Chromosome Studies in *Fritillaria*, III
Chiasma Formation and Chromosome Pairing in
Fritillaria imperialis

By **C. D. DARLINGTON**
John Innes Horticultural Institution, Merton

Received September 16, 1930

Introduction

Consideration of chromosome pairing in polyploids and especially of the mechanical conditions at prophase of meiosis and the frequency of the formation of trivalents has led me to the view that the formation of chiasmata is a *conditio sine qua non* of the pairing of chromosomes (DARLINGTON 1929 a & b).

Fritillaria imperialis (v. DARLINGTON 1929 b) seemed particularly suitable material with which to test this hypothesis by a statistical study of the pairing of fragment chromosomes at meiosis. Chiasmata are formed at random in the large chromosomes, and the fragments which occur in many clonal varieties, are a small fraction of the length of the large chromosomes. These should therefore fail to pair, on my hypothesis, in a proportion of cases while, on the hypothesis that the pairing of chromosomes is conditioned by a generalised affinity, they should pair, if at all, with the same regularity as the larger chromosomes.

The methods used have been described in earlier papers two of which were concerned with *Fritillaria* (DARLINGTON 1929 b; NEWTON and DARLINGTON, 1929, 1930).

Observations

1. Observations on Somatic Chromosomes

Several varieties of *Fritillaria imperialis* were examined and had the following chromosome complements :—

Var. "No. 2"	$2n=24$
"No. 3"	$2n=24$
"No. 6"	$2n=24$
"Maxima Yellow"	$2n=24$
"Orange Brilliant"	$2n=24+1f.$ Ⓢ
"Maxima Red"	$2n=24+1f.$
"No. 4"	$2n=24+3ff.$
"No. 10" *	$2n=24+3ff.$
"Crown upon Crown" *	$2n=24+3ff.$
"Yellow" *	$2n=24+6ff.$
	and $24+12ff.$
"No. 13" *	$2n=24+6ff.$

* Pollen mother-cells studied in detail. Ⓢ "f" is the abbreviation used for "fragment".

The 24 chromosomes of the somatic complement resemble those of *F. Meleagris* (NEWTON and DARLINGTON 1930) and *F. latifolia* (DARLINGTON 1929 a). Four

have the attachment constrictions sub-medial, twenty sub-terminal (Fig. 1). The illustrations (Figs. 1-3) indicate that the chromosomes fill an approximately spherical space at metaphase. All the pairs cannot be constantly distinguished and on account of their contorted shape it is impossible to arrive at the exact length of each type. In order to obtain an approximation for the mean length of

Fig. 1.

Fig. 2.

Figs. 1-3. Somatic mitoses from the root tips of clonal varieties of *Fritillaria imperialis*. $\times 2160$.

Fig. 1. "No. 10." $2n=24+3ff.$ Plan with ends of chromosomes broken. Fig. 2. "No. 5," $2n=24+6ff.$, polar view with chromosomes drawn separately. The secondary constriction is visible in one pair.

Fig. 3. "Crown upon Crown," $2n=24+3ff$. M, medianly constricted chromosomes. S, subterminally constricted chromosomes. T¹ and 2-6 "terminally" constricted chromosomes.

Fig. 4. Fragments from somatic mitoses. A, "Crown upon Crown"; B, "No. 10"; C, "Yellow." $\times 4300$.

the members of the complement as a whole the gross length of the chromosomes in Fig. 3 was taken as equivalent to the actual length seen at an angle of 45° to the axis of vision. In this way the estimated mean length of the chromosomes was $(12.5 \times \sqrt{2}) \mu$ or 18.1μ .

The fragments in all varieties seem to be almost the same length (viz. 2μ) although they have their constrictions sometimes median and sometimes subterminal (Fig. 4).

