

Cytogenetic Studies in Non-Tuberous *Solanum* Species, Hybrids and Amphiploids*

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All the ten taxa studied revealed a regular course of meiosis. The twentyfour hybrids produced fell into six groups depending upon the nature of meiosis and the extent of pollen fertility in them. Irregularities in the form of non-orientation of bivalents on metaphase plates, anaphase bridges, laggards and unequal distribution of chromosomes at anaphase I were observed in the hybrids. The six amphidiploids produced by colchicine treatment from the hybrids representing all the six groups led to the conclusion that sterility observed in respective hybrids was mainly due to cryptic and gross structural differences of which the former appeared to be more predominant.

Although considerable cytogenetic work has been done on the tuber-bearing group of the genus *Solanum* to which potato (*S. tuberosum*) belongs, little attention has been paid in this respect towards the non-tuberiferous group involving the popular vegetable brinjal (*S. melongena*) and its wild relatives. The wild species of the genus *Solanum* possess attributes like hardiness and resistance to pests and diseases which most of the high yielding varieties of brinjal lack. A knowledge of the cytogenetic relationships among the species would be helpful in evolving a satisfactory breeding programme for improvement of the crop utilising the germplasm of wild species of *Solanum*. In the studies presented herein, a detailed cytogenetic analysis of ten taxa of the non-tuberous group of the genus *Solanum* and their hybrids and amphiploids was made with the view to gain

an insight in to the cytogenetic relationships among the species and to understand the nature of differentiation of species in this group of *Solanum*.

MATERIAL AND METHODS

The material involved in the present investigation consisted of nine-tuberous species of *Solanum*, viz., (1) *S. melongena* Linn. which has represented by one cultivar, pusa purple long and one wild variety, *insanum* Prain, (2) *S. incanum* Linn, (3) *S. xanthocarpum* Schrad. and Wendl. (4) *S. indicum* Linn, (5) *S. integrifolium* Poir, (6) *S. gilo* Raddi, (7) *S. khasianum* Clarke, (8) *S. sisymbriifolium* Lam. and (9) *S. zuccagnianum* Dun. and their hybrids and amphiploids.

The flower buds in suitable stage were fixed between 8.30 and 9.00 a.m. in a mixture of 3 parts of alcohol, 4

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parts of chloroform and 1 part of propionic acid with traces of ferric acetate. The material was kept for 24 hours in a refrigerator maintained at 10°C. The flower buds were then washed under tap water several times until the chloroform was completely washed off. Then the flower buds were transferred to 70 per cent alcohol. Propiono-carminic PMC smear method was adopted for preparation of slides.

