MEIOTIC BEHAVIOR OF SPECIES AND HYBRIDS IN THE GENUS *SOLANUM* SECTION *TUBERARIUM*

By

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INTRODUCTION

The wild species of the genus Solanum section Tuberarium are potential sources of desirable characters which would be of value if they were incorporated in the cultivated varieties of potato, Bukasov (2) and Hawkes (10). The characters of major interest to the potato breeder are resistance to late blight, virus resistance, insect resistance, frost resistance, drought resistance, and high protein content.

Rybin (24) established the existence of a polyploid series in the wild and cultivated species. Species exist with a somatic chromosome number of 24, 36, 48, 60, and 72.

Several cytological investigations have been reported in regard to meiotic behavior of species, secondary association of chromosomes, nature of polyploidy, interspecific hybridization, and sterility. The previous cytological work has been summarized by Koopsman (14).

The survey of the literature indicated several opinions in regard to the nature of polyploidy and the basic number of the genus. Some investigators have proposed a basic number of six instead of twelve. The proposals of a basic number of six has been based on the high degree of chromosome pairing in triploids, secondary association of chromosomes, and complex genetical behavior. The original basic number of the genus may have been six; however, considering the regular bivalent formation reported in diploid species, it is evident that a basic number of twelve is well stabilized.

The meiotic behavior of certain species and interspecific hybrids was studied in this investigation. The crossability of the species also was investigated. An interpretation, other than the pairing of chromosomes within a genome, is proposed in regard to the high frequency of chromosome pairing in triploids.

MATERIALS AND METHODS

The species investigated cytologically and used in hybridization are listed in table 1. The species are arranged in a taxonomical scheme after Bukasov (3). The somatic chromosome numbers of the species are listed in the third column of the table.

All material was obtained from the United States Department of Agriculture, Bureau of Plant Industry. The plants were grown in the greenhouse at the Plant Industry Station, Beltsville, Maryland, during the spring months of 1951 and 1952. All plants were grown from seed with the exception of the following species which were grown from tubers:

S. tuberosum L. var. Earlaine and Katahdin
S. semidemissum Juz.

In regard to S. chacoense Bitt. two lots of seed were selected from the material available. One packet of seed was marked S. caldasii; and the other, S. commersonii. The plants grown from both lots of seed were found to have a somatic chromosome number of 24 and differed only slightly in morphological characteristics. Both agreed with the description of S. chacoense Bitt. and are considered by the author to be forms of that species. As used in this report S. chacoense refers to the material obtained under the name S. caldasii and S. chacoense var. latisectum (Hassler) Bitt. refers to material received under the name of S. commersonii.

Table 2 lists the hybrids that were examined cytologically. The second column of the table gives the somatic chromosome numbers of the hybrids.

TABLE 1. Scheme of taxonomic relation of the species of Solanum, section Tuberarium investigated (after Bukasov).

Group	Species	Chromosome number
Stellata		
Commersoniana	S. chacoense Bitt.	24
	S. chacoense var. latisectum (Hassler) Bitt.	24
Rotata		
Articulata		
Polyadenia	S. polyadenium Greenm.	24
Tuberosa		
Eutuberosa	S. tuberosum L.	
	var. Earlaine	48
	var. Katahdin	48
Demissa	S. semidemissum Juz.	60
	S. demissum Lindl.	72
Acaulia	S. acaule Bitt.	48

TABLE 2. Interspecific hybrids investigated in this study.

Hybrid	Chromosome number
S. acaule x S. chacoense	36
S. acaule x S. chacoense var. latisectum	36
S. demissum x S. chacoense	60
S. demissum x S. tuberosum var. Earlaine	60

In an attempt to obtain interspecific hybrids pollinations were made among the species. These were made without regard to taxonomic relationship or to chromosome number. All possible combinations were made except in cases where a limited number of flowers made this impossible. Pollinations were made on flowers which had been emasculated

before the anthers started to dehisce.

Buds for cytological investigation were collected in the morning and fixed for 24 hours in 3 parts 95% alcohol to 1 part glacial acetic acid. After fixation they were transferred to 70% alcohol and stored until used. Material fixed and stored in this manner was satisfactory. However, freshly fixed material was superior, especially for diakinesis.

Smears of the microsporocytes were made by the aceto-carmine smear technique. Observations were made with the aid of 40X and 90X apochromatic objectives and 15X compensating oculars. All photomicrographs were taken from temporary mounts.

An attempt was made to study all stages of meiosis from diakinesis through the sporad stage. However, diakinesis was not found in some of the material collected.

Somatic chromosome counts were made of the hybrid seedlings to establish their chromosome number and hybridity at an early stage of development. Smears of young leaves and root tips were attempted. The material was pretreated with a saturated solution of paradichlorobenzene for one hour before fixation in 3 parts 95% alcohol to 1 part glacial acetic acid. Smears were made by the aceto-carmine technique. Both young unexpanded leaves and root tips were satisfactory for chromosome counting. The pretreatment with paradichlorobenzene shortened the chromosomes and inhibited the formation of the spindle which resulted in a good spread of the chromosomes (Fig. 1).

RESULTS

Interspecific Pollinations

The results of the interspecific pollinations made in 1951 are summarized in table 3. The diploid S. polyadenium was the only species which failed as both a male and female parent. In the crosses involving species with differences in chromosome number, the cross was more successful when the species with the higher chromosome number was used as the female parent. The one exception was the cross S. chacoense x Katahdin and its reciprocal. In this case a comparison is not justifiable because of the few number of pollinations made when Katahdin was used as the female parent. From the cross S. acaule x S. demissum, 168 aborted seed were obtained. This would indicate that fertilization had taken place, but viable seed was not obtained due to some cause other than the failure of fertilization.

Hybrid seedlings were obtained from the following crosses:

S. chacoense x Katahdin
S. chacoense var. latisectum x Katahdin
S. acaule x S. chacoense
S. acaule x S. chacoense var. latisectum
S. semidemissum x Katahdin
S. demissum x S. chacoense
S. demissum x S. acaule
S. demissum x Earlaine

TABLE 3. Summary of interspecific pollinations made in 1951.

Species	Number of flowers pollinated	Number of fruit set	Number of plump seed
S. polyadenium			
x *S. chacoense*	62	0	-
x *S. chacoense* var. *latisectum*	39	0	-
x *S. acaule*	24	0	-
x Katahdin	57	0	-
x *S. demissum*	26	0	-
S. chacoense			
x *S. polyadenium*	156	0	-
x *S. acaule*	128	0	-
x Katahdin	64	28	13
x *S. semidemissum*	19	0	-
x *S. demissum*	99	0	-
S. chacoense var. *latisectum*			
x *S. polyadenium*	120	0	-
x *S. acaule*	51	0	-
x Katahdin	46	11	6
x *S. semidemissum*	110	2	0
x *S. demissum*	129	0	-
S. acaule			
x *S. chacoense*	6	1	137
x *S. chacoense* var. *latisectum*	34	12	1906
x Katahdin	3	0	-
x *S. demissum*	22	6	0
Katahdin			
x *S. polyadenium*	99	2	0
x *S. chacoense*	12	0	-
S. semidemissum			
x Katahdin	10	3	84
S. demissum			
x *S. chacoense*	77	53	205
x *S. chacoense* var. *latisectum*	120	42	0
x *S. polyadenium*	90	0	-
x *S. acaule*	123	78	6
x Earlaine	22	3	99
x *S. semidemissum*	49	0	-

Cytological Investigation of Species

S. chacoense (2n=24).--Five plants of this species were investigated. Twenty microsporocytes from each of the five plants were studied at diakinesis. The results of these observations are summarized in table 4. From the results summarized in table 4, S. chacoense has a chiasmata frequency of 1.032 (1238/1200) per bivalent. The terminalization coefficient is 80.61% (998/1238 x 100). A cell at diakinesis in which all of the chiasmata may be seen is shown in figure 2.

TABLE 4. Types of bivalent formation and chiasmata in S. chacoense as determined from an analysis of 20 cells per plant.

Plant Number	Bivalents Rod	Bivalents Ring	Univalents	Chiasmata Terminal	Chiasmata Interstitial	Total	Average per cell
12	229	10	2	229	20	249	12.45
14	225	15		192	63	255	12.75
15	232	7	2	176	70	246	12.30
21	235	3	4	179	62	241	12.05
31	231	8	2	222	25	247	12.35
Total	1152	43	10	998	240	1238	

A cell at I-Metaphase in which 12 bivalents are seen is shown in figure 3. All the bivalents are of the rod type. Two of the bivalents show interstitial chiasmata.

The results of observations of the other stages of meiosis are summarized in table 5. The microsporocytes at I-Anaphase, II-Prophase, and II-Telophase were considered normal if twelve chromosome configurations were counted in each group. One of the cells observed at

I-Anaphase with a bridge and fragment is shown in figure 4.

Figure 5 shows a cell at I-Telophase. A cell at II-Prophase is shown in figure 6. These cells are normal with twelve chromosome configurations in each group. Figure 7 shows a cell at II-Prophase in which an unequal segregation of the dyads occurred during I-Anaphase. One group has eleven dyads and the other group has thirteen. A cell at II-Telophase with twelve chromosomes in each of the four groups is shown in figure 8.

TABLE 5. Summary of meiosis in S. chacoense

Stage of meiosis	Number of microsporocytes observed		
	Normal	Abnormal	Nature of abnormalities
I-Anaphase	364	2	Bridge and fragment
II-Prophase	522	11	Unbalanced groups with number of chromatid dyads ranging from 10 to 14.
II-Telophase	437	10	Unbalanced groups with chromosome number ranging from 11 to 13.
Sporad	594	32	Dyads, pentads, hexads, and septads.

S. chacoense var. latisectum (2n=24).--On the basis of 20 cells from each of five plants the results of observations at diakinesis are summarized in table 6. From the data presented in table 6 S. chacoense var. latisectum has a chiasmata frequency of 1.073 (1288/1200) per bivalent. The terminalization coefficient is 64.91% (836/1288 x 100). A cell at diakinesis is shown in figure 9.

