THE DETERMINATION OF POSITION IN CROSSING-OVER

III. THE EVIDENCE OF METAPHASE CHIASMATA

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(With Thirteen Text-figures)

1. Introduction

The mean positions of chiasmata in bivalents, and higher configurations, at metaphase of the first meiotic division vary from species to species. At one extreme falls *Mecostethus*, where all or nearly all of the chiasmata lie very close to the centromere. At the other end of the scale are types like *Campanula*, where all the chiasmata are terminal. The majority of organisms are intermediate, with some terminal connexions, but also having a number of interstitial chiasmata. The positions of these interstitial chiasmata are variable, sometimes being near to the chromosome end and sometimes nearer to the centromere.

The distribution of chiasmata as seen at metaphase is clearly dependent on two factors, viz. their original positions at the time of formation and any movement which they may have experienced subsequently. Now there is abundant evidence that terminal chiasmata are derived from interstitial positions by the movement which Darlington has called terminalization. Similar evidence of movement is not, however, available for the chiasmata which remain interstitial, and, though attempts have been made to describe their positions in terms of terminalization movements, there has been no real means of distinguishing the effects of the two factors which determine the metaphase positions. Such an attempt may now be made.

In an earlier paper of this series (1937) I have shown that the relation between chromosome length and chiasma frequency, in organisms with a large chromosome size range, provided evidence for the hypothesis that chiasmata do not occur haphazardly along the bivalents but arise in certain definite regions, most probably related in position to the centromere. The positions of these regions may be described in terms of two parameters, the *differential* and *interference* distances. These are, respectively, the distance between the centromere and the mean position of

the proximal chiasma, and the mean distance between the proximal or first and the next proximal or second chiasma. The distances between the second and third, third and fourth chiasmata etc. are equal, so far as can be judged, to that between the first and second. Though the interference distance is constant from bivalent to bivalent within a nucleus, the differential distance is positively correlated with chromosome length.

The comparisons on which the analysis was based were wholly of one bivalent with another. The variables used were the chromosome length and mean number of chiasmata of each bivalent. No account was taken of the internal characteristics of the bivalents. It is then legitimate to make such inferences as this hypothesis allows about the distribution of chiasmata within bivalents and to compare these with the observable diakinesis and metaphase positions. These need not necessarily coincide, as the positions deducible from the analysis of the chromosome length and chiasma frequency relation will be the positions of original formation of chiasmata. Thus, by such a comparison, evidence may be obtained as to the movements of chiasmata between their origin and the attainment of metaphase. Furthermore, as will be seen below, the results of this comparison add greatly to the evidence for the validity of the hypothesis of determinate positions of chiasma formation.

2. Analysis of the chromosome length-chiasma frequency curve

A typical chromosome length-chiasma frequency curve is shown in the lower portion of Fig. 1 (line *ABCD*). By my earlier analysis (1937), the distance *AB* may be recognized as the maximum differential distance and *BE* (= *EF*) is the interference distance. There is probably a smooth change from the region *AB*, where one chiasma is formed independently of chromosome length, to the region *BCD*, where the chiasma frequency goes up in linear proportion to the chromosome length. Short chromosomes, whose length is less than *AB*, regularly form one chiasma, and larger chromosomes show a mean chiasma frequency deducible from the line *BCD*. This curve does not relate the differential distance to the centromere in an unambiguous manner, but merely demands that some fixed point in the chromosome be the effective origin of chiasma formation. On general grounds the centromere seems the most likely point, and an analysis of *Drosophila* data definitely indicates this relation (Mather, 1936). As a working hypothesis we may take the centromere as the origin of chiasma formation. The picture of the distribution of chiasmata in a long chromosome then takes the form shown in the upper portion of

Fig. 1, A being the centromere. The mean position of the first formed or proximal chiasma is at B, of the second at C and so on. AB is the differential distance. The variance of the position of any chiasma presumably increases as we proceed away from A. The variance of the first formed

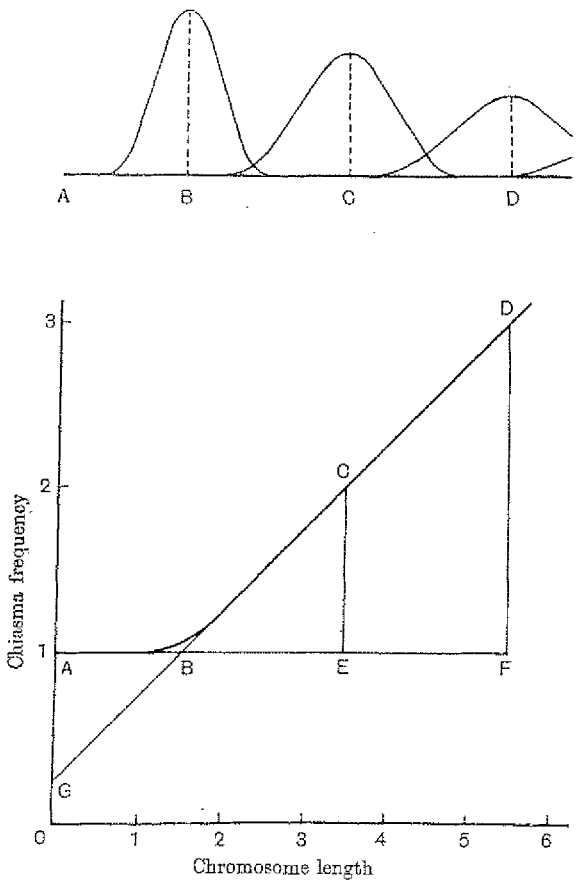

Fig. 1. Diagram to illustrate the relation between the distribution of chiasmata along the chromosome (upper) and the chromosome length-chiasma frequency graph (lower). A is the centromere and B, C, D the mean positions of the first formed, second formed, etc., chiasmata. For further explanation, see text.

chiasma is that of the differential distance. That of the second chiasma is the sum of the variances of the differential and interference distances, as the position of this second one is dependent on that of the first. These variances are however of no great importance for the present analysis, which is solely concerned with the mean position of the chiasmata.

