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Chromosome Arrangement.

VII. The Pollen Mother Cells of Spinacia oleracea, MILL. and Vicia faba, L.

By

TAKESHIGE MAEDA AND KAZUO KATÔ.

With Plate XXX and 23 Text-figures.

(Received January 26, 1929)

It has been emphasized by DONCASTER (1920), that the resemblance between the arrangement of chromosomes in the equatorial plate and that of floating magnets in a magnetic field is especially conspicuous "when the chromosomes are short and of nearly uniform size," and he pointed out that "this fact may have some bearing on the theory concerning the mechanism of nuclear division." It seems to us very desirable to analyze the phenomenon statistically, and to obtain some idea to what extent a similar statement is applicable to those cases where all chromosomes are not uniform in length and size as we frequently meet with such in both plant and animal kingdoms.

The pollen mother cells of *Spinacia oleracea*, MILL. and *Vicia faba*, L. were found to be suitable for this purpose of investigation as in each of them there has been found a small number of chromosomes, one of which conspicuously differs from the others in its size or length. The results obtained will be mentioned briefly in the following pages.

A. OBSERVATION OF THE POLLEN MOTHER CELLS OF Spinacia oleracea, Mill.

Material for this observation was get from the spiny-fruited garden variety commonly known as "Japanese spinach." The material was 328 TAKESHIGE MAEDA AND KAZUO KATÔ:--

fixed with NAWASCHIN'S fixative for three hours, with a previous treatment with CARNOV'S mixture for several minutes, and then was passed directly, without rinsing with water, through graded alcohols beginning with 30%. It was imbedded in paraffin in the usual manner and sections were cut 8μ thick and stained exclusively with HEIDENHAIN'S iron alum haematoxylin.

I. In the Heterotype Division.

As has been reported by STOMPS (1911), we can find six chromosomes in the equatorial plate of heterotype division of pollen mother cells. One of them is marketly larger in size than the others and in most-cases makes its appearance in the shape of a compact ring or a C in side view (Text-fig. 1). Thus, it can easily be distinguished from the other five chromosomes by its larger size and particular shape. The



Text-figs. 1-3. I. Meta-anaphase in heterotype division in side view, showing the atclomitic J-shaped chromosome.

- 2. Chromosomes in the heterotype nuclear plate showing a type of arrangement. The chromosome occupying the central position is larger than the others.
- 3. Diakinesis. One of six bivalents is ring-shaped and the other five V-shaped (ZEISS 1/12 \times K. 18).

other five chromosomes are all nearly of the same size, in the majority of cases being of the shape of dumb-bells, or rods, constricted in the middle, and look like small solid circles when viewed from the pole (Text-fig. 2).

In the diakinesis, six bivalent chromosomes are distributed in the nuclear cavity at the same distance from one another. One geminus represents itself as a ring in shape and the other five appear in the form of V's (Text-fig. 3). The ring-shaped bivalent chromosome is that one which appears as the large round chromosome in the heterotype metaphase when viewed from the pole. In the side view of anaphase of the division, both univalent sides of the geminus assume a J-shape, their spindle-fiber attachment being sub-median.

In the metaphase these six chromosomes are very regularly arranged on the equatorial plane without coming in contact with each other or without being disposed one above another. Careful observations in this stage revealed the fact that there are the following different cases in arrangement of these six chromosomes :—

1. One of the five small chromosomes is situated at the centre of the equatorial plate and the other five chromosomes, one large and four small, are arranged surrounding this central chromosome, forming a regular circle in the majority of cases (Text-fig. $_4$).

2. The large chromosome occupies the central position instead of a small chromosome, the arrangement in other respects being the same as in I (Text-fig. 5).

3. All chromosomes take part in the formation of the ring without any chromosome in the centre. In this case the ring is not a regular circle in most case (Text-fig. 6).

4. Besides these three main types of arrangement there are a few cases where configurations differ from any of the types. These are grouped into one as case 4 (Taxt-figs. 7 and 8).

To obtain numerical results of the frequency of occurrence of these cases, counting was carried out in preparations made from material fixed by the method described above. The results obtained are summarized in Table I.

As is seen in the table, configurations belonging to Case I are the most numerous, being 67.2% of all the cases observed, and those belonging to Cases III and II come next in frequency in the order named,



Text-figs. 4-8. Chomosome arrangement in the heterotype nuclear plates. Explanation in the text.

