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CYTOLOGY OF A FERTILE MONOPLOID TOMATO.

by

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CYTOLOGY OF A FERTILE MONOPLOID TOMATO.

Introduction.

The term monoploid is used here rather than haploid, not merely because it is replacing haploid in recent literature, but because monoploid signifies "true haploidy" (Darlington, 1932.) Thus the strain of the Earliana variety of tomato used in this investigation is considered to be a monoploid, since it is naturally occuring, has twelve chromosomes or the basic number of the genus, in somatic cells as well as in the gametes. The pollen is highly fertile and ovule development is apparently parthenocarpic resulting in abundant fruit with viable seeds. This is the first highly fertile monoploid tomato to be reported, and as far as can be ascertained the first fertile monoploid flowering plant.

The observations to be reported in this paper are part of a series of investigations carried on for the past ten years at the Dominion Experimental Station at Summerland, British Columbia, in an attempt to determine the cause of roughness in the Earliana tomato. A rough fruit may be described as one, which, instead of having a regular smooth and round shape, is irregular in shape, - that is with corrugations and grooves. These rough fruits are rejected by the canners, resulting in serious losses to the growers. Breeding, selection, and nutritional studies have been of no avail in the elimination of roughness. Temperature, especially the cold

night temperatures of the early summer seem to have some effect, giving an increase in the ammount of roughness. Besides cold the other main factor influencing roughness is heterozygosity in the plants, a condition which is in accord with our present day knowledge of monoploids. To date, cytological study has not contributed greatly to the explanation and solution of roughness, as only microsporogenesis has been thoroughly investigated. However, this process is of interest since it differs from that described for other monoploid plants in that there is an equal distribution of the chromosomes at the two divisions, which are, in effect, two successive mitoses during which each chromosome divides twice.

Material and Methods.

The material for this investigation was grown during 1933, 1934 and 1935 at the Dominion Experimental Station, Summerland, B.C. Two strains of the Earliana variety were used; A common diploid variety, John Baer, was used for comparison. Buds and blossoms were collected at random throughout the field plots in order to insure that the material was representative of the variety and not of one particular plant.

Two killing and fixing solutions were used. One was weak chrom-acetic solution (Schaffner's formula), and the other was an alcohol-acetic fluid known as B.C. Fixing Solution. It has the following constituents:- 95 per cent alcohol, 100cc; acetic acid (glacial), 2cc; formalin, 5 cc; and water, 25 cc. Both caused some plasmolysis but the B.C. Fixative was the superior, and was very convenient because material could be left in it for an indefinite length of time. The material was imbedded in parafin and sections were cut 8 to 10 microns in thickness and stained with iron alum and a hematoxylin.

Anther smears were made with both the monoploid and diploid material, fixed with Navaschin's solution and stained with Gentian Violet (La Cour, 1931). This method proved quite satisfactory but the parafin method was used almost entirely as it gave series of stages in single anthers.

Experimental Results.

Somatic chromosome counts.

Chromosome counts were made in root tip cells of the monoploid Earliana tomato and twelve chromosomes or the x number were observed. (Fig. 1). In order to be sure that each bud used for microsporogenesis studies was a monoploid, chromosome counts were made in somatic cells of the sepals, petals, anthers, and style. Fig. 2 shows a metaphase plate in a petal cell; Fig. 3 shows a side view of metaphase chromosomes of three levels of a nucleus in an anthertip cell; and Fig. 4 shows a late anaphase stage in a cell of the style. All stages show twelve chromosomes which is the monoploid number for the tomato.

Microsporogenesis.

In the following descriptinn of microsporogenesis in the monoploid, terms used to describe stages analogous to those occuring in the diploid, particularly the prophase stages, will be placed in quotation marks to show that they are not strictly applicable here.

The nucleus at the last resting stage preceding meiosis in the microsporocytes consists of a fine reticulum of chromatic substance. Scattered along this reticulum are an indefinite number of dark staining bodies (Fig.5).