TABLE 6. Types of bivalent formation and chiasmata in S. chacoense var. latisectum as determined from an analysis of 20 cells per plant.

Plant Number	Bivalents Rod	Bivalents Ring	Univalents	Chiasmata Terminal	Chiasmata Interstitial	Total	Average per cell
1	201	34	10	161	108	269	13.45
21	227	13		175	78	253	12.65
23	231	9		150	99	249	12.45
24	191	40	18	181	90	271	13.55
25	230	8	4	169	77	246	12.30
Total	1080	104	32	836	452	1288	

The results of the other stages of meiosis are given in table 7. In regard to the data presented in table 7, the majority of the abnormalities were observed in the two plants, numbers 1 and 24. Figure 10 shows two cells at I-Anaphase. One cell is normal with twelve dyads in each group. In the other cell a precocious centromere split has taken place in two dyads and four chromatids are lagging in the cytoplasm. Both of the two large groups have eleven configurations.

A cell at II-Prophase with the normal complement of dyads is shown in figure 11. An abnormal distribution of eleven and thirteen is shown in the cell in figure 12.

Figure 13 shows a cell at II-Metaphase with one dyad excluded from the groups.

Figures 14 and 15 show cells at II-Telophase showing normal distribution of chromosomes and three excluded chromosomes respectively.

A cell at the sporad stage is shown in figure 16. In this cell there are three large nuclei and three smaller nuclei.

TABLE 7. Summaryof meiosis in S. chacoense var. latisectum.

Stage of meiosis	Number of microsporocytes observed: Normal	Abnormal	Nature of abnormalities
I-Anaphase	100	6	Unbalanced groups, dyad number in the group varying from 11 to 13. Lagging dyads.
II-Prophase	469	82	Unbalanced groups, dyad number in the group varying from 9 to 15. Dyads excluded. Precocious division of the centromere.
II-Telophase	444	56	Unbalanced groups, chromosome number in the group varying from 10 to 14. Chromosomes excluded.
Sporad	472	35	Dyads, triads, pentads, and hexads.

S. polyadenium (2n=24).--Meiosis was studied in five plants of this species. At diakinesis it was difficult to distinguish between bivalents with one chiasma (rod type) and bivalents with two chiasmata (ring type). The majority of the rod type bivalents had an interstitial chiasma which held the chromatic regions of the chromosomes very close together. As a result it was often impossible to determine whether a bivalent was of the rod or of the ring type. It was possible to determine with accuracy all 12 bivalents in only 22 cells. The results of the observations on these 22 cells are summarized in table 8.

TABLE 8. Types of bivalents and chiasmata frequency in S. polyadenium.

Number of microsporocytes	Bivalents with two chiasmata	Bivalents with one chiasma	Average chiasmata: Per cell	Per bivalent
22	223	41	22.136	1.845

Figures 17 and 18 show cells at diakinesis.

The only abnormalities observed in this species was a bridge and fragment at I-Anaphase (Fig. 19) and occasional monads, dyads, and triads at the sporad stage (Fig. 20).

Figure 21 shows a cell at II-Prophase. Figure 22 shows two cells at I-Metaphase. The three cells shown in these two figures are normal.

S.acaule (2n=48).--At diakinesis in this tetraploid species only bivalents were observed in 60 cells. Two bivalents were attached to the nucleolus. The majority of the bivalents were of the ring type (Fig. 23). Counts of the chromosomes in each group were made in 100 cells at II-Prophase. In all cells there was an equal distribution of chromosomes (Fig. 24). The production of four microspores at the sporad stage was characteristic of this species. In only one of the five plants investigated was any meiotic abnormality observed. In this plant four microsporocytes out of 100 had produced pentads at the sporad stage.

S. tuberosum (2n=48).--Meiosis was studied in the two varieties, Katahdin and Earlaine, of this tetraploid species. In the variety Katahdin 40 cells were classified at diakinesis. The results of these observations are presented in table 9. In Earlaine it was possible to interpret diakinesis in only two cells. These two cells showed the following configurations:

3 quadrivalents, 2 trivalents, 13 bivalents, and 4 univalents, and

5 quadrivalents, 0 trivalents, 13 bivalents, and 2 univalents.

Figures 25, 26, 27, 28, and 29 show cells of Katahdin at diakinesis. The majority of the quadrivalents in Katahdin were the open chain type. Diagrammatic configurations of the different types of quadrivalents and their frequencies are shown in table 10.

TABLE 9. Frequencies of configurations at diakinesis in Katahdin as determined from an analysis of 40 cells.

Configurations	Total	Range	Average per cell
Quadrivalents	112	0-6	2.80
Trivalents	65	0-6	1.63
Bivalents	606	9-22	15.15
Univalents	65	0-5	1.63

TABLE 10. Types of quadrivalents observed in Katahdin.

Type of configuration	Number of chiasmata	Frequency
	3	68
	3	11
	3	3
	4	15
	4	6
	4	5
	4	2
	4	2
	Total	112

At diakinesis usually only one nucleolus, to which a single bivalent was attached, was observed. A few cells, however, were observed in which there were two nucleoli with a bivalent attached to each. Figure 25 shows this condition.

Counts at II-Prophase were made to determine the percentage of microsporocytes in which normal segregation occurred. A cell was considered normal if there were 24 dyads in each group. The results of the counts at II-Prophase are summarized in table 11.

TABLE 11. Distribution of dyads at II-Prophase.

	Cells with normal distribution	Cells with unbalanced groups. Number of dyads ranging from 20 to 27
Katahdin	60	48
Earlaine	21	22

Figure 30 shows a cell of Katahdin at II-Prophase with the normal distribution of dyads. A cell with an unequal distribution of 23 and 25 chromosomes is shown in figure 31.

Besides the unequal distribution of dyads during the first meiotic division, dyads were also eliminated in some of the cells. Such dyads were observed in the cytoplasm during the second division. Observations were made at II-Metaphase to determine the number and frequency of the elimination of dyads. As seen in table, 12 dyads were more frequently eliminated in the variety Earlaine than in Katahdin. A cell of Earlaine in which there has been one dyad eliminated is shown in figure 32. A cell at II-Metaphase showing two groups but no eliminated dyads is shown in figure 33.

TABLE 12. Frequency of eliminated dyads at II-Metaphase in Earlaine and Katahdin.

	Cells with the following number of eliminated dyads			
	0	1	2	3
Earlaine	70	39	6	2
Katahdin	86	5	9	0

Observation of the sporads disclosed that 67% of the sporads of Earlaine and 17% of the sporads of Katahdin had more than the normal number of 4 microspores. The detailed results of the observations at the sporad stage are shown in table 13. Figure 34 shows two cells of Katahdin at the presporad stage. One of the cells is normal with four nuclei; the other, abnormal with five nuclei.

TABLE 13. Microspore formation in Earlaine and Katahdin

	Sporads with the following number of microspores				
	4	5	6	7	8
Earlaine	33	34	28	3	
Katahdin	83	17			

Other than the elimination of chromosomes and the resulting production of more than the usual number of four microspores, the meiotic behavior of Earlaine and Katahdin was quite regular. A bridge and fragment was observed in a single cell at I-Anaphase (Fig. 35) in Katahdin. Figure 36 shows a cell at II-Metaphase in Earlaine in which there is a chromatin bridge remaining in the cytoplasm from the first division.

S. semidemissum (2n=60).--Good fixation of the first division was not obtained. Consequently, detailed conclusions cannot be made in regard to the meiotic behavior of this species. During the second division configurations were observed excluded in the cytoplasm (Figs. 37 and 38). At the sporad stage only 35 cells from a total of 200 showed the formation of the normal number of four microspores. In the other cells from five to seven microspores were observed.

S. demissum (2n=72).--Meiosis in this hexaploid species was very regular. Only bivalents were observed at diakinesis. At II-Prophase there was usually an equal distribution of 36 configurations in each group (Fig. 39). In only one cell in the 500 observed was there a chromosome eliminated. At the sporad stage only 19 cells from a total of 400 showed the formation of a fifth microspore.

Cytological Investigation of Hybrids

S. acaule x S. chacoense (2n=36).--Somatic chromosome counts were made on 15 of the F_1 hybrids from this cross. All had a somatic chromosome number of 36. Diakinesis was studied in 65 cells. The results are summarized in table 14. Figure 40 shows a cell at diakinesis.

TABLE 14. Types of configurations at diakinesis in the triploid hybrid S. acaule x S. chacoense as determined from an analysis of 65 cells.

Type of configurations	Total	Range per cell	Average per cell
Trivalents	248	1-7	3.82
Bivalents	558	5-13	8.58
Univalents	480	2-12	7.38

Sufficient material has not been examined to draw conclusions on the other stages of meiosis. However, unequal distribution of dyads (Fig. 41) and the elimination of chromosomes have been observed.

S. acaule x S. chacoense var. latisectum (2n=36).--The F_1 plants from this cross were all triploid hybrids with a chromosome number of 36. Twenty cells were observed at diakinesis. The results of the observations at this stage of meiosis are summarized in table 15. Figures 42 and 43 show a cell at diakinesis.

TABLE 15. Types of configurations at diakinesis in the hybrid S. acaule x S. chacoense var. latisectum as determined from an analysis of 20 cells.

Type of configurations	Total	Range per cell	Average per cell
Trivalents	90	1-7	4.50
Bivalents	175	5-12	8.75
Univalents	99	2-7	4.95

At I-Anaphase a bridge and fragment were observed in six cells. Three of these cells are shown in figures 44, 45, and 46.

Unequal distribution and lagging dyads occurred at the end of the first division. Counts were made in 112 cells at II-Prophase and II-Metaphase to determine the distribution of the dyads and the frequency of eliminated dyads. The results of these counts are given in table 16. A cell at II-Prophase with a distribution of 19 and 17 dyads is shown in figure 47; one with a distribution of 18 and 18 is shown in figure 48.

TABLE 16. Distribution and elimination of dyads at II-Prophase and II-Metaphase in S. acaule x S. chacoense var. latisectum.