Case	I	II	III	IV	Total
Heterotype metaphase	. 90	17	19	8	134
Percentage	* 67.2 <i>%</i>	12.7%	14.2%	6.0%	

TABLE I.

those belonging to Case IV being the smallest in number. The numerical ratio between Case I and Case II is 5.3:1.

If there are one large and five small chromosomes arranged on a plane in the shape of a ring, and if which chromosome will occupy

the central position is determined merely by chance irrespective of its size, the chance for the large chromosome would be 1/6 and for its remaining on the ring 5/6.

The numerical ratio between Cases I and II may, therefore, be regarded as showing that, in *Spinacia oleracea*, which chromosome occupies the central position is determined merely by chance irrespective of its size.

In the anaphase, while all the small chromosomes have been separated into their homologous components, being nearly round in shape, the large chromosome yet remains having its homologous components in contact with each other at the distal ends, each component presenting itself in the shape of a J or an odd V directing its apex towards the pole (Text-fig. 9). As the division proceeds the two J-shaped components progressively draw apart and finally become separated completely from each other. This chromosome is denoted for the sake of convenience, by the letter "J" in the following pages. While the component chromosomes are separating, the longitudinal split for the next division become clearly observable in some of the chromosomes (Text-figs. 9 and 10). The second small chromosome from the left in the lower group of Text-fig. 9 looks as if it is a bent one, but this is really due to the opening out of the longitudinal fission visible commonly in the subsequent stages.



Text-figs. 9 and 10. 9. Typical side view in heterotype anaphase. Most of the separating chromosomes are near the poles except those of the large geminus which is still in contact at the ends. 10. The salle; longitudinal doubleness is recognizable in some of the chromosomes (ZEISS $1/12 \times K.18$).

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In Text-fig. 10, a later anaphase than in Text-fig. 9, the longitudinal split is visible more or less clearly in some of the separating chromosomes.

In the polar view of the anaphase, the forms of arrangement can generally be grouped into four cases as in the metaphase, but in this case, owing to the tendency of the chromosomes to put their longitudinal axes obliquely to the optical axis, it was sometimes difficult to distinguish the J-chromosome from the others, and, therefore, the results are given in Table II without distinguishing Cases I and II. Text-figs. 11 and 12 represent figures for Cases I+II, and Case III respectively and Textfigs. 13 and 14 are some examples of Case IV.



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Text-figs. 11-14. Three forms of chromosome arrangement in the heterotype anaphase. Explanation in the text.

Case	I+II	III	IV	Total
Heterotype anaphase	76	25	12	113
Percentage	67.3%	22.1%	10.6%	Ш. 12

TABLE II

Table II shows that Case I+II occurs more frequently than Case III. The ratio between the frequency of occurrence of these two cases is 3:1. In the metaphase this ratio is, as will be readily seen from Table I, 5.6:1. These results show that the case where five chromosomes are arranged in the form of a ring having the remaining one in its centre occurs less frequently in the anaphase than in the metaphase.

II. In the Homotype Division.

Text-fig. 15 shows two sister homotype nuclear plates. They lie perpendicular to each other. In side view the chromosomes are nearly as large as those in the heterotype metaphase and most of them are



Text-fig. 15. Homotype metaphase showing arrangement of chromosomes in polar view and dumb-bell-shaped chromosomes in side view (ZEISS 1/12× K.18).

of the dumb-bell shape. The forms of arrangement of the six chromosomes can generally classifiel into four categories as in the case of the heterotype anaphase, but, since discrimination of the J-chromosome from the other five small ones was sometimes difficult, no special attention was paid also in this case to the position of the J-chromosome in the arrangement.

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In Table III, all the forms of arrangement where the chromosomes are arranged in the form of a ring with one of them in its centre are grouped together in Case I+II, irrespective of whether the J-chromosome occupies the central position or not. Text-fig. 16 is respresentative of Case I+II, Text-figs. 17 and 18, of Case III, and Text-figs. 19 and 20, of Case IV.



Text-figs. 16-20. Chromosome arrangement in the homotype metaphase. Explanation in the text.

The frequency of occurrence of these cases of the chromosome arrangement in the homotype metaphase is as shown in Table III.

