darlington (1965) demonstrated that the chromosomes in Fritillaria are more deeply stained in centromere region and that it is near here that pairing probably begins. In some cases three or four chromosomes are involved in pairing. In such instances pairing occurs in two out of three or four chromosome threads in a particular segment. At the end of pairing, the chromosomes at pachytene become thicker and shorter, the double nature of chromosome threads is well shown at certain regions (Fig. 2). Pairing is incomplete in certain segments of chromosomes probably because the time for pairing is short and the regions lie farthest apart from the point at which pairing begins. It may happen that when pairing is delayed it may never be

completed (Fig. 2) since division of homologous threads interrupts pairing (Darlington, 1965).

Diplotene stage is of short duration so it was not possible to follow up, although at diakinesis it was possible to follow 12 bivalents in the nuclei; multivalents in form of hexavalents, quadrivalents, and trivalents are not infrequent. The frequency of these multivalents are shown in Table 24.

TABLE 24

Multivalent frequency at diakinesis in S. pinnatisectum Dun.

Chromosome complements	No. of PMC observed	Percentage
12 bivalents	280	79.77
10 bivalents, 4 univalents	22	6.27
1 trivalent, 10 bivalents, 1 univalent	10	2.85
1 quadrivalent, 10 bivalents	15	4.27
1 hexavalent, 9 bivalents	5	1.43
1 hexavalent, 1 quadrivalent, 7 bivalents	8	2.28
1 hexavalent, 2 quadrivalents, 5 bivalents	6	1.70
2 quadrivalents, 8 bivalents	5	1.43
	351	

At diakinesis the chromosomes are held by a single or two chiasmata. The average frequency of chiasmata at this stage varies from 1.0 to 1.2 per bivalent and the result of analysis is shown in Table 25.

TABLE 25

Frequency of chiasmata at diakinesis in S. pinnatisectum Dun.

No. of PMC observed	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
22	18	1.5
19	16	1.4
17	15	1.3
15	14	1.2
12	13	1.1
10	12	1.0
3	11	0.9
Total 98	Average frequency	1.2

At first metaphase 12 bivalents are usually seen, and it was not possible to follow multivalents clearly owing to overcrowding of chromosomes at equatorial region of the spindle. The univalents could be seen at side view where they fail to orientate on the equatorial region of the spindle (Fig. 5).

The bivalents often fail to orientate or lie off the equatorial region of the spindle (35.3%), these bivalents are mostly rod-type (Fig. 6). Similar non-orientation of bivalents were demonstrated in diploid potatoes by Choudhuri (1943). Darlington (1965) considered the non-orientation of bivalents to increased distance between the centromeres, with consequent decrease in repulsion since he regarded repulsion as the effective agent in orientation. On this assumption, therefore, rod-bivalents should be more liable to non-orientation than ring-bivalents, indeed, this has been the case here. The frequency of non-orientation of rod-bivalents is considerably higher (4.7%) than that of ring-bivalents (0.6%).

At first anaphase, the bivalents and multivalents disjoin and move towards the poles while the univalents which fail to orientate at the equatorial region of spindle, move slowly in between the poles. Such univalents, lag, divide or are eliminated (Fig. 7, 11). First anaphase figures were also characterized by presence of chromatid bridges (Fig. 8). The frequency of bridges, fragments, lagging and eliminated chromosomes have been analysed at first anaphase and the results are shown in Table 26.

TABLE 26

Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. pinnatisectum Dun.

No. of PMC showing clean separation	No. of chromatid bridges	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
218	-	-	-	-	218	74.15
-	1	-	-	-	8	2.72
-	-	1	-	-	4	1.36
-	-	-	1	1	10	3.40
-	-	-	1	2	7	2.38
-	-	-	1	-	15	5.11
-	-	-	2	1	9	3.06
-	-	-	3	1	6	2.04
-	-	-	3	-	5	1.70
-	-	-	4	-	4	1.36
-	-	-	-	2	8	2.72
					294	

The distribution of chromosomes in the second metaphase is not equal. In Fig. 18 is shown a distribution of 12-11 chromosomes along with 1 eliminated chromosome while in Fig. 16 is shown an equal distribution of 12-12 chromosomes. The frequency of distribution of chromosomes observed on second metaphase plates is shown in Table 27.

TABLE 27

Frequency of different chromosomes distribution on second metaphase plates in S. pinnatisectum Dun.

No. of chromosomes on second metaphase plate	No. of eliminated chromosomes	No. of PMC observed	Percentage
12 - 12	-	420	94.18
12 - 11	1	10	2.24
12 - 10	2	12	2.69
11 - 11	2	4	0.89
		446	

Secondary association was observed in the second metaphase plates. These were analysed and are presented in Table 28. The most frequent secondary association is 3 groups of 3 chromosomes and the range of association is greater than the other species studied.

TABLE 28

Showing character and frequency of secondary association in second metaphase in S. pinnatisectum Dun.

No. of single chromosomes	No. of chromosomes in Groups of 2	3	4	5	6	Frequency
12	.	.	.	.	.	18
10	1	.	.	.	.	8
9	.	1	.	.	.	6
8	.	.	1	.	.	10
7	1	1	.	.	.	4
5	.	1	1	.	.	8
3	.	3	.	.	.	9
2	5	.	.	.	.	2
			Total PMC analysed			65

Second anaphase-telophase figures were also characterized by the presence of lagging and eliminated chromosomes. In Fig. 22 is shown a lagging chromosome along with 1 eliminated chromosome while Fig. 23 shows 2 eliminated chromosomes at second telophase. The frequency of chromatid bridges, lagging and eliminated chromosomes at second anaphase has been analysed and the results are presented in Table 29.

TABLE 29

Showing frequency of bridges, lagging and eliminated chromosomes at second anaphase in *S. pinnatisectum Dun*.

No. of PMC showing clean separation	No. of chromatid bridges	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
202	-	-	-	-	202	72.92
-	1	-	-	-	4	1.44
-	-	-	1	1	10	3.62
-	-	-	1	2	7	2.52
-	-	-	2	2	4	1.44
-	-	-	1	-	10	3.62
-	-	-	-	1	25	9.02
-	-	-	-	2	15	5.42
					277	

Pollen

Pollen formation in the diploid S. pinnatisectum Dun. is not very regular as has been imagined. The formation of micronuclei from eliminated chromosome is not an unsual feature. Table 30 shows the frequency of micronuclei formed during pollen formation.

TABLE 30

Frequency of micronuclei during pollen formation in S. pinnatisectum Dun.

No. of normal tetrads	No. of micronuclei	No. of PMC observed	Percentage
285	-	285	87.96
-	1	11	3.39
-	2	25	7.72
-	3	3	0.93
		324	

As expected from above certain amount of dwarf, morphologically deformed pollen grains occur along with morphologically good ones (Fig. 25). Analysis of chromosome irregularities during second division (c.f. Table 29) shows 27.08% irregularities along with 12.04%

formation of micronuclei. The percentage of morphologically good pollen was 64.75 and 35.25% being deformed. The percentage of aberration during second division which is the final phase of formation of pollen seems to indicate that there is connection between cytological aberration and deformity of pollen. The incidence of malformation of pollen (35.25%) is close to the percentage of aberration during second division (27.08).

(xi) PLATES V and VA

Figs. 1-32, showing meiosis in pollen mother cells of *S. stenotomum* Juz. et Buk.

Fig. 1. Pachytene showing completely paired chromosomes along with unpaired segments.

Fig. 2. Diplotene showing 2 bivalents. The number of chiasmata varies from 1 to 3 per bivalent.

Fig. 3. Diakinesis showing 12 bivalents.

Fig. 4. Diakinesis showing 10 bivalents and 4 univalents.

Fig. 5. Diakinesis showing 1 quadrivalent and 10 bivalents.

Fig. 6. First metaphase showing 12 bivalents.

Fig. 7. First metaphase, side view, with 4 non-orientated univalents.

Fig. 8. First metaphase, side view, with 2 non-orientated univalents.

Fig. 9. First metaphase, side view, with 2 non-orientated chromosomes, one of them is presumably a bivalent.

Fig. 10. First anaphase showing 2 chromatid bridges.

Fig. 11. First anaphase showing 1 laggard and 1 eliminated chromosomes along with a small chromosome which is presumably a fragment.

Fig. 12. First anaphase showing 1 laggard and 1 eliminated chromosomes.

Fig. 13. First anaphase with 1 laggard which is dividing.

Fig. 14. First anaphase with remanant of broken chromatid bridge along with a laggard which is dividing.

Fig. 15. Different configurations of (a) (b) (i) quadrivalents, taken from different cells at diakinesis.

PLATE VA

Fig. 16. First anaphase showing 2 laggards.

Fig. 17. First anaphase showing 1 eliminated chromosome.

Fig. 18. First anaphase showing 4 lagging chromosomes all of which are dividing.

Fig. 19. First anaphase with 1 laggard which is in the process of division.

Fig. 20. First anaphase showing 2 laggards 1 of which is dividing.

Fig. 21. First anaphase with 3 laggards. Note the unseparated chromatid bridge included in one of the poles.

Fig. 22. First anaphase showing a chromatid bridge and a laggard.

Fig. 23. First anaphase showing 1 laggard.

Fig. 24. Second metaphase showing 2 eliminated chromosomes.

Fig. 25. Second metaphase showing 12-11 distribution of chromosomes on different plates along with 1 eliminated chromosome.

Fig. 26. Second metaphase showing 11-7 distribution of chromosomes along with 5 eliminated chromosomes.

Fig. 27. Second anaphase showing 2 eliminated chromosomes along with 2 fragments which are forming micronuclei.

Fig. 28. Second anaphase showing 1 eliminated chromosome.

Fig. 29. Second telophase showing 2 eliminated chromosomes which is forming a micronucleus.

Fig. 30. Second telophase showing 4 eliminated chromosomes which are forming micronuclei.

Fig. 31. Tetrads along with a chromatid bridge which failed to separate in the second division and has been eliminated and may eventually form a micronucleus.

Fig. 32. Morphologically good and deformed pollen grains x 1000.

PLATE V

Meiosis in S. stenotomum Juz. et Buk.