The chromosome length-chiasma frequency curve allows of the calculation of the relative magnitudes of the differential and interference distances. The triangles ABG and BCE are similar and hence the ratio AG/AO $(=AG/CE)$ is the same as AB/BE, i.e. differential distance/interference distance, which may for convenience be written d/i. Thus it is possible to form an idea of how the chiasmata should be distributed in a long chromosome. Where G lies between A and O, $AG/AO = d/i < 1$ and the proximal chiasma is on the average nearer to the centromere than it is to the second chiasma. With G and O coincident, $d/i = 1$, and the distances between first chiasma and centromere on the one hand, and first and second chiasmata on the other, should be equal. Where G falls on the ordinate below O, $d/i > 1$ and the chiasmata should be nearer to one another than the proximal one is to the centromere. These expectations are clearly verifiable in a general way from illustrations of metaphase bivalents.

3. Two-armed chromosomes

Before proceeding to a consideration of the published data from which d/i values have been obtained, it is necessary to discuss the use of chromosomes with median or submedian centromeres.

The starting-point of chiasma formation in the above analysis is taken to be the centromere, and the differential distance is the mean distance from the centromere to the most proximal chiasma. Applying this to the two-armed chromosomes it is clear that there will be two differential distances, one on each side of the centromere, and the centric loop will have a circumference of twice the sum of the differential distances. The acentric loops will have circumferences of twice the interference distance (see Fig. 2). Where the two arms are equal or nearly so the differential distances on each side of the centromere will be equal and, the interference distance being at least approximately constant in any case, the chiasma frequency of the chromosome will be twice that of a single arm or twice that of any other chromosome with subterminal centromere and length equal to one of the arms. This is the case in *Vicia Faba* where the M chromosome has two arms each about equal to the single long arm of the m chromosomes. The M chromosome was found to average 7·06 and the m 3·42 chiasmata per bivalent (Mather, 1934). Such data give no information about d/i as the observed proportionality is dependent solely on the presence of one or two long arms.

Where, however, a series of chromosomes of varying length but all with median centromeres exist, the d/i relation can be obtained, as the

bivalents are comparable. Each will have a length and chiasma frequency twice that of the single arms. Since the first two chiasmata in such chromosomes will in general each be proximal, one on each side of the centromere, the interference distance does not come into play until a chiasma frequency of more than two is obtained. Consequently the length-chiasma frequency curve is, as it were, drawn on twice the scale