The ratio between Case I+II and Case III is 2.4:1, while the same ratio in the heterotype anaphase 3:1. As mentioned above, in the heterotype metaphase the ratio between the sum of Cases I and II and Case III is 5.6:1. Case I+II in the homotype metaphase seems to occur remarkably seldom as compared with Cases I and II of the

Case Stage	I+II	III	IV	Total
Homotype metaphase	98	41	17	156
Percentage	62.8%	26.3%	10.9%	

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heterotype metaphase.

If we sum up the numerical results in each case obtained in the different phases of the meiotic divisions, we have the results tabulated in Table IV.

Case	1+11	111	IV	Total
Heterotype metaphase	107 (90+17)	19	8	134
Heterotype anaphase	76	25	12	113
Homotype metaphase	98	41	17	1 56
Total	281	85	37	403
Percentage	69.7%	21.1%	9.2 <i>%</i>	

TABLE IV

From this table we see that the configurations grouped into Cases I and II in the heterotype metaphase and into Case I+II in the heterotype anaphase, and homotype metaphase, or, configurations which resemble the stable form of MAYER's floating magnets are the most numerous, being nearly 70% of all the configurations observed.

The forms of arrangement belonging to Case III and some of those belonging to Case IV may be regarded as representing the less stable forms of floating magnets given by physicists, or those which are in stages of transition to forms more or less stable. (Comp. Text-figs. 21a-b and 22).

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Text-fig. 21 a-b. Six floating magnets carrying one magnetized needle each. a. Transient stage. b. Stable form of a.

Text-fig. 22. Six floating magnets carrying one magnetized needle each, except the large one which carries 2 needles. Transient form.

The fact that Case III occurs more frequently in the homotype division than in the heterotype division might have a causal relation to the fact that in this plant there is no separating wall between two sister homotype spindles.

B. OBSERVATION OF THE POLLEN MOTHER CELLS OF Vicia faba, L.

Material for these observations was taken from the variety *megalosperma*. A part of the material was fixed with NAWASCHIN'S fixative for 3 hours, and another part for 5 hours and both were then transferred directly into 30% alcohol without rinsing with water, and the third part was fixed with the Bonn modification of FLEMMING'S solution for 24 hours after being treated with CARNOV'S mixture for half a minute. They were imbedded in paraffin in the usual manner. Sections were cut $10-12\mu$ thick and stained exclusively with HEIDENHAIN'S iron alum haematoxylin.

It has been made clear by SHARP (1913, 1914) and SAKAMURA (1915, 1920) that in the somatic cells of *Vicia faba* there are 12 chromosomes, 2 of which are about twice as long as the other 10, the mode of spindle fiber attachment being median in these longer ones and sub-terminal in all the others, and, especially by SAKAMURA, that in the stages

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of diakinesis and metaphase of heterotype division in the pollen mother cells, there are found 6 gemini or double chromosomes, one of which, the "M-geminus", as it is called by him, is about twice as long as the other 5. As has been investigated exhaustively by SAKAMURA, the mode of spindle fiber attachment in these gemini is the same as in the corresponding chromosomes in the somatic cells. In careful observations one of the authors (M) has found that in the stages of diakinesis and metaphase these chromosomes clearly manifest themselves as so called "compound rings": the M-geminus comes to sight in the shape of a chain of many rings disposed perpendicularly to each other successively, while the other chromosomes take rather simpler configurations of chains composed of 3 or 4 rings in the majority of cases, presenting certain conspicuous differences from one another in their appearance (see Figs. 1-6, Pl. XXX). In later stages, however, no such conspicuous morphological difference in either size or shape was to be seen among these small chromosomes. This seems to show that the apparent size differences among them often found in the metaphase are simply due to differences in their "compound ring" configurations in this stage. In diakinesis the 6 gemini are not so regularly distributed near the periphery of the nuclear cavity as is the case with Spinacia oleracea, but some of them, very often the M-geminus, are found lying in the central region of this cavity. If the M-geminus occupies this position, it is straightened out from one side to the other across the center of the cavity. In an earlier stage of metaphase the 6 chromosomes¹ are not arranged so regularly in the equatorial plate, but some of them are found to lie above or below this plate, showing not so a clear radiating figure as in the later But sooner or later all of them come to lie in the equatorial stage. plate so as to form a clear radiating figure.