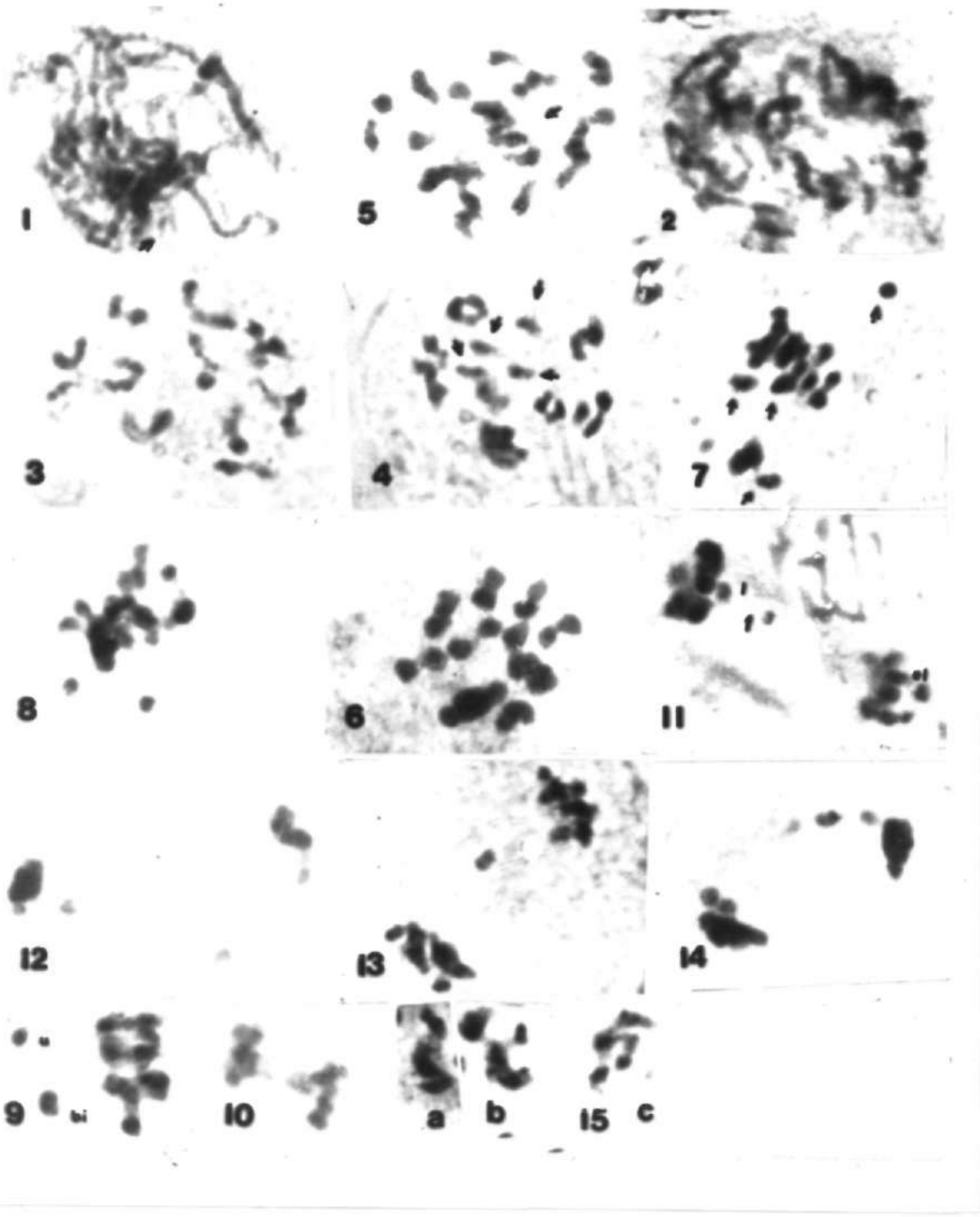
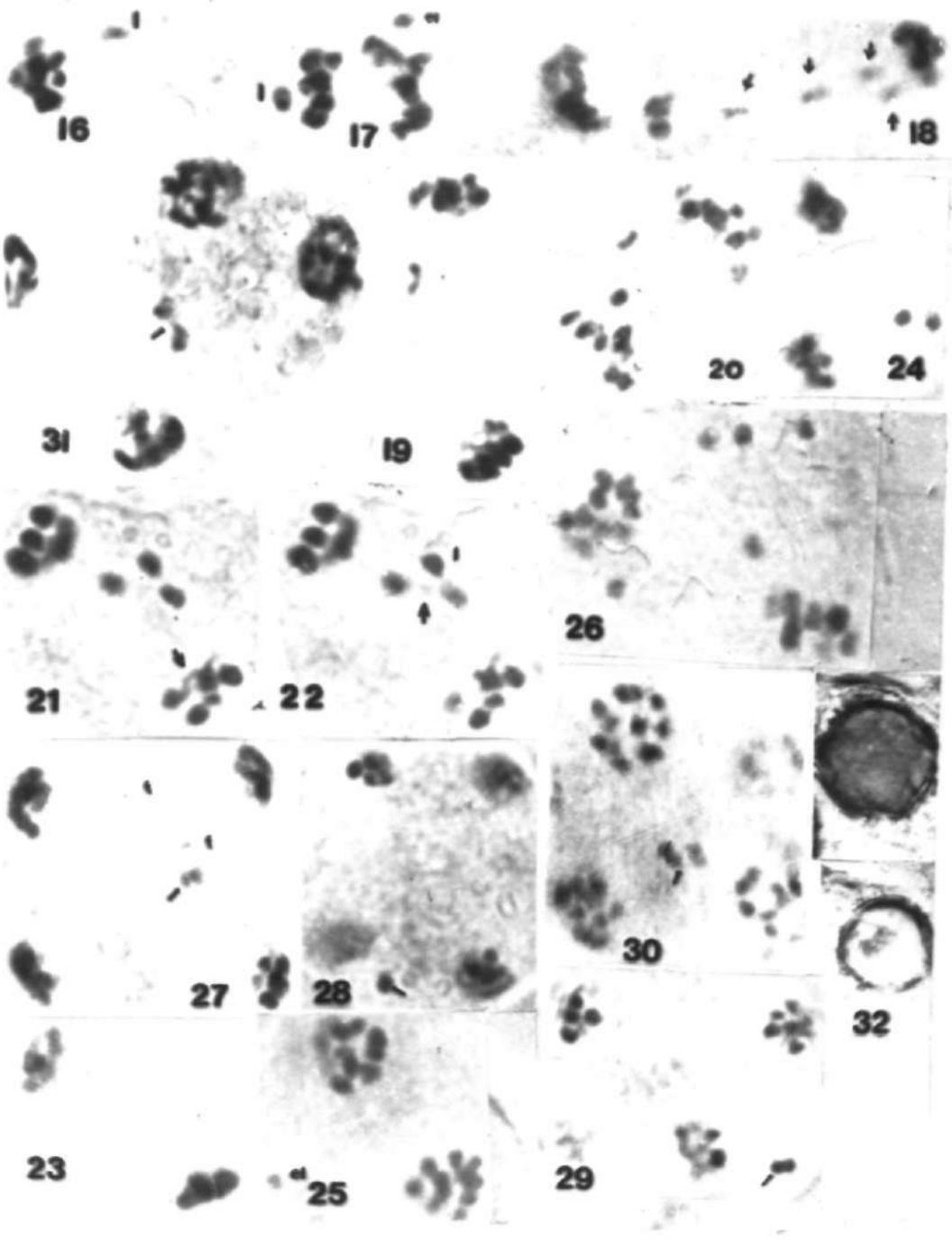


PLATE VA

Meiosis in S.stenotomum Juz. et Buk.



(xii) S. stenotomum Juz. et Buk.

Choudhuri (1943) studied the secondary pairing during meiosis in S. stenotomum var. Juz. et Buk. The material studied in the present investigation is a different clone of S. stenotomum and morphologically somewhat dissimilar.

The early prophase stages of meiotic division was not found suitable for critical studies, although at pachytene, it was possible to follow paired chromosome threads (Plate V, Fig. 1). Pairing is also found to be incomplete in certain segments of chromosomes. This is due either to their non-homologous nature of these segments or due to the short time available for pairing. It often happens that when pairing is delayed, it may not be completed since division of homologous threads interrupts pairing (Darlington, 1965).

At diplotene it is possible to follow the 12 bivalents in the nuclei. The paired chromosomes are separated completely along their length except at the points of chiasmata. In Fig. 2 is shown a nucleus with as many as 29 chiasmata. The frequency of chiasmata varies from 1.7 to 2.1 per bivalent, the results of analysis of which are presented in Table 31.

TABLE 31

Frequency of chiasmata at diplotene in S. stenotomum Juz. et Buk.

No. of PMC observed	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
6	29	2.5
10	28	2.4
6	27	2.3
15	26	2.2
14	25	2.1
18	24	2.0
8	22	1.8
6	21	1.7
Total 83	Average frequency	2.1

Although most of the chromosomes were usually seen in form of bivalents at diakinesis, multivalents in form of pentavalents, quadrivalents were not infrequent. The frequency of these various multivalents are shown in Table 32.

TABLE 32

Multivalent frequency at diakinesis in S. stenotomum Juz. et Buk.

Chromosome complements	No. of PMC observed	Percentage
12 bivalents	203	81.20
10 bivalents, 4 univalents	15	6.00
1 quadrivalent, 10 bivalents	10	4.00
2 quadrivalents, 8 bivalents	9	3.60
1 trivalent, 10 bivalents, 1 univalent	8	3.20
1 pentavalent, 2 quadrivalents, 5 bivalents, 1 univalent	5	2.00
	250	

Pattern of different configurations of pentavalents and quadrivalents are shown in Fig. 15a, b, c. At diakinesis, the chromosomes are held together by a single chiasma or two chiasmata. Choudhuri (1943) reported presence of polyvalents in form of trivalents in S. stenotomum var. Juz. et Buk. and their frequency was very low.

The frequency of chiasmata varies from 0.9 to 1.2 per bivalent and the results of analysis are present in Table 33.

TABLE 33

Frequency of chiasmata at diakinesis in S. stenotomum Juz. et Buk.

No. of PMC observed	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
12	18	1.5
16	17	1.4
11	16	1.3
18	15	1.2
9	14	1.1
12	12	1.0
10	11	0.9
Total 88	Average frequency	1.2

At first metaphase 12 bivalents are easily followed as might be expected from diakinesis. Some of the chromosomes at times fail to orientate at the equatorial region of the spindle and these non-orientated chromosomes are mainly univalents (Fig. 8). The multivalents could not be followed because of the overcrowding of chromosomes at equatorial region of spindle.

At first anaphase the bivalents and polyvalents disjoin and move towards the poles while the univalents which failed to orientate during metaphase move slowly in between the poles (Plate VA, Figs. 16, 17). First anaphase

figures were also characterized by the presence of chromatid bridges and fragments (Fig. 10). The presence of fragments without any chromatid bridge seemed to indicate that the bridge had either been disjoined early or carried to one of the poles leaving the fragments in between the separating groups of chromosomes. The chromatid bridges are short, and hence, they break at mid-anaphase and move to the poles (Fig. 14). The frequency of chromatid bridges, fragments, laggards and eliminated chromosomes are analysed and results are shown in Table 34.

TABLE 34

Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. stenotomum Juz. et Buk.

No. of PMC showing clean separation	No. of chromatid bridge	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
274	-	-	-	-	274	71.16
-	1	-	-	-	6	1.56
-	2	-	-	-	8	2.08
..	-	1	1	1	5	1.29
..	..	..	1	1	12	3.12
..	1	..	1	..	6	1.56
-	..	-	1	..	22	5.72
-	-	-	2	-	14	3.64
-	-	-	3	-	7	1.82
-	-	-	4	-	11	2.86
-	-	-	-	1	20	5.19
					385	

Choudhuri (1943) demonstrated the presence of chromatid bridges, fragments along with lagging and eliminated chromosomes at first anaphase in S. stenotomum var. The frequency of chromatid bridges and fragments was somewhat high (11.41%) whereas the percentage of lagging and eliminated chromosomes was low (8.21) in comparison to results obtained in the present study.

As expected, the distribution of chromosomes at second metaphase is not regular due to division and elimination of univalents. In Fig. 26 is shown an unequal distribution of 11-7 chromosomes along with 5 eliminated chromosomes while in Fig. 25 is shown a distribution of 12-11 along with 1 eliminated chromosome. The frequency of distribution of chromosomes on second metaphase plate is shown in Table 35.

TABLE 35

Frequency of different chromosome distribution on second metaphase plates in S. stenotomum Juz. et Buk.

No. of chromosomes in second metaphase plates	No. of eliminated chromosomes	No. of PMC observed	Percentage
12 - 12	-	287	83.92
12 - 11	1	35	10.24
12 - 10	2	15	4.38
11 - 7	5	5	1.46
		342	

Second anaphase-telophase figures were also characterized by presence of chromatid bridges, fragments, lagging and eliminated chromosomes. In Fig. 27 is shown a second anaphase figure with 2 eliminated chromosomes along with 2 fragments. While in Fig. 30 is shown a second telophase with 4 eliminated chromosomes. The frequency of chromatid bridges, fragments, lagging and eliminated chromosomes have been analysed at second anaphase and results are shown in Table 36.

TABLE 36

Showing frequency of bridges, fragments, lagging and eliminated chromosomes at second anaphase in S. stenotomum Juz. et Buk.

No. of PMC showing clean separation	No. of chromatid bridges	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
276	-	-	-	-	276	77.09
-	1	-	-	-	5	1.39
-	-	1	-	-	7	1.95
-	-	2	-	-	9	2.52
-	-	-	1	-	10	2.70
-	-	2	-	2	8	2.24
-	-	-	-	1	22	6.15
-	-	-	-	2	15	4.19
-	-	-	-	4	6	1.68
					358	

Similar occurrences of chromatid bridges and fragments along with lagging and eliminated chromosomes in the final phase of pollen formation had also been reported by Choudhuri (1943) in S. stenotomum var.

Pollen

Pollen formation in S. stenotomum Juz. et Buk. is not as regular as one would expect in diploid form. The formation of micronuclei from eliminated chromosomes and fragments is not uncommon feature (Fig. 30, 31). The frequency of micronuclei has been analysed and results are presented in Table 37.

TABLE 37

Frequency of micronuclei during pollen formation in S. stenotomum Juz. et Buk.

No. of normal tetrad	No. of micronuclei	No. of PMC observed	Percentage
262	-	262	85.90
-	1	10	3.28
-	2	19	6.23
-	3	6	1.93
-	4	8	2.62
		305	

The occurrence of dwarf and morphologically deformed pollen grains (69.90%) resulting from irregularities during division, along with morphologically good pollen grains (30.10%) were observed (Fig. 32). An analysis of aberration during second division (c.f. Table 36) shows 22.91 irregularities.

The percentage of aberration (22.91) during second division the final divisional phase in the formation of pollen seems to indicate there is no direct connection between cytological aberrations and malformation of pollen. The incidence of deformity (69.90) far exceeds the percentage of aberrations during second division (22.91). It seems that pollen deformity in the present case is presumably due to gene mutation (Beadle, 1932). Choudhuri (1943), however, demonstrated that there is certain amount of correlation in the percentage of deformed pollen with the amount of bridge formation.

(xiii) PLATES VI and VIA

Figs. 1 - 21, showing meiosis in pollen mother cells of S. chacoense Bitt.

Fig. 1. Pachytene showing completely paired chromosomes along with unpaired segments.

Fig. 2. Diplotene showing 12 bivalents. The number of chiasmata varies from 1 to 3 per bivalent.

Fig. 3. Diakinesis showing 1 quadrivalent and 10 bivalents. There is small chromatid body judging from its size it may be regarded as a centromere.

Fig. 4. First metaphase showing 12 bivalents.

Fig. 5. First metaphase showing non-orientated bivalent.

Fig. 6. First anaphase showing delayed separation of bivalents.

Fig. 7. First anaphase with 1 lagging chromosome which is dividing.

Fig. 8. First anaphase showing a fragment lying in between separating groups of chromosomes.

Fig. 9. First anaphase showing a chromatid bridge.

Fig. 10. First anaphase showing elimination of 1 chromosome which is dividing.

Fig. 11. First anaphase with 1 lagging chromosome.

Fig. 12. Different configurations (a,b,c) of quadrivalents taken from different cells at diakinesis.

PLATE VIA

Fig. 13. First anaphase showing normal separation of chromosomes.

Fig. 14. Second metaphase showing presumably distribution of 12-11 chromosomes along with 1 eliminated chromosome. Note the secondary association of chromosomes.

Fig. 15. Second metaphase showing presumably distribution of 12-10 chromosomes along with 2 eliminated chromosomes. Note the secondary association of chromosomes in 2 groups of 5 chromosomes in each.