	Groups with a dyad number of:									Eliminated dyads per cell				
	14	15	16	17	18	19	20	21	22	0	1	2	3	4
Frequency	5	14	32	46	50	38	27	10	2	87	12	10	2	1

S. demissum x S. chacoense (2n=60).--Twenty-four of the hybrids from this cross were checked for the somatic number of chromosomes. All had the pentaploid chromosome number of 60. This indicates either the formation of unreduced gametes or spontaneous chromosome doubling resulting in S. chacoense gametes with the diploid number.

Configurations from univalents to pentavalents have been observed at diakinesis. The results of observations of ten cells are summarized in table 17.

TABLE 17. Types of configurations at diakinesis in the hybrid S. demissum x S. chacoense as determined from an analysis of 10 cells.

Type of configurations	Total	Range per cell	Average per cell
Pentavalents	3	0-3	0.30
Quadrivalents	27	1-7	2.70
Trivalents	48	3-7	4.80
Bivalents	134	8-18	13.40
Univalents	65	4-10	6.50

Counts were made at II-Prophase to determine the distribution of the dyads and also the elimination of dyads during the first division. The results of the counts in 154 cells are shown in table 18.

TABLE 18. Distribution and elimination of dyads at II-Prophase in S. demissum x S. chacoense as determined from an analysis of 154 cells.

	Groups with a dyad number of:										Eliminated dyads per cell				
	25	26	27	28	29	30	31	32	33	34	0	1	2	3	4
Frequency	2	7	22	51	54	71	46	34	16	5	102	33	15	1	3

The results of observations at the sporad stage are summarized in table 19. The majority of the sporads had a number of microspores greater than the normal number of four.

TABLE 19. Microspore formation in S. demissum x S. chacoense.

	Number of microspores per sporad				
	4	5	6	7	8
Frequency	51	150	171	25	3

S. demissum x S. tuberosum var. Earlaine (2n=60).--Good preparations of diakinesis were not obtained. Consequently it was not possible to determine the frequency of the types of association during the first division. Univalents, bivalents, trivalents, and quadrivalents were observed. Figures 49 and 50 show a cell at diakinesis in which univalents, bivalents, and trivalents occurred.

Lagging dyads were frequent at I-Anaphase (Fig. 51). A bridge and fragment at I-Anaphase was observed in four cells, one of which is shown in figure 52. Counts were made at II-Metaphase to determine the frequency and number of eliminated dyads. These results are presented in table 20. Figure 53 shows a cell at II-Metaphase with six dyads

eliminated.

TABLE 20. Eliminated dyads at II-Metaphase in the pentaploid hybrid S. demissum x Earlaine.

	Number of dyads eliminated per cell						
	0	1	2	3	4	5	6
Number of cells	22	30	40	7	1	2	1

Only a small percentage of the microsporocytes produced the normal number of four microspores at the sporad stage. The results of observations on 500 sporads are given in table 21. Figure 54 shows a cell at the presporad stage with five nuclei, a single chromosome, and a group of five chromosomes.

TABLE 21. Microspore production in S. demissum x Earlaine

	Number of microspores per sporad					
	4	5	6	7	8	9
Frequency	22	93	200	131	44	10
Percentage of total	4.4	18.6	40.0	26.2	8.8	2.0

DISCUSSION

The fact that pairing takes place in the interspecific hybrids indicates homology between the chromosomes of the different species. Pairing was observed in all interspecific hybrids studied. Choudhuri (4), Emme (9), Koopsman (14), Lamm (16), Propach (23), Rybin (25), and Swaminathan (28) observed as high a degree of pairing in hybrids between diploid species as in the diploid species themselves. Propach (23) considers that speciation on the diploid level has been genetic in nature. However, it is equally possible that structural differentiation has also taken place. If structural aberrations involve small segments of the chromosomes, they would have little affect on bivalent formation. However, sterility of the hybrids could result. That gross structural differences exist is demonstrated by the occurrence of bridges and fragments in the diploid species S. chacoense and S. polyadenium and also in the interspecific hybrids, S. acaule x S. chacoense var. latisectum and S. demissum x S. tuberosum.

That polyploidy has played an important part in the speciation of the genus is obvious from the large number of polyploid species. The exact nature of the polyploids is not known since in no case have diploid ancestors been identified.

The polyploid species, S. acaule and S. demissum, studied in this investigation have the meiotic behavior of allopolyploids. In the case of S. demissum, the only hexaploid species in the group, polyhaploid plants have been reported by Bains and Howard (1) and Doods (6). In these polyhaploid plants of S. demissum bivalents were

observed at I-Metaphase. The number of bivalents per cell observed by these investigators ranged from 2 to 6 and from 1 to 8 respectively. The formation of bivalents indicates that there is some degree of homology of chromosomes between at least two of the three genomes. In view of these facts S. demissum is either an allohexaploid of the segmental type with three different genomes or an allohexaploid with two different genomes one of which has been duplicated. The regular formation of bivalents in this hexaploid species would seemingly indicate that three different genomes are present in S. demissum.

The formation of quadrivalents in S. tuberosum indicates an autopolyploid condition. Tetrasomic inheritance has also been reported for this species by Lunden (19) and Müller (20). However, both of these conditions can occur in segmental allotetraploids. Ivancvskaja (12) and Lamm (15) observed bivalent formation in a polyhaploid S. tuberosum plant. Univalents were also observed and I-Anaphase bridges and fragments were frequent. The plant was completely sterile. Ivanovskaja considers S. tuberosum to be an allotetraploid which developed from a hybrid between two closely related diploid species.

Considering the distribution of chromosomes during meiosis in S. tuberosum, pollen grains are formed with the normal complement of 24 chromosomes, with a number of chromosomes greater than 24, and with a number of chromosomes less than 24. It would seem that the pollen grains with aneuploid numbers should function occasionally. However, a survey of the literature fails to reveal a single such report. Forty-five varieties counted by Ellison (7) and 37 varieties counted by Longley and Clark (18) had the normal somatic chromosome number of 48. The varieties in which chromosomes have been counted have all

been selections of the plant breeder. It is possible that weak aneuploid plants were eleminated. Counts in an entire seedling population from either selfs or intervarietal crosses have not been made. It is possible that such an investigation would reveal the presence of aneuploid plants. However, it seems likely that aneuploid gametes or zygotes of S. tuberosum are under selective disadvantage. The only incidences of aneuploid plants in the genus Solanum section Tuberarium have been in the progeny of triploid and pentaploid species and hybrids or in the progeny of fertile aneuploids originating from triploids or pentaploids.

All the hybrids from the cross S. demissum x S. chacoense were pentaploids. This indicates that the barriers to interspecific hybridization between S. demissum and S. chacoense were overcome by the functioning of S. chacoense gametes with the diploid number of chromosomes. The failure to obtain any tetraploid hybrids from this cross emphasizes this fact. Livermore and Johnstone (17) and Swaminathan (28) have reported increased crossability and self-fertility effected by the artificial doubling of the chromosomes in certain species. The natural occurrence of chromosome doubling or artificially induced doubling may make possible otherwise difficult crosses.

The high frequency of trivalents and bivalents (Tables 14 and 15) in the triploid hybrids S. acaule x S. chacoense and S. acaule x S. chacoense var. latisectum is of interest. This same high frequency has been reported in other triploid species and hybrids, Emme (8), Ivanovskaja (13), Lamm (16), v. Olah (21), Propach (22), and Schwarz (26). The sum of trivalents and bivalents has often exceeded 12, the basic number of the genus. This has been interpreted as the

result of pairing of chromosomes within a genome.

Another interpretation, consistent with the present concepts of polyploidy, Stebbins (27), seems more plausible. For an illustration the triploid hybrid S. acaule x S. chacoense will be discussed. Since trivalents and bivalents were observed in this triploid hybrid, pairing must take place between the genomes of S. acaule and S. chacoense. This indicates homology of chromosomes of the two species. However, this is probably homology of chromosome segments and not necessarily entire chromosomes. If this is the case this hybrid is a segmental allotriploid. It is also probable that the tetraploid S. acaule is a segmental allotetraploid in which only bivalents are formed due to differential affinity, Darlington (5; pp. 198-300). However, it is possible that heterogenetic pairing can take place between chromosomes of the two genomes of S. acaule when their exact homologs are not present. Consequently, heterogenetic pairing between the two genomes of S. acaule could account for some of the bivalents observed in the triploid hybrid. A chromosome of S. chacoense could be composed of segments of which the homologs in S. acaule are distributed in two or more chromosomes. Considering that chromosomes pair segment by segment, a chromosome from S. chacoense would then have more than one possible partner within the two genomes of S. acaule. If the chromosomes of the two genomes of S. acaule do pair, and a chromosome from S. chacoense has more than one possible partner within the two genomes of S. acaule, a type of pairing could take place which would account for the high frequency of trivalents and bivalents observed in this triploid hybrid. A polyhaploid plant of S. acaule would probably furnish the answer to the possibility of pairing between the two

genomes of S. acaule. However, such a plant has not been reported.

The utilization of the wild species in transferring desirable genes to the cultivated S. tuberosum should probably be undertaken on the tetraploid level. Elimination of chromosomes in the triploids and pentaploids, as pointed out by Howard and Swaminathan (11), could result in the elimination of desirable genes from many of the functional gametes.

The solution to the problem of speciation of the group, whether mainly genetic or due to small structural differences, should be looked for in the diploid species. Before the diploid species and their hybrids have been thoroughly investigated both cytologically and genetically, it will be difficult to interpret in detail the behavior of the polyploid species.

SUMMARY

Eight species and varieties and four interspecific hybrids in the genus Solanum section Tuberarium were investigated in regard to their meiotic behavior. The crossability of the species was also investigated.

Pentaploid hybrids were obtained from the cross, hexaploid S. demissum x diploid S. chacoense. Since no tetraploid hybrids were obtained from this cross as would be expected, it seems that the barriers to interspecific hybridization were overcome by the functioning of S. chacoense gametes with the diploid number of chromosomes.