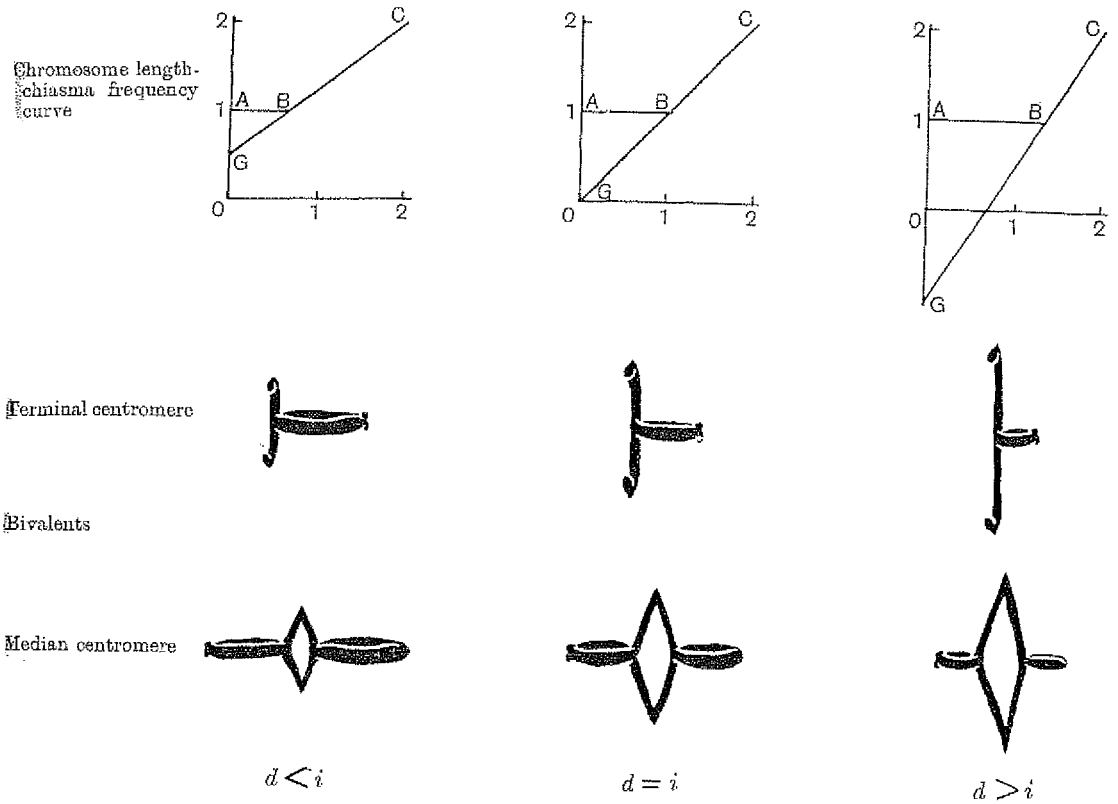

Fig. 2. Diagrammatic representation of the appearance of metaphase bivalents corresponding to certain types of chromosome length-chiasma frequency relations. d = differential distance, i = interference distance.

of that obtained when single-armed chromosomes are used, and the d/i ratio is AG/AO where A is at the point 2·0 on the ordinate and not at the point 1·0 as in the case of single-armed chromosomes. Failure to follow this rule will give false estimates of d/i except when this ratio equals one. In such cases it clearly makes no difference where A is located.

When both single- and double-armed chromosomes are present together the material is difficult to analyse. Perhaps the easiest thing to do

is to halve the length and chiasma frequency of each two-armed bivalent and treat it as single-armed. This is, however, not accurate if the arms are very unequal in length. In such cases some idea of the d/i value can be obtained as the estimate can always be correctly observed to be more than, equal to, or less than unity, no matter how the analysis is done, even though the precise numerical value is unobtainable. Since the final comparison of expectation with the metaphase positions is visual, and hence crude, a very precise knowledge of the d/i value is of little value. A really false impression can be gained only if a direct comparison is made of chromosomes having nearly equal length but some of which have subterminal and the rest submedian centromeres. It may happen that the differential and interference distances are very different, and since one type of chromosome includes one and the other two differential distances, the chiasma frequencies can be highly discrepant. This difference will not be much in evidence when the frequency is low, as the differential distance is correlated with chromosome length. For this reason it is not observable in Levan's data for *Allium zebdanense*.

There are a number of further points that can be raised concerning the relations of the individual arms of chromosomes with median centromeres, especially with regard to interference across the centromere, but as they are not immediately related to the present analysis, full discussion must be deferred. It is sufficient for the present to notice that such interference is not of the same nature as that within a single arm, and so should vary independently of the latter. This has been found to be the case by Pätau (1939), thus giving additional support to the hypothesis that the centromere is the origin of crossing-over.

4. Observations

In *Locusta migratoria* males there are eleven pairs of autosomes and a single X; all have nearly terminal centromeres. The autosomal bivalents

TABLE I

Locusta migratoria, 70 *nuclei*

Chromosomes	Long (2)	Long-medium (1)	Medium (5)	Short (3)
Length in μ	5·3	3·9	2·9	1·2
Chiasmata	2·15	1·49	1·07	1·02

$d/i = 1{\cdot}1$.
All have subterminal centromeres.

may be visually distinguished into four classes at meiosis. These classes are denoted as long (L), long medium (LM), medium (M) and short (S),

and contain 2, 1, 5 and 3 bivalents respectively. The average lengths of the four classes of chromosome based on four spermatogonial metaphases, together with their average frequencies of chiasma formation in 70 nuclei are given in Table I. The data are plotted in Fig. 3. As all the centromeres are nearly terminal we put A at the point 1·0 on the ordinate and AG is slightly greater than unity. The d/i value being a trifle larger than one, we should expect the centric free arm (chiasmata in the short arm are non-existent) to be about equal to the length of the acentric loop on the average, i.e. the distance between the first and second chiasmata should be about equal to that between the centromere and the first

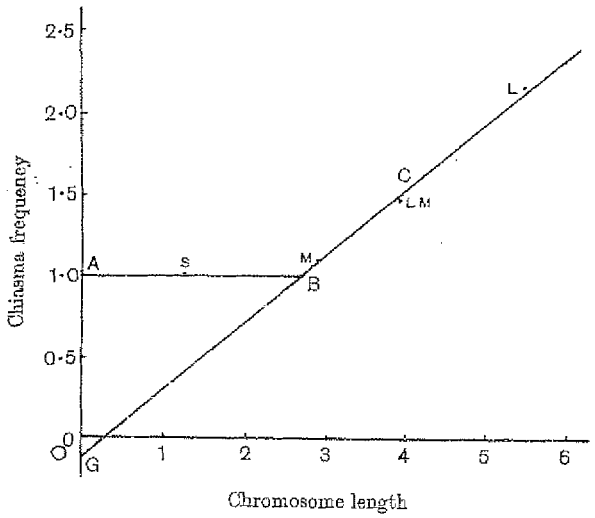

Fig. 3. The chromosome length-chiasma frequency graph of *Locusta migratoria*. L=long, LM=long medium, M=medium, S=short bivalents.