With the beginning of the early prophase the number of anastomosing reticular threads becomes greatly reduced. Those remaining thicken slightly, forming single

leptotene threads which are joined together by finer strands (Fig. 6). Sometimes the remains of the chromatic bodies that were scattered on the reticulum are still present, but these disappear later. At late leptotene the threads become a little thicker and the fine connecting fibres become less distinct, (Fig. 7).

As the prophase progresses the threads continue to thicken and show considerable variation in diameter (Fig. 8). This corresponds to zygotene at which stage synapsis normally takes place. The contraction known as synizesis has not been observed in this monoploid although some contraction of the nuclear constitients takes place. It is probably an artifact caused by fixation. At late "zygotene" there is no evidence of pairing between the chromosomes or any part of them as would be expected in a diploid.

The next stage is "pachytene"where the chromosomes thicken and begin to shorten in length. Again they show a evidence of having paired (Fig. 9).

"Diplotene", where in normal diploid meiosis it is customary for the chromosomes to shorten and thicken and for loops to occur between the paired parts. Whereas in the monoploid Earliana there is shortening and thickening of the chromosomes but no looping,- a further evidence that no pairing took place. Figures 10 and 11 show two consecutive stages of this. The fine connecting fibres are still present but this is the last stage at which they were seen. Fig. 10 A. shows a special case of a nucleus at "diplotene".

Nuclei of this sort occasionally occur and the parallel position of some of the threads and chromosomes might easily be interpreted to be the result of pairing, but nothing was observed previous to this stage that would substantiate this. Perhaps it is an accidental parallelism or else the chromosomes are beginning to form daughter chromatids.

At "diakinesis" the chromosomes present an unexpected appearance. They are "doubled". Apparently a longitudinal splitting has taken place giving them an appearance similar to that of the paired chromosomes of a diploid, but instead of being in the form of tetrads they are diads, and the number of diads is 12. Individuality of the chromosomes is prominent at this stage, but they do not possess the same characteristics as those of the usual diploid tomato. The split univalents are scattered throughout the nucleus and one noticeable feature about them is that the univalent halves widely repulse each other to varying extents but they are not entirely separated and wandering (Fig. 12). During late "diakinesis"the univalent halves draw together and the nucleolus and nuclear membrane disappear (Fig. 13). This compacting process continues until the chromosomes become rounded and shrunken to form small spheres losing their individuality entirely. Now a metaphase plate is formed at which the split in the greatly contracted chromosomes can be observed only with difficulty, (Fig. 14).

At metaphase of the first division the chromosomes line up regularly at the equatorial plate and a bi-polar

spindle is always present. In early anaphase the twelve daughter univalents (or halved univalents)pass regularly to each pole (Fig. 15). In a few odd cases as shown in Figure 16 the dividing univalents are scattered on the spindle, a regular metaphase plate not being formed in these cases. Figure 17 shows the individuality of the 12 chromosomes at "disjunction" during first metaphase, eleven of which show varying degrees of telomitic or terminal spindle attachment, and the other one a telomitic attachment, the spindle being attached to the centre of the arc-shaped chromosome. At early anaphase these chromosomes do not pull apart in the form of V's as is characteristic of paired diploid chromosomes. Late anaphase shows 12 chromosomes moving regularly to each pole (Fig. 18). At telophase 1 the chromosomes mass together in a loose aggregation (Fig. 19).

At interphase there is a definite reorganization of the nucleus. Figure 20 shows the two nuclei at early interkinesis. Figure 21 shows a later stage where the nuclei are complete with nucleoli and definite chromosomes. The chromosomes at this stage show doubleness and individuality. It was observed that the individuality of the chromosomes was consistent and the same types could be identified at diakinesis, metaphase 1, and interkinesis, - see figures 12, 17, 21, which are placed side by side to facilitate comparison.