Fig. 16. Second metaphase showing presumably distribution of 12-12 chromosomes. Note the secondary association of 9 chromosomes.

Fig. 17. Second metaphase showing distribution of 12-12 chromosomes. Note the secondary association of chromosomes in 2 groups of 5 chromosomes.

Fig. 18. Second anaphase showing 1 lagging chromosome.

Fig. 19. Second anaphase showing equal separation of chromosomes.

Fig. 20. Tetrads with an eliminated chromosome forming a micronucleus.

Fig. 21. Showing morphologically good and deformed pollen grains x 1000.

PLATE VI

Meiosis in S. chacoense Bitt.

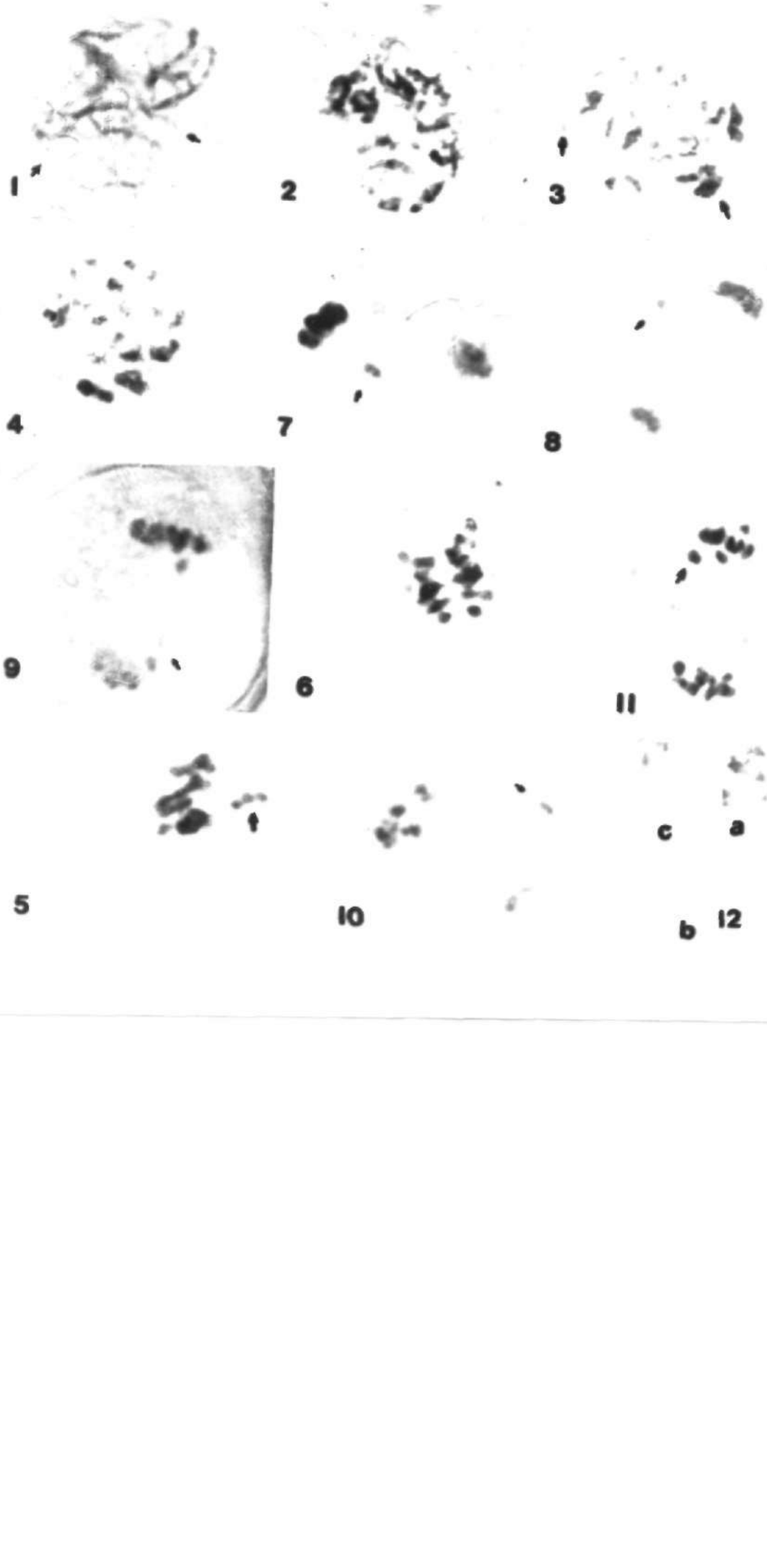


PLATE VIA

Meiosis in S. chacoense Bitt.



14



15



16



18



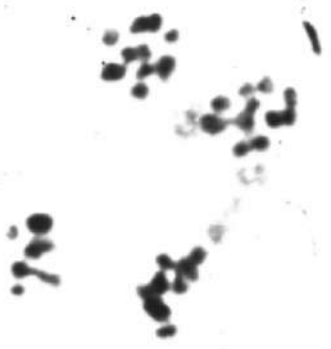
0



13



17



19



21

(xiv) S. chacoense Bitt.

Early stages of meiosis was found unsuitable for critical studies although at pachytene it was possible to follow the paired chromosomes which becomes thicker and shorter at the end of pairing. Pairing is incomplete in certain segments of chromosomes (Plate VI, Fig. 1), presumably because the time available for pairing is short. The occurrence of such case was reported by Darlington (1965) who demonstrated that when pairing is delayed it may never be completed, since the division of homologous chromosomes interrupts pairing.

It was possible to follow 12 bivalents at diplotene in the nuclei. The paired chromosomes separate completely except at points of chiasmata. Fig. 2 shows a nucleus at diplotene with as many as 26 chiasmata. The frequency of chiasmata at diplotene varies from 1.8 to 2.2 per bivalent are shown in Table 38.

TABLE 38

Frequency of chiasmata at diplotene in S. chacoense Bitt.

No. of PMC observed	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
8	30	2.6
15	29	2.5
12	28	2.4
9	27	2.3
11	26	2.2
10	25	2.1
14	24	2.0
16	22	1.8
Total 95	Average frequency	2.2

Although 12 bivalents are usually seen at diakinesis multivalents in form of quadrivalents are not rare (Fig. 3). The frequency of multivalents and bivalents is presented in Table 39.

TABLE 39

Multivalent frequency at diakinesis in S. chacoense Bitt.

Chromosome complements	No. of PMC observed	Percentage
12 bivalents	320	90.65
1 quadrivalent, 9 bivalents, 2 univalents	5	1.42
1 quadrivalent, 10 bivalents	10	2.83
11 bivalents, 2 univalents	5	1.42
2 quadrivalents, 8 bivalents	9	2.55
2 trivalents, 9 bivalents	4	1.13
	353	

At diakinesis, the chromosomes are held together by a chiasma or two chiasmata. In some cells a small chromatin body is seen near chromosomes and it may be judging from the size considered to be a centromere (Fig. 3). The frequency of chiasmata is reduced and varies from 1.0 to 1.3 per bivalent, the result of the analysis is presented in Table 40.

TABLE 40

Frequency of chiasmata at diakinesis in S. chacoense Bitt.

No. of PMC observed	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
10	19	1.6
9	18	1.5
11	17	1.4
14	16	1.3
12	15	1.2
8	14	1.1
6	12	1.0
Total 70	Average frequency	1.3

At first metaphase as might be expected from diakinesis 12 bivalents are easily seen (Fig. 4). The multivalents could not be followed. The univalents and bivalents could be seen at side view where they fail to orientate at the equatorial region (Fig. 5). The bivalents often lie off the equatorial region at metaphase (6.1%), these bivalents are mostly rod-type (Fig. 5). Similar non-orientation of bivalents were demonstrated in diploid potatoes by Choudhuri (1943). Darlington (1965) considered non-orientation of bivalents to increased distance between the centromeres, with

consequent decrease in repulsion since he regarded repulsion as the effective agent in orientation. On this assumption, therefore, rod bivalents should be more liable to non-orientation than ring-bivalent, indeed this is the case. In this material the frequency of non-orientation of rod-bivalents is considerably higher (5.9%) than that of ring-bivalent (0.2%).

At first anaphase the bivalents and multivalents disjoin and move towards the poles, while the univalents which failed to orientate on the metaphase plate, move slowly in between the poles. These univalents lag, divide, or are eliminated (Figs. 10, 11). First anaphase figures were characterized by the presence of chromatid bridges and fragments (Fig. 9). The presence of fragments at anaphase without any bridge seemed to indicate that the bridge had either been disjoined early or carried to one of the poles (Fig. 8) leaving a fragment between separating groups of chromosomes. The chromatid bridges are short and as a consequence they break at mid-anaphase and move to the poles leaving the fragments in the equatorial region of the spindle. The frequency of bridges, fragments, lagging and eliminated chromosomes are analysed and the results of which are presented in Table 41.

TABLE 41

Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. chacoense Bitt.

No. of PMC showing clean separation	No. of chromatid bridge	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
308	-	-	-	-	308	82.13
-	1	-	-	-	8	2.13
-	-	1	-	-	5	1.33
-	-	-	1	1	7	1.87
-	-	-	1	-	15	4.00
-	-	1	-	1	4	1.07
-	-	-	-	1	22	5.87
-	-	-	-	2	6	1.60
-	-	-	-		375	

The chromosomes of bivalents often show difficulty in separation and consequently they lag behind their fellows between separating groups of chromosomes (Fig. 6). The configuration of such belated separation of chromosomes of bivalents is distinct from bridge formation (c.f. Figs. 6 and 9). It may be that delayed separation of chromosomes is due to the difficulty in movement of chiasmata. Such instances of delayed separation of chromosomes of a bivalent owing to arrest of terminalisation has been noted in Lachenalia glaucina (Moffett, 1936) and Brassica oleracea (Richharia 1937). It has been suggested that the prevention of movement of chiasmata may be due to change in homology of chromosomes (Lawrence 1931). The occurrence of this phenomenon in S. chacoense Bitt. suggests that sructural change has taken place in the chromosome complement of the species.

The distribution of chromosomes at second metaphase is not equal because of the division and elimination of univalents. In Figs. 16 and 17 are shown equal distribution of 12 chromosomes on each of the second metaphase plates while in Fig. 14 is shown a distribution of 12-11 chromosomes along with an eliminated chromosome. The frequency of distribution of chromosomes observed on second metaphase plates is shown in Table 42.

TABLE 42

Frequency of different chromosome distribution on second metaphase plates in S. chacoense Bitt.

No. of chromosomes on second metaphase plates	No. of eliminated chromosomes	No. of PMC observed	Percentage
12 - 12	-	315	89.48
12 - 11	1	20	5.68
12 - 10	2	15	4.27
11 - 11	2	2	0.57
		352	

Secondary association of chromosomes is observed in this material with a frequent combination of 2 groups of 5 chromosomes. The analysis of secondary association of chromosomes is shown in Table 43.

TABLE 43

Showing character and frequency of secondary association in second metaphase in S. chacoense Bitt.

No. of single chromosomes	No. of chromosomes in Groups of 2	3	4	5	6	8	9	Frequency
12	.	.	.	.	.	.	.	15
9	.	1	.	.	.	.	.	8
8	2	.	.	.	.	.	.	10
8	.	.	1	.	.	.	.	6
7	1	1	.	.	.	.	.	4
6	.	2	.	.	.	.	.	3
6	1	.	1	.	.	.	.	4
4	1	2	.	.	.	.	.	2
3	.	.	.	.	.	.	1	5
2	.	.	.	2	.	.	.	14
								Total PMC analysed 71

Lagging and eliminated chromosomes were observed at second anaphase (Fig. 18). The frequency of chromatid bridges, fragments, lagging and eliminated chromosomes have been analysed and the results are presented in Table 44.

TABLE 44

Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at second anaphase in S. chaccense Bitt.

No. of PMC showing clean separation	No. of chromatid bridge	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
317	-	-	-	-	317	89.29
-	1	-	-	-	3	0.85
-	-	1	-	-	4	1.13
-	-	-	1	-	8	2.25
-	-	-	1	1	5	1.41
-	-	-	-	1	12	3.38
-	-	-	1	2	6	1.69
-	-	-			355	

Pollen

Pollen formation in the diploid S. chacoense Bitt, is not so regular as has been imagined. The formation of micronuclei from eliminated chromosomes is not unusual (Fig. 20). The frequency of micronuclei during pollen formation is shown in Table 45.

TABLE 45

Frequency of micronuclei during pollen formation in S. chacoense Bitt.

No. of normal tetrad	No. of micronuclei	No. of PMC observed	Percentage
321	-	321	94.13
-	1	12	3.52
-	2	8	2.35
		341	

As might be expected from the above certain amount of dwarf and morphologically deformed pollen grains occur (Fig. 21) resulting from irregularities during formation of pollen. An analysis of aberration during second division (c.f. Table 44) shows 10.71% irregularities with 5.87% formation of micronuclei. The percentage of morphologically good pollen was 74.25 and 25.75 being deformed.

The percentage of aberration (10.71) during second division seems to indicate that there is no direct connection between cytological aberration and malformation of pollen. The incidence of deformity of pollen (25.75%) exceeds the percentage of aberrations during second division (10.71). It seems that pollen deformity in the present case is presumably due to gene mutation (Beadle, 1932).

(xv) PLATES VII and VIIA

Figs. 1 - 29, showing meiosis in pollen mother cells of S. kuntzianum Bitt. et Wittm.

Fig. 1. Pachytene showing completely paired chromosomes along with few unpaired segments. Note the highly condensed regions in some areas of the chromosomes.