chiasma. Fig. 4 includes illustrations of diplotene and diakinetic bivalents of *Locusta*. (The metaphase bivalents are too contracted to be of any value for the comparison.) Only the long class have two chiasmata with any regularity. In addition to four whole nuclei, the long chromosomes from four other nuclei are shown. (These were drawn from unselected nuclei, being the only usable nuclei in one section on the slide.) Though some variability occurs, the proximal chiasma being sometimes very close to the centromere and sometimes a long way away, the average state of affairs agrees reasonably well with the expectation of d about equal to i, if we assume that the longest free arm in each bivalent is the centric arm. At metaphase, though detailed comparison is impossible, it

would appear that the centric free arm is longer than the arm at the distal end, and so the above assumption is justifiable. The agreement between

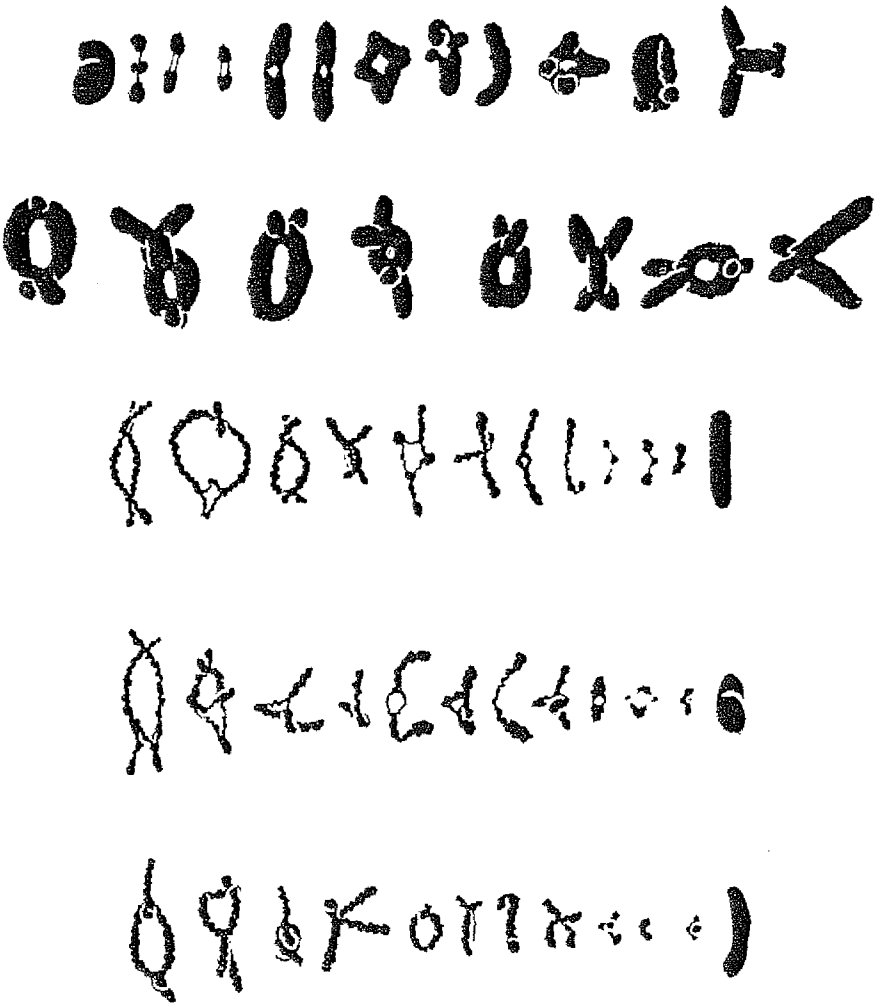

Fig. 4. Diplotene and diakinesis bivalents of *Locusta migratoria*. (*a*) Complete nucleus at diakinesis. (*b*) Long bivalents from four diakinetic nuclei. (*c*) Three complete diplotene nuclei [smaller magnification than (*a*) and (*b*)].

the *d*/*i* value obtained from the graph and the diakinetic chromosomes is good, and no great movement of chiasmata can have occurred.

Similar data have been given for nine other organisms in Tables II–X and illustrations of the metaphase bivalents in Figs. 5–13. These are

TABLE II

Allium macranthum (*Levan*, 1933), 8 *nuclei*

Chromosomes	Long (6)	Medium (4)	Short (4)
Length in μ	8·5	6·4	2·8
Chiasmata	4·60	3·06	1·41

$d/i = 1{\cdot}0$.

"Long" and "short" have median and "medium" submedian centromeres.

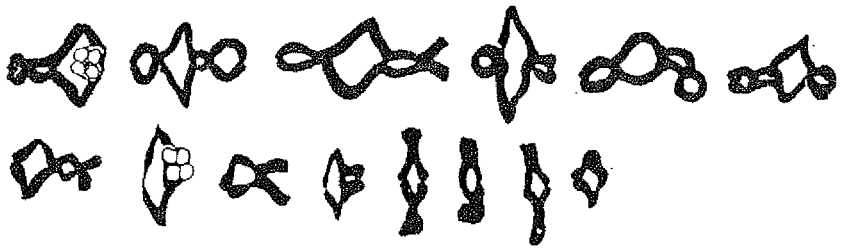

Fig. 5. A complete metaphase nucleus of *Allium macranthum* (Levan, 1933).

TABLE III

Allium zebdanense (*Levan*, 1935), 20 *nuclei*

Chromosome	1	2	3	4	5	6	7
Length in μ	10·2	9·1	9·0	7·9	6·6	4·7	4·5
Chiasmata	2·95	2·60	2·60	2·35	2·10	1·60	1·45

$d/i = 1{\cdot}0$.