Abortive seed were obtained from the cross tetraploid S. acaule x hexaploid S. demissum. Viable seed were not obtained presumably due to some cause other than the failure of fertilization.

In the diploid species, S. chacoense and S. chacoense var. latisectum, the majority of the bivalents at diakinesis were rod shaped. Ring type bivalents were less frequent. Univalents were also occasionally observed. This resulted in the unequal distribution of chromosome configurations in some of the microsporocytes during the first division. Precocious division of the centromere was occasionally observed at I-Anaphase.

In the diploid species, S. polyadenium, ring bivalents were more frequent than rod bivalents at diakinesis.

The observation of bridges and fragments at I-Anaphase in both species and interspecific hybrids indicated that gross structural

differences of the chromosomes occurred. The pairing of chromosomes observed in all interspecific hybrids indicated a degree of homology between the chromosomes of the different species.

The tetraploid S. acaule and the hexaploid S. demissum had the meiotic behavior of allopolyploids. Considering the behavior reported in polyhaploid S. demissum plants and the probable pairing of S. acaule chromosomes in triploid hybrids, it is likely that these species are segmental allopolyploids. The formation of quadrivalents in the cultivated S. tuberosum indicated an autopolyploid condition.

Numerous trivalents and bivalents were observed in the triploid hybrids, S. acaule x S. chacoense and S. acaule x S. chacoense var. latisectum. A high frequency of chromosome elimination was observed in the triploid and pentaploid hybrids. The fact that desirable genes may be eliminated with these chromosomes makes these types undesirable for a practical breeding program.

The diploid species and hybrids should be investigated cytogenetically to determine whether speciation has been mainly genetic in nature or has involved structural differences. Before this has been accomplished, it will be impossible to interpret in detail the behavior of the polyploids.

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PLATE I

Chromosomes in cell of root tip. Meiosis in S. chacoense.

Fig. 1. Chromosomes in cell of root tip in the pentaploid hybrid S. demissum x Earlaine, 2n=60. 600X.

Figs. 2-8 Meiosis in S. chacoense, 2n=24. 1350X.

Fig. 2. Diakinesis. One ring and 11 rod bivalents. Interstitial chiasmata indicated by arrows. All other chiasmata are terminal.

Fig. 3. I-Metaphase. Two bivalents in upper left with interstitial chiasmata.

Fig. 4. I-Anaphase. Bridge and fragment.

Fig. 5. I-Telophase.

Fig. 6. II-Prophase.

Fig. 7. II-Prophase. Unequal distribution, 11 and 13, of chromatid dyads.

Fig. 8. II-Telophase

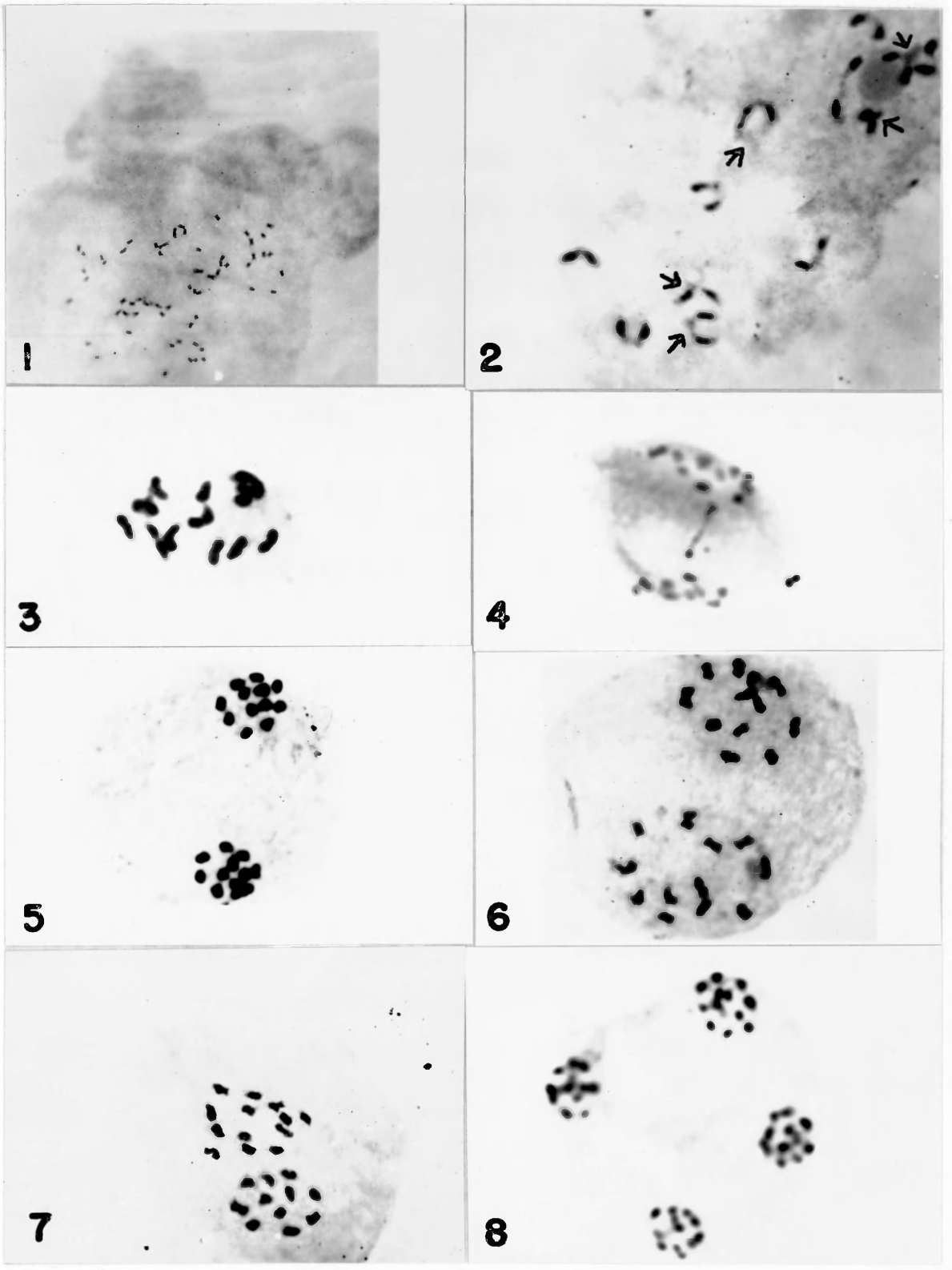

PLATE I

PLATE II

Meiosis in *S. chacoense* var. *latisectum*, 2n=24. 1350X.

Fig. 9. Diakinesis. Two ring and 10 rod bivalents. Interstitial chiasmata indicated by arrows. All other chiasmata are terminal.

Fig. 10. I-Anaphase. Cell on right, normal. Cell on left, 4 chromatids lagging in cytoplasm.

Fig. 11. II-Prophase.

Fig. 12. II-Prophase. Unequal distribution, 11 and 13, of chromatid dyads.

Fig. 13. II-Metaphase. One dyad excluded.

Fig. 14. II-Telophase.

Fig. 15. II-Telophase. Three chromosomes excluded.

Fig. 16. Early sporad. Three large nuclei and three smaller nuclei.

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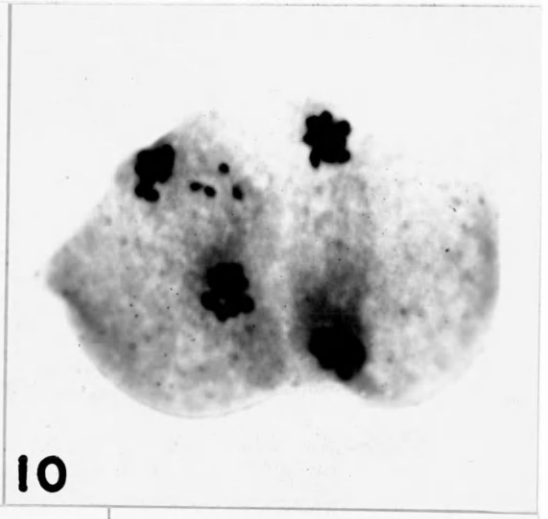

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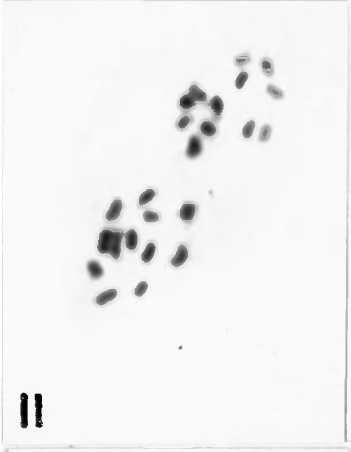

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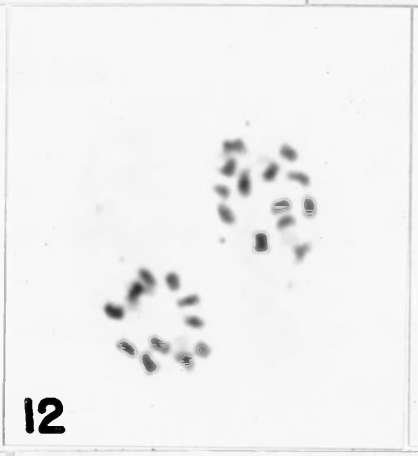

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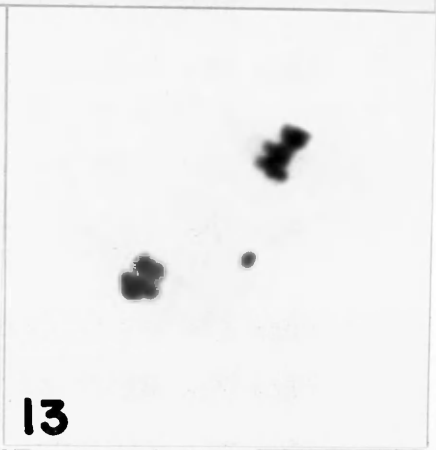

