THE HOMŒOLOGOUS NATURE OF THE NON-HOMOLOGOUS MEIOTIC PAIRING IN *TRITICUM ÆSTIVUM* DEFICIENT FOR CHROMOSOME V (5B)

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Received 5.i.63

1. INTRODUCTION

THE common wheat of agriculture, *Triticum æstivum* ($2n = 6x = 42$) is an allohexaploid which has disomic inheritance and in which there are 21 bivalents at meiosis. Each chromosome, therefore, normally pairs at meiosis with its fully homologous partner only, despite the close genetic and structural correspondence of equivalent, homœologous, chromosomes of the three component genomes (Sears, 1954; Riley, 1960). The efficiency of the suppression of homœologous affinity is further demonstrated by the small amount of meiotic pairing in 21-chromosome haploids in which homologous competition is absent (Riley, 1960).

However, the pattern of pairing is greatly modified in 40-chromosome nullisomics and 20-chromosome nullisomic haploids deficient for chromosome V (5B). In plants nullisomic for chromosome V (5B) there is a mean of approximately one multivalent per cell. Some cells have several multivalents and while trivalents and quadrivalents are most common there are also associations of five and six. In 20-chromosome haploids, deficient for chromosome V (5B), there is a marked increase in pairing compared with the level in 21-chromosome euhaploids. There are many bivalents and trivalents, but quadrivalents and higher associations are rare (Riley and Chapman, 1958; Riley, 1960).

Clearly, chromosome V (5B) carries one or more genes which are normally responsible for the extreme rarity of a form of non-homologous pairing in wheat. Moreover, it has been demonstrated that chromosome V (5B) alone is involved in the suppression of this type of non-homologous association and that the activity is confined to its long arm (Riley, Chapman and Kimber, 1960; Riley, 1960).

The question remains, however, as to the precise relationships between the chromosomes which pair non-homologously in the chromosome V (5B)-deficient situation. This abnormal pairing could result either from random synapses, or from the association of randomly distributed duplicate segments, or from homœologous pairing between corresponding chromosomes of the three genomes. The nature of the pairing in V (5B)-nullisomics and particularly the high frequency of trivalents in V (5B)-deficient haploids indicated that the hypothesis of homœologous association was probably correct. However, while

the inference of homœologous pairing seems reasonable it is nevertheless necessary to attempt to determine the exact relationships between the chromosomes which pair non-homologously. The present paper describes the results of work designed to ascertain these relationships.

2. MATERIAL

All the plants used in the present work were derivatives of *Triticum æstivum* L. emend. Thell ssp. *vulgare* MacKey variety Chinese Spring. In this variety the three classes of material listed below were used ; all were generously supplied by Dr E. R. Sears.

(*a*) In the first category there were euploid individuals which had 42 chromosomes and each member of the complement was complete and disomic.

(*b*) In the second class there was a set of lines, all with 42 chromosomes, but each disomic in turn for a telocentric condition of a different chromosome. In all, 20 chromosomes of the haploid complement were separately marked in the ditelocentric lines. In the remaining line, chromosome IV (4A) was carried as one telocentric and one complete chromosome. The ditelocentric lines were completely deficient for one arm of the appropriate chromosome but were otherwise identical to each other, and to the euploid stock, in chromosome structure. Since the telocentric condition is readily recognisable in somatic and meiotic preparations, it provides a cytological marker by which the behaviour of particular chromosomes can be followed.

(*c*) The final class of material consisted of a 42-chromosome stock which was nullisomic for chromosome V (5B) and tetrasomic for chromosome XVIII (5D). Chromosomes V (5B) and XVIII (5D) are homœologous (Sears, 1954) and tetrasomy for XVIII (5D) removes the sterility otherwise caused by the deficiency of chromosome V (5B) without interfering with the non-homologous pairing which also occurs when V (5B) is deficient. The difference in fertility makes nullisomic-V (5B) tetrasomic-XVIII (5D) plants much easier to use than those which are simply nullisomic for V (5B), although in the present work the extra dosage of chromosome XVIII (5D) caused difficulty in the diagnoses of the cytological status of occasional derivatives. The nullisomic-V (5B) tetrasomic-XVIII (5D) stock had been maintained by Dr E. R. Sears, in Missouri, and by the present authors, in Cambridge, for some generations prior to its use in the work described. In addition it should be indicated that all the material discussed in the present paper was derived from a hybridisation with a single individual of the stock.