Chromosomes 8 and 9 aré omitted as having very unequal arms. Then rest have medium centromeres.

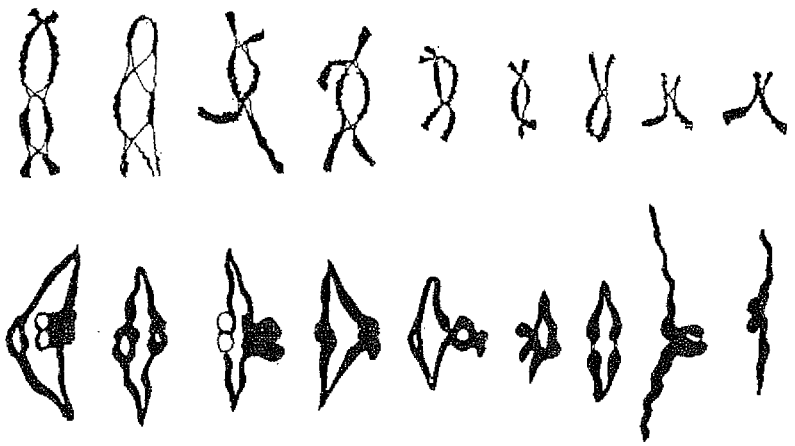

Fig. 6. Complete diakinesis and metaphase nuclei of *Allium zebdanense* (Levan, 1935).

TABLE IV

Eremurus spectabilis (*Upcott*, 1936), 100 *nuclei*

Chromosomes	Long (5)	Short (2)
Length in μ	7·1	3·5
Chiasmata	3·89	1·61

$d/i = 0{\cdot}7$.

All have subterminal centromeres.

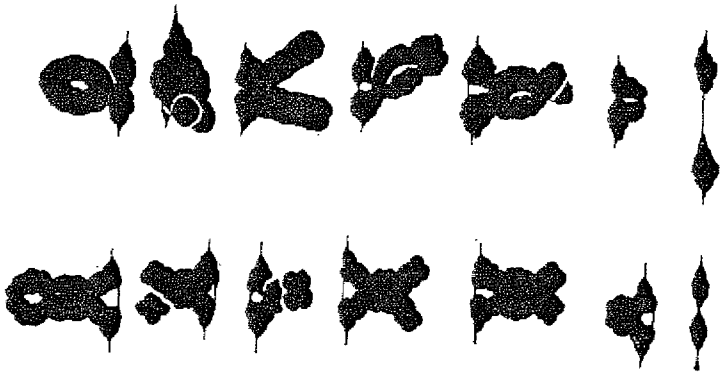

Fig. 7. Two complete metaphase nuclei of *Eremurus spectabilis* (Upcott, 1936).

TABLE V

Mecostethus grossus (*White*, 1936)

All chromosomes have subterminal centromeres and a mean chiasma frequency of 1·0+. Their lengths vary from 9·8 μ to 1·2 μ. *d/i* very small.

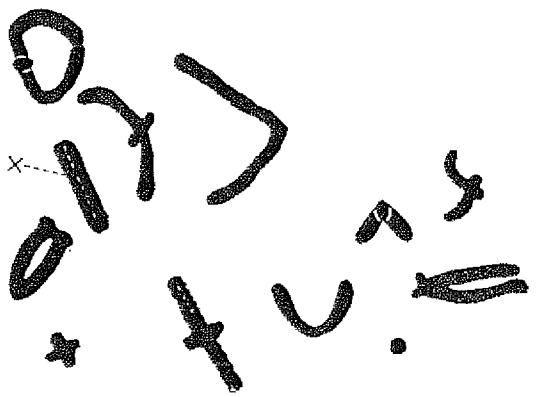

Fig. 8. Metaphase nucleus of *Mecostethus grossus* (White, 1936).

TABLE VI

Melanoplus femur-rubrum (*Hearne & Huskins*, 1935), 83 *nuclei*

Chromosomes	Long (4)	Medium (4)	Short (3)
Length (arbitrary units)	7	3	1
Chiasmata	1·70	1·03	1·00

$d/i = 0{\cdot}5$.

See text for note on chromosome lengths. All have subterminal centromeres.

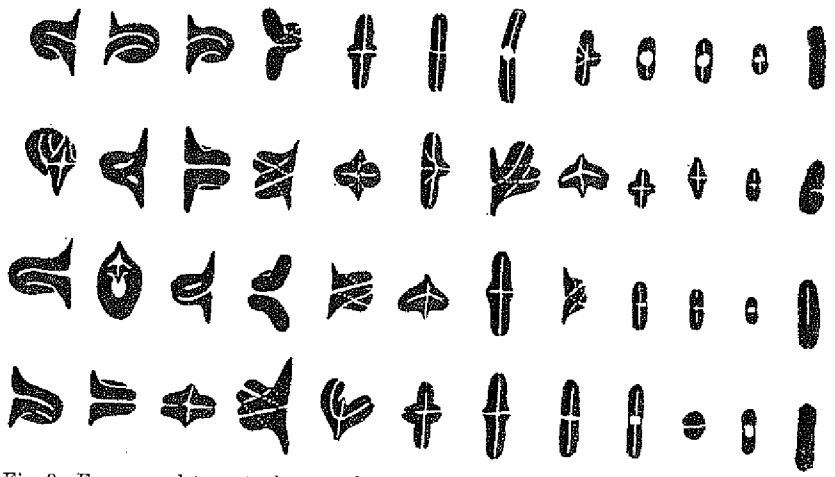

Fig. 9. Four complete metaphase nuclei of *Melanoplus femur-rubrum* (Hearne & Huskins, 1935).