2. Chiasma Formation and the Pairing of Fragments in the Pollen Mother-Cells

The prophase of meiosis follows the general course of development described by NEWTON for *Tulipa* (1927). An exchange of partners between chromatids is assumed to occur at every one of the "nodes" (BELLING 1928) or "points of intersection" (MAEDA 1930) observed at diplotene and later stages. These exchanges or chiasmata are formed at random.

The justification for interpreting "nodes" as chiasmata is three-

Figs. 5-8. The whole complement drawn separately. The numbers of fragments illustrated; trivalent fragment and numbers of chiasmata given below. Fig. 5. Late diplotene, "No. 13"; mean number of chiasmata, 3.2.

Fig. 6. Late diplotene, "No. 10"; mean number of chiasmata, 4.8. $\times 2600$

Fig. 7. Side view of metaphase, "No. 13."

Fig. 8. Side view of metaphase, "No. 10." Inset 3 fragments from another division, 2 paired and 1 free. M, medianly constricted chromosomes. $\times 1950$.

fold. (i) Whenever they can be examined at prophase from a suitable point of view the exchange of partner can be directly observed (Figs. 5 and 6). (2) At metaphase the points of intersection (which correspond numerically with prophase chiasmata) are always accompanied by a change of the plane in which the loop between the two pairs of chromatids lies (Figs. 7-10). (3) The special arrangements of separating chromatids at anaphase can be shown to agree with this assumption and, apparently, with no other, in the bivalent configurations most suited for such studies (NEWTON and DARLINGTON, 1930, on *F. Meleagris*). Fig. 11 shows a characteristic anaphase separation in *Fritillaria imperialis*, with the asymmetry of the chromatids which must follow the unravelling of chiasmata. At anaphase, therefore, separation of the pairs of chromatids takes place without breakage.

There is no change perceptible in the arrangement of the chromatids (i.e. no definite evidence of terminalisation: DARLINGTON 1931) between diplotene and metaphase. The chromosomes merely contract longitudinally and as they do so, successive loops arrange themselves at right angles to one another.

The pairing of fragments, as distinct from that of whole chromosomes, has not been observed at pachytene. The threads are too long

Fig. 9

Fig. 10

Figs. 9 and 10. Polar views of first metaphase of the pollen mother-cell division, showing numbers of chiasmata of each bivalent. Fig. 9. "No. 10"; one pair of fragments, one free fragment. Fig. 10. "No. 13"; 12 free fragments. $\times 2340$.

to be identified individually. But their later association (when it occurs) is normal except that at diakinesis and metaphase it is usually terminal (exception: Fig. 12) and it is possible that a slight amount of terminalisation may occur in the fragments which either does not occur or cannot be detected in the whole chromosomes (see Appendix). They form bivalents and trivalents. They may also pair with whole chromosomes, terminally and interstitially (i.e. by lateral chiasmata, DARLINGTON, 1929 b, 1931).

The fragments, therefore, unlike the small chromosomes of *Lygaeus* and *Metapodius* (WILSON, 1905, 1909) pass through comparable stages in development to the whole chromosomes (Fig. 6). When unpaired they usually lie on or near the equatorial plate at the first metaphase and divide at the first anaphase after the bivalent chromosomes (Fig. 7.) They may also pass without division to one pole, presumably after having been lying to one side of the plate at metaphase.

In the variety ("No. 10") where three fragments form trivalents occasionally, and are therefore to be regarded as homologous, their pairing shows that they are homologous with different parts of different chromosomes (Figs. 8 and 9). This must be ascribed to a reduplication of part of the material in the diploid set. Such a change would ordinarily escape notice (although it can be observed genetically in *Drosophila*). Apparent quadrivalent whole chromosomes were observed

twice, but not under good conditions for observation. This would also suggest reduplication.