3. METHODS

Diagnoses of somatic chromosome constitutions were made on Feulgen-orcein stained squashes of root-tips which had been pretreated with mono-bromonaphthalene.

Meiotic examinations were made on permanent squashes of pollen mother cells from anthers stained by the Feulgen procedure, with the stain intensified by the use of propionic orcein.

4. THE CHROMOSOME STRUCTURE OF *TRITICUM ÆSTIVUM*

Before considering the details of the tests to determine the nature of non-homologous chromosome pairing, it is necessary briefly to describe the classification of the chromosomes of *T. æstivum*. This classification, by Sears (1954) and Okamoto (1962), depended upon the use of various aneuploid combinations. Each chromosome was assigned to its particular genome by the comparison of the pattern of meiotic pairing in hybrids between the monosomics of *T. æstivum*

and various other parents deficient for one or other of the three genomes. In this way the complement was classified into three categories each of seven chromosomes—each category stemming from one of the original diploid parents of the hexaploid.

The second pattern emerged from the study of the 21 nullisomics, available in the variety Chinese Spring, completely deficient for each chromosome of the complement in turn. Each nullisomic condition caused a pronounced and often distinctive modification of the euploid phenotype. However, it was discovered by Sears (1954) that in certain instances tetrasomy for one chromosome would compensate for the phenotypic disturbance caused by deficiency for

TABLE 1

The classification of the chromosomes of T. æstivum *into genomes and homœologous groups (after Okamoto, 1962)*

Homœologous groups	Genomes		
	A	B	D
1	XIV (1A)	I (1B)	XVII (1D)
2	XIII (2A)	II (2B)	XX (2D)
3	XII (3A)	III (3B)	XVI (3D)
4	IV (4A)	VIII (4B)	XV (4D)
5	IX (5A)	V (5B)	XVIII (5D)
6	VI (6A)	X (6B)	XIX (5D)
7	XI (7A)	VII (7B)	XXI (7D)

another. There were seven groups, each of three chromosomes, within which nullisomic-tetrasomic compensation occurred; there was no compensation between chromosomes of different groups. Clearly, the capacity of one chromosome, in extra dosage, to compensate for the disturbance caused by the deficiency of another is an indication of similarity in their genetic activities. Chromosomes in the same group may be described as homœologous.

Fitting together the classifications into genomes and homœologous groups showed that each homœologous group had one chromosome in each genome and that each genome had one chromosome in each homœologous group (table 1). Consequently, it is reasonable to conclude that homœologues derive from corresponding chromosomes of the diploid parents which were the sources of the genomes of the hexaploid. They may thus have had a common origin in the chromosomes of an ancestral diploid prototype.