TABLE VII

Schistocerca gregaria (*White*, 1934), 96 *nuclei*

Chromosomes		Long (3)	Medium (5)	Short (3)
Length in μ		8·0	4·0	2·0
Chiasmata	2° C.	2·40	1·53	1·00
	15° C.	2·69	1·73	1·02
	26° C.	2·50	1·56	1·00
	45° C.	2·38	1·48	1·00

d/i	2° C.	0·35
	15° C.	0·25
	26° C.	0·40
	45° C.	0·40

All have subterminal centromeres.

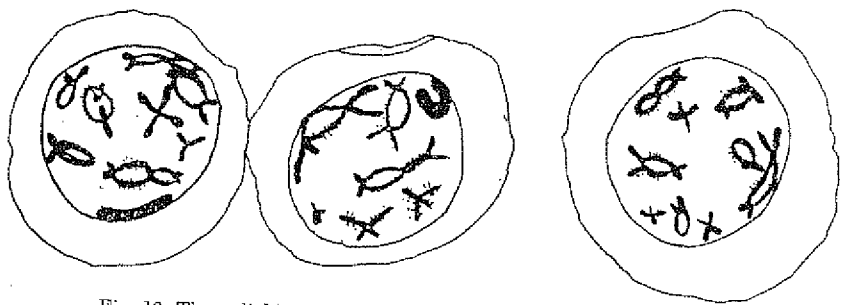

Fig. 10. Three diakinetic nuclei of *Schistocerca gregaria* (White, 1933).

TABLE VIII

Scilla italica (*Dark*, 1934), 25 *nuclei*

Chromosomes	Long (4)	Medium (2)	Short (2)
Length in μ	10·7	6·5	3·8
Chiasmata	2·95	2·02	1·52

$d/i = 0{\cdot}3$.

The positions of the centromeres vary among the chromosomes.

Fig. 11. Metaphase nucleus of *Scilla italica* (Dark, 1934).

TABLE IX

Spironema fragrans (*Richardson*, 1934), 109 *nuclei*

Chromosomes	SM 1 and 2	SM 3	ST, 1, 2 and 3
Length in μ	36	26	20
Chiasmata	3·53	1·98	1·81

$d/i = 0{\cdot}9$.

SM = submedian centromere. ST = subterminal centromere.

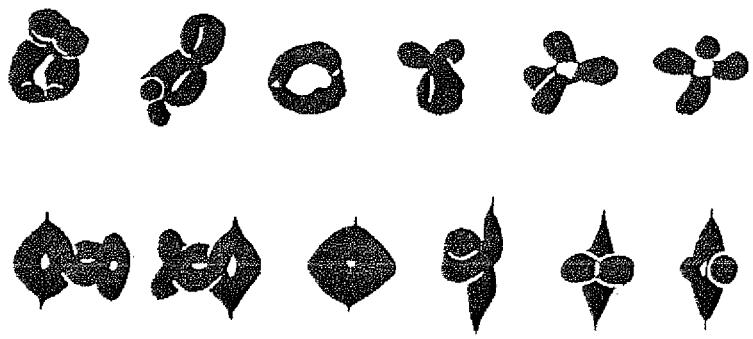

Fig. 12. Diakinesis and metaphase nuclei of *Spironema fragrans* (Richardson, 1934).

TABLÆ X

Stenobothrus parallelus (*Darlington & Dark*, 1932), 28 *nuclei*

Chromosomes	Long	Medium	Short
Length in μ	11·3	4·1	1·6
Chiasmata	3·31	1·45	1·04

$d/i = 0{\cdot}7$.

The long chromosomes have submedian, and the rest subterminal, centromeres.

Fig. 13. Two metaphase nuclei of *Stenobothrus parallelus* (Darlington & Dark, 1932).

taken from the various authors cited in the tables and the legends. Some of the figures are less reliable than others, for various reasons. *Scilla italica*, *Spironema fragrans* and *Stenobothrus parallelus* have some chromosomes with median and some with subterminal centromeres, thus introducing an element of uncertainty into the estimation of d/i, as described in the previous section. In *Melanoplus femur-rubrum* it is difficult to determine from Hearne & Huskins's table what the correct ratios of the chromosome lengths are, so I have taken the ratio given in their text, which agrees with their Graph 2. Diakinesis illustrations are the only ones available for *Schistocerca*. As this insect has all subterminally centric chromosomes however it is easy to compare the differential and interference distances by noting the lengths of the free arms relative to those of the loops.

In general the agreement between the d/i values estimated from the chromosome length-chiasma frequency graphs and those apparent from the figures of metaphase bivalents is strikingly good. It is impossible to get the metaphase intrachromosome ratio exactly, but there is little difficulty in forming some idea of it.