Fig. 2. Late-diplotene showing 24 bivalents. The number of chiasmata varies from 1 to 2 per bivalent.

Fig. 3. Diplotene showing 24 bivalents. The number of chiasmata varies from 1 to 3 per bivalent.

Fig. 4. Diakinesis showing 24 bivalents.

Fig. 5. Diakinesis showing 1 quadrivalent and 22 bivalents.

Fig. 6. First metaphase, side view, with 1 non-orientated bivalent.

Fig. 7. First metaphase, side view, with 2 non-orientated univalents.

Fig. 8. First anaphase showing a chromatid bridge along with 1 fragment.

Fig. 9. First anaphase showing 3 lagging chromosomes all of which are dividing along with 1 fragment.

Fig. 10. First anaphase showing 2 lagging chromosomes and 2 fragments.

Fig. 11. First anaphase showing presumably a broken chromatid bridge along with 1 lagging and 1 eliminated chromosomes.

Fig. 12. First telophase with a lagging chromosome.

Fig. 13. First anaphase showing 1 lagging chromosome which is dividing along with 2 fragments.

Fig. 14. Different configurations of (a,b) quadrivalent taken from different cells at diakinesis.

PLATE VIIA

Fig. 15. First anaphase showing 1 lagging chromosome which is dividing along with a fragment.

Fig. 16. First anaphase showing a chromatid bridge along with a fragment, 3 lagging chromosomes 1 of which is dividing.

Fig. 17. First anaphase with 1 eliminated chromosome and a fragment.

Fig. 18. First anaphase showing 1 lagging chromosome which is dividing along with a fragment.

Fig. 19. First anaphase showing a chromatid bridge along with 2 lagging chromosomes and 1 fragment.

Fig. 20. Second metaphase showing presumably distribution of 21 chromosomes in each plate along with 6 eliminated chromosomes.

Fig. 21. Second metaphase showing distribution of 24 chromosomes in one of the plates, the other plate presumably have 24 chromosomes.

Fig. 22. Second metaphase showing presumably 24-23 distribution of chromosomes along with 1 eliminated chromosome.

Fig. 23. Second metaphase showing distribution of 24 chromosomes in one of the plates, the other plate presumably contain 24 chromosomes.

Note the secondary association of chromosomes in 7 groups of 3 chromosomes.

Fig. 24. Second metaphase showing equal distribution of 24-24 chromosomes on each plate. Note the secondary association of the chromosomes in 4 groups of 4.

Fig. 25. Second anaphase showing a chromatid bridge.

Fig. 26. Second anaphase with 2 lagging chromosomes.

Fig. 27. Second anaphase showing 1 lagging chromosome which is dividing.

Fig. 28. Second telophase showing 4 eliminated chromosomes forming micronuclei.

Fig. 29. Showing morphologically good and deformed pollen grains x 1000.

PLATE VII

Meiosis in S. kuntzianum Britt. et Wittm.

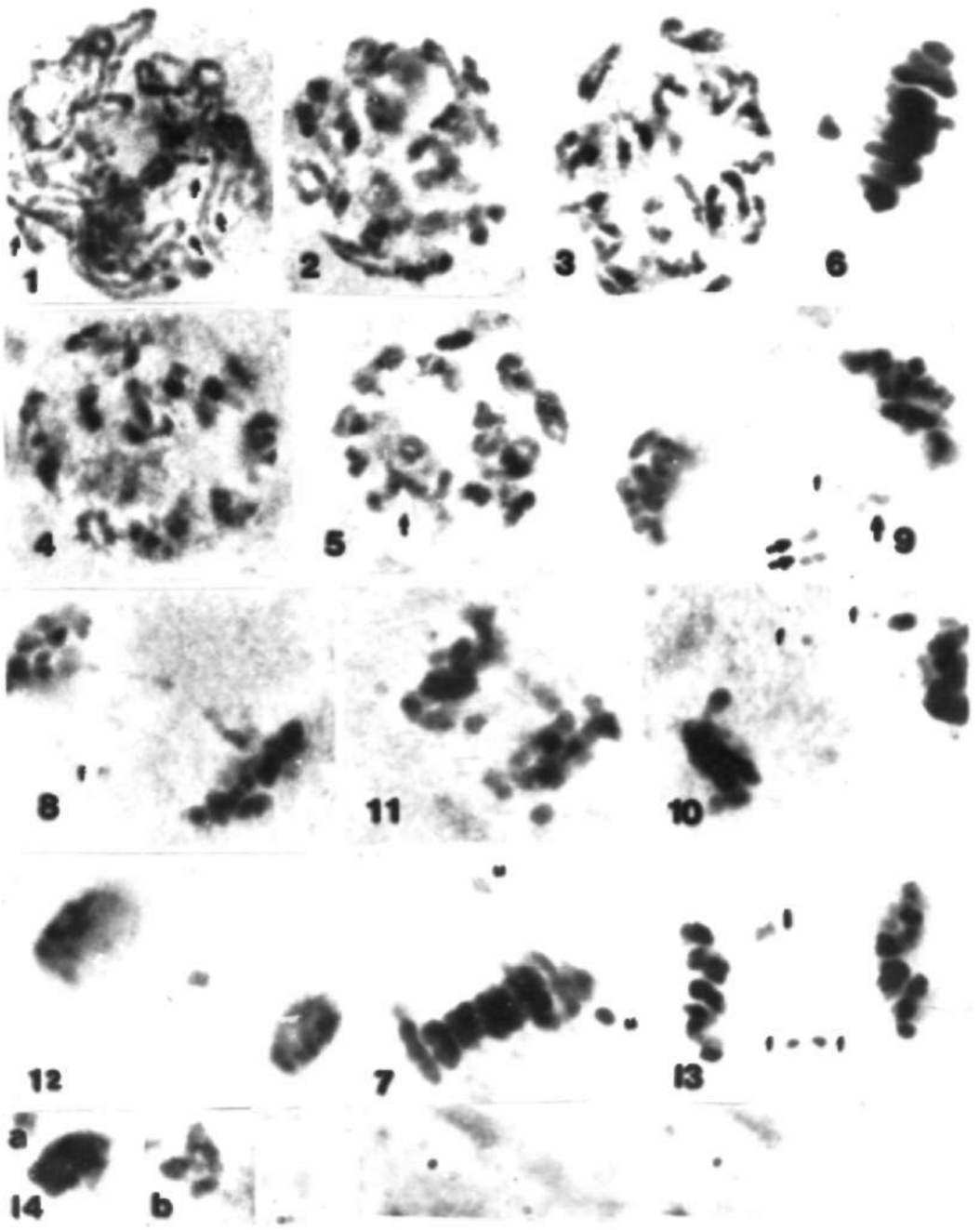
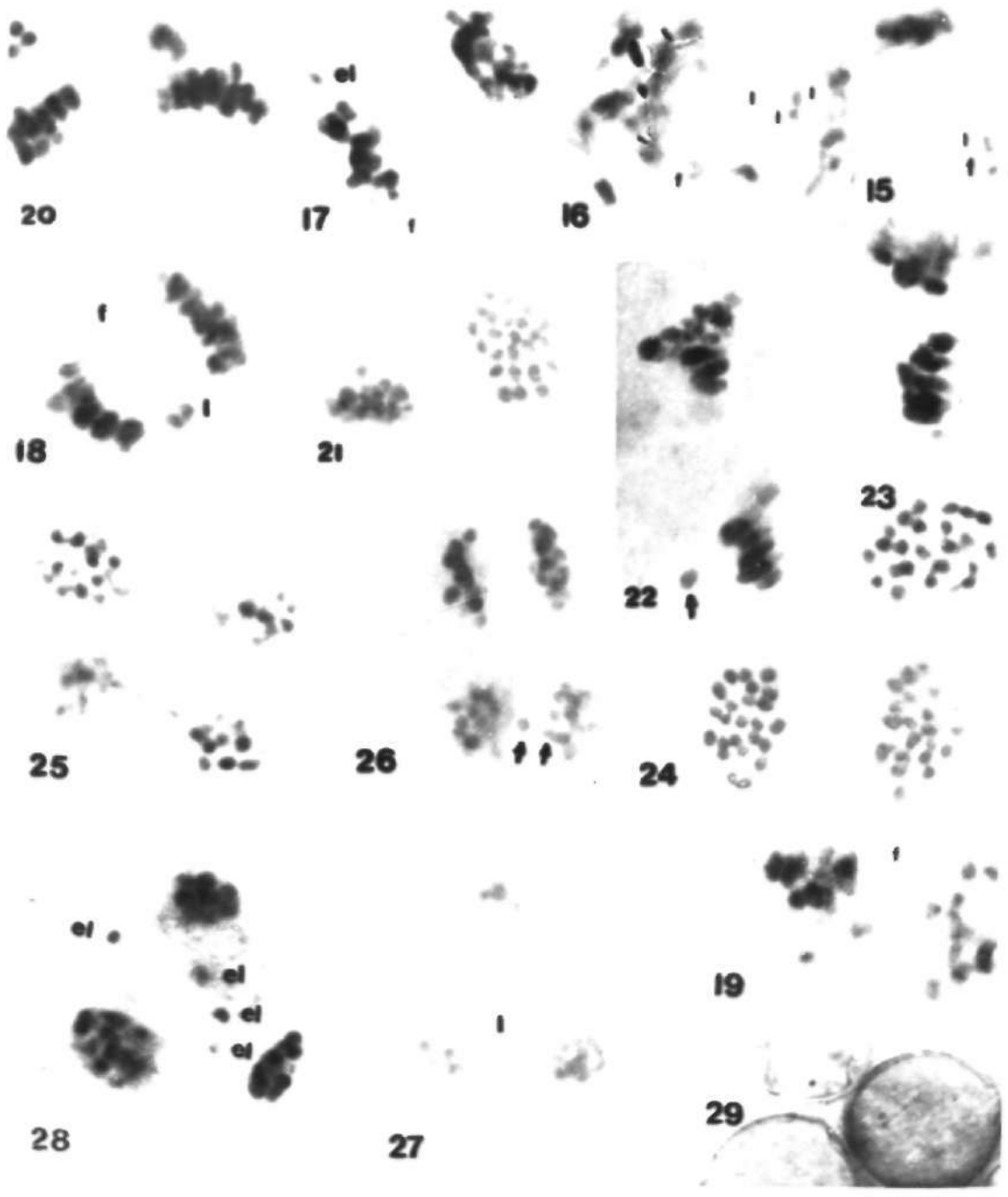


PLATE VIIA

Meiosis in S. kuntzianum Bitt. et Wittm.



(xvi) Meiosis in wild tuber-bearing tetraploid Solanum species

(xvii) S. kuntzianum Bitt. et Wittm.

The behaviour of chromosomes in a tetraploid during meiosis is determined by the same properties that determine their behaviour in a diploid. The difference follow only from each chromosome being represented four, instead of twice.

If pairing between the four homologous chromosomes is complete they will either be associated in two bivalents or all held together in a single quadrivalent. If pairing is incomplete they may form one bivalent and two univalents, one trivalent and one univalent or even four univalents.

Early prophase stage of meiotic division was not very suitable for critical studies. However at pachytene it was possible to follow completely paired chromosome threads along with chromosomes and certain regions which remained unpaired. Such cases of unpaired chromosomes of tetraploids at pachytene was reported in Hyacinthus, and Primula sinensis by Darlington (1929a,b). The completely paired region shows homology of the chromosomes. The position of the centromere is conspicuous as these appeared as gap in chromosomes thread surrounded on both sides by deeply stained chromatic regions. (Whelan 1969) (Plate VII, Fig. 1).

At diplotene it was possible to follow 24 bivalents in the nuclei. The paired chromosomes are separated

completely along their length except at points of chiasmata (Figs. 2 and 3). The average frequency of chiasmata varies from 1.45 to 1.60 per bivalent. Analysis of chiasma frequency at diplotene is shown in Table 46.

TABLE 46

Frequency of chiasmata at diplotene in S. kuntzianum Bitt. et Wittm.

No. of PMC observed	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
8	42	1.75
10	41	1.70
12	40	1.66
7	39	1.62
14	38	1.58
5	37	1.54
11	36	1.50
6	35	1.45
Total 73	Average frequency	1.60

Although 24 bivalents are usually seen at diakinesis (Fig. 2), quadrivalents are not rare (Figs. 5, 14). The presence of quadrivalents in the tetraploid species of potato was reported by Swaminathan (1954a,b) in his studies of nature of chromosome pairing at diakinesis

in a number of commercial potato varieties. Lamm (1945) also found multivalents in two varieties of potato while Thomas (1946) demonstrated presence of quadrivalents in S. tuberosum. The frequency of quadrivalents and bivalents is presented in Table 47.

TABLE 47

Quadrivalent and bivalent frequency at diakinesis in S. kuntzianum Bitt. et Wittm.

Chromosome complements	No. of PMC observed	Percentage
24 bivalents	153	31.56
23 bivalents, 2 univalents	36	7.94
1 quadrivalent, 22 bivalents	100	22.07
2 quadrivalents, 20 bivalents	102	22.51
22 bivalents, 4 univalents	62	13.68
	453	

At diakinesis the chromosomes are held together by single chiasma or two terminal chiasmata one at each end, the latter forming ring bivalents (Fig. 4). The occurrence of such ring bivalents in tetroploids was reported in Primula (Darlington 1931). The frequency of chiasmata is reduced on an average from 1.08 to 1.22 per bivalent and the result of analysis is shown in Table 48.