RESULTS AND DISCUSSION

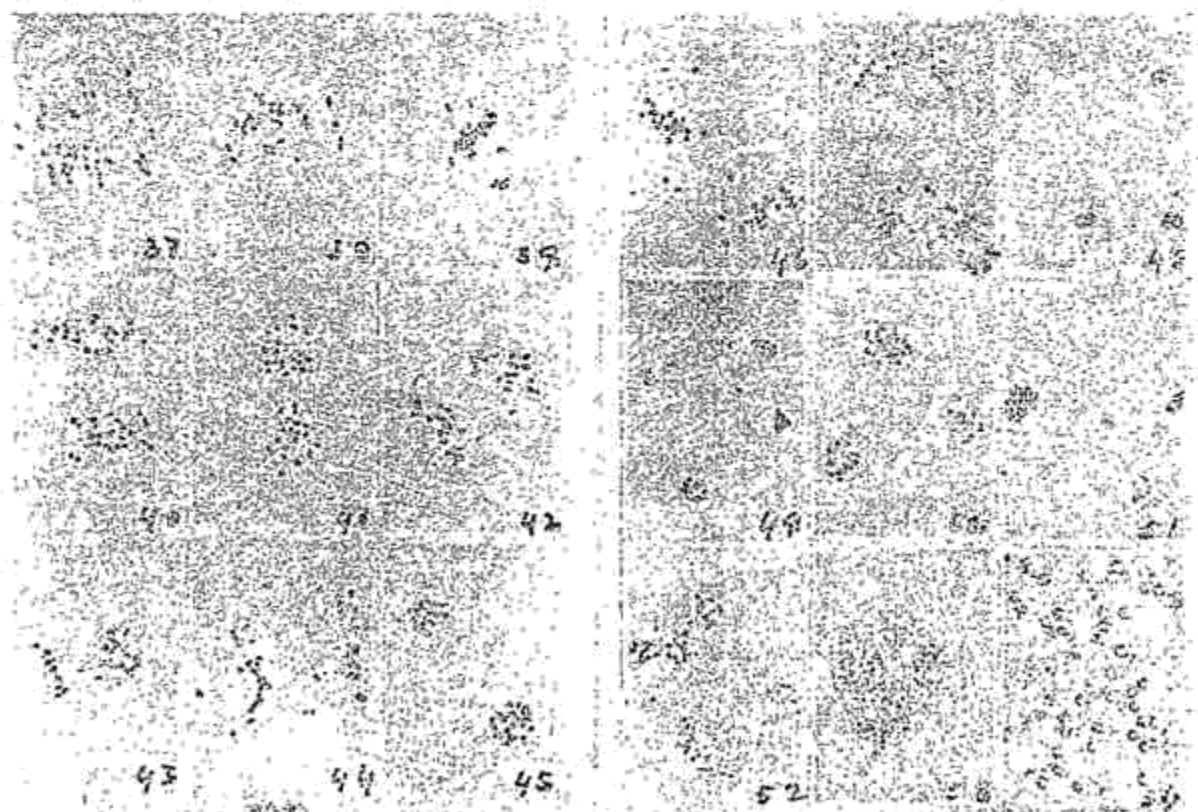
A. Meiosis in parents: (plate I-1 to 9)

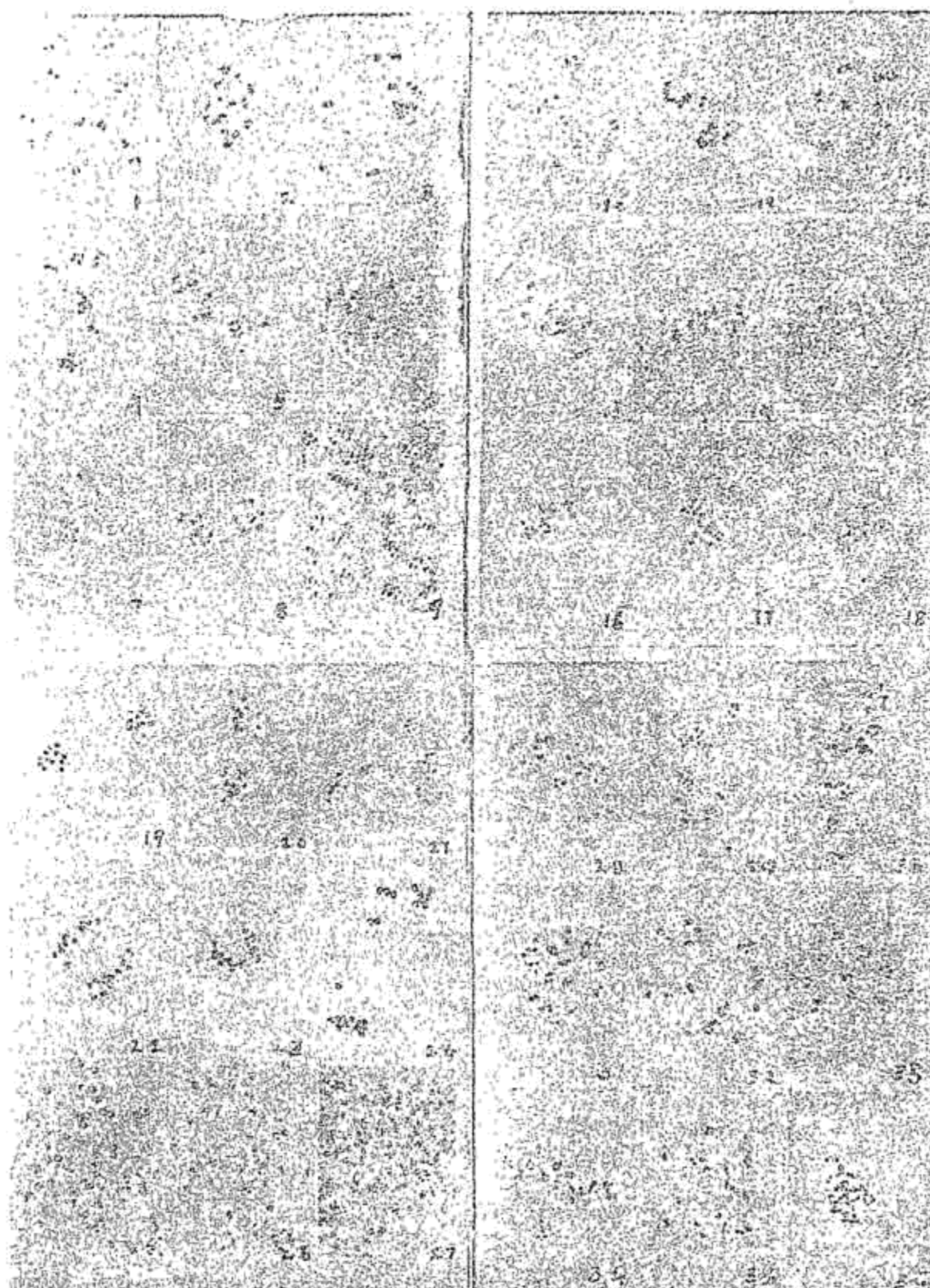
All the ten parents, except *S. sisymbriifolium*, showed regular course of