Examination of individual nuclei, particularly in the clones "No. 10" and "Yellow," suggests a correlation between chiasma formation in the large bivalent chromosomes and the frequency of pairing of fragments (cf. Figs. 7, 9 and 11 with Figs. 8, 10 and 12). To determine this more satisfactorily I have recorded the results of examining large numbers of nuclei of different varieties at stages between diplotene and metaphase. This method supplies a corrective to errors of interpretation (which are always present) in that these errors are of a different kind at different stages. For example: the method used is to determine the mean number of chiasmata formed by whole chromosomes from the formula $M = \frac{\sum fv}{n}$. The

observations are taken as far as possible at random, usually from two to six from a single prophase nucleus and nine or ten from polar views

Fig. 11. Separation of a bivalent at anaphase of the first pollen mother-cell division in "No. 13." Side view. $\times 4300$.

Fig. 12. Fragments at various stages of mitosis and meiosis. A, 3 unpaired fragments at diplotene in "Crown upon Crown." B, 6 fragments in "Yellow" at diplotene, trivalent, bivalent and univalent. C, D and E, 3 fragments of "No. 10" at early diakinesis (C, a triple chiasma; E only one pair). F, 3 fragments of "No. 10." G, one pair and one univalent in side view of first metaphase in "Crown upon Crown." $\times 4000$.

of metaphase. The error of sampling should exaggerate the lower frequencies since a short chromosome is more often to be interpreted completely than a long one. This is not usually true of

Fig. 13

Fig. 14

Figs. 13-14. Diakinesis showing numbers of chiasmata in each bivalent. Fig. 13. "No. 13" showing two pairs and four unpaired fragments. $\times 2600$. Fig. 14. "Crown upon Crown," 3 unpaired fragments. Inset: fragment paired terminally with chromosome. $\times 3000$.

metaphase but a comparison of metaphase and prophase shows that any such error is probably slight. Again pairing of fragments with parts of chromosomes can be seen more readily at prophase than at metaphase.

The method used in calculating the frequencies of chiasmata from the observation of their pairing is based on the theory of terminalisation outlined in connection with *Tradescantia* (1929). The process there described hypothetically has since been observed in studying the origin of multiple chiasmata in *Primula sinensis* (1930). Each fragment is treated as a potential half-bivalent and one half-chiasma is therefore calculated for the pairing of a fragment with a chromosome, two half-chiasmata for the pairing of three fragments (since one of them must have formed two chiasmata). The average number of chiasmata

per potential bivalent fragment is calculated by dividing the sum of these half-chiasmata by the total number of fragments.

In calculating the simple expectation for chiasma-formation in the fragments the value of 18μ is taken for the average length of the whole chromosomes, 2μ for the length of the fragments. The width and thickness being comparable the assumption is made that the chiasma frequency of the fragments should be one-ninth that of the whole chromosomes.

Differences occur between the four clones studied in the numbers of fragments and in their relationship to one another, as follows:—

<i>F. imperialis</i> "No. 10"	3 homologous fragments (=1 ^{III}) ¹⁾
<i>F.</i> " " "Crown upon Crown"	3 fragments (1 ^{II} , 1 ^I , not 1 ^{III})
<i>F.</i> " " "Yellow"	6 fragments (1 ^{III} , 1 ^{II} , 1 ^I or perhaps 1 ^{VI})
<i>F. imperialis</i> "No. 13"	12 fragments ²⁾

The first two varieties are the most important.

The large number of fragments in "No. 13" prevented any exact study of their pairing, for incomplete observations are relatively valueless (the fragments overlooked are likely to be the ones paired with whole chromosomes, v. Table 3 B) and the proportion of complete observations is too small to be statistically reliable. The illustrations show that the frequency of pairing of fragments (although every one has at least one potential mate) was low. There was the same difficulty (but to a much less extent) in "Yellow" with 6 fragments. Here incomplete observations have been quoted for comparison.

Table 1
Observations on *Fritillaria imperialis* "No. 10" (3 fragments)
A. Chiasma-formation.