TABLE 48

Frequency of chiasmata at diakinesis in S. kuntzianum Bitt. et Wittm.

No. of PMC	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
12	33	1.37
8	32	1.33
10	31	1.29
7	30	1.25
11	29	1.20
9	28	1.16
14	27	1.12
6	26	1.08
Total 77	Average frequency	1.22

24 bivalents are easily followed at first metaphase as it was not possible to follow quadrivalents clearly owing to overcrowding of chromosomes at equatorial region of spindle. The extent of corresponding chromosome association at metaphase has been described by a number of workers in tetraploids viz Canna (Belling, 1921), Datura (Belling 1927), Primula sielboldii (Ono 1927), Hyacinthus (Belling, 1928). They reported that the chromosomes associate fully while incomplete and variable association involving different numbers of quadrivalents was discovered

in tetraploid Solanum lycopersicum (Lesley and Lesley, 1930; Upcott, 1935) and in Primula sinensis (Darlington, 1931a). The univalents are easy to follow at side view where they fail to orientate on equatorial region of spindle (Fig. 7). The bivalents often lie off equatorial plate at metaphase (11.2%) these are mainly rod-type (Fig. 6) Similar non-orientation of bivalents were demonstrated in diploid potatoes by Choudhuri (1943). Darlington (1965) considered the non-orientation of bivalents to increased distance between the centromeres, with consequent decrease in repulsion since he regarded repulsion as the effective agent in orientation. With this assumption rod-bivalents should be more liable to non-orientation than ring-bivalents and this is indeed, the case in this species. The frequency of non-orientation of rod-bivalents is higher (10.8%) than the ring bivalent (0.4%).

At first anaphase the bivalents and quadrivalents disjoin and move towards the poles. The behaviour of univalents varies, they lag, divide or are eliminated (Figs. 17, 18). First anaphase stages were characterized by the presence of chromatid bridges and fragments (Figs. 8, 16). The presence of fragments at anaphase without any chromatid bridge seemed to indicate that the bridge had been disjoined early or carried to one of the poles leaving the fragment between separating groups of chromosomes (Figs. 10, 17). The frequency of chromatid bridges, fragments, lagging and eliminated chromosomes

have been analysed, the results of which are presented in Table 49.

TABLE 49

Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. kuntzianum Bitt. et Wittm.

No. of PMC showing clean separation	No. of chromatid bridge	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
335	-	-	-	-	335	68.64
-	1	-	-	-	19	3.89
-	-	1	-	-	14	2.86
-	-	2	-	-	11	2.25
-	1	1	-	-	16	3.27
-	1	-	1	1	14	2.86
-	-	2	1	-	11	2.25
-	-	2	2	-	10	2.04
-	-	1	1	-	12	2.45
-	1	1	1	1	5	1.02
-	-	1	-	1	12	2.45
-	1	1	2	-	8	1.63
-	1	1	1	-	10	2.04
					488	

Usually 24 chromosomes are seen as second metaphase but the distribution is not equal. In Fig. 20 is shown an unequal distribution of 21-21 chromosomes with 6 eliminated chromosomes whereas in Fig. 22 is shown presumably distribution of 24-23 with 1 eliminated chromosome. Fig. 24 shows an equal distribution of 24 chromosomes on each plate. The frequency of distribution of chromosomes on second metaphase plates is shown in Table 50.

TABLE 50

Frequency of different chromosome distribution on second metaphase plates in S. kuntzianum Bitt. et Witt.

No. of chromosomes on second metaphase plates	No. of eliminated chromosomes	No. of PMC observed	Percentage
24 - 24	-	216	52.04
24 - 23	1	85	20.48
24 - 22	2	50	12.04
21 - 21	6	64	15.44
		415	

At second metaphase the bivalents show secondary association of chromosomes the frequency of various types of association is tabulated in Table 51.

TABLE 51

Showing character and frequency of secondary association in second metaphase plate in S. kuntzianum Bitt. et Wittm.

No. of single chromosomes	No. of chromosomes in Groups of 2	3	4	5	6	Frequency
24	.	.	.	.	.	28
22	1	.	.	.	.	18
20	.	.	1	.	.	9
20	2	.	.	.	.	4
16	.	.	2	.	.	4
14	3	.	1	.	.	3
14	.	.	1	.	1	5
8	.	.	4	.	.	10
8	4	.	2	.	.	6
3	.	7	.	.	.	11
					Total no. of PMC analysed	98

Second anaphase figures are characterized by the presence of chromatid bridges, lagging and eliminated chromosomes, the frequency of these have been analysed and the results of which are presented in Table 52. In Fig. 25 is shown anaphase with chromatid bridges while Fig. 26 shows 2 lagging chromosomes.

TABLE 52

Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at second anaphase in S. kuntzianum Bitt. et Wittm.

No. of PMC showing clean separation	No. of chromatid bridge	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
249	-	-	-	-	249	50.20
-	1	-	-	-	28	5.64
-	-	2	-	-	18	3.63
-	-	-	1	1	35	7.06
-	-	-	1	-	47	9.48
-	-	-	2	-	29	5.85
-	-	-	-	1	44	8.87
-	-	-	-	2	27	5.44
-	-	-	-	3	19	3.83
					496	

Pollen

Pollen formation in the tetraploid S. kuntzianum is also not regular. Irregularities during pollen formation include formation of micronuclei from eliminated chromosome (Fig. 28). Table 53 shows the frequency of micronuclei during pollen formation.

TABLE 53

Frequency of micronuclei during pollen formation in S. kuntzianum Bitt. et Wittm.

No. of normal tetrad	No. of micronuclei	No. of PMC observed	Percentage
274	-	274	61.85
-	2	58	13.09
-	3	79	17.83
-	4	32	7.23
		443	

Some dwarf and morphologically deformed pollen grains occur resulting from irregularities during pollen formation (Tables 49, 51, 52). The occurrence of dwarf and morphologically deformed pollen grains (63.56%). resulting from irregularities during division, along with morphologically good pollen grains (36.44%) were observed (Fig. 29). An analysis of aberration during

second division (Table 52) shows 49.80% irregularities along with the amount of bridge formation during first division (14.71%) and these indicate that there is some correlation between cytological aberrations including bridge formation (49.80 + 14.71 = 64.51%) and deformation of pollen (63.56%). Similar correlation between chromatid bridge formation and deformity of pollen have been demonstrated by Choudhuri (1943) in wild diploid potatoes.

(xviii) PLATES VIII and VIIIA

Figs. 1 - 29, showing meiosis in pollen mother cells of S. polytrichon Rydb.

Fig. 1. Pachytene showing completely paired chromosomes along with unpaired segments.

Fig. 2. Pachytene with completely paired chromosomes. Note the highly condensed regions of certain chromosomes.

Fig. 3. Diplotene showing 24 bivalents. The number of chiasmata varies from 1 to 3 per bivalent.

Fig. 4. Diplotene showing 24 bivalents. The number of chiasmata varies from 1 to 4 per bivalent.

Fig. 5. Diakinesis with presumably 2 quadrivalents and 20 bivalents.

Fig. 6. Diakinesis showing 24 bivalents.

Fig. 7. First metaphase, side view, with 1 non-orientated bivalent.

Fig. 8. First metaphase, side view, showing 2 non-orientated univalents.

Fig. 9. First anaphase showing 2 eliminated chromosomes.

Fig. 10. First anaphase with 1 eliminated chromosome.

Fig. 11. First anaphase showing 4 eliminated chromosomes along with 1 fragment.

Fig. 12. First telophase with 1 lagging chromosome which is dividing with a fragment.

Fig. 13. Configurations of (a, b) quadrivalents taken from different cells at diakinesis.

PLATE VIIIA

Fig. 14. First anaphase showing 2 lagging chromosomes.

Fig. 15. Second metaphase showing 4 eliminated chromosomes. The distribution of chromosomes is presumably 22-22.

Fig. 16. Second metaphase showing 5 eliminated chromosomes. The distribution is presumably 22-21 chromosomes.

Fig. 17. Second metaphase showing a distribution of 24 chromosomes in one of the plates along with 2 eliminated chromosomes. There are presumably 22 chromosomes on the other plate.

Fig. 18. Second metaphase showing 2 eliminated chromosomes. There are presumably distribution of 24-22 chromosomes on the plates.

Fig. 19. Second metaphase showing distribution of 24-24 chromosomes. Note the secondary association of chromosomes in 4 groups of 3 and 2 groups of 2 chromosomes.

Fig. 20. Second anaphase with 2 lagging chromosomes along with 2 eliminated chromosomes.

Fig. 21. Second anaphase showing 1 eliminated chromosome.

Fig. 22. Second anaphase showing 1 eliminated chromosome along with 1 fragment.

Fig. 23. Second anaphase showing a chromatid bridge along with a fragment and 1 lagging chromosome.

Fig. 24. Second telophase showing 3 lagging chromosomes and a fragment.

Fig. 25. Tetrads showing 4 eliminated chromosomes which are forming micronuclei.

Fig. 26. Tetrads x 3500.

Fig. 27. Tetrads with 3 eliminated chromosomes and a fragment which are forming micronuclei.

Fig. 28. Morphologically deformed pollen grain x 1000.

Fig. 29. Showing morphologically good pollen grain x 1000.

PLATE VIII

Meiosis in S. polytrichon Rydb.

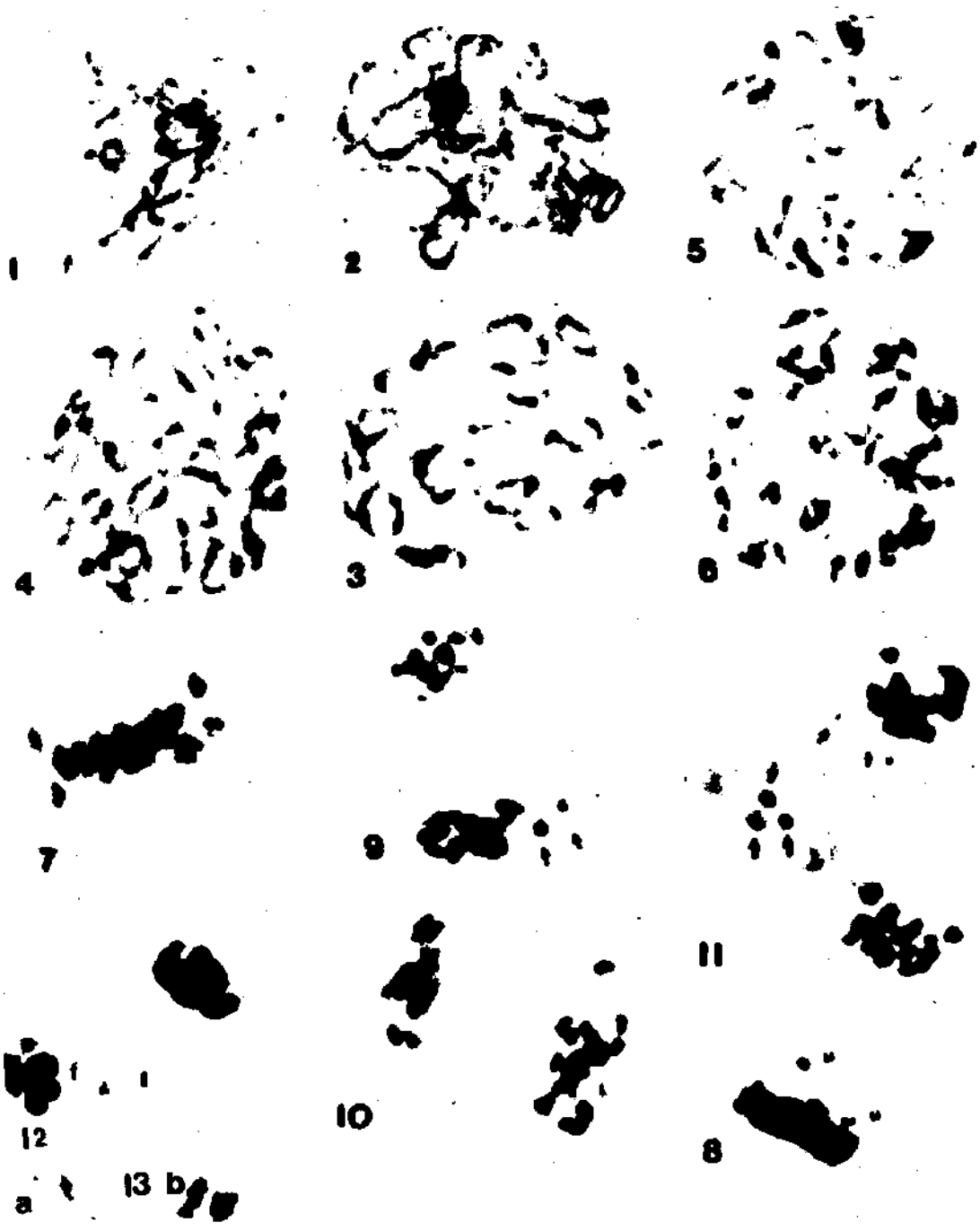
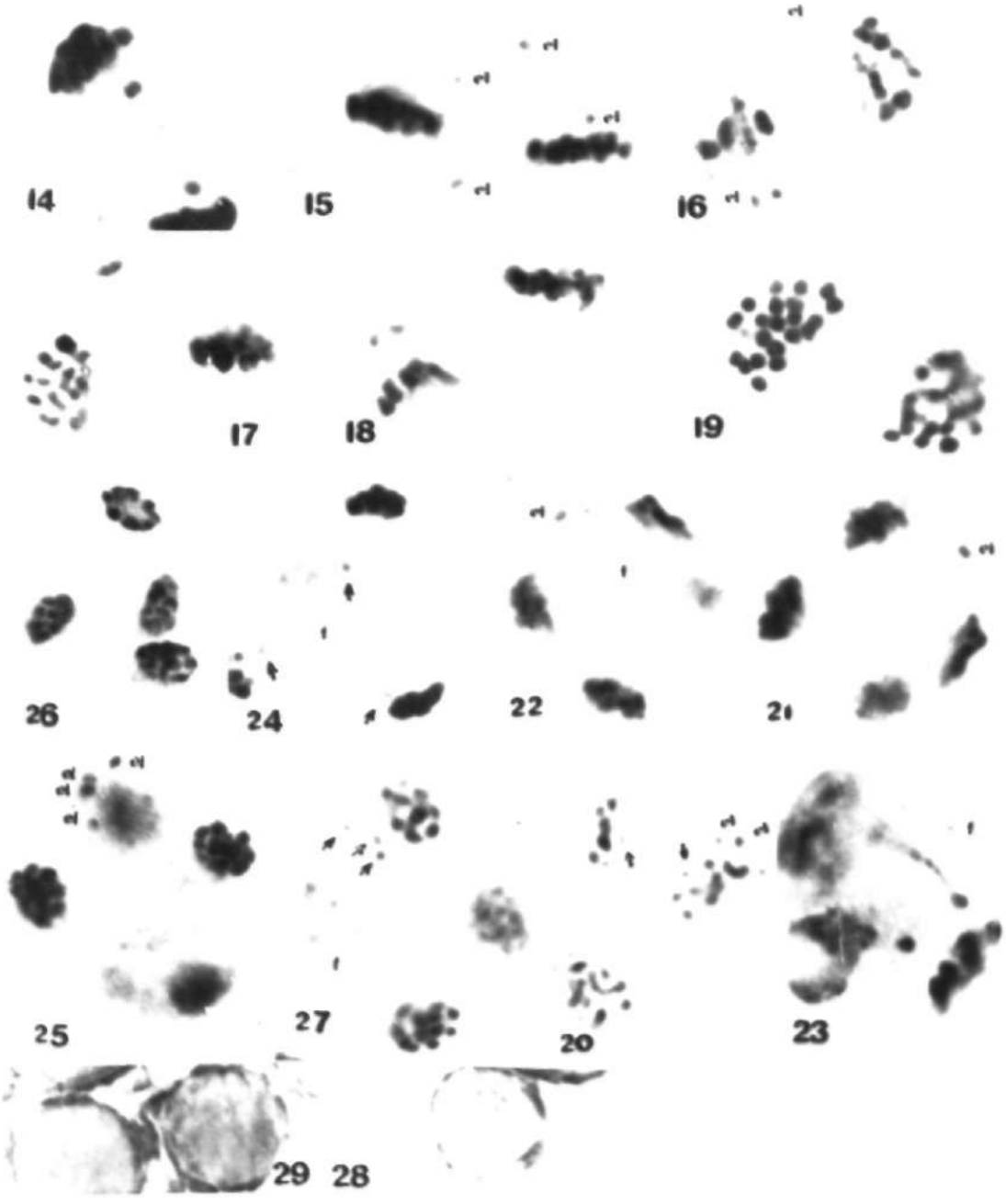