Following the double stage during interphase the chromosomes become smaller and rounded, the nuclear membrane and nucleolus disappear, and the second metaphase plates are

formed with well-defined spindles (Fig. 22). Both groups of chromosomes divide simultaneously and pass to the poles in regular and orderly manner (Fig. 23). At late anaphase the spindle fibres near the poles are not clearly defined (Fig. 24). Upon reaching their respective poles the chromosome groups are surrounded by a nuclear membrane and a nucleolus appears. The chromosomes at this stage lose their spherical shape and become elongated (Fig. 25).

Pollen tetrads are formed and these break apart and develop into pollen grains. Pollen is about 90 per cent fertile although this figure varies for different buds. This was determined from counts made of heavily stained, well-rounded full pollen grains in various anthers. Pollen germinates readily on the stigma and the style is packed with pollen tubes passing down it.

Pollen nuclei were seen to enter the embryo sac, but fertilization was not observed to take place, however there is not sufficient evidence on this point yet, and many more embryos will have to be examined before it can be proved that parthenogenesis takes place. Endosperm development appears normal but there are certain peculiarities in the embryo development that require a great deal more research before it can be described completely.

Review of Literature and Discussion.

Haploid sporophytes have been described in eight genera of flowering plants. Datura, Oenothera, Nicotiana, Triticum, Crepis, Brassica, Matthiola, and Solanum. The haploids are smaller than the diploids, with smaller cells and certain other alterations in form and character. They are almost completely sterile. These have appeared (a) after crossing with a distantly related species, (b) after subjection to cold at the time of fertilization and (c) in the tomato, "spontaneously". (From a summary of Gates and Goodwin, 1930).

The monoploid Earliana tomato does not conform to any of the above described general characteristics for haploids. This monoploid plant is not noticeably smaller than the diploid, yet it is slightly smaller. Among the most noticeable differences observed in the field are the following: slightly smaller leaves with edges curling inwards exposing lighter colored under surface; an increase in the number of floral parts , usually two more parts than in most diploids and often more than two extra stamens; fruits are, as a rule, borne in large numbers on a truss instead of a hanging cyme as is customary for other varieties. The size of the cells is approximately mid-way between the measurements reported for the cell size of haploid and diploid tomatoes by Humphrey, (1934). It appears that this monoploid originated "spontaneously". The following history is copied from U.S.D.A.

Miscellaneous Publication No. 160: "Earliana was introduced in 1900 by the firm of Johnson and Stokes, of Philadelphia. The original stock was produced by George Sparks, of Salem, N.J. and is reported to have been developed from a single plant selection made in a field of tomatoes grown from seed purchased under the name of Stone." The author does not know whether all Earliana tomatoes are monoploid or if this condition only exists in the strains developed by Mr. W.M. Fleming at the Summerland Experimental Station and described in this paper.

The cytology of the monoploid Earliana tomato differs from that of any haploid previously described. Belling and Blakeslee (1927, 1927) give an account of the cytology of Datura haploids produced by subjecting the plants to low temperature at the time of fertilization. The 12 chromosomes show no attraction for each other at the metaphase of the heterotypic mitosis in the microsporocytes but either move at random to the poles (in assortments of 1 and 11, 2 and 10, 3 and 9, 4 and 8, 5 and 7, 6 and 6), or there may be non-reduction. If there is segregation the groups of chromosomes after a short interphase pass through a homeotypic metosis where each divides and the halves are distributed in the usual manner. Such microsporocytes form 4 small microspores, usually 2 equal and smaller and 2 equal and larger. Polyspores are developed when irregularities during anaphase of the first division give chromosomes independent of the main groups and these organize very small cells in

addition to the 4 principal cells. All of these small grains constitute the mass of abortive pollen which is developed. Non-reduction takes place when the 12 chromosomes split and the halves are distributed in two sets, 12 + 12, and two pollen grains result each with the haploid set of chromosomes. These constitute the good pollen grains which make up about 12 percent of the total. The Datura haploid and Earliana tomato monoploid are not similar since in the latter there are two divisions in the tomato and the chromosomes divide at the first division as well as at the second and 12 halves pass regularly to the poles in each division resulting in fertile pollen.