Nos. of chiasmata	3	4	5	6	7	8	Total Bivalents	Total Chi- asmata	Mean No. Chi- asmata per Bivalent
Diplotene	5	10	8	10	4	3	40	207	5.2
Diakinesis	9	9	13	13	3	0	47	227	4.8
Metaphase	1	8	10	2	1	1	23	112	4.9
Total Bivalents	15	27	31	25	8	4	110	546	4.9
„ Chiasmata	45	108	155	150	56	32	546	—	—

1) I, II III and VI give the maximum possible valency of configuration formed at meiosis.

2) The 12 fragments appeared in the flower buds of a plant having 6 fragments in the root-tip (DARLINGTON 1929 b) without doubling of the large chromosomes.

B. Pairing of Fragments.

Nos. of $\frac{1}{2}$ chiasmata	0	1	2	3	3	4	Total No. of fragments	Total $\frac{1}{2}$ chiasmata	Mean No. $\frac{1}{2}$ chiasmata per fragment
Type of pairing	f.f.f.	f+c.f.f.	f+f.f	f+f.f+c	f+c+f. f+c	f+f+f.			
Diplotene	8	2	9	—	—	3	66	32	0.48
Diakinesis	11	2	12	—	—	—	75	26	0.34
Metaphase	15	8	4	1	1	—	87	22	0.25
Total number of nuclei	34	12	25	1	1	3	228	80	0.35

Notes: (i) Considering observations of diplotene, diakinesis and metaphase together: there is a chance of one-fifth ($\chi^2=13.6217$; $n=10$; $P=0.20$) of such samples being taken at random from the same population. (ii) Considering observations of metaphase as opposed to those at diplotene and diakinesis the chance is a little over one-twentieth ($\chi^2=10.833$; $n=5$; $P=0.05+$). There is therefore a difference between diakinesis and metaphase; this difference is more likely to be due to different conditions of interpretation than to randomness alone.

Table 2

Observations on *Fritillaria imperialis* "No. 13" (12 fragments)

Chiasma formation: all metaphase observations.

Nos. of chiasmata per bivalent	2	3	4	5	6	Totals
Nos. of bivalents	32	34	27	—	1	94
Nos. of chiasmata observed	64	102	108	—	6	280
Mean number of chiasmata per bivalent						2.98

For note on pairing of fragments, see text.

Table 3

Fritillaria imperialis "Yellow."

A. Chiasma formation

No. of chiasmata per bivalent	1	2	3	4	Total bivalents	Total chiasmata	Mean No. of chiasmata per bivalent
No. of bivalents observed							
(1) Slide 2. Metaphase only	11	43	44	13	111	281	2.53
(2) Slide 5. Comparable metaphase and diakinesis	5	31	36	12	84	223	2.65
Total	16	74	80	25	195	504	2.58
Total nos. of chiasmata observed	16	148	240	100	504	—	—

B. The pairing of fragments

No. of $\frac{1}{2}$ chiasmata	0	1	2	2	3	3	4	4	5	Total
Type of pairing	all free	c+f	c+f c+f	f+f	f+f c+f	f+f +c	f+f f+f	f+f c+f c+f	f+f+f f+f	
Sl. 2. 6 ff. observed (i)	8	10	3	6	2	—	1	1	1	32
5 ff. observed	3	2	—	2	—	—	1	—	—	8
Sl. 5. 6 ff. observed (ii)	5	—	—	—	—	1	1	—	—	7
5 ff. observed	—	1	—	—	—	—	—	—	—	1
Sl. 2 and 6 ff. obsd. (ii) nos. of chiasmata	0	10	6	12	6	3	8	4	5	54
(iii) Mean no. $\frac{1}{2}$ chiasmata per fragment (with complete observation)										$\frac{54}{6 \times 39} = 0.22$

Note: The low proportion of C+f observations in cells where only 5 ff were observed indicates that the sixth fragment was paired with a large chromosome and was on this account overlooked.

Table 4

Fritillaria imperialis "Crown upon Crown" (3 ff.)