As to the arrangement of these 6 chromosomes the following cases were found in the equatorial plate of heterotype metaphase:

I They are really double chromosomes but we describe them here as simply chromosomes in the broad sense of the term.

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I. The M-chromosome bends back at its point of spindle fiber attachment into a V with arms of about equal length, and the 5 small chromosomes are arranged radially in the equatorial plate, having their points of spindle fiber attachment near the center; the arms of the former and the distal ends of the latter being directed towards the periphery of the equatorial plate. Thus a clear radiating figure is composed of the 5 shorter chromosomes and the 2 arms of the M-chromosome with no chromosomes in the center of the figure (see our Fig. 1, Pl. XXX and also comp. SHARP, 1926, Fig. 63 F and FRASER, 1914, Fig. 18, though the latter figure is interpreted by the author in another way).

II. The same arrangement as in case I with the exception that one of the shorter chromosomes occupies the central position, and owing to this, the radiating figure is rendered more or less irregular (Fig. 2).

In these two cases, I and II, both arms of the V-shaped M-chromosome are not often situated in the equatorial plate but on a plane more or less oblique to this plate: they sometimes open out very wide to make an obtuse angle, and, rarely, almost a straight line. In such cases the arrangement of the small chromosomes in the remaining space of the equatorial plate seems to have been disturbed, not being arranged in one and the same optical plane, probably owing to lack of sufficient room for them.

IIIa. The M-chromosome, its arms opening out in a straight line, takes up its position across the center of the equatorial plate straight from one side of the periphery to the other : the 5 shorter chromosomes, 3 of them lying on one side of the M-chromosome and the remaining 2 on the other side, are arranged having their proximal ends near the center of the equatorial plate and their distal ends directed towards the periphery of this plate (Fig. 3, also comp. SAKAMURA's Text-fig. 7, 1915 and his Fig. 16, 1920).

IIIb. Nearly the same mode of arrangement as in Case IIIa with the exception that one of the three shorter side chromosomes which lies near one end of the straightened-out M-chromosome takes up such a position that it is overlaid by that part of the M-chromosome. In this

case, the latter chromosome is bent upwards or downwards, and in most cases, the point of spindle fiber attachment does not lie at the center of the equatorial plate, but on the supposed circle to be formed by connecting the points of spindle fiber attachment of the 5 shorter chromosomes, being slightly shifted towards the periphery of the arrangement figure (Fig. 4, cf. Text-fig. 23, Schema D).

IVa. The position of the M-chromosome is nearly the same as in Cases I and II, but the arms open out more widely to form an obtuse angle, within which one of the shorter chromosomes is found. The other 4 are radially arranged outside of this angle (Fig. 5).

IVb. A similar arrangement to that of Case IVa, but here, one of the arms of the M-chromosome comes to be overlaid by one of the shorter chromosomes situated outside the angle of the former as is shown in Fig. 6.

T 1	Prepa-	Number of Cases						The fact
Fixation	ration	Case I	Case II	Case IIIa	Case IIIb	Case IVa	Case 1Vb	TOTAL
NAWASCHIN 5 hs.	A B	10 8	13 18	5 3	2 3	3 5	I I	34 38
NAWASCHIN 3 hs.	A B	6 5	9 12	2 2	I I	3 1	1 I	20 24
C ¹ _2–Bonn	$egin{array}{c} A \ B \end{array}$	5 16	8 27	1 13	о 3	2 13	1 2	17 74
Total		50	87	26	10	27	7	207
%		24.2	42.0	12.6	4.8	13.0	3.4	100

TABLE V.

Abbreviations :

 NAWASCHIN 5 hs.:
 Fixing with NAWASCHIN'S fixative for 5 hours.

 NAWASCHIN 3 hs.:
 Fixing with NAWASCHIN'S fixative for 3 hours.

 C1-Bonn:
 Fixing with the Bonn modification of FLEMMING'S solution after treating for half a minute with CARNOY'S mixture.

Figures of the chromosome arrangement such as in Cases IIIb and IVb may be easily misinterpretted as representing those of the earlier

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metaphase, when the arrangement of chromosomes have not been yet finished. But, as in these figures the beginning of the chromosome disjunction is recognizable, we are led to the conclusion that the chromosomes maintain these relative positions, through the stage of the metaphase, up to the beginning of the anaphase.