Chipman and Goodspeed (1927) made a cytological study of meiosis in the microsporocytes of the haploid from Nicotiana tobacum, var.purpurea, one of the two haploids reported by Clausen and Mann (1924). This haploid had 24 chromosomes and was female sterile but some viable pollen was produced. There was pairing of the threads before synizesis in the diploid but not in the haploid. Synizeses in the haploid is followed by pachynema and the single spireme then segments into the haploid set of 24 chromosomes. Bipolar spindles are often formed resulting in a random distribution of the 24 chromosomes some of which occasionally pass into the cytoplasm. Univalents sometimes divide during the heterotypic mitosis and when rarely all 24 divide there results a giant spindle and the formation of dyads which might develop into pollen grains with a full set of haploid chromosomes.

Here there is a division of all univalents at the first division, but this is not followed by a second division as in the tomato and pollen dyads and not tetrads are formed.

A haploid occuring in a pure line of N. glutinosa was described by Goodspeed and Avery (1929). This plant was one of a culture which had been subjected to x-rays as seedlings but its origin was "spontaneous" and unconnected with the treatment received. The 12 chromosomes were distributed at random in pollen meiosis.

Clausen and Lammerts (1929) crossed N. digulata, an allahexaploid with carmine flowers and 36 bivalent chromosomes, with the pollen of a form of N. tabaccum, identical with var. purpurea except in having white flowers. The latter had 24 bivalents. The F_1, consisting of 173 plants had a single plant with small white flowers and was identical in other features with haploid purpurea. It was completely sterile, had 24 univalent chromosomes in its pollen mother cells and these were usually distributed at random. In one mother cell 19 of the univalent chromosomes were seen to divide, while the rest separated, one half-univalent being fragmented into two.

Kostoff (1929), obtained a haploid by pollinating an aberrant plant of Nicotiana Tabaccum macrophylla having 70-72 chromosomes with pollen of N. Langsdorffii ($n = 9$). Out of 1000 seedlings one reached maturity. This was a haploid Langsdorffii, somewhat smaller than the diploid and having 9 Langsdorffii chromosomes. In pollen mother cells

the 9 chromosomes do not form an equatorial plate, but spread out towards the poles of the spindle and separate at random. Sometimes some of the chromosomes divide in the first division. When all the chromosomes remain in a group at interkinesis they all frequently divide in the second division forming pollen dyads. They may separate into two or more groups, each of which forms its own spindle, with resulting pollen triads, pentads or even octads. About 8% of the pollen appears good.

With Nicotiana haploids, random distribution of the undivided univalent chromosomes seems to be the general rule. Such is not the case in the monoploid Earliana tomato where all univalents divide at the first division.

Gaines and Aase (1926) obtained a haploid with 21 chromosomes by pollenating winter wheat, Triticum compactum humboldtii (42 chromosomes), with Aegilops cylindrica. The haploid could not be distinguished from the female parent No. 128 until the time of flowering when peculiarities characteristic of sterility appeared. The plant was about 99.8 percent sterile. There was no pairing of chromosomes during meiosis in the microsporophytes because there were probably three dissimilar sets of 7 chromosomes each. The chromosomes are generally distributed irregularly during the heterotypic mitosis or there may be a mixture of the two processes. The homeotypic mitosis continues the disorderly distribution of the chromsomes giving many irregularities and forms of polyspory. No normal pollen grains were observed to develop

although such might rarely be found. Pollen mother cells sometimes coalesce forming giant pollen grains. In some respects this haploid ressembles the tomato,- the haploid being indistinguishable from the others, and the univalent chromosomes splitting lengthwise at the first dicision. However this is not the rule as it is in the tomato.