A. Observations of Chiasmata in the Bivalents

No. of Chiasmata per Bivalent	2	3	4	5	6	7	Total bivalents	Total chiasmata	Mean No. of chiasmata per bivalent
No. of Bivalents									
(i) diplotene-diakinesis	3	40	64	58	27	4	196	862	4.40
(ii) metaphase	2	14	9	7	5	—	37	147	3.97
(iii) total	5	54	73	65	32	4	233	1009	4.33
No. of chiasmata observed	10	162	292	325	192	28	1009	—	

B. Observations of the Pairing of Fragments

No. of $\frac{1}{2}$ Chiasmata	0	1	2	3	Total No. of nuclei	Total No. of ff.	Total No. of $\frac{1}{2}$ Xta	Mean No. of $\frac{1}{2}$ Xta per f.
Type of Pairing	3 free	C+f 2 free	f+f 1 free	C+f f+f				
Diplotene-diakinesis	40	3	19	—	62	186	41	.22
Metaphase	10	5	3	1	19	57	14	.25
Total	50	8	22	1	81	243	55	.23

Significance of the Observations

To consider first chiasma frequencies in the large bivalents: it will be seen that in two clones a slight decrease was found between diplotene and metaphase. This is of doubtful significance but agrees in direction with the observations of NEWTON and of BELLING (cf. BELLING 1928). BELLING however differs from me in interpretation owing to his not recognising as such what I call "terminal chiasmata." This accounts for the greater part of the diminution he observes, for slight terminalisation probably occurs between diplotene and diakinesis in *Lilium* and *Tulipa*. Thus, in BELLING's figure 2, I make 28 instead of 24 chiasmata. In NEWTON's figure 31 (1927) I make 28 chiasmata instead of BELLING's 21. Such slight difference as remains between my interpretation of diakinesis and diplotene in *Lilium* and *Tulipa* I am inclined to ascribe as in *Fritillaria* to the different conditions of observation at the two stages, although a diminution as a result of slight terminalisation is indicated by the formation of triple chiasmate amongst fragments.

Different clones in *Fritillaria imperialis* vary in mean chiasma frequency from 2.58 to 4.96. This may be ascribed to one of three causes, viz. (i) Structural hybridity. (ii) Environmental differences. (iii) Genetic variation.

The first seems unlikely in view of the general regularity of behaviour, the second unlikely in view of the uniformity of the different preparations of the same individual (Table 3). While therefore these sources of variation cannot be excluded (and doubtless contribute to the result) the third appears much the most important in *Fritillaria imperialis*. This conclusion is reinforced by the differences I have observed in chiasma formation between different species of *Fritillaria* to be described later (cf. also NEWTON and DARLINGTON 1930). The observations of differences observed in the large chromosomes, as a group, should therefore be applicable to the fragments.

The effect on the chiasma frequency however is comparable with that produced by external conditions found elsewhere. MAEDA (1930) has examined chiasma frequencies in particular distinguishable bivalents at metaphase in different preparations. He has not commented on the differences observed but they seem to me of particular importance, not only in connection with my own observations but also in connection with KIHARA's observations of the frequency of chromosome pairing in *Triticum-Aegilops* hybrids (1929). For comparison I reproduce percentage tables of certain examples of these two series of results (Table 5).

The pairing of the fragments on my hypothesis should be governed directly by the formation of chiasmata, but there are three respects in which the observations of chiasmata in the large bivalents are perhaps not directly applicable. Pairing at zygotene takes place in *Fritillaria*

Fig. 15. Single bivalents with fragments from early metaphase in "No. 10." Numbers of chiasmata marked. A, one fragment paired with chromosome interstitially. B, two homologous fragments paired interstitially with different parts of the same chromosome; probably opposite ends of the homologous segment. C, one fragment paired terminally with chromosome. D and E, fragments paired interstitially with whole chromosome. D, two free chromosomes. E, two paired chromosomes. $\times 2600$.