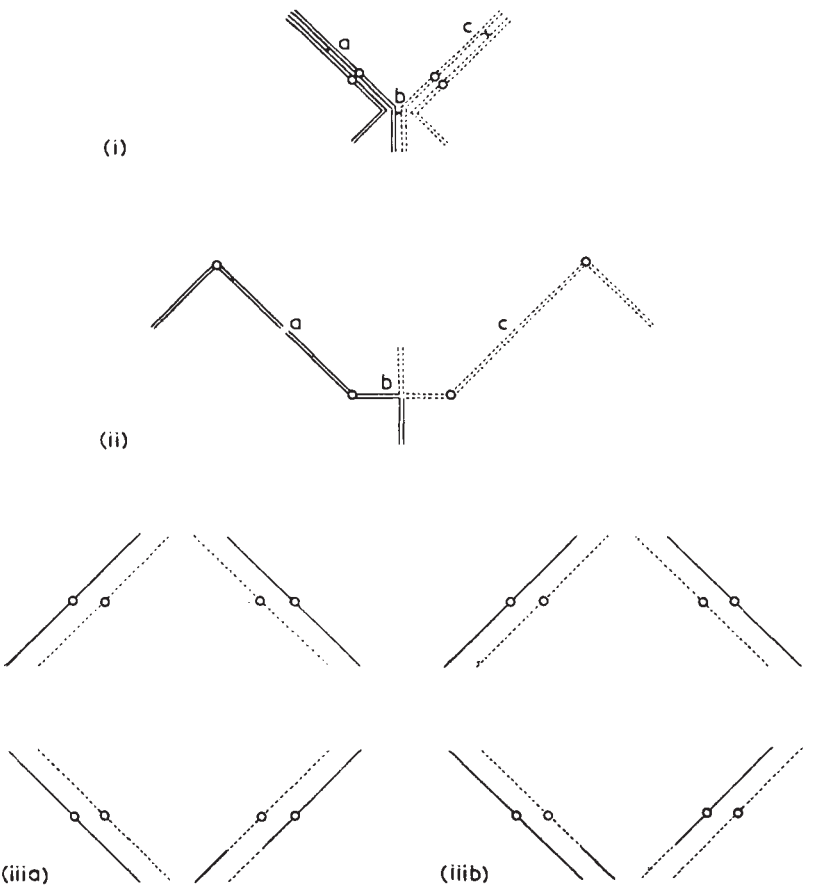
5. CHROMOSOME DESIGNATIONS

For a considerable time it has been the practice to number the chromosomes of *T. æstivum* with roman numerals. More recently, Sears (1958) has suggested that it might be more convenient to

designate them with arabic figures and with letters in a way which indicated the genome and homœologous group to which they belong. Thus, for example, chromosome XIV in homœologous group 1 and the A genome would become 1A, and I and XVII would become 1B and 1D respectively (table 1). Because both systems are currently in use, both designations will be applied in the present paper, the genome-group symbols being placed in brackets.

6. THE TEST TO DETERMINE THE CHROMOSOMES CONCERNED IN NON-HOMOLOGOUS PAIRING

Chiasma-formation and recombination between non-homologous chromosomes will lead to the occurrence of changes that must formally



TEXT-FIG. 1.—A diagram to illustrate a possible mode of origin of translocations by non-homologous meiotic pairing in plants of *T. æstivum* deficient for chromosome V (5B). (i) Two pairs of chromosome have paired homologously at prophase and have formed chiasmata at *a* and *c*. One member of each pair has paired non-homologously and formed a chiasma at *b*. (ii) A possible orientation, at first metaphase, following such pairing. (iii) The second anaphase segregations which might follow such a metaphase orientation showing the segregation of a reciprocal translocation condition (iii*a*) and two duplication-deficiency conditions (iii*b*).

be recognised as translocations relative to the original chromosome structure. Text-fig. 1 illustrates one way in which such a translocation might arise. It may be noted that, since there is usually only one chiasma per arm in wheat, most recombinational translocations will be terminal and interstitials will be rare. Therefore most models used in the present work have assumed the translocations to be terminal. The production of translocation heterozygotes in the derivatives of nullisomic-V (5B) plants has been described by Riley and Chapman (1958) and attributed to recombination. Consequently the determination of the chromosomes concerned in translocations, originating in this