meiosis. *S. symbrifolium* exhibited two univalents in five per cent of P. M. Csak diakinesis. Even though meiosis was regular, precocious disjunction involving one to five bivalents was observed, in all the species. *S. xanthocarpum* exhibited the maximum precocious disjunction (32 per cent) and *S. indicum* and *S. integrifolium* exhibited the minimum (10 per cent). All the species were highly fertile.

B. Meiosis in hybrids: (plate I-10 to 27)

For presenting the cytological data, the twentyfour hybrids that could be produced and studied in this investiga-





tion have been grouped into six categories, depending upon the nature of meiosis and the extent of pollen fertility in them. Meiotic behaviour was classified into regular and irregular ones and the hybrids were accommodated in three fertility ranges viz, low fertility group having the pollen fertility from 0 to 25 per cent medium fertility group having fertility from 26 to 80 per cent and high fertility group having the fertility from 81 to 100 per cent. All the hybrids which exhibited normal bivalent associations classified as undergoing normal meiosis and the rest which showed multivalent associations are classified as undergoing abnormal meiosis. Accordingly the twentyfour hybrids fell into the following six groups.

1. Normal meiosis with high pollen fertility.
2. Abnormal meiosis with high pollen fertility.
3. Normal meiosis with medium pollen fertility.
4. Abnormal meiosis with medium pollen fertility.
5. Normal meiosis with low pollen fertility.
6. Abnormal meiosis with low pollen fertility.

1. The hybrids, *S.melongena* cultivar x *S.melongena* var. *insanum*, *S.melongena* cultivar x *S.incanum* and the reciprocals would fall in to the first group. Abnormalities such as non-orientation of bivalents on the metaphase plates, precocious disjunction and chromatin

bridges were noticed in certain of the hybrids in this group.

2. The hybrids, *S.melongena* var. *insanum* x *S.incanum* and the reciprocal one fell in the second group. High pollen fertility (90.7 to 92.1 per cent) was observed in spite of higher association of chromosomes and other abnormalities. Univalents to quadrivalents were noticed during diakinesis and metaphase I. Precocious disjunction of bivalents and chromatin bridges were also seen in the P.M.Cs. Even though multivalent association was noticed, the anaphase I separation was regular and equal (12/12) in all the P.M.Cs studied.