In some Matthiola hybrids, Lesley and Frost (1928) obtained in F_2 two extreme dwarfs, one of which was diploid (14 chromosomes with two extra chromosome fragments, the other haploid with one such fragment. In some cases there is random segregation of the haploid chromosomes followed by other irregularities. Frequently the chromosomes split and separate (except sometimes the extra fragment) the heterotypic mitosis evidently being omitted. This results in pollen dyads.

Hollingshead (1928) described two haploid individuals of Crepis capillaris ($n = 3$) among progeny of a cross C. capillaris x C. tutorem. It is not certain whether cold or foreign pollen is the exciting cause for the haploid being formed. The cytology of the haploid is not described in this article, and unfortunately the 1930 paper by this same author which deals with the cytological study was not available.

Emerson (1929) describes the reduction division in an atypical plant appearing in the F_1 from the cross Oenothera franciscana x the hybrid franciscana sulphurea. The spireme in the pollen mother cells of this haploid is not

continuous and parallelism of the threads is common at synapsis. Pairing was seen at many stages but not as frequently as in the diploid. Later the spireme appears continuous and is thrown into loops, the arms of which are twisted about each other. After second contraction the thread thickens and segments into 7 chromosomes formed end to end. Anaphase chromosomes have not the typical v's with spindle fibres attached to the center. There is no similarity between this and the tomato as there is no pairing in the prophase stages of the tomato and the chromosomes divide at the first division and are distributed regularly.

An account of another haploid in Oenothera is given by Davis and Kulkarni (1930). This one is a haploid mutation in Oe. franciscana and is called "pointed tips". In the pollen mother cells the spireme segments into 7 chromosomes which do not pair. Irregular distribution of the chromosomes in the heterotypic mitosis (6 + 1), (5 + 2) (4 + 3) gives a mass of sterile pollen. Functional pollen grains are the result of the multipolar spindle becoming unipolar, the 7 chromosomes all becoming attached to the spindle fibres from that pole. The heterotypic mitosis being omitted, the nucleus is reconstituted and the chromosomes split. This corresponds to the period of interkinesis and is followed by an ordinary homeotypic mitosis in which seven chromosomes pass to each pole of the spindle and a dyad of pollan grains is formed. Here the formation of a dyad of full sized pollen grains by omission of the reduction division is similar to that

found by Belling and Blakeslee in Datura, but is not at all comparable to the tomato where two divisions occur.

Other Oenothera haploids have been reported by Gates and Goodwin (1930), Stomps (1930 a and b) and Catcheside (1932). The cytology of these is somewhat similar to those described above.

A haploid tomato mutant with 12 chromosomes has been described by Lindstrom (1929). It appeared in the F_2 numbering 327 plants of a varietal cross showing complete fertility, and may therefore be regarded as spontaneous. It is dwarf and completely sterile. An account of the cytology of the haploid is given by Lindstrom and Koos (1931). Little attention was given to the prophase but it was believed that a continuous spireme was present. No metaphase plate was formed. Distribution was irregular but all combinations were observed. Occasional micronuclei were present. The results of cytokinesis were not uniform, groups of from two to six cells appeared. Humphrey (1934) describes the cytology of this particular haploid with special emphasis on the prophase. He found single leptotene threads with lack of pairing and thickening and shortening of these to form chromosomes which existed as unpaired univalents at diakinesis. The author's observations of the prophase stages in the monoploid Earliana tomato agree very closely with those of Humphrey. But at diakinesis the chromosomes of the Earliana tomato are longitudinally split and the first division is a regular mitosis, in which 12 halved univalents pass to each

pole and are distributed regularly and not at random as in the other haploid. Humphrey sometimes observed three spindles at the second division whereas in this monoploid three were never observed. Also normal spores occasionally result from non-reduction at the first division, and hexads are occasionally formed, but in the Earliana tetrads are always formed.