Fig. 16. Side view of first anaphase in "No. 13," the univalent fragments lagging slightly. One pair at one pole. Two more missing. $\times 2600$.

fragments must be affected by the homologies of the fragments in the different varieties. If there is an odd number of fragments the

without polarisation of the nucleus. Pairing of one part of a chromosome follows that of the part immediately adjoining it. It therefore seems possible that small and exceptional fragments may sometimes altogether fail to meet at pachytene. This might reduce the

expectation of pairing at metaphase in very small chromosomes (1929 b).

Another more definite source of divergence is the occurrence in one pair of fragments of two chiasmata (cf. Fig. 12 B) which might terminalise to the same end. This would give (without direct evidence of the cause) a lower pairing frequency than on the simple assumption. For these two reasons I have given the calculated chiasma-frequency as a maximum in Table 6.

Thirdly the relationship of chiasma formation in the large chromosomes to the pairing of

Table 5 (cf. Fig. 17)

Comparison in Percentages of Chiasma Formation and Chromosome Pairing in Different Forms

A. Present Observations of Chiasmata in <i>Fritillaria</i>									
Percentages of Bivalents		Numbers of Chiasmata							
		1	2	3	4	5	6	7	8
<i>F. imperialis</i> "No. 10" (110)		0	0	13.6	24.5	28.2	22.7	7.3	3.6
" " "No. 13" (94)		0	34.0	36.2	28.7	0	1.1	0	0
" " "Yellow" (195)		8.2	37.9	41.3	12.8	0	0	0	0
" " "C. upon C." (233)		0	2.1	23.2	31.3	27.6	13.7	1.7	0

B. NEWTON and DARLINGTON's observations of chiasmata in the major limb of "s" bivalents in <i>F. Meleagris</i> (1930)					
Percentages of Bivalents		Numbers of Chiasmata			
		1	2	3	4
		52.7	38.0	8.7	0.7

C. MAEDA's observations of chiasmata in "m" bivalents in <i>Vicia</i> (1930)							
Percentages of bivalents		Numbers of Chiasmata					
		1	2	3	4	5	6
Prepn. no. C ₁ -B (1) (204 obsns)		0.5	6.8	24.5	43.2	21.6	3.4
" " C ₁ -N (4) (244 " ")		1.2	20.1	50.0	24.6	4.1	0

D. KIHARA's observations of pairing in <i>Triticum dicoccoides</i> × <i>Aegilops ovata</i> (1929)								
Fixation no. No. of observations		Numbers of bivalents and trivalents						
		0	1	2	3	4	5	6
80	100	73	23	4	0	0	0	0
93	100	1	18	36	27	11	6	1

Fig. 17

frequency of pairing should be below the expectation, for there can only be one complete length of paired chromosomes at pachytene amongst the three (NEWTON and DARLINGTON 1929, cf. DARLINGTON 1930 b). If there is an odd fragment, its pairing frequency should be specially reduced, for although it is evidently capable of pairing with the parts of whole chromosomes it is in a specially disadvantageous position, for it must do so in competition, since these parts are presumably bivalent.

This source of divergence (directly shown in the case of trivalent whole chromosomes in *Hyacinthus*) (DARLINGTON 1929 a) can be accurately allowed for: where there are three fragments the pairing frequency must be calculated as for two. On this basis (Table 6) it will be seen that the observations approach the maximum calculated from the observations on chiasma frequency in the large chromosomes.

It may be argued that the agreement between chiasma frequency in major chromosomes and in fragments merely shows the conditions of chiasma formation to be the same in the two types. But this is not so, for the chiasmata are observed in the whole chromosomes according

Table 6
Summary of Observations
Comparison of Mean Frequencies of Chiasmata and Fragment Pairing

	"No. 10" 3 homol. ff.	"Yellow" 6 ff.	"Crown upon Crown" 2 homol. ff. 1 non-hom. f.	"No. 13" 12 ff.
Mean for pairs of bivalents	4.96	2.58	4.33	2.98
Max. expected mean for pairs of fragments	0.55	0.29	0.46	0.37
Max. expected mean fre- quency allowing for 3 fragments having the same chance as two	0.37	0.29	0.31	0.37
Mean calculated from pair- ing of fragments	0.35	0.22	0.23	Less than 0.37

to certain indisputable criteria. In the fragments on the other hand the chiasmata are inferred from the observation of pairing. I interpret them as "terminal chiasmata" merely because the chromosomes are paired. The observations are directly a verification of this interpretation and therefore indirectly a verification of the theory that chromosome pairing depends on chiasma formation.