To obtain numerical results for each case, two preparations for each were selected from material fixed by the three different methods, and observations were made exclusively in pollen mother cells which were just in the stage of heterotype metaphase and which had not been cut through by the microtome knife and show clearly and simultaneously all the chromosomes in polar view. The results are given in Table V.

As is shown schematically in Text-fig. 23, if only the position of the points of spindle fiber attachment of chromosomes be considered, the 6 cases described above may be classified into 3 cases of arrangement which are similar to the 3 cases found in *Spinacia* (compare Text-figs. 4, 5 and 6 with Schemas G, H and I respectively).



Text-fig. 23. A-F, schemas for 6 cases of chromosome arrangement found in the pollen mother cells of *Vicica faba*: H-I, schemas for 3 cases of chromosome arrangement similar to those found in the pollen mother cells of *Spinacia oteracea*: the arrows show that if in Schemas A-F only the position of the points of spindle fiber attachment (black solid circles in the figure) be considered, the Schemas can be reduced to Schemas G-I.

If the numerical results given in Table V are grouped together after this manner of classification, the results will be as follows:

" Schema H (" " Case II " ")......60(29.0%) Schema I (" " Case III " ").......60(29.0%)

From these results we see that the ratio between the frequency of occurrence of G and H is 42:29. In comparing it with the corresponding ratio obtained in the case of *Spinacia* (5.3:1), we come to the conclusion that the chance for the long chromosome of entering the chromosome ring of arrangement is much greater than that of the larger chromosome in Spinacia and also is greater than that for any of its companion chromosomes of shorter length.

If we add together the results of all the cases of arrangement having one chromosome in the center of the ring of arrangement, irrespective of whether it is the long chromosome or the short, that is, the results for Schemas G and H together, we have 147 cases, or 71% of all the Thus we may say that in Vicia, too, chromosome cases observed. arrangement resembles the arrangement of MAYER's floating magnets in the majority of cases.

CONCLUSION.

"If there are six magnets" in the experiment of MAYER's floating magnets, "they do not arrange themselves at corners of a hexagon but five take up positions at the corners of a pentagon while the sixth passes to the centre of the figure" (CANNON, 1923, P. 55). It has been made clear from the results of observations in the pollen mother cells of Spinacia oleracea as described in the foregoing chapter that throughout the different phases of the meiotic divisions, in nearly 70% of all the figures of chromosome arrangement observed in the equatorial plate they resemble the arrangement of MAVER's floating magnets, and that the ratio between the frequencies of Cases I and II in the heterotype metaphase is nearly equal to 5:1, a fact which shows that which position, inner or outer, a chromosome takes in the arrangement in the equatorial plate is determined merely by chance, the larger chromosome behaving

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quite similarly to the other small ones.

Now it is clear from these facts that there is a marked coincidence between the forms of arrangement of chromosomes of different sizes in the pollen mother cells of *Spinacia oleracea* and those of MAVER's floating magnets, notwithstanding CANNON's presumption that "the equilibrium arrangement of such a group would not conform to the same laws as those predicted for groups of chromosomes of the same size" (CANNON, 1923, P. 55).

The two cases of arrangement, Cases III and IV, which were found to occur in a lower percentage than the other cases throughout all stages of meiotic divisions in *Spinacia oleracea* are to be regarded as the transient state of arrangement before the final state of equilibrium is attained, as suggested by KUWADA (1928).

In the pollen mother cells of *Vicia faba* 6 cases of chromosome arrangement could be found as described in the foregoing chapter, and, therefore, there seems at first glance to be some difference between *Vicia* and *Spinacia*. But, as since it has been shown in the same chapter that if only the position of the points of spindle fiber attachment be considered, these 6 cases of chromosome arrangement can be reduced to 3 cases of arrangement similar to those found in the pollen mother cells of *Spinacia oleracea* (Schemas A-I), we may conclude that the mode of the chromosome arrangement in the equatorial plate is the same in principle in these two apparently different cases of *Vicia faba* and *Spinacia oleracea*. This interpretation is naturally based upon the assumption that the point of spindle fiber attachment plays some important rôle in the determination of the position of the chromosome in the arrangement.