3. The two hybrids, *S.indicum* x *S.melongena* cultivar and *S.gilo* x *S.zuccagnianum* could be grouped under third category. Precocious disjunction of 1-4 bivalents, chromatin bridges and laggards were noticed in a low frequency.

4. The fourth group consisted of the hybrids, *S.indium* x *S.melongena* var. *insanum* and *S.incanum* x *S.indicum*. The pollen fertility was 36.1 per cent in the former hybrid and 39.2 per cent in the later. Precocious disjunction of one to three bivalents, chromatin bridges and laggards were noticed in low frequency. At anaphase I, unequal separation of 13/11 was seen in 6 to 10 per cent of the P.M.Cs.

5. The hybrids, *S.melongena* cultivar x *S.integrifolium*, *S.integrifolium* x *S.melon-*

gena cultivar, *S. melongena* var. *insanum* x *S. integrifolium*, *S. integrifolium* x *S. melongena* var. *insanum*, *S. incanum* x *S. integrifolium*, *S. integrifolium* x *S. incanum*, *S. melongena* cultivar x *S. gilo* fell in this group. In the hybrids, *S. melongena* cultivar x *S. integrifolium*, *S. incanum* x *S. integrifolium* and their reciprocals as well as *S. incanum* x *S. gilo* and *S. indicum* x *S. gilo*, 1-2 bivalents were seen to be non-orienting on equatorial plates in one to five per cent of the P.M.Cs. Precocious disjunction of one to five bivalents was also noticed in 16 to 34 per cent of the P.M.Cs. Either chromatin bridges or laggards or both together were recorded to occur in a low frequency in all the hybrids except in *S. indicum* x *S. integrifolium*.

6 The hybrids, *S. xanthocarpum* x *S. melongena* var. *insanum*, *S. zuccagnianum* x *S. melongena* var. *insanum* and *S. xanthocarpum* x *S. indicum* constituted the six groups. In the first and the last hybrids, abnormal meiosis was accompanied by low fertility. In the second hybrid, abnormal meiosis was recorded but the extent of fertility could not be assessed as the flower buds dropped off in early stages before flower opening but after microsporogenesis. Since all the tetrads were seen degenerating, this hybrid was grouped in this category. The pollen fertility in the other two hybrids was very low (0.2 to 0.4 per cent). The chromosome associations ranged from hexavalent to bivalents in the hybrid *S. xanthocarpum* and *S. indicum* while the other hybrids recorded associations ranging from quadrivalents to univalents

at both diakinesis and metaphase plates. Non-orientation of chromosome bodies on the equatorial plates, precocious disjunction, laggards, bridges and unequal separation were observed in these hybrids. Bivalents or multivalents ranging from one to three did not orient on the metaphase plate in four to nine per cent of P.M.Cs. examined. Precocious disjunction of one to seven bivalents was noticed in 38 to 62 per cent of the P.M.Cs. In the two hybrids involving *S. xanthocarpum* one to three laggards were seen in 10 to 16 per cent of the P.M.Cs at anaphase I where as in the hybrid, *S. zuccagnianum* x *S. melongena* var. *insanum*, one chromatin bridge was noticed in 12 per cent of the P.M.Cs and also one to two laggards were recorded in 12 per cent of the P.M.Cs. In the hybrids involving *S. xanthocarpum*, the chromosomes separated as 13/11 and 14/10 at anaphase I in a low frequency while in the hybrid, *S. zuccagnianum* x *S. melongena* var. *insanum*, unequal disjunction of 13/11 was observed in a few cells.

In order to gain an insight in to the nature of differentiation the chromosomes of a hybrid in each of the above six groups were doubled by colchicine method.

C. Meiosis in amphiploids

1. Amphiploid of *S. melongena*, cultivar x *S. incanum*:

The chromosome associations ranged from univalents to quadrivalents at diakinesis and metaphase I. The

pollen fertility recorded was 60.5 per cent.