The observations therefore show the expected correlation between chiasma-formation in large bivalents and in fragments, *on the assumption that the fragments only pair by chiasmata*. They also explain in terms of chiasma formation the very general observation of the failure of pairing of small new chromosomes arising by fragmentation. This type of observation has an important bearing on the theory of meiosis (DARLINGTON 1931).

The observations also show that genetical as well as environmental conditions affect chiasma formation (as they do crossing-over, cf. PLOUGH 1917, GOWEN 1923, BRIDGES 1929 and chromosome pairing, cf. KIHARA 1929).

Note. It might be thought that this failure of pairing in small chromosomes would preclude the perpetuation of forms with extreme size-differences in chromosomes (*Brachystola*, SUTTON 1902; *Uvularia*, BELLING, 1926; *Yucca filamentosa*, MORINAGA et alii 1929). The perpetuation of such forms must depend on a localisation of chiasmata such as that observed in *Fritillaria Meleagris*. A number of such forms are being studied.

Summary and Conclusion

Species and varieties of *Fritillaria* vary in regard to both the frequency and the distribution of the chiasmata formed by the pairing chromosomes at the prophase of meiosis, but each type has a constant average behaviour. Four species behave like *F. Meleagris* in having concentration of the chiasmata near the attachment constriction. But in *F. imperialis* the chiasmata are formed at random with a mean frequency constant for each variety (taking the complement as a whole). Varieties differ in their frequency, some having as low a mean as 3, others as high a mean as 5. Fragment chromosomes one-ninth the length of the ordinary chromosomes occur in these varieties. These fragments fail to pair (either with one another or with whole chromosomes) in a proportion of cases. And the frequency of their pairing is lower in varieties with lower frequency of chiasma formation.

It is shown that both these results could be predicted on the hypothesis that the pairing of chromosomes at metaphase depends on the formation of chiasmata amongst the associated chromatids at prophase. This hypothesis makes it possible to present the relationship of meiosis to mitosis fairly in simple terms, for at both there is an association of chromatids in pairs; the occurrence of chiasmata makes an effective difference between them at metaphase (DARLINGTON 1931). Or, we may say, chromosomes have no more affinity for one another at the metaphase of meiosis than at the metaphase of mitosis.

Appendix

Evidence of the conditions affecting terminalisation may be gathered from some recent work. I have noticed in the illustrations of KIHARA and NISHIYAMA (1930) that the fewer the pairs of chromosomes in *Triticum-Aegilops* hybrids the higher is the proportion with terminal association as the following table shows.

Hybrid	No. of divisions	No. of Chrs.	No. of chiasmata per chromosome		Proportion interstitial
			Total	Interstitial	
<i>T. durum</i> × <i>vulgare</i> (5n)	2	70	0.71	0.27	0.38
<i>T. aegilopoides</i> × <i>dicoccum</i> (3n)	5	105	0.48	0.15	0.31
<i>T. Spelta</i> × <i>aegilopoides</i> (4n)	6	169	0.30	0.06	0.20

The observations of PHILP and HUSKINS on *Matthiola* (1931) on the other hand indicate an increase in the proportion of interstitial chiasmata where there is a reduction in the total number. Here the reduction in prophase chiasmata in the long-chromosome race is probably much greater than that in metaphase chiasmata, for the maximum of two at metaphase (terminalisation being usually complete in *Matthiola*) limits the variation.