Jorgensen 1928, gives an interesting description of some Solanum haploids. These were produced by attempts to cross two species that would cross only with difficulty. The pollen tube of Solanum luteum may enter the embryo sac of S. Nigrum and discharge its two sperm nuclei but they fail to fuse with the egg and endosperm nucleus and finally disintegrate. From some of the unfertilized eggs embryos begin to develop and it is more than likely that the seeds which produce haploids come from parthenogenetic development. During meiosis in the microsporocytes the 30 chromosomes of the haploid at diakinesis show some degree of pairing, the number of pairs ranging from 3 to 11 or 12. The large number of pairs suggest a reduction of the $12_2 + 12_1$ type. At the heterotypic metaphase only the bivalents are constantly present on the equatorial plate, the univalents being scattered through the cells and most often in the polar regions. The number of bivalents on the plate range from 3 to 12 with numbers of 5 to 8 most frequent. Univalent chromosomes lying near the plate may divide and their products can be recognized by their small size. The

chromosomes pass irregularly to the poles in numbers ranging from 15 to 22 with 18 most frequent. The homeotypic mitosis more commonly presents 18 chromosomes at metaphase, these divide and anaphase proceeds regularly giving 4 pollen grains usually with 18 chromosomes.

A striking peculiarity of the Solanum haploid is the pairing of certain chromosomes in the heterotypic mitosis. This, as Jorgensen (1928) points out, suggests that the 36 chromosomes of the haploid constitute a group composed of 3 sets of 12, two of these sets contain homologues of sufficient similarity to bring them together in a true synapsis. Such behavior could not be expected to occur in the tomato where twelve, the haploid number, is the basic chromosome number of the genus.

Jorgensen found that parthenogenetic embryo development in Solanum nigrum was the result of a fertilization stimulus caused by the nuclei from pollen of distantly related S. luteum entering the embryo sac but failing to fuse with the egg nucleus. In the tomato the pollen tube was seen to enter the embryo sac and discharge its two nuclei, though they came from the same plant, fusion of the egg and pollen nucleus was not observed. This is a difficult proceedure to see at any time, but it is a still more difficult task to prove that fertilization does not take place, and many more embryo sacs will have to be examined before parthenogenesis can be definitely demonstrated. If parthenogenesis is shown to take place in the tomato and the pec-

uliarities of the ensuing embryo development cleared up it will explain how viable seeds are produced, and how the life life cycle of this monoploid perpetuated.

The Earliana when used in crosses with other tomatoes seems to act normally. There are no apparent irreguliarities in the progeny of these crosses, but as yet no cytological examination of these has been made.

This monoploid, though there are but one set of non-homologous chromosomes in its cells, it is not homozygous. This was demonstrated by Mr. Fleming at Summerland when he developed by selection (self-fertilization not being necessary as the tomato is self-pollinated) strains which were homozygous for smooth fruit shape. Later these same strains became hopelessly rough. This can perhaps be explained by considering that mutations resulted from non-disjunction, translocation, or reduplication of small portions of the chromosomes of the monoploid as suggested by East (1930) and Darlington (1932).

Summary.

1. Chromosome counts made in the cells of root tips, sepals, petals, anthers and style, revealed the somatic number of chromosomes to be 12, the monoploid number and the basic number for the genus.

2. Early prophase stages show single leptotene threads with no pairing.

3. Later prophase stages show a thickening and shortening of these threads to form chromosomes, and there is no evidence of pairing having taken place.

4. At diakinesis the chromosomes are "doubled" due to a longitudinal splitting. There are 12 diads or 24 monovalent halves.

5. A regular metaphase plate is formed and the univalent halves pass regularly to each pole exactly as in a homeotypic mitosis.