2. *Amphiploid of S.indicum x S.melongena, cultivar:*

The chromosome associations ranged from univalents to quadrivalents. The pollen fertility was estimated to be 66.8 per cent.

3. *Amphiploid of S.melongena, cultivar x S.integrifolium:*

Chromosome associations ranging from univalents to quadrivalents were recorded. The pollen fertility in this amphiploid was estimated to be 62 per cent.

4. *Amphiploid of S.melongena var. insanum x S.incanum:*

The chromosome associations ranged from univalents to hexavalents. The pollen fertility recorded was 65.3

5. *Amphiploid of S.xanthocarpum x S.melongena var. insanum:*

The chromosome associations ranged from univalents to octovalents. The pollen fertility in this amphidiploid was 70.7 per cent.

6. *Amphiploid of S.incanum x S.indicum:*

The chromosome associations ranged from univalents to hexavalents. The pollen fertility was 69.0 per cent in this amphidiploid.

All this six amphidiploids were characterised by disturbances like non-orientation of chromosomes or chromo-

some association equatorial plates, precocious disjunction, laggards and bridges and unequal separations during first and second meiotic divisions. Triads and pentads were observed among tetrads in a low frequency in all the amphidiploids.

The occurrence of 11 bivalents and two univalents was recorded in *S.sisymbriifolium* by Swaminathan et.al. (1954) also. The presence of such univalents was noticed even in diploid tuber-bearing species of *Solanum* by Bains (1951), who interpreted such univalents as being due to precocious separation of rod bivalents at metaphase I. From the common occurrence of precocious disjunction in *Solanum* species at metaphase I, it can be suggested that the occurrence of two univalents in *S.Sisymbriifolium* at diakinesis might be due to precocious disjunction.

The occurrence of quadrivalents in the amphidiploids is an indication of close homology between the parental genomes. The extent of homology can be compared to that of intervarietal genomes since the maximum number of quadrivalents (7) formed in these amphidiploids exceeded the maximum number of quadrivalents (5) recorded by Rajasekaran and Desai (1965) in an autotetraploid of *S.melongena*.

In the groups of hybrids where there was normal and abnormal meiosis with medium and low fertility, the fertility improved after chromosomal doubling. The quadrivalent frequency

recorded was less than that of the amphiploids of *S. melongena* cultivar \times *S. incanum* and *S. melongena* var. *insanum* \times *S. incanum*. This may be attributed to the greater degree of structural differentiation of the parental genomes which led to the formation of more number of bivalents in the amphiploids because of preferential pairing due to differential affinity (Darlington, 1937). The presence of structural differences between the parents is also evident from the occurrence of chromatin bridges during the course of meiosis in the hybrids. However, the frequency of quadrivalents in these amphiploids is also very high which suggests a close homology between the parental sets of chromosomes. The genomes of the parents of these hybrids, though similar to a great extent, differ by either gross or cryptic structural differences or both. These differences are not large enough to prevent pairing but at the same time can cause sterility in the hybrids.

The sterility noticed in all the six amphiploids may be entirely or partly due to formation of higher associations. The genic causes for sterility cannot be disentangled in such causes. However, the evidence for the existence of such factors bringing in sterility through disturbances at the second division of meiosis could be obtained in all the amphiploids.

The occurrence of a hexavalent or a pentavalent in the amphiploids of *S. melongena* var. *insanum* \times *S. indicum* and *S. incanum* \times *S. indicum* and an octo-