The differences between the various species are specially informative. For example, *Locusta*, *Schistocerca* and *Melanoplus*, all having sub-

terminally constricted chromosomes, show *d/i* values determined graphically from the chiasma frequencies of the length classes of 1·1, 0·25–0·40 and 0·5. Though the published illustrations of *Schistocerca* are poor it is obvious that the proximal chiasma is closer to the centromere, relative to its distance from the second chiasma, in the last two species than in *Locusta*, just as would be expected from the chromosome length-chiasma frequency graphs. The same type of comparison can be made between the other organisms and gives good agreement with expectation. Thus not only do the graphical and metaphase *d/i* values agree for individual species, but the interspecific comparison shows that where a certain difference in *d/i* is expected on the basis of the length-chiasma frequency graphs, it is shown by the metaphase bivalents. There is thus no evidence of movement of interstitial chiasmata between formation and metaphase.

There is one striking exception to these agreements, viz. *Scilla italica*. Here the graphically determined *d/i* value is less than one, probably nearer to 0·5, yet the first or proximal chiasma is much farther from the centromere than it is from the second chiasma at metaphase. This discrepancy may be due to (*a*) movements of chiasmata and (*b*) a breakdown of the method of analysis. Though the former possibility cannot be ruled out it would be strange to find one species having movement when nine others do not. There is, furthermore, a way in which the analysis might break down to give just the result observed. The graphical method of determining the *d/i* ratio is dependent on the assumption that the centromere is the effective origin of crossing-over. This presupposes that pachytene pairing is complete. If, however, pachytene pairing is incomplete this assumption may lead to false conclusions. With incomplete pairing localized proximally the centromere is still the effective origin of crossing-over, as in *Fritillaria Meleagris* and, presumably, *Mecostethus*. The behaviour of the latter confirms this view as the graphically determined *d/i* ratio is very small, agreeing with the metaphase bivalents where usually a single chiasma is found proximally localized. If a second chiasma occurs it is placed in a very distal position.

If, on the other hand, pachytene pairing occurs only at the ends of the chromosomes, away from the centromere, the effective origin of the subsequent crossing-over will presumably be at the proximal limit of the paired region in a chromosome arm. Then the true differential distance may be much smaller than the distance from the centromere to the average position of the proximal chiasma. This is just what is observed in *Scilla italica*. Two further points may be noted in connexion with this argument. In the first place the central region of a medianly centric

chromosome may appear to be paired at pachytene when in fact the pairing is purely of an ineffective nature due to relational coiling developing interstitially in the region between the truly paired ends of the chromosomes. So the pachytene figures may give no clue to the real situation. Secondly, the assumption that the effective origin of crossing-over is the proximal limit of the effectively paired section of the arm implies that the sequence of crossing-over is still controlled from the centromere, by progressive splitting perhaps, but the mechanism cannot begin to operate until the paired region is reached.

Distal localization of pairing and, in consequence, of chiasma formation is also believed to occur in *Tradescantia* and other organisms with large chromosomes like *Scilla italica*. *S. peruviana*, with smaller chromosomes than *S. italica*, seems to show no evidence of incomplete pairing. Sato (1934) gives figures of chromosome lengths and chiasma frequencies which on plotting indicate a *d/i* ratio of 1. This agrees as far as can be determined with his illustration of metaphase bivalents. The case is not very critical however as Sato's drawings do not allow of a clear judgment being made. If *S. peruviana* does not in fact show incomplete pairing, it would appear that the extent of pairing is a function of chromosome size, being less complete in larger chromosomes.

The distinction between the manner of pairing of the chromosomes at zygotene-pachytene and the manner of crossing-over cannot be over-emphasized. Distal localization of the pachytene pairing does not of necessity imply that crossing-over starts, or is controlled, from the ends of the chromosomes. The region near the centromere may be unpaired, or ineffectively paired, at pachytene and yet the sequence of crossing-over may commence at the centromere, though actual crossing-over cannot occur until the paired distal region is reached. This is perhaps the situation in *Drosophila*, where the coincidence of crossing-over in regions near the centromere may exceed one, suggesting failure of pachytene pairing in that region (Kikkawa, 1933), even though there is evidence of the centromere being the origin of crossing-over. (There is, however, an alternative explanation of such coincidence values. Any factor affecting the magnitude of the differential distance would tend to produce abnormally high coincidences as its effect would, presumably, be correlated in the two arms of one chromosome.)

The general conclusion to be drawn from the observations is, then, that the relative sizes of the differential and interference distances and the extent of chiasma formation, as expressed by the graphically determined *d/i* value, agrees well with the positions of the interstitial chiasmata

at anaphase. Chiasmata which are interstitially placed at metaphase have not moved since they originated. The sole apparent exception is capable of alternative explanation.

Apart from their bearing on the theory of terminalization, which is discussed below, these results immensely strengthen the hypothesis that the centromere is, in general, the origin of crossing-over. Whatever the mechanism, whether progressive splitting, as I have postulated in an earlier paper (1938), or not, it commences at the centromere. Two observations which would provide material evidence on this point seem obvious. One would be the occurrence of the first chiasma nearer to the centromere in *Locusta* after subjection to high temperatures, as White (1934) has found evidence that this gives a chromosome length-chiasma frequency graph showing a much lower *d/i* ratio than that found in low temperature material (see Mather, 1937). Unfortunately he published no drawings of the diakinesis and metaphase bivalents. The second test of the hypothesis lies in finding two chromosomes of clearly similar length but with subterminal and median centromeres respectively, in an organism with a fairly high chiasma frequency. These two chromosomes should show somewhat unequal chiasma frequencies, where the differential and interference distances are very unequal.