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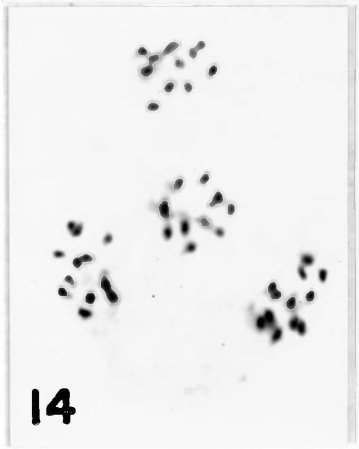

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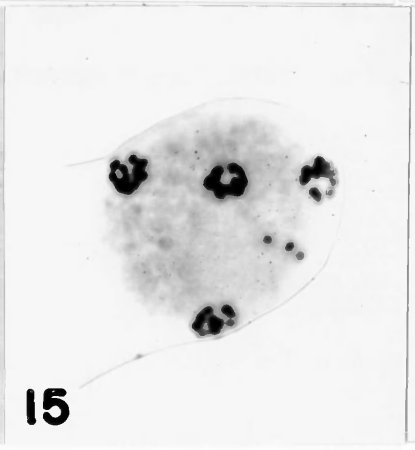

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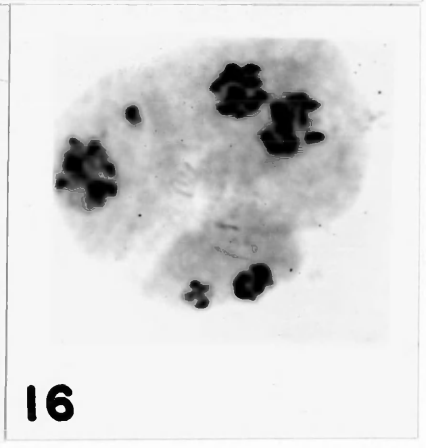

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PLATE II

PLATE III

Meiosis in *S. polyadenium*. 2n=24. 1350X.

Figs. 17-18. Diakinesis.

Fig. 19. I-Anaphase. Bridge and fragment.

Fig. 20. Sporad. Monads, dyads, triads.

Fig. 21. II-Prophase.

Fig. 22. Two cells at I-Metaphase.

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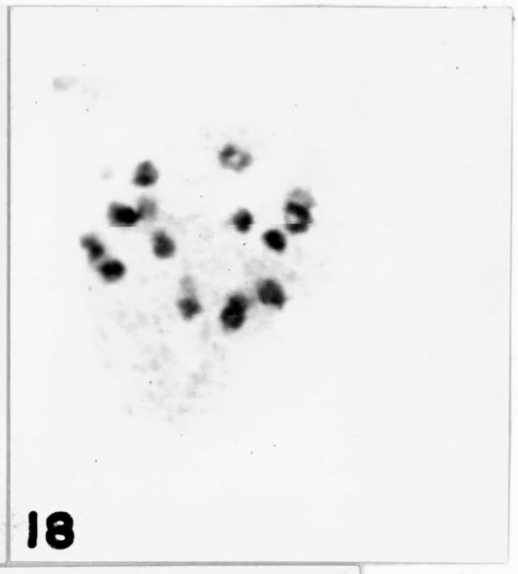

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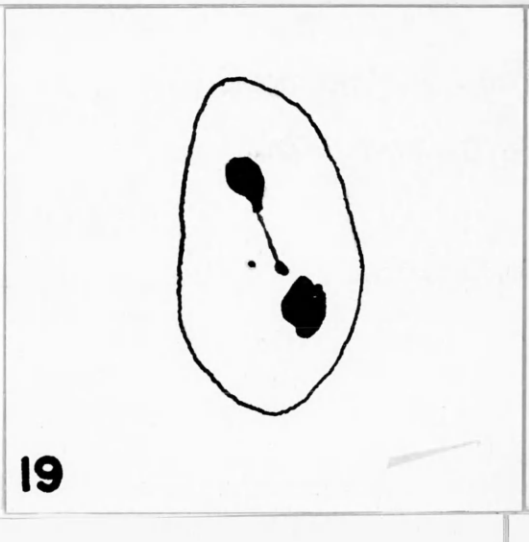

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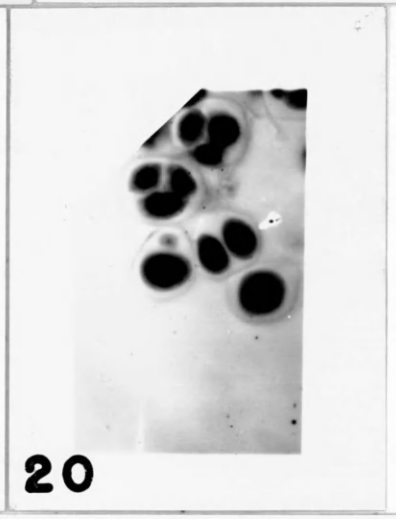

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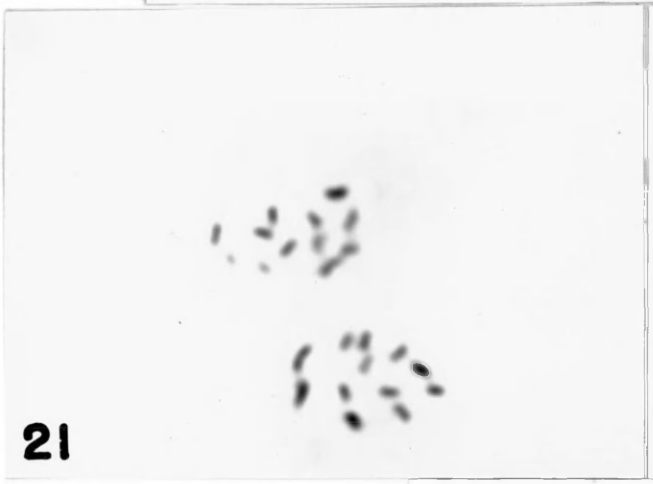

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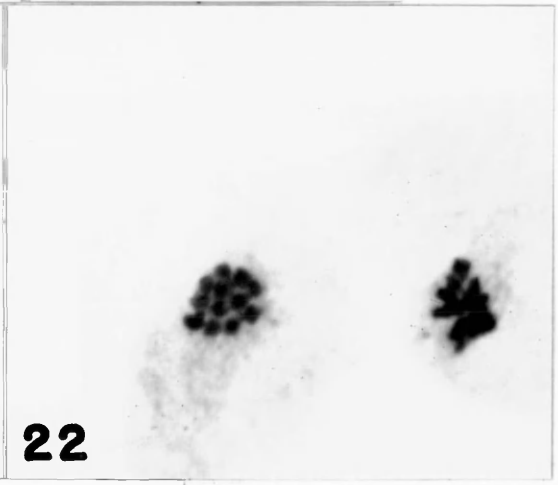

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PLATE III

PLATE IV

Meiosis in tetraploids. 2n=48. 1350X.

Fig. 23-24. *S. acaule*

Fig. 23. Diakinesis.

Fig. 24. II-Prophase.

Figs. 25-29. Diakinesis in *S. tuberosum* var. Katahdin.

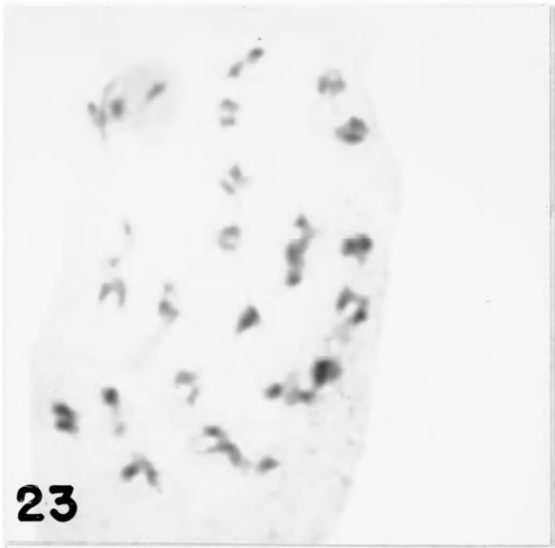
Fig. 25. Two quadrivalents, one trivalent, and 18 bivalents. Two nucleoli.

Fig. 26. Diagrammatic presentation of Fig. 25. Nucleoli, N.

Fig. 27. Two quadrivalents, two trivalents, 16 bivalents, and two univalents.

Fig. 28. Diagrammatic presentation of Fig. 27.

Fig. 29. Zigzag quadrivalent.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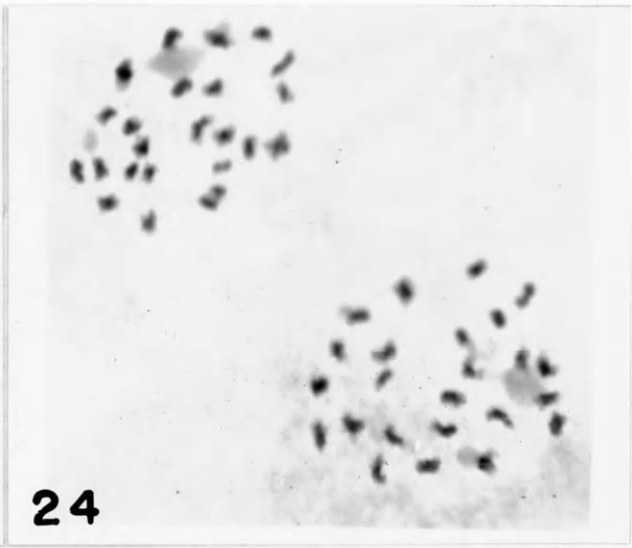
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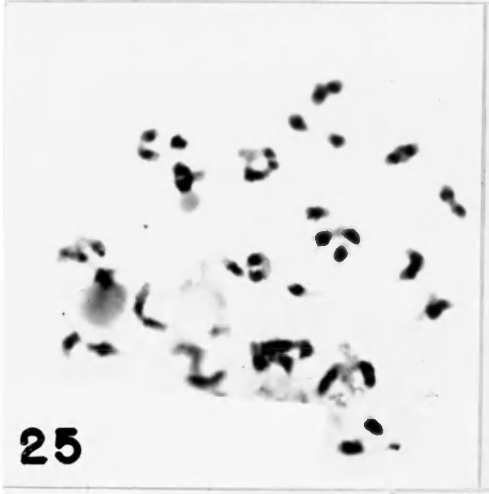
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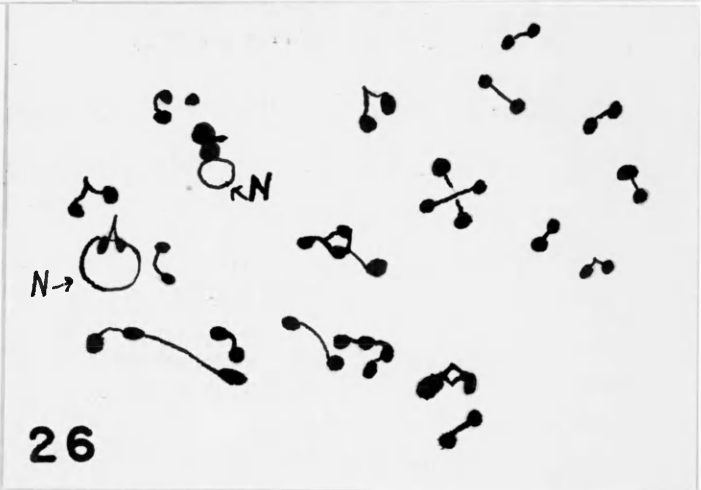