valent or a lower association higher than quadrivalent in the amphiploid of *S. xanthocarpum* \times *S. melongena* var. *insanum* suggests that quadrivalents observed in the corresponding F_1 hybrids are due to the heterozygosity for a translocation involving large segments. The occurrence of multivalent associations of the kinds mentioned in the hybrids and amphiploids suggests at first glance that the quadrivalents formed in the hybrids are due to quadruplicate nature of chromosomes. But such possibility is ruled out because no parental species studied showed quadrivalent formation. And also if the segments involved in the translocation are small, the chromosomes involved in the quadrivalents would have formed 4 bivalents in the amphiploids. However, one of the two quadrivalents formed in the hybrid, *S. xanthocarpum* \times *S. melongena* var. *insanum*, might be due to translocation involving small segments. This assumption is made based on the fact that only one octovalent, septavalent, hexavalent, or pentavalent was observed in the amphiploid corresponding to one quadrivalent of the hybrid. The four chromosomes which formed the other quadrivalent would have formed only quadrivalents or lower associations in the amphiploid. The occurrence of two quadrivalents was also observed in the hybrids, *zuccagnianum* \times *S. melongena* var. *insanum* and *S. xanthocarpum* \times *S. indicum*. Formation of a hexavalent or a pentavalent in the hybrid, *S. xanthocarpum* \times *S. indicum* indicates that three pairs of chromo-

somes should have been involved in translocations in the parents.

The occurrence of a quadrivalent in *Solanum* hybrids due to heterozygosity for translocations was also reported by earlier workers. Swaminathan and Magoon (unpublished, cited by Magoon et al., 1962) in *S.torvum* x *S.hispidum* and Babu Rao (1965) and Rajasekaran (1968) in *S.xanthocarpum* x *S.melongena* var. *insanum*.

From the foregoing analysis, it is evident that cryptic structural changes have played a more predominant role than the gross structural changes like inversions and translocations in the evolution of these species through the latter types of structural changes are not uncommon. Similar views were expressed by Westergaard (1948) and Rajasekaran (1968) in respect of *Solanum* species.

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- PLATE I — 1 to 9 Meiosis in parents — 10 to 27. Meiosis in Hybrids — 28 to 54 Meiosis amphiploids.
1. 12 II at diakinesis
 2. 11 II + 2 I at diakinesis
 3. 12 II at Prometaphase I
 4. 12 II at M I
 5. Precocious disjunction of one bivalent at M I
 6. Precocious disjunction of two bivalents at M I
 7. Precocious disjunction of four bivalents at M I
 8. 12/12 separation at A I
 9. Pollen grains (Normal)
 10. 12 II diakinesis
 11. 1 IV + 10 II at diakinesis
 12. 2 IV + 8 II at diakinesis
 13. 12 II at prometaphase
 14. 12 II at M I (precocious separation of one bivalent)
 15. 1 IV + 10 II at M I
 16. 1 VI + 9 II at M I
 17. Non-orientation of a bivalent on M I Plate
 18. Precocious separation of three bivalents at M I

19. 12/12 distribution at A I
20. 13/11 distribution at A I
21. 14/10 distribution at A I
22. One bridge at A I
23. Two bridges at A I
24. Laggards at A I
25. Pollen grains—high fertility group
26. Pollen grains—medium fertility group
27. Pollen grains—low fertility group
28. 1 VI + 22 II at late diakinesis
29. 24 II at M I
30. 3 IV + 18 II at M I
31. 4 IV + 16 II at M I
32. 4 IV + 2 III + 13 II at M I
33. 6 IV + 1 III + 10 II + 1 I at M I
34. 1 V + 3 IV + 1 III + 14 II at M I
35. 1 VI + 3 IV + 15 II at M I
36. 1 VI + 5 IV + 2 III + 8 II at M I
37. 1 VII + 1 IV + 18 II + 1 I at M I
38. 1 VIII + 2 IV + 3 III + 11 II + 1 I at M I
39. Non-orientation of some bodies on M I plate
40. 24/24 separation at A I
41. 25/23 separation of A I
42. 26/22 distribution at A I
43. bridges at A I
44. Laggards at A I
45. T I
46. Non-orientation on M II Plate
47. Laggards At A II
48. T II
49. T II with laggards
50. A triad
51. A triad with expulsion of a mass of chromatin
52. A Pentad
53. A normal tetrad and
54. Pollen grains.