6. At interkinesis the nucleus is definitely reconstituted and the chromosomes appear double.

7. The chromosomes show characteristic individuality at diakinesis, first metaphase disjunction, and interkinesis.

8. The second division is normal in all respects, 12 chromosomes passing to each of the four poles.

9. Pollen tetrads are formed and the resulting pollen is 90 per cent fertile.

10. Evidence suggests parthenogenetic embryo development and the seed produced is about 85 per cent viable.

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Description of Plates.

All drawings were made with a camera lucida giving a magnification of 3700 diameters. In reproduction the drawings were reduced one half.

Plate 1.

Fig. 1. Metaphase plate in a root tip cell showing 12 somatic chromosomes.

Fig. 2. Metaphase plate in a petal cell with 12 chromosomes. Adjacent to it is a resting nucleus also with 12 chromosomes.

Fig. 3. Three levels of a nucleus in an anther tip cell showing a side view of the 12 chromosomes at metaphase.

Fig. 4. Late anaphase in a cell of the style, 12 chromosomes passing to each pole.

Fig. 5. Microsporocyte nucleus at last resting stage prior to meiosis.

Fig. 6. Early leptotene, threads beginning to thicken.

Fig. 7. Late leptotene, single threads becoming thicker, the connecting fibres are less distinct.

Fig. 8. "Zygotene" with lack of pairing between the chromosomes.

Fig. 9. "Pachytene". The chromosomes show no evidence of having been paired.

Fig. 10. Early "diplotene". The chromosomes lack the characteristic looping of paired parts as in diploids.

Fig. 10 A. Some of the chromosomes have the appearance of being paired, but this is believed to be a stage in the formation of daughter chromatids.

Fig. 11. Shortened and thickened irregular chromosomes of late "diplotene" and diakinesis.

Fig. 12. Diakinesis. The chromosomes are "doubled" due to a longitudinal splitting. The univalent halves repulse each other widely and show marked individuality.

Fig. 17. Side view of metaphase 1 at the time of disjundtion. The chromosomes are separated in the drawing in order to bring out their individuality.

Fig. 21. Interkinesis. Note that certain individual chromosomes can be picked out at this stage, diakinesis, and metaphase.

Plate 11.

Fig. 13. Late diakinesis. The univalent halves of the diads are drawing closer together and the nucleolus has disappeared accompanied by the breakdown of the nuclear membrane.

Fig. 15. Early anaphase 1, daughter univalents passing regularly to poles.

Fig. 16. Exceptional case where a regular equatorial plate is not formed.

Fig. 18. Late anaphase, 12 chromosomes passing to each pole.

Fig. 14. Metaphase plate of first division with contracted spherical chromosomes.

Fig. 19. Telophase 1.

Fig. 20. Early interkinesis, the chromosomes have not yet acquired their characteristic shapes.

Fig. 22. Metaphase 11.

Fig. 23. Early anaphase 11, the chromosomes indicate that a regular division has taken place.

Fig. 24. Late anaphase 11, 12 chromosomes passing to each of the four poles.

Fig. 25. Four nuclei result from the second division.

Fig. 26. Tetrad of pollen grains.

Plate 1.