	No. of divisions	No. of chromosomes	Chiasmata per chromosome		
			Total	Interstitial	Proportion interstitial
Long chromosome race	35	490	0.77	0.09	0.12
Short chromosome race	35	490	0.81	0.02	0.03

The reduction in number of chiasmata in this case proceeds however, not from hybridity, but from a distinct genetic character correlated with the lack of contraction of the chromosomes. On the precocity theory (DARLINGTON 1931) this correlation is inevitable, for less contraction means a shorter prophase, insufficiently anticipating the splitting of the chromosome, and hence incomplete pachytene pairing, and a reduction of diplotene chiasmata; this would lead to the variation in metaphase pairing and consequent "non-disjunction" observed by LESLEY and FROST (1927). Evidently therefore we have the correlation of a reduced chiasma frequency and reduced time during which terminalisation can take place, expected on the basis of the precocity theory. The metaphase chromosomes of the long chromosome variety probably correspond to early diakinesis chromosomes of the short chromosome variety. This case is therefore exceptional.

The *Triticum* results suggest that, other things being equal, the fewer the chiasmata formed, the more effective or complete is their terminalisation. Comparison of fragments with whole chromosomes supports this conclusion. If this is the case, then the difference depends not on the frequency of the chiasmata per given length of chromosome but on the number of chiasmata per single chromosome.

Bibliography

- BELLING, J. 1926. Single and double rings at the reduction division in *Uvularia*. Biol. Bull. 50.
- 1928. Nodes and chiasmata in the bivalents of *Lilium* with regard to segmental interchange. Biol. Bull. 54.
- BRIDGES, C. B. 1929. Variation in crossing over in relation to age of female in *Drosophila melanogaster*. Carnegie Pub. 399.
- DARLINGTON, C. D. 1929 a. Meiosis in polyploids II. J. Genet. 21.
- 1929 b. Chromosome behaviour and structural hybridity in the Tradescantiae J. Genet. 21 (2).
- 1930. Meiosis in *Primula sinensis*. J. Genet. 22.
- 1931. Meiosis. Biol. Rev. (in press).
- GOWEN, M. S. and GOWEN, J. W. 1922. Complete linkage in *Drosophila melanogaster*. Amer. Nat. 56.
- KIHARA, H. 1929. Conjugation of homologous chromosomes in the genus hybrids *Triticum* × *Aegilops* and species hybrids of *Aegilops*. Cytologia 1.
- and NISHIYAMA, I. 1930. Genomaffinitäten in tri-, tetra- und pentaploiden Weizenbastarden. Cytologia 1.
- LESLEY, M. M. and FROST, H. B. 1927. Mendelian inheritance of chromosome shape in *Matthiola*. Genetics, 12.
- MAEDA, T. 1930. On the configurations of gemini in the pollen mother-cells of *Vicia Faba* L. Mem. Coll. Sci. Kyoto B. 5.
- MORINAGA, T. et alii. 1929. Chromosome numbers of cultivated plants. Bot. Mag. Tokyo 43.
- NEWTON, W. C. F. 1926. Chromosome studies in *Tulipa* and related genera. J. Linn. Soc. 47.
- and DARLINGTON, C. D. 1929. Meiosis in polyploids I. J. Genet. 21 (1).
- 1930. *Fritillaria Meleagris*: Chiasma formation and distribution. J. Genet. 22.
- PHILP, J. and HUSKINS, C. L. 1931. The Cytology of *Matthiola incana* (in press). J. Genet.
- PLOUGH, H. H. 1917. The effect of temperature on crossing over in *Drosophila*. J. Exper. Zool. 24.
- SUTTON, W. S. 1902. On the morphology of the chromosome group of *Brachystola magna*. Biol. Bull. 4.
- WILSON, E. B. 1905. Studies on chromosomes I. The behaviour of the idiochromosomes of the Hemiptera. J. Exper. Zool. 2.
- 1909. Studies on chromosomes V. The chromosomes of *Metapodius*, a contribution to the hypothesis of the genetic continuity of the chromosomes. J. Exper. Zool. 6.
-