PLATE VIIIA

Meiosis in S. polytrichon Rydb.



(xix) S. polytrichon Rydb.

As usual the early prophase stages were found unfavourable for critical studies although at pachytene it was possible to follow completely paired chromosomes with highly condensed regions in certain parts (Plate VIII, Fig. 2). In paired chromosomes, certain segments often remain unpaired. Darlington (1929b) reported the presence of unpaired segments of chromosomes in the tetraploid Primula sinensis.

At diplotene, 24 bivalents could be followed in the nuclei. The paired chromosomes are completely separated and only remain connected at points of chiasmata (Figs. 3, 4). The frequency of chiasmata varies from 1.41 to 1.55 per bivalent and analysis of chiasma frequency is shown in Table 54.

TABLE 54

Frequency of chiasmata at diplotene in S. polytrichon Rydb.

No. of PMC observed	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
11	41	1.70
8	40	1.66
10	39	1.62
15	38	1.58
9	37	1.54
7	36	1.50
5	35	1.45
6	34	1.41
Total 71	Average frequency	1.55

Although 24 bivalents were usually seen at diakinesis, multivalents in form of quadrivalents and trivalent are common. Lamm (1945) discovered multivalents in autopolyploid - S. rybinii and the same occurrence in Lycopersicum esculentum (Upcott, 1935). The frequency of these multivalents observed at diakinesis were analysed and shown in Table 55. In Fig. 5 is shown a nucleus with 2 quadrivalents and 20 bivalents.

TABLE 55

Multivalent frequency at diakinesis in S. polytrichon Rydb.

Chromosome complements	No of PMC observed	Percentage
24 bivalents	148	32.83
23 bivalents, 2 univalents	20	4.43
22 bivalents, 4 univalents	24	5.32
1 quadrivalent, 22 bivalents	97	21.50
4 quadrivalents, 16 bivalents	103	22.83
1 quadrivalent, 22 bivalents, 1 univalent	59	13.09
	451	

The chromosomes are held together by a single or two chiasmata and the frequency of chiasmata is reduced at this stage and varies from 1.04 to 1.18 per bivalent. The results of this is presented in Table 56.

TABLE 56

Frequency of chiasmata at diakinesis in S. polytrichon Rydb.

No. of PMC observed	Total No. of chiasmata per nucleus	Average frequency of chiasmata per bivalent
6	32	1.33
12	31	1.29
8	30	1.25
9	29	1.20
16	28	1.16
8	27	1.12
6	26	1.08
5	25	1.04
Total 70	Average frequency	1.18

At first metaphase as might be expected from diakinesis 24 bivalents are usually seen. The multivalents could not be followed due to overcrowding of chromosomes at the equatorial region of spindle. The univalents are easily followed at metaphase where they failed to orientate at the equatorial region of the spindle (Fig. 8).

At first anaphase the polyvalents and bivalents disjoin and move towards the poles while the univalents move slowly between the poles. These univalents lag, divide or are eliminated (Figs. 10, 14). First anaphase is also characterized by the presence of fragments (Fig. 11). The presence of fragments at anaphase without any chromatid bridge seemed to indicate that the bridge had either been disjoined early or carried to one of the poles (Fig. 11) leaving a fragment between separating groups of chromosomes. The frequency of bridges, fragments, lagging and eliminated chromosomes at first anaphase is shown in Table 57.

TABLE 57

Frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in S. polytrichon Rydb.

No. of PMC showing clean separation	No. of chromatid bridge	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
399	-	-	-	-	399	78.54
-	1	-	-	-	5	0.98
-	-	1	1	-	8	1.57
-	-	1	-	-	4	0.79
-	-	-	1	-	22	4.33
-	-	-	2	-	18	3.54
-	-	1	-	4	5	0.98
-	-	-	-	1	25	4.93
-	-	-	-	2	15	2.96
-	-	-	-	4	7	1.38
					508	

As might be expected, the second metaphase shows unequal distribution of chromosomes. This is due to division and elimination of univalents. In Fig. 15 is shown metaphase with a distribution of 22-22 along with 4 eliminated chromosomes, whereas in Fig. 19 is shown an equal distribution of 24 chromosomes on each of the second metaphase plates. A distribution of 22-21 chromosomes along with 5 eliminated chromosomes is shown in Fig. 16. The frequency of distribution of chromosomes observed on second metaphase plates is shown in Table 58.

TABLE 58

Frequency of different chromosome distribution on second metaphase plates in S. polytrichon Rydb.

No. of chromosomes on second metaphase plates	No. of eliminated chromosomes	No. of PMC observed	Percentage
24 - 24	-	305	68.86
24 - 23	1	25	5.66
24 - 22	2	65	14.69
22 - 22	4	23	5.20
22 - 21	5	15	3.39
		443	

The presence of secondary association of chromosomes is analysed and the results of which are presented in Table 59.

TABLE 59

Showing character and frequency of secondary association in second metaphase in S. polytrichon Rydb.

No. of single chromosomes	No. of chromosomes in Groups of 2	3	4	5	6	Frequency
24	.	.	.	.	.	36
20	.	.	1	.	.	10
18	.	2	.	.	.	5
15	3	1	.	.	.	7
14	1	.	2	.	.	9
14	2	2	.	.	.	8
10	7	.	.	.	.	11
8	2	4	.	.	.	6
8	.	.	4	.	.	12
				Total PMC analysed		104

Second anaphase - telophase figures were characterized by the presence of chromatid bridges, fragments, lagging and eliminated chromosomes. The frequency of chromatid bridges, lagging, and eliminated chromosomes is shown in Table 60. In Fig. 23 is shown a chromatid bridge along with a fragment and 1 laggard, whereas in Fig. 24 is shown second telophase with 3 lagging chromosomes and a fragment.

TABLE 60

Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at second anaphase in S. polytrichon Rydb.

No. of PMC showing clean separation	No. of chromatid bridge	No. of fragments	No. of laggards	No. of eliminated chromosomes	Frequency	Percentage
372	-	-	-	-	372	78.65
-	1	-	-	-	8	1.69
-	1	1	1	-	6	1.27
-	-	1	3	-	5	1.06
-	-	1	-	1	10	2.11
-	-	1	-	3	4	0.85
-	-	-	2	2	7	1.48
-	-	-	-	1	25	5.29
-	-	-	-	2	16	3.38
-	-	-	-	3	11	2.32
-	-	-	-	4	9	1.90
					473	

Pollen

Pollen formation in this species is not as regular as expected. The formation of micronuclei from eliminated chromosomes and fragments was noted and is not an usual feature. Table 61 shows the frequency of micronuclei during pollen formation.

TABLE 61

Frequency of micronuclei during pollen formation in S. polytrichon Rydb.

No. of normal tetrad	No. of micronuclei	No. of PMC observed	Percentage
240	-	240	55.94
-	1	77	17.94
-	3	42	9.79
-	4	70	16.33
		429	

As expected certain amount of dwarf and morphologically deformed pollen grains occur (Figs. 28, 29) resulting from irregularities during formation of pollen. The percentage of deformed pollen was 27.90 while that of good pollen was 72.10%. An analysis of aberration during second division shows (21.35%) irregularities along with 6.28% formation of micronuclei. The percentage of aberration (21.35) during second division, seems to indicate that there is direct connection between cytological aberration and malformation of pollen. The incidence of deformity of pollen (27.90%) is very close to the percentage of aberration during second division (21.35).

4. DISCUSSION

(i) Pairing and association of chromosomes in diploid and tetraploid Solanum species

The tuber producing Solanum species used in this investigation have been found to be either diploids or tetraploids with 24 and 48 chromosomes, 2n = 24, 2n = 48, respectively. In a basic diploid species where each chromosome is present twice, pairing usually occurs between any two homologous chromosomes. Therefore, an association of more than two chromosomes is not expected in diploids. In the tetraploids where there is complete pairing between the four homologous chromosomes they will all be held together as a quadrivalent. If pairing is incomplete as demonstrated in the tetraploid species studied they may form two bivalents, one bivalent and two univalents, one trivalent and one univalent or even four univalents.

Although early prophase pairing could not be followed in all the species of Solanum under investigation here, however, in S. pinnatisectum Dun. a diploid, it was possible to follow pairing in zygotene. In this species, pairing was found to occur between any two or three, four or more homologous segments. In such an instance pairing appeared in two of the four, five or more homologous segments of chromosomes threads. At later stages of division chiasmata may be formed in the paired regions of segments and this may result in formation of multiple

associations of three, four or more chromosomes. The formation of multivalents in form of trivalents, quadrivalents, pentavalents, hexavalents, etc., in diploids can be explained only on the assumption of the presence of translocation heterozygotes. When such an exchange occured in organisms, pairing between interchanged segments showed configurations of multivalents. The configuration depended on the number and position of chiasmata. The occurrence of such multiple association has been demonstrated by Darlington (1929a) and Choudhuri (1971, 1972, 1975) in diploid Rhoeo and Solanum, respectively.

The incidence of multivalents present in various diploid species under consideration is reasonably moderate. It is apparent from Table 62 that the percentage of multivalents varies from 13.10 to 17.04

TABLE 62

Incidence of multivalents, bivalents and univalents in diploid species

Species	Frequency of multivalents	Frequency of bivalents	Frequency of univalents
S. mochicense Ochoa	13.10	76.19	14.28
S. boliviense Dun.	14.68	71,67	16.39
S. raphanifolium Cárd et Hawkes	17.04	77.04	11.48
S. pinnatisectum Dun.	13.96	79.77	9.12
S. stenotomum Juz. et Buk.	14.68	81.20	11.20
S. chacoense Bitt.	17.04	90.65	2.84

Considering the fact that Solanum chromosomes are small, the interchanged segments are expected to be small and since the chiasmata could be restricted to larger interchanged segments only, then the frequency of association of multivalents would be expected to be limited to moderate level, as the smaller interchanged segments may fail to form any chiasma. This would presumably increase the percentage of univalents. Indeed, this has been the case in most of diploid Solanum species under consideration except S. chacoense where the percentage of univalents varies from 2.84 to 16.39 (Table 62).

It may also be that mechanical interference is also limiting the incidence of multivalents (Darlington, (1965).