It seems to be worthy of emphasis here that the ratio between the frequency values of those two cases represented by Schemas H and G in *Vicia* (29:42) is larger than the ratio between those of the corresponding cases in *Spinacia* (ca. 1:5). This fact may show that the long chromosome in *Vicia* has a stronger tendency to occupy the central position in the arrangement than the large chromosome in *Spinacia*, or than any of its companion chromosomes of shorter length. If the shorter

chromosomes are comparable with floating magnets with a smaller number of magnetized needles, the long chromosome should be comparable with that having a greater number of such needles.

SUMMARY.

I. In the pollen mother cells of *Spinacia oleracea* the arrangement of chromosomes can be classified into the following 4 cases :---

1. One of the small chromosomes takes the central position, while the other 4 small and one large ones are so arranged as to compose a ring surrounding the central one.

The large chromosome takes the central position instead of a small one, the other 5 small ones being arranged around it in a circular form.
 All the 6 chromosomes are arranged in a ring having none in it. In this case the ring is generally more or less crooked.

4. Forms of arrangement which can not be classified into any of these 3 cases.

The frequency of occurrence of these different cases were found to be as follows :

	Case I and	l Case II	Case III	Case IV	
Heterotype metaphase :	67.2%	12.7%	14.2%	6.0%	
Heterotype anaphase :	67.3%		22.1%	10.6%	
Homotype metaphase :	62.8%		26.3%	10.9%	
Average :	70.4%		21.3%	8.3%	

From these results it was pointed out that in the pollen mother cells of *Spinacia oleracea* Cases I and II occur more frequently than Cases III and IV both in the heterotype division and in the homotype metaphase, and also that in the heterotype metaphase the ratio between Cases I and II is nearly 5:1.

II. In the heterotype metaphase of the pollen mother cells of *Vicia faba* 6 cases of the chromosome arrangement in the equatorial plate could be found. If only the points of spindle spindle fiber attachment of the chromosomes be taken into consideration, these 6 cases can

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be reduced to 3 cases which are quite similar to the first 3 cases found in the pollen mother cells of *Spinacia*. The frequency of occurrence of these 3 cases of arrangement are: 42.0%, 29.1%, and 29.0%. In this case the ratio between the two cases which correspond to Cases I and II in *Spinacia* is not 5:1, but 42:29 or about 1.5:1.

III. From these results, we see that in both *Spinacia* and *Vicia* cases where the chromosome arrangement resembles that of MAYER's floating magnets are the most numerous in frequency, being 69.7% on an average in the case of *Spinacia*, and 71.1% in *Vicia*, and also that the larger chromosomes may be comparable with floating magnets consisting of more magnetized needles than those comparable with the small chromosomes.

This investigation was carried out under the direction of Prof. Y. Kuwada, of Botanical Institute, College of Science, Kyoto Imperial University, to whom the authors wish to take this opportunity of expressing their cordial thanks.

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EXPLANATION OF PLATE XXX.

All the figures have been drawn from equatorial plates in heterotype division in pollen mother cells of *Vicia faba*, L. with the aid of an ABBE's camera lucida using Zeiss' apoch. imm. 2mm. and comp. oc. 18 for outlines and comp. oc. 12 for studies in detail. Figs. I and 2 are from material fixed with NAWASCHIN's fixative for 3 hours and all the other figures from material fixed with the same fixative for 5 hours.

- Fig. 1. M-chromosome is bent back into a V at its point of spindle fiber attachment: the two arms of the V together with the other chromosomes form a radiating figure.
- Fig. 2. Similar arrangement as Fig. 1, except that one of the small chromosomes is situated at the center of the arrangement.
- Fig. 3. M-chromosome is found straight across the center of the equatorial plate and 3 of the small chromasomes are situated on one side and the remaining 2 on the other side of the M-chromosome.
- Fig. 4. A similar arrangement to Fig. 3, except that one of the small chromosomes is situated so as to have a part of it overlaid by a part of the M-chromosome.
- Fig. 5. The M-chromosome is slightly bent at its point of spindle fiber attachment to make an obtuse angle; one of the small chromosomes is situated inside this angle and the other 4 are arranged radially outside of the angle.
- Fig 6. A similar arrangement to Fig. 5, but one of the small chromosomes is overlaid by a part of the M-chromosome.



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