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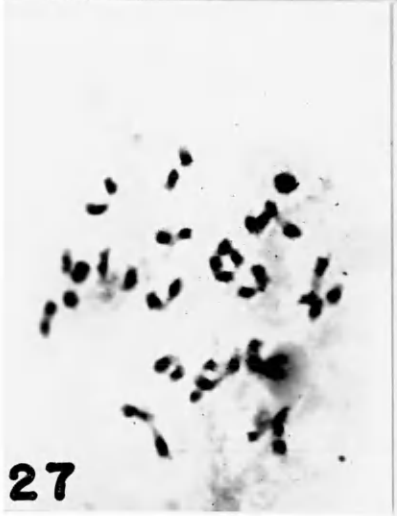
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PLATE IV

PLATE V

Meiosis in tetraploids, continued from Plate IV.

Fig. 30. II-Prophase in Katahdin. Equal distribution, 24 and 24, of chromatid dyads.

Fig. 31. II-Prophase in Katahdin. Unequal distribution, 23 and 25, of chromatid dyads.

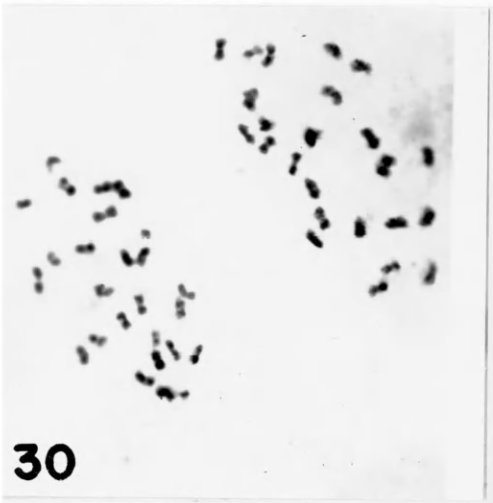
Fig. 32. II-Metaphase in Earlaine. One dyad excluded.

Fig. 33. II-Metaphase in Earlaine.

Fig. 34. Prespored in Katahdin. One cell with four nuclei. Other cell with five nuclei.

Fig. 35. I-Anaphase in Katahdin. Bridge and frament.

Fig. 36. II-Metaphase in Earlaine. Chromatin bridge from first division.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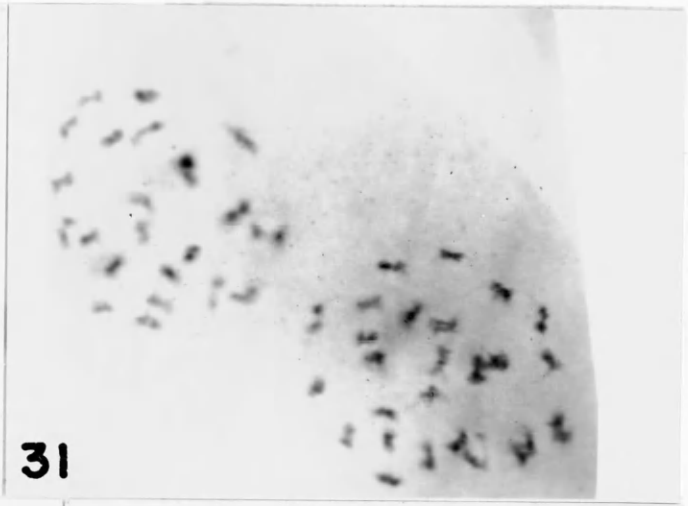
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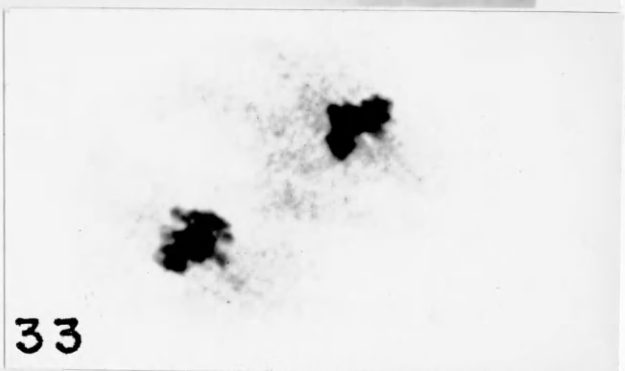
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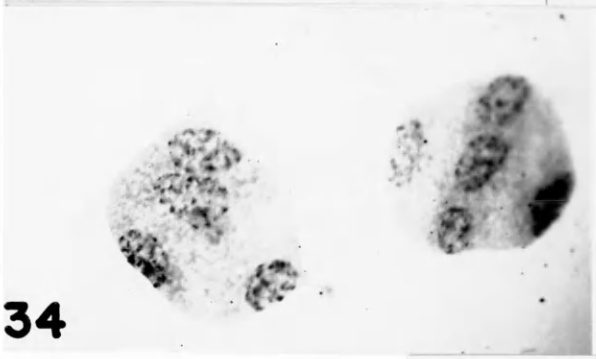
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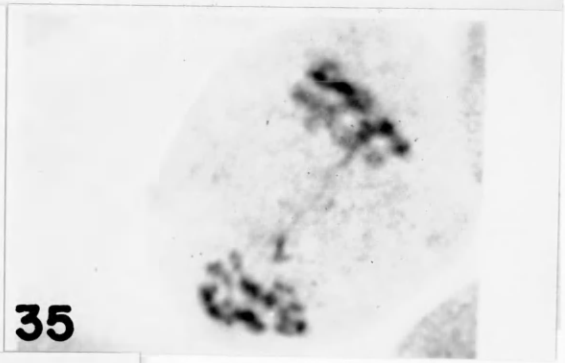
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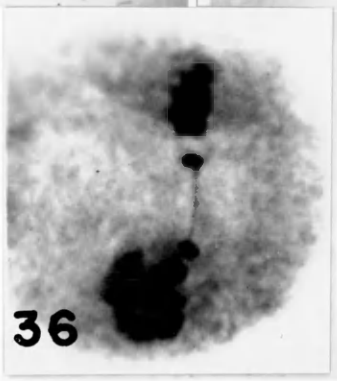
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PLATE V

PLATE VI

Meiosis in S. semidemissum, 2n=60, S. demissum, 2n=72, and S. acaule x S. chacoense, 2n=36. 1350X.

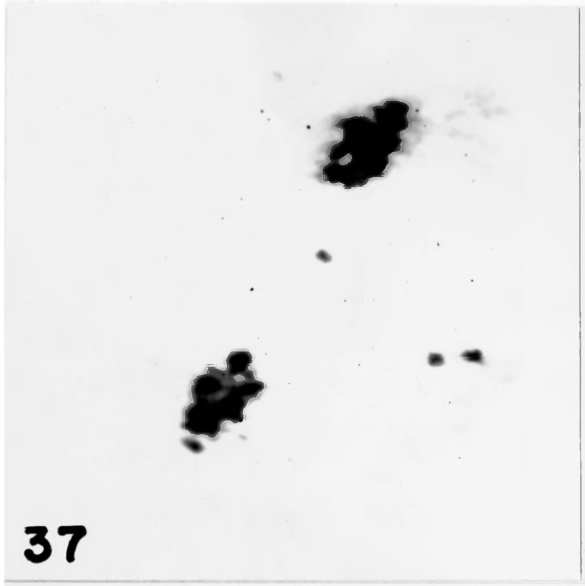
Fig. 37. II-Metaphase in S. semidemissum. Three chromosome configurations excluded.

Fig. 38. II-Telophase in S. semidemissum. Two chromosomes excluded.

Fig. 39. II-Prophase in S. demissum.

Fig. 40. Diakinesis in the triploid hybrid S. acaule x S. chacoense. Five trivalents, 7 bivalents, and 7 univalents.

Fig. 41. II-Prophase in S. acaule x S. chacoense. Distribution of chromatid dyads, 14 and 22.