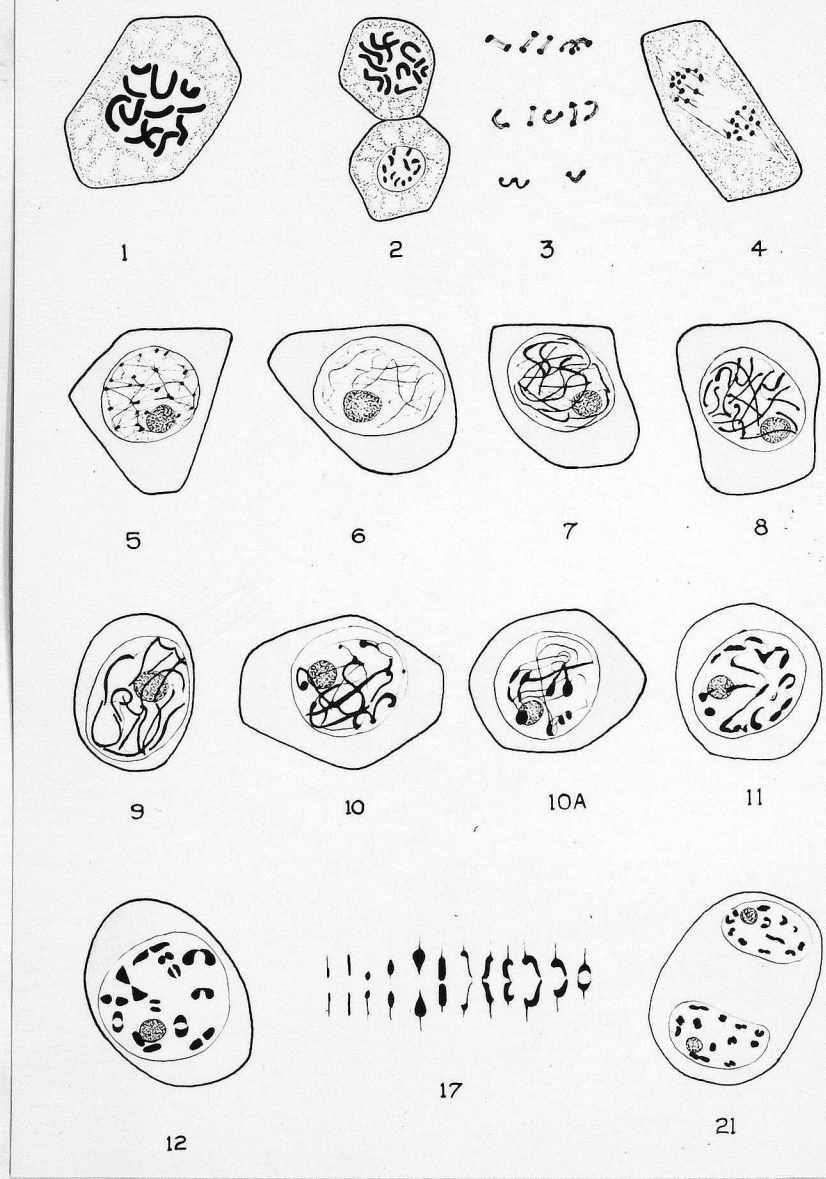
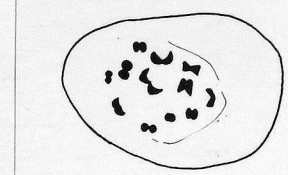


Plate 11.



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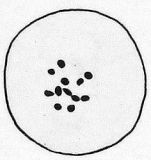

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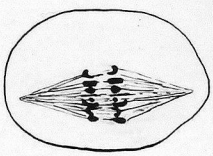

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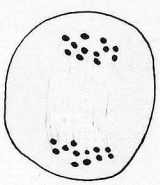

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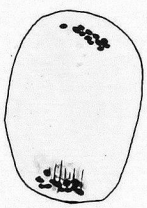

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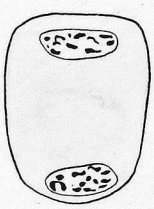

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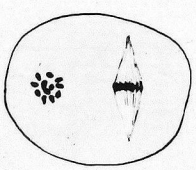

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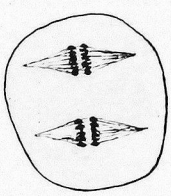

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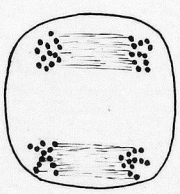

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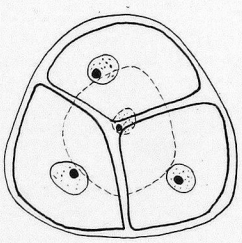

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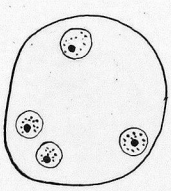

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