5. The terminalization of chiasmata

The hypothesis of terminalization of chiasmata was introduced by Darlington to reconcile terminal junctions of chromosomes at metaphase, especially in *Oenothera*, with his two analytical principles, that chiasmata always arise by interstitial crossing-over and that metaphase association is solely by chiasmata. The general validity of these two principles cannot be doubted, though some exceptions to the latter one have been found, notably in the male *Drosophila* by Darlington himself.

There is good evidence that movement of chiasmata to the ends of chromosomes does occur. In such plants as *Campanula persicifolia* (Gairdner & Darlington, 1931) interstitial chiasmata are visible at diplotene but decrease to a frequency of zero at metaphase, while terminal junctions correspondingly increase in frequency. Similar observations have been made in other plants, for example, *Primula verticillata* and *P. floribunda* (Upcott, 1939). The terminalizing movements of chiasmata are most reasonably ascribed to a special action of the centromere.

Similar movements of interstitial chiasmata have been postulated by a number of authors to account for the metaphase positions of the

interstitial chiasmata. The necessity for supposing that this movement occurs has originated from the assumption of what has been called "random" formation of the chiasmata along the chromosome, i.e. that the frequency of crossing-over per unit cytological length is constant along the chromosome.

I have now presented reasons for believing (*a*) that chiasmata always tend to have determinate positions, and (*b*) that there is no detectable change in these positions after the time of formation except, of course, in cases where complete terminalization occurs or where potentially complete terminalization is arrested by the onset of metaphase, leaving an intermediate condition. Two illustrative cases may be considered. In *Melanoplus femur-rubrum* the proximal chiasma in the long chromosomes lies very close to the centromere at diakinesis and metaphase, and in order to explain its regular occurrence in this position Hearne & Huskins have postulated that this chiasma actually moves *towards* the centromere. We have seen above, however, that there is no need to postulate such movement because there is internal evidence that the chiasma actually forms in that position. Secondly in such plants as *Agapanthus* (Darlington, 1933) the centric loop at metaphase is about twice as large as the distal loops, which are themselves all of the same size in any given arm of an individual bivalent. It would be necessary to postulate movement to explain this if chiasmata were supposed to form indifferently in all parts of the bivalent. Accepting the hypothesis of position determination from the centromere, these observations merely mean that $d=i$, and there is no need to postulate movement.

Thus we can distinguish on one hand the chiasmata which are terminalized and on the other those that remain interstitial, as moving and non-moving chiasmata. It is only necessary for the theory of terminalization to account for movement of the former type. This removes an awkward dilemma. Previously it was necessary to suppose that, of adjacent acentric loops, the smaller would grow at the expense of the larger. In the case of adjacent centric and acentric loops, the former would grow until its larger size, as compared with its neighbour, neutralized the effect of the included centromeres. Carrying this argument to its logical conclusion, complete terminalization of two chiasmata in the same arm would be impossible, as at some stage in the process the acentric loop must reach a very small size as compared with its centric neighbour and so a balance should be reached and terminalization of the interstitial chiasma should cease. It is unnecessary now to postulate that small loops grow at the expense of the larger ones, other things being equal,

because the more or less equal sizes of the distal acentric loops and the relative size of the centric loop may be considered as determined by the positions of formation of the chiasmata. Then larger loops may be deemed to grow at the expense of adjacent smaller ones, and terminalization will be a process which, once initiated, will go on at an ever-increasing speed. Small differences in loop size will lead to no change, as the chiasma movement involves what may be termed a "friction". This depends on the fact that, in order to move a chiasma, paired chromatids must be separated and so the terminalization force must attain a certain minimal value before it can become effective by breaking this pairing. Loops will in general grow at the expense of open arms provided the movement forces can overcome the friction of the chiasmata. This will lead to the occurrence of terminal chiasmata in otherwise unaltered bivalents as, for example, in *Agapanthus* and *Melanoplus*.

Thus, in general, terminalization is an all or none process. Either the chiasmata all terminalize in a bivalent or, at most, only the most distal ones move to the ends, there being no reduction in chiasma frequency. Different bivalents of the same nucleus may show the two alternative types of behaviour, but more often the whole nucleus will be of one kind or the other, for example, *Campanula* on the one hand, and *Lilium* on the other. The only types which may be said to show intermediate terminalization are (*a*) those in which some but not all of the bivalents show complete movement, while the others show none, or at most, movement of the most distal chiasma only, and (*b*) those in which terminalization movement is arrested as the later stages of meiosis begin before it can be completed. Such cases may be expected to be rare.

6. Summary

The positions of chiasmata at metaphase are dependent on (*a*) their positions at the time of formation, and (*b*) subsequent movement. These two factors may now be separated analytically.

A method is given for determining the mean positions of formation of chiasmata relative to the centromere and to one another, by comparison between the size classes in organisms with a large chromosome size range. The original positions as determined in this way seem to be retained at metaphase. There is thus no need to suppose that interstitial chiasmata have moved between their formation and the attainment of metaphase.

Thus terminalization is an all or none process. Either all the chiasmata terminalize or they do not move, except for occasional movement of the

most distal chiasma to the end of the bivalent as a result of absorption of the free distal arm.

Some properties of chiasma formation in two-armed chromosomes are discussed and certain observations which would be critical for the hypothesis of centromeric determination of the position of chiasmata are described.

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