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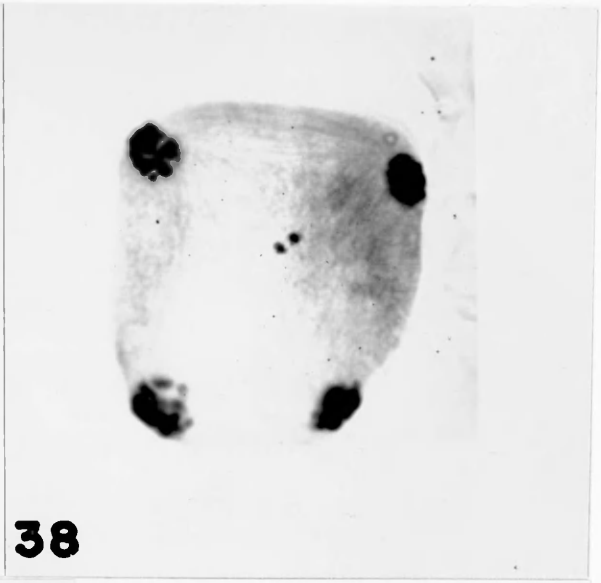

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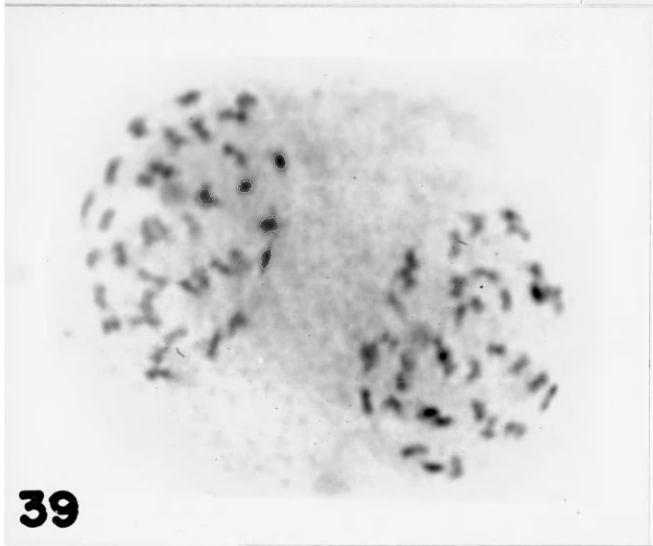

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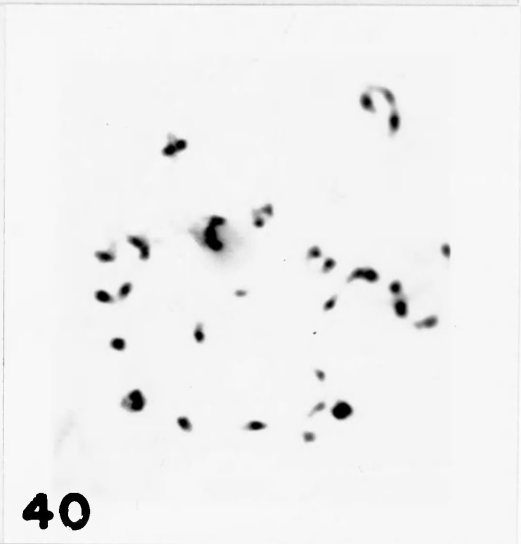

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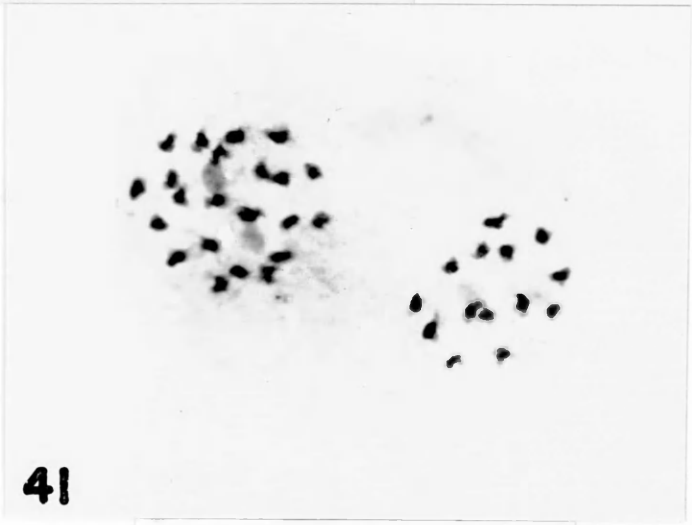

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PLATE VI

PLATE VII

Meiosis in the triploid hybrid S. acaule x S. chacoense var. latisectum. 2n=36. 1350X.

Fig. 42. Diakinesis. Three trivalents, 10 bivalents, and 7 univalents.

Fig. 43. Diagrammatic presentation of Fig. 42.

Figs. 44-46. I-Anaphase showing bridges and fragments.

Fig. 47. II-Prophase. Unequal distribution, 17 and 19, of chromatid dyads.

Fig. 48. II-Prophase. Equal distribution, 18 and 18, chromatid dyads.

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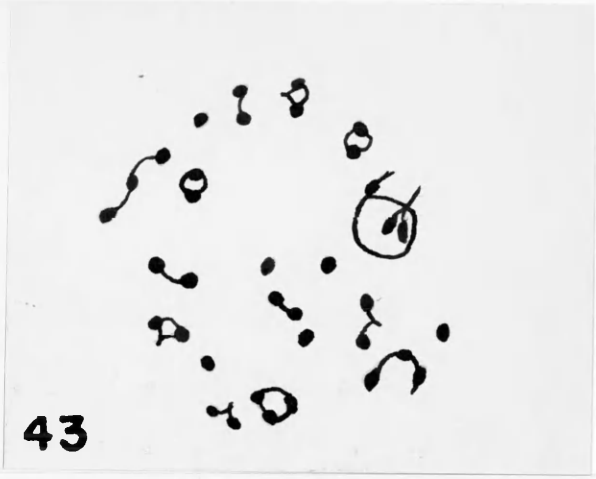

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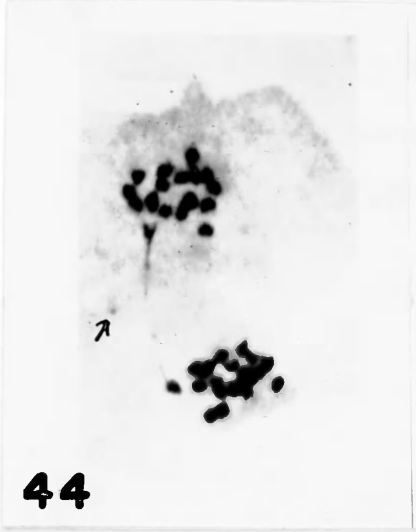

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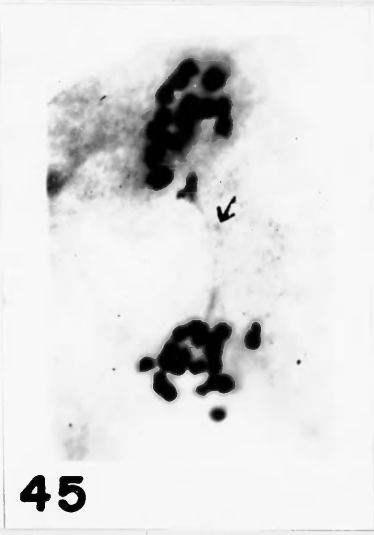

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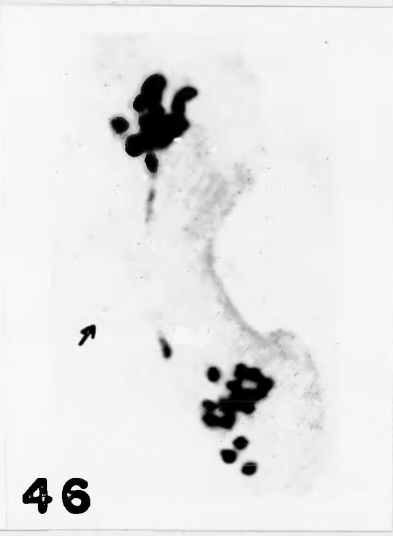

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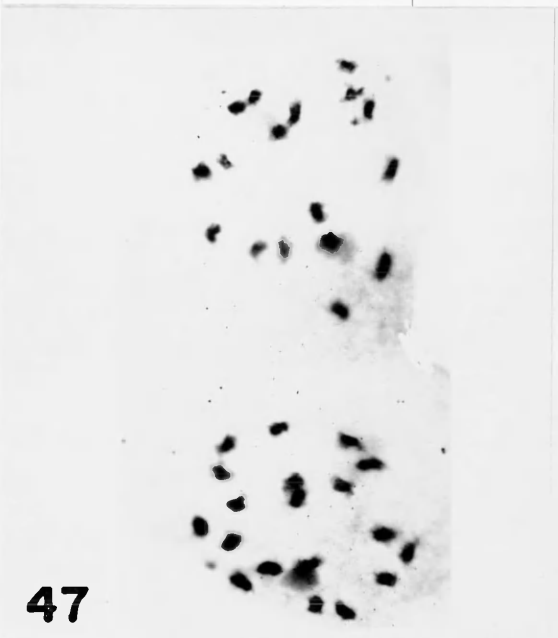

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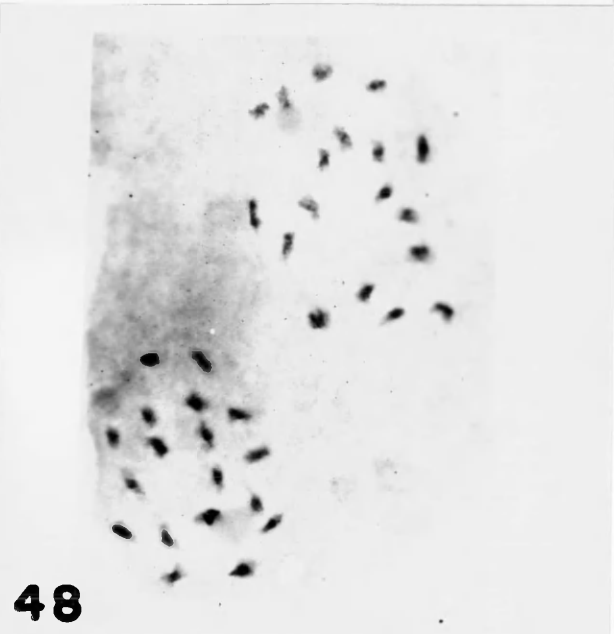