Magoon et al. (1958) showed the occurrence of quadrivalents in certain clones of some diploid species and interpreted this as possibly being due to the structural heterozygosity of the clones. The occurrence of four quadrivalents in early division stages in the diploid S. polyadenium was reported by Giles (1955). The considerable reduction in the number of quadrivalents from the earlier stages of meiosis to metaphase I has been suggested by Magoon et al. (1958) to be due to slipping off of chiasmata in view of the shortness of the chromosomes and localization of the chiasmata to the ends.

Choudhuri (1943) also demonstrated the occurrence of a trivalent in a diploid species (S. stenotomum) and suggested that this was due to pairing within one of the haploid sets and that therefore S. stenotomum may not be a real diploid. Lamm (1945) frequently noted a quadrivalent both at diakinesis and first metaphase in two diploid species and also found cells having trivalent plus a univalent instead of a quadrivalent.

Cadman (1943), demonstrated the presence of multivalents in form of trivalents and quadrivalents in S. tuberosum, which is a tetraploid. Schnell (1948) also reported the occurrence of trivalents and quadrivalents in some frequency along with bivalents and univalents.

Association higher than quadrivalents was also reported in S. tuberosum (Longley and Clark, 1930, Meurman and Rancken, 1932, Muntzing, 1933, Ellison, 1936, and Giles, 1955). They interpreted such higher association as resulting from the presence of heterozygosity for structural changes.

TABLE 63

Incidence of quadrivalents in tetraploid species

Species	Frequency of tetravalents	Frequency of chromosome association over tetravalents	Frequency of univalents
S. kuntzianum Bitt. et Wittm.	44.58	-	21.62
S. polytrichon Rydb.	44.33	-	22.84

The incidence of quadrivalents in tetraploid species under consideration is high and varies from 44.33 to 44.58 percent. This gives indication that they are autotetraploid and therefore shows a high degree of affinity between the four sets of chromosomes. Swaminathan (1954a,b) also recorded such a high incidence of multivalents in a number of commercial potato varieties.

The low frequency of multivalents in a hybrid of S. tuberosum variety Deodora by Kawakami and Matsubayashi (1954 and 1957) was interpreted by them as being indicative of low degree of affinity between the two sets from S. tuberosum parent and thus of the allotetraploid nature of the cultivated variety.

(ii) Chiasma and terminalisation values

The homology of chromosomes is determined by the degree of pairing followed by crossing over and free gene exchange manifested at the diplotene stage of meiotic division. This occurs at every chiasma.

Since the enunciation of "chiasmatype hypothesis" (Janssen 1909, 1924, Darlington 1930a, 1930b), it has been generally accepted that chiasma is a physical basis of "genetic crossover" in a chromosome. It has now been universally accepted that chiasmata are the points where two of the four chromatid of homologous chromosomes exchange their partners. The function of chiasmata is primarily the reassortment of the genes between the chromosomes, so that new recombination of genes may take place in the daughter gametes. As a result the greater the number of chiasmata the greater will be the chances of recombination in the offspring.

Chiasmata first arises interstitially, and very rarely at the ends. They vary in number but their range of variation is characteristic and peculiar for each bivalent. In organism where the size of the chromosomes is small, the mean number of chiasmata per bivalent is approximately proportional to the length of the paired chromosomes.

Organisms with very large chromosomes usually experience incomplete pairing at pachytene due to the

'time limit' for pairing. In Frittilaria, the pairing usually begins near the centromere and it is in distal region that the pairing fails. The chiasmata are formed in the paired parts of chromosomes and thus localised near the centromere (Darlington, 1935). In the extreme minimal case, one chiasma is formed in every bivalent. The number, however is not constant but vary in different nuclei and a study of the chiasma frequency indicates how pairing varies in different chromosomes, in different nuclei and in different species and varieties. It seems that in shorter chromosomes pairing is completed quickly than longer ones and hence they have a chance of forming chiasma proportional to the length of the paired segments of chromosomes.

The diploid Solanum species investigated have short chromosomes and as might be expected the chiasma frequency per bivalent in diplotene is moderate ranging from 2.2 to 1.9 per bivalent (Table 64). As expected, the frequency of chiasmata per bivalent at diplotene in the tetraploid species is lower and varies from 1.55 to 1.60 per bivalent due presumably to the presence of large number of chromosomes and hence competition for pairing and time factor.

It is noted from Table 64 that there is reduction in the number of chiasmata at diakinesis and the range of reduction in diploid species varies from 0.8 to 0.9 per bivalent while in tetraploid species it varies from 0.37 to 0.38 per bivalent. This reduction in the number of chiasmata from diplotene to diakinesis is due to terminalization (Darlington, 1929a,b).

TABLE 64

Frequency of chiasmata at diplotene and diakinesis in different Solanum species

Species	Average chiasma frequency per bivalent at diplotene	Average chiasma frequency per bivalnet diakinesis	Terminalization value per bivalent
S. mochicense Ochoa	-	1.2	-
S. boliviense Dun.	1.9	1.1	0.8
S. raphanifolium Cárd et Hawkes	-	1.3	-
S. pinnatisectum Dun.	-	1.2	-
S. stenotomum Juz. et Buk.	2.1	1.2	0.9
S. chacoense Bitt.	2.2	1.3	0.9
S. kuntzianum Bitt. et Wittm. (tetraploid)	1.60	1.22	0.38
S. polytrichon Rydb (tetraploid)	1.55	1.18	0.37

It is apparent from Table 64 that different species have different terminalization value. This has been regarded by Darlington (1965) as due to different degrees of centromere repulsion in relation to the length of the chromosome. Thus it is seen here that the terminalization value is low because of the reduction of the length of the chromosome. This can also be due to interference in the movement of chiasmata owing to change of homology of chromosomes. Indeed this has been the case in diploid S. boliviense Dun. where terminalization was arrested due to change of homology. Similar arrest of terminalization due to change of homology in Lachenalia, Brassica and Solanum have been demonstrated by Moffett (1936), Richharia (1937), and Choudhuri (1975) respectively.

(iii) Dicentric chromatid bridge

Chromatid bridges were frequently observed in all the species of Solanum investigated. These bridges separated with difficulty while at times they break at late telophase. Fragments are produced as a result of the break in bridges, but since fragments at times occur along with bridges, it means that they may be produced before the breakage occurs.

The presence of dicentric chromatid bridge along with acentric chromatid fragment may be explained on the basis of crossing over within an inversion. The presence of this bridge along with a fragment furnishes a cytological method for detecting inversion at meiotic division. At times loop chromatid are formed in the first anaphase. When chiasmata occur between the inverted region and the centromere as well as within inversion, the dicentric chromosomes which is formed will pass to one of the poles without separation and form chromatid bridge at second anaphase. Such an instance is found in S. mochicense.

It is not necessary to discuss the detailed process leading to formation of chromatid bridges at first and second divisions, since it has exhaustively been dealt with by several authors e.g., Smith (1935), Richardson (1936) in Trillium and Lilium respectively.

The chromatid bridges occur in varying proportion in all the Solanum species studied (Table 65).

These chromatid bridges may break at any point during chromosome separation at the anaphase stages, and thus give rise to chromosomes with additional segments or to chromosomes lacking certain segments, this may result in formation of a new chromosome, a deficient or duplicated with certain segments.

TABLE 65

Showing percentage of chromatid bridges along with percentages of morphologically good and deformed pollen in Solanum species

Species	Total percentage of chromatid bridges	Total percentage of morphologically good pollen	Total percentage of morphologically deformed pollen
S. mochicense Ochoa	3.60	88.46	11.54
S. boliviense Dun.	4.76	88.42	11.58
S. raphanifolium Card et Hawkes	8.52	56.74	43.26
S. pinnatisectum Dun.	4.16	64.75	35.25
S. stenotomum Juz. et Buk.	5.03	30.10	69.90
S. chacoense Bitt.	2.98	74.25	25.75
S. kuntzianum Bitt. et Wittm. (tetraploid)	20.35	36.44	63.56
S. polytrichon Rydb. (tetraploid)	3.94	72.10	27.90

A chromosome with deficient or added segment may prove lethal to the gamete which contained it, but not in all cases, provided the missing segments were small. New chromosome could also undergo further changes by crossing over in different regions of the homologous segments.

Thus interspecific crosses may lead not only to numerical differences in chromosome complements as in Viola and Saccharum, but also to structural differences and consequently the structural appearance of new chromosomes as demonstrated in Crepis (Navashin 1934). It is probable that such structural alterations have occurred in the species under investigation as a result of translocation heterozygote, the evidence of which has been demonstrated in the present instance in the formation of multivalents in the diploid species.

Upcott (1937) correlated sterility with bridge formation in Tulipa, she considered that more than 10 percent inversion causes considerable sterility.

It is apparent from Table 65 that a fairly high percentage of morphologically good pollen occurs in some species. It is however, to be emphasised that such apparent fertility may be misleading since Becker (1939) showed that in S. demissum nearly half of the morphologically good pollen was nevertheless non-viable.

Within the tetraploids it is noticed that there is some relationship between the chromatid bridge and deformity of pollen. A high percentage of chromatid bridge formation present in S. kuntzianum (20.35) is somewhat correlated with high incidence of deformity of pollen (63.56). In S. polytrichon which has a low value of chromatid bridge (3.94%), the percentage of deformed pollen is low (27.90%). Magoon et al. (1958, 1962) recorded a low percentage of pollen fertility in some tetraploid Solanum species. They concluded from cytogenetical studies that in addition to meiotic irregularities some genetic, physiological or environmental factors appear to be involved in pollen sterility. Such may be the case in the tetraploid species of potatoes under investigation here.

(iv) Secondary Pairing or Association in Solanum species

In the present investigation little attention has been given to study of secondary pairing of chromosomes at meiosis in diploid and tetraploid species. This is primarily due to paucity of materials. The growth and development of flower buds are very much restricted due to unfavourable climatic condition. Furthermore, very few first metaphase figures, polar view were available, as a result secondary association of bivalents at first metaphase could not be analysed.

Secondary association studies were therefore restricted to second metaphase only and this analysis could not be carried out in a wider scale also due to paucity of materials.

There are two different types of pairing observed in Solanum. First is the prophase pairing, arising from particulate attractions which lead to pairing of homologous chromosomes at zygotene. This prophase pairing is extended to the first metaphase by maintenance of chiasmata formed at pachytene. Whereas the secondary pairing or secondary association is the result of general affinity between chromosomes which are phylogenetically related, and is not due to presence of chiasmata. Secondary association of chromosomes occur in all the Solanum species investigated.

It is unnecessary to embark on a full discussions on its mechanism since it has already been dealt with by several authors viz Lawrence (1931a), Müntzing (1933b). Secondary association has been used as one of the criteria for determining the polyploid nature of many plants (Lawrence 1931a,b). Its significance in Solanum has been a subject of great controversy.

Choudhuri (1943) demonstrated that the occurrence of secondary pairing which involves the aggregation of chromosomes into groups at first metaphase is very conspicuous in six "diploid" wild tuber bearing Solanum; the extent of such secondary pairing of bivalents at first metaphase is analysed. The secondary associations have been observed until second metaphase when they were further analysed. It is evident from the results of analysis that there is preponderance of two over other groups and the most frequent combination of secondarily paired chromosomes either at first or second metaphase is four groups of 2 and four free chromosomes, although the maximum number of groups of 2 noted is five. From the amount of evidence of secondary pairing of chromosomes in the "diploid" species of Solanum, there is good reason for assuming that the primary

basic number of chromosomes is lower than 12 and may be perhaps 6. This view is in harmony with the findings of Müntzing (1933).

(v) Failure of pairing in homologous chromosomes - cause and consequence

Although a high degree of homology exists between chromosomes of diploid species of Solanum, inspite of this, occurrence of failure of pairing is not unusual (Table 66). The presence of all chromosomes in bivalents at metaphase in a large number of cases however, shows that univalents are homologous at least to segments. It is often considered that failure of pairing among chromosome which are potentially capable of doing so, may be due to segmental differences or to mechanical interference with pairing of chromosomes (Darlington 1937, 1965; Moffett 1936).

TABLE 66

Showing incidence of paired chromosomes and univalents in diploid Solanum species

Species	Percentage of paired chromosomes*	Percentage of univalents
S. mochicense Ochoa	84.53	15.47
S. boliviense Dun.	83.61	16.39
S. raphanifolium Cárd. et Hawkes	88.52	11.48
S. pinnatisectum Dun.	90.88	9.12
S. stenotomum Juz. et Buk.	88.80	11.20
S. chacoense Bitt.	97.16	2.84

*bivalents and multivalents.

The effects of hybridization (Karpechenko 1928) and genetic factors in reducing chromosome pairing (Beadle 1930) is well known. It is also demonstrated that in some cases it may be due to severe reduction in chiasma frequency resulting in univalents during meiotic stages of division. This reduction in chiasma frequency has been due to the action of a recessive gene in Pisum sativum (Gottschalk and Baquar, 1971).

The percentage of failure of pairing is much higher in tetraploids than in diploids (Table 67).

TABLE 67

Incidence of paired chromosomes and univalents in tetraplid Solanum species

Species	Percentage of paired chromosomes*	Percentage of univalents
S. kuntzianum Bitt. et Wittm.	76.14	21.62
S. polytrichon Rydb.	78.16	22.84

*bivalents and quadrivalents.

Although strong homology exists between four sets of chromosomes (being autotetraploids) which is demonstrated by high percentage of pairing varying from 76.14 to 78.16, the percentage of occurrence of univalents is not negligible ranging from 21.62 to 22.84.