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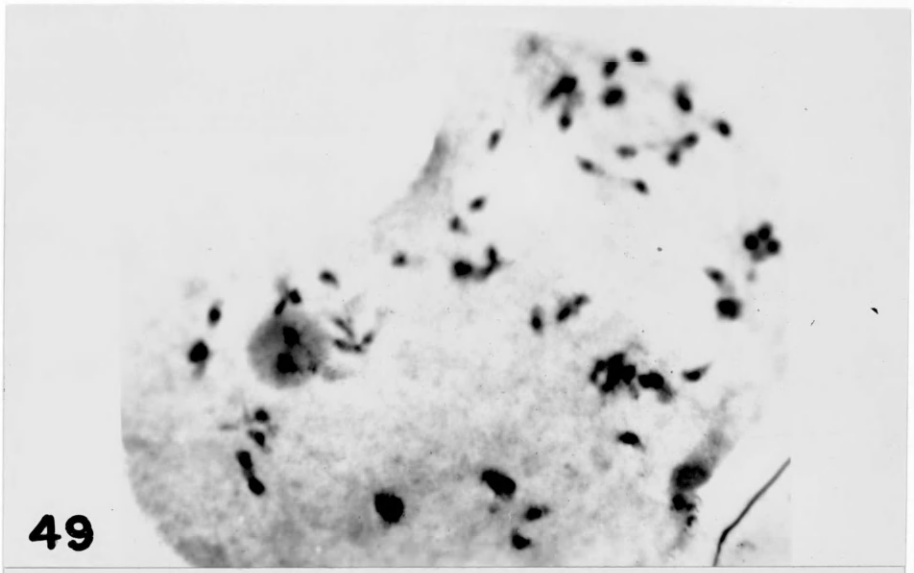
PLATE VII

PLATE VIII

Meiosis in the pentaploid hybrid S. demissum x Earlaine, 2n=60. 1350X.

Fig. 49. Diakinesis. Five trivalents, 16 bivalents, and 13 univalents.

Fig. 50. Diagrammatic presentation of Fig. 49.



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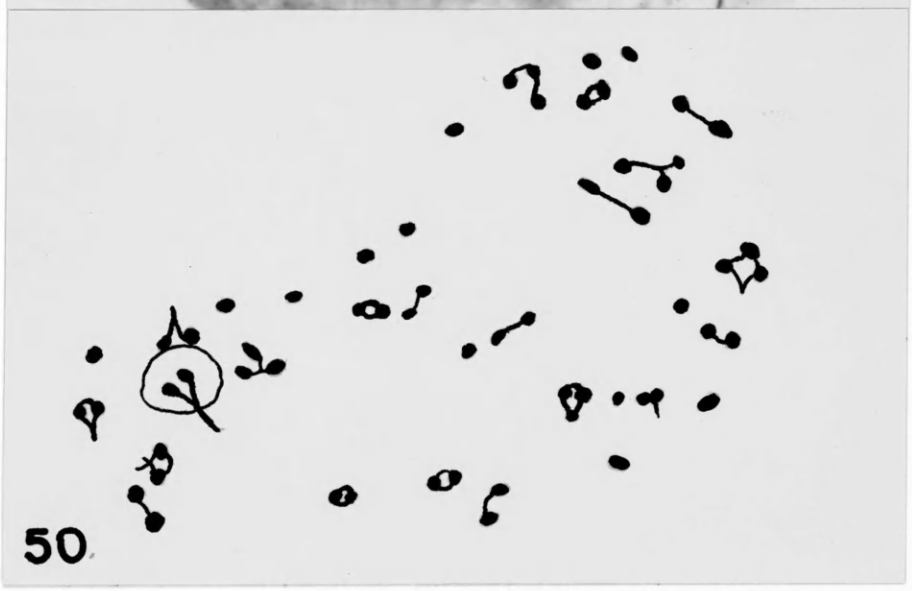

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PLATE VIII

PLATE IX

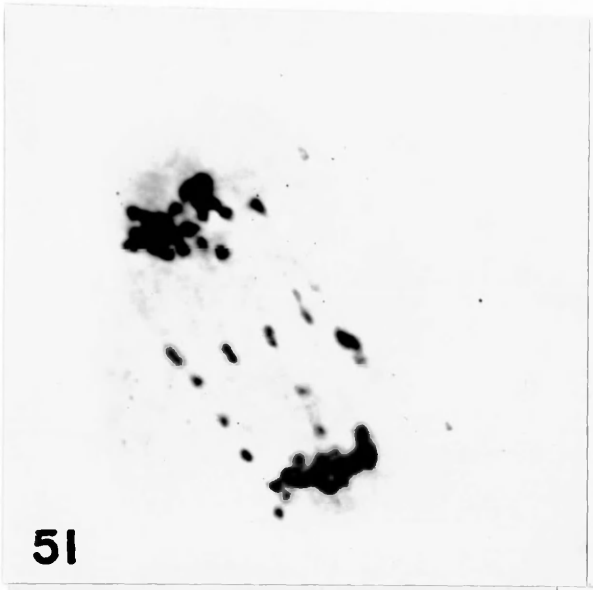
Meiosis in *S. demissum* x Earlaine, continued from Plate VIII.

Fig. 51. I-Anaphase. Lagging chromosome configurations.

Fig. 52. I-Anaphase. Bridge and fragment.

Fig. 53. II-Metaphase. Six chromosome configurations excluded.

Fig. 54. Presporad. Five nuclei, a single chromosome, and a group of five chromosomes.



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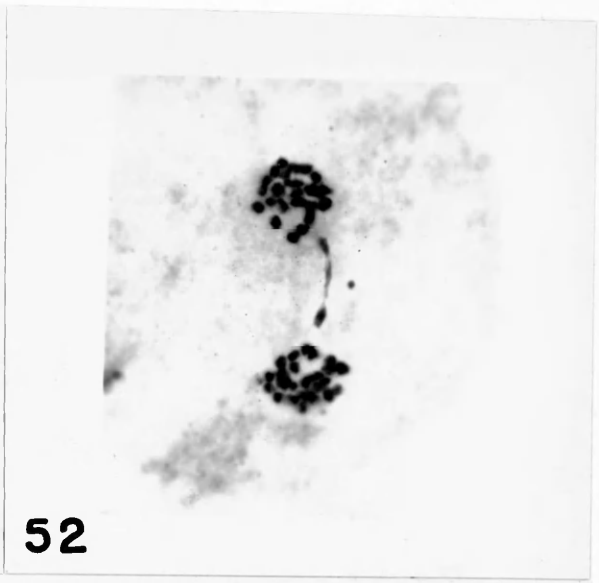

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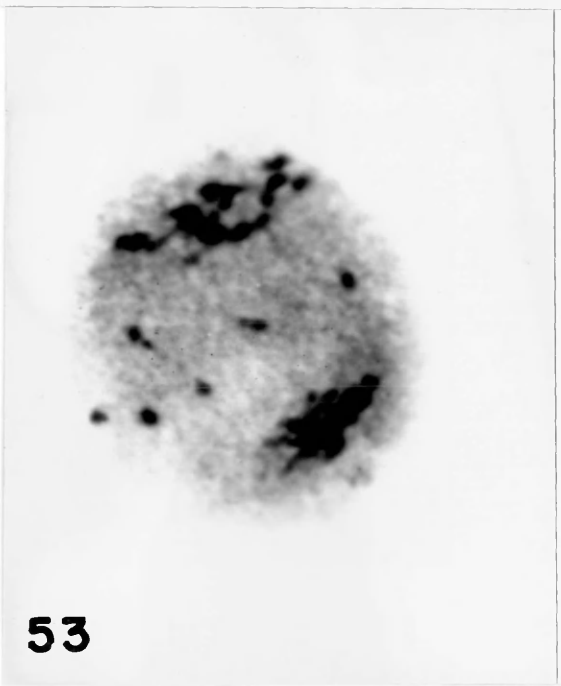

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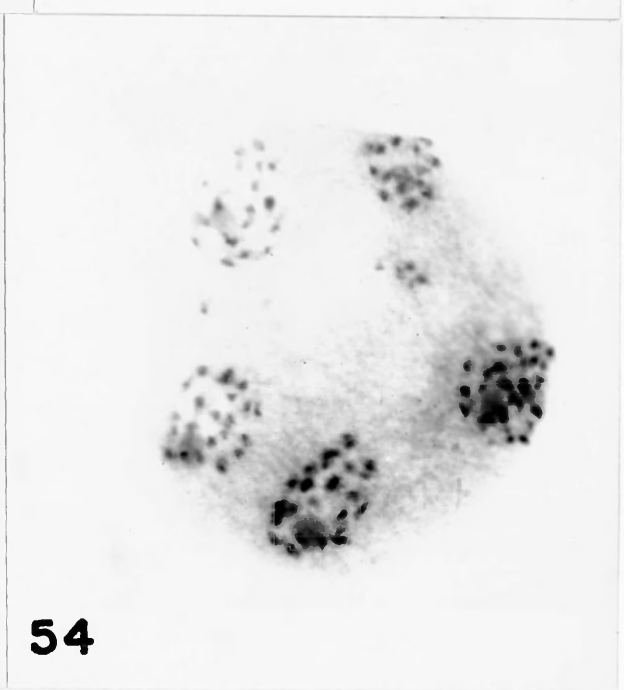

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PLATE IX

VITA

Full Name: Raymond Wilbur Buck, Jr.

Permanent Address: Monticello, Maine

Degree to be Conferred; date: Doctor of Philosophy; June 7, 1952

Date of birth: April 20, 1919

Place of birth: Monticello, Maine

Secondary Education: Ricker Classical Institute, Houlton, Maine

Collegiate Institutions attended	Dates	Degree	Date of Degree
University of Maine	1937-1942	B.S.	June, 1941
University of Maryland	1948-1952	M.S.	June, 1950

Positions held:

Graduate Fellow, University of Maine, Orono, Maine 1941-1942

Pvt. to S/Sgt., U. S. Army Air Forces, United States 1942-1946

Instructor in Botany, University of Maine, Orono, Maine 1946-1948

Graduate Assistant, University of Maryland, College Park, Maryland 1948-1950

Agent, United States Department of Agriculture, Bureau of Plant Industry, Beltsville, Maryland 1950-