The causes of failure of pairing among pairable mates in diploids and tetraploids are probably not much different. Of course, the mechanical interference with pairing owing to presence of four sets of homologous chromosomes is likely to cause more failure of pairing in tetraploid than in diploids. Indeed, this has been the case in Solanum species under investigation. However, it is probable that genetic dissimilarity of individual chromosomes is also responsible for certain amount of failure of pairing amongst pairable chromosome metes in Solanum.

The univalents which fail to orientate at first metaphase as they do generally behave in different ways. This is determined by the relative position of the univalents in relation to the equator of the spindle at first metaphase. At first anaphase they may pass to the poles intact or may split or divide while lagging. The consequence of such splitting and division of univalents at first anaphase is the unequal distribution of chromosomes at second metaphase plates. The lagging or eliminated chromosomes which fail to be included in the daughter nuclei at later stages of division form micronuclei.

TABLE 68

Showing percentage of micronuclei during pollen formation in Solanum species

	Percentage of laggards at second anaphase	Percentage of eliminated chromosomes at second anaphase	Percentage of micronuclei
S. mochicense Ochoa	4.86	10.29	7.21
S. boliviense Dun.	4.86	14.80	3.44
S. raphanifolium Card et Hawkes	7.90	9.63	4.95
S. pinnatisectum Dun.	11.20	22.02	12.04
S. stenotomum Juz. et Buk.	2.79	14.26	14.10
S. chacoense Bitt.	5.35	6.48	5.87
S. kuntzianum Bitt. et Wittm.	22.39	25.20	38.15
S. polytrichon Rydb.	3.81	17.33	44.06

From the results obtained (Table 68) it can be deduced that only few of the univalents have a chance to be included in the normal gametes while a large number of lagging and eliminated chromosomes form micronuclei.

(vi) Species Formation and the Status of Diploid and Tetraploid Solanum

The discovery of a complete euploid series in potatoes shows without doubt the important role which has been played by euploidy in the evolution of the species. The existence of polyploid series in the wild relatives of domestic potato was first established by Smith (1927), Vilmorin and Simonet (1927a and 1927b). Rybin (1930, 1933) in his study of 26 wild species of cultivated potatoes discovered the occurrence of polyploid series. This indicates a great role played by euploidy in the evolution of the potatoes. Although there exists considerable controversy regarding the basic number in genus Solanum, it is generally considered by several authors that the basic number in Solanum is 12. The obvious line of evolution in potatoes must have been the establishment of amphidiploid forms with high chromosome numbers whose ancestors are not known and autopolyploids. In these amphidiploids and autopolyploids slight modification in segments of individual chromosomes has taken place, and the comparatively frequent presence of fragmentation of chromosomes and bridge formation and presence of translocation heterozygote in diploids supports such an assumption.

Cytological investigation of diploid dealt with here shows that there is good evidence for regarding them as of hybrid origin. It is known that hybrids are characterized

by meiotic irregularities, and the obvious question is whether these so-called "diploid" potatoes behave like known hybrids. Failure of pairing in pairable chromosome mates, lagging and elimination of chromosomes, along with frequent formation of chromatid bridges and deformity of pollen may be regarded as conclusive evidence of hybridity in the Solanum species under consideration. Similar chromosome aberrations have been demonstrated in Dahlia, Galeopsis and Solanum hybrids by Lawrence (1929, 1931b), Müntzing (1932) and Choudhuri (1944) respectively. Winge (1917) also suggested the hybrid origin in tetraploids.

The behaviour of chromosomes in Solanum species studied are not in any way different from that of hybrids. It can therefore be suggested that one of the main lines of evolution in Solanum species investigated is that of interspecific hybridization. This is in conformity with the genetical and cytological findings demonstrated by Choudhuri (1943, 1944, 1975, 1976) in his studies of Solanum species.

5. SUMMARY

1. The haploid number of chromosomes in six out of eight species of tuber-bearing wild Solanum species investigated is found to be 12 (n= 12). They are therefore, diploids (2n = 24). The species are (1) S. mochicense Ochoa, (2) S. boliviense Dun., (3) S. raphanifolium Card et Hawkes, (4) S. pinnatisectum Dun., (5) S. stenotomum Juz. et Buk., (6) S. chacoense Bitt.

2. In two other species spicies investigated namely, S. kuntzianum Bitt. et Wittm. and S. polytrichon Rydb. the haploid number of chromosomes is found to be 24 (n= 24). They are therefore, tetraploids.

3. The diploid number of chromosomes in S. mochicense is determined from tapetal cell and is found to be 24 (2n= 24). Endoreduplication with a degree of ploidy was observed in tapetal cells. Chromosomal reduplication was so marked that normal diploid chromosome number reached 48. All chromosomes have either metacentric or submetacentric centromeres. Four satellite chromosomes are seen among them.

4. In meiosis pairing begins generally at a point and passes regularly along the length of chromosomes. The point at which pairing begins is more deeply stained than the other parts of the chromosomes and are probably the centromere regions. Where three, four or more homologous chromosomes lie together pairing occurs in two of three

or four homologous chromosomes threads in a particular segment. In a tetraploid if pairing between the four homologous chromosomes is complete they will either be associated in two bivalents or all held together in a single quadrivalent, if pairing is incomplete they may form one bivalent and two univalents, one trivalent and one univalent or even four univalents. However, there are cases of unpaired segments of the chromosomes at pachytene presumably because these regions are non-homologous or due to the time available for pairing is short and the region lie farthest apart from the point at which pairing begins.

5. Frequencies of chiasmata at diplotene and diakinesis are analysed in the different species. In the diploid, the frequencies varied from 2.2 to 1.9 and 1.3 to 1.1 per bivalent at diplotene and diakinesis, respectively. The highest frequency of chiasmata per bivalent (2.2) is seen in S. chacoense Bitt. whereas the lowest frequency (1.9) per bivalent occurs in S. boliviense Dun. in diplotene. In diakinesis, the highest frequency of chiasmata (1.3) per bivalent is found in S. raphanifolium Cárd et Hawkes and S. chacoense Bitt. and the lowest (1.1) per bivalent is seen in S. boliviense Dun.

6. The terminalization value varies in different species. In the diploids, it varies from 0.8 in S. boliviense to 0.9 in S. stenotomum and S. chacoense.

The different terminalization values had been regarded as due to different degrees of centromere repulsion in relation to the length of the chromosome. Within the tetraploids it varies from 0.38 in S. kuntzianum to 0.37 in S. polytrichon. The low terminalisation value in the species investigated is due to reduction of the length of the homologous chromosome segments.

7. In the tetraploid the highest frequency of chiasmata per bivalent (1.60) is in S. kuntzianum Bitt. et Wittm. whereas the lowest frequency (1.55) occurs in S. polytrichon Rydb in diplotene. At diakinesis, the highest frequency of chiasmata (1.22) per bivalent is found in S. kuntzianum Bitt. et Wittm. and the lowest 1.18 per bivalent is found in S. polytrichon Rydb.

8. Although at diakinesis 12 bivalents and 24 bivalents are usually noted in diploids and tetraploids respectively, occasionally in the diploid S. mochicense Ochoa. 13 chromosomes are observed owing presumably to the presence of 11 bivalents and 2 univalents while in the tetraploids S. kuntzianum and S. polytrichon one or two bivalents are represented by corresponding number of univalents resulting in 23 bivalents, 2 univalents or 22 bivalents, 4 univalents. Such univalents fail to orientate at the equatorial region of the spindle.

9. Association of chromosomes in three, four or more are seen in the diploid species of Solanum investigated with the corresponding number of bivalents and univalents. The frequencies of multivalents have been analysed and the incidence of their occurrence have been estimated in percentage, namely, 13.10, 14.68, 17.04, 13.96, 14.68, 17.04, in S. mochisense, S. boliviense, S. raphanifolium, S. pinnatisectum, S. stenotomum and S. chacoense, respectively. The occurrence of multivalents seemed to indicate the presence of translocation heterozygotes in the diploid species of Solanum under consideration.

10. In the tetraploids the percentage of tetravalents varied from 44.58 to 57.42 in S. kuntzianum and S. polytrichon, respectively.

11. The incidence of pairing of chromosomes were analysed in the diploid and estimated in percentage viz. 84.53, 83.61, 88.52, 90.88, 88.80, 97.16 in S. mochicense, S. boliviense, S. raphanifolium, S. pinnatisectum, S. stenotomum, and S. chacoense respectively. The high percentage of incidence of pairing indicates a high degree of homology existing between chromosomes of diploid species of Solanum.

12. In the tetraploids the percentage of paired chromosomes varied from 76.14 in S. kuntzianum to 78.16 in S. polytrichon which is much lower in comparison to diploid species.

13. The frequency of failure of pairing was calculated in percentage in all the species. These were 15.47, 16.39, 11.48, 9.12, 11.20 and 2.84 in S. mochicense, S. boliviense, S. raphanifolium, S. pinnatisectum, S. stenotomum and S. chacoense respectively. In the tetraploids the frequency varies from 21.62 to 22.84% in S. kuntzianum and S. polytrichon respectively. The cause of failure of pairing among pairable mates in diploids and tetraploids are probably not much different. Of course, the mechanical interference with pairing owing to presence of four sets of homologous chromosomes is likely to cause more failure of pairing in tetraploid than in diploids in Solanum species under investigation. It is also probable that genetic dissimilarity of individual chromosomes is also responsible for certain amount of failure of pairing amongst pairable chromosome mates in Solanum.

14. The univalents behave in different ways, they either pass to the poles or lag in between separating groups of chromosomes or divide. The division and elimination of univalents causes unequal distribution of chromosomes on second metaphase plates. The extent

of unequal distribution of chromosomes in diploid were analysed and are shown in percentage viz, 8.35, 9.27, 7.13, 5.82, 16.08, 10.52, in S. mochicense, S. boliviense, S. raphanifolium, S. pinnatisectum, S. stenotomum, and S. chacoense respectively.

15. The extent of unequal distribution of chromosomes in tetraploid varies from 47.96 S. kuntzianum to 31.14 in S. polytrichon. The high percentage is probably due to large number of univalents formed in tetraploids.

16. The incidence of lagging and eliminated chromosomes in diploids are shown in percentage viz, 15.15, 19.66, 17.53, 33.22, 17.05 and 11.83 in S. mochicense, S. boliviense, S. raphanifolium, S. pinnatisectum, S. stenotomum, and S. chacoense respectively.

17. In the tetraploids the percentage of laggard and eliminated chromosome varied from 21.14 to 47.59 in S. polytrichon and S. kuntzianum respectively. From the results obtained it is deduced that only few of the univalents have a chance to be included in the normal gametes while a large number of lagging and eliminated chromosomes form micronuclei.

18. The incidence of formation of micronuclei has been analysed in S. mochicense (7.21%), S. boliviense (3.44%),

S. raphanifolium (4.95%), S. pinnatisectum (12.04%), S. stenotomum (14.10%), and S. chacoense (5.87%). In the tetraploids the percentage of micronuclei varies from 38.15 to 44.06 in S. kuntzianum and S. polytrichon respectively.

19. The formation of dicentric chromosomes involving chromatid bridges and fragments is found to be an usual phenomenon, its significance and bearing on sterility is discussed. The frequency of chromatid bridge formation in diploids has been analysed and their occurrence varied in percentage from 3.60, 4.76, 8.52, 4.16, 5.03 and 2.98 in S. mochicense, S. boliviense, S. raphanifolium, S. pinnatisectum, S. stenotomum and S. chacoense, respectively.

20. In the tetraploid the frequency of chromatid bridge was 20.35 in S. kuntzianum, and 3.94 in S. polytrichon. There seems to be no correlation between bridge formation and deformation of pollen in tetraploids.

21. Secondary association of chromosomes occur in all the species under consideration and the frequency of various types at second metaphase has been analysed, There is preponderance of two over other groups and the most frequent combination of secondarily paired chromosomes

at second metaphase is four groups of 2 and four free chromosomes, although the maximum number of groups of 2 noted is five.

22. The occurrence of spontaneous chromosome irregularities has been fully analysed and their significance discussed. There are some correlations between the percentage of chromosome irregularities 18.58, 20.15, 27.08 and abortion of pollen 11.54, 11.58, 35.25 in the diploid species, S. mochicense, S. boliviense, S. pinnatisectum, respectively. Similar correlations between incidence of chromosome irregularities 64.51, 21.35, and percentage of abortion of pollen 63.56, 27.90 occur in the tetraploid species, S. kuntzianum and S. polytrichon, respectively. However, wide disparity exists between incidence of chromosome irregularities 20.97, 22.91, 10.71, and abortion of pollen 43.26, 69.90, 25.75 in S. raphanifolium, S. stenotomum and S. chacoense, respectively. It may be that abortion of pollen grains in these species is presumably due to gene mutation.

23. Cytological studies in diploid Solanum species under consideration indicate that there is good evidence for regarding them as of hybrid origin. The hybrids are characterised by meiotic irregularities. Failure of pairing in pairable chromosome mates, lagging

and elimination of chromosomes along with frequent formation of chromatid bridges and deformity of pollen may be regarded as characteristic and conclusive evidence of the hybrid nature of Solanum species.

24. The cytological studies of the tetraploids show formation of very high percentage of quadrivalent formation varying from 57.4 to 44.6 in S. polytrichon and S. kuntzianum respectively. The strong homology between four genomes indicate that they are probably of autopolyploid origin.

25. It can therefore be suggested that the main lines of evolution in Solanum species investigated is that of interspecific hybridization and occurrence of polyploidy.

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