TABLE 2

Meiotic pairing in T. æstivum *nullisomic-V (5B) tetrasomic-XVIII (5D)*

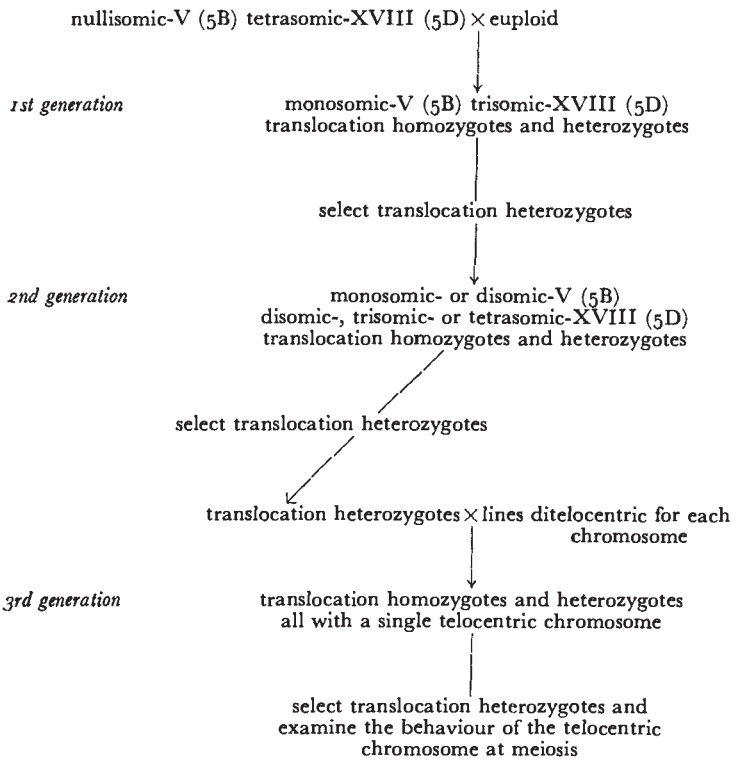
Plant no.	No. cells	Mean per cell					Range			Mean chiasmata per cell
		univ.	biv.	triv.	quadriv.	hexav.	triv.	quad.	hex.	
nulli-V tetra-XVIII 1	44	0·80	18·70	0·25	0·73	0·02	0-2	0·2	0-1	39·91±0·49
nulli-V tetra-XVIII 2	49	0·80	17·45	0·47	1·16	0·04	0-4	0-3	0-1	42·04±0·40
nulli-V tetra-XVIII 3	50	0·78	18·16	0·38	0·88	0·04	0-2	0-3	0-1	40·20±0·27
nulli-V tetra-XVIII 4	50	0·20	19·92	0·04	0·46	...	0-2	0-2	...	40·78±0·32
euploid . .	30	0·20	20·90	...	...	...	...	...	...	43·60±0·40

way, will also lead to the recognition of the chromosomes which have been involved in non-homologous meiotic pairing. The purpose of the present work, therefore, has been to ascertain between which chromosomes translocations had occurred, and meiotic pairing could be inferred to have taken place, in V (5B)-deficient situations.

The arrangement of the test is illustrated in text-fig. 2 and is described below. In the first instance it was planned to pollinate plants nullisomic for chromosome V (5B) and tetrasomic for chromosome XVIII (5D) with the pollen of normal, euploid, individuals. This form of V (5B)-deficient parent was chosen because of the restoration of fertility resulting from tetrasomy for chromosome XVIII (5D). There is a pronounced departure from a purely bivalent-forming pattern of meiotic pairing in the nullisomic-V (5B) tetrasomic-XVIII (5D) stock. The level of multivalent formation is considerably in excess of the single quadrivalent, or trivalent plus univalent, to be expected simply from the tetrasomy of chromosome XVIII (5D) (table 2). The non-homologous pairing, characteristic of the deficiency of chromosome V (5B), is displayed despite the extra dosage of chromosome XVIII (5D) (plate I, fig. 1). However,

all the multivalents formed in this stock, other than that associated with XVIII (5D), should not necessarily be attributed to contemporary non-homologous pairing since some might be due to heterozygosity for translocations originating from non-homologous recombinations in earlier generations. However, for the purposes of the present test it is immaterial whether the translocated chromosomes, extracted at the first cross, had originated at the immediately preceding or at some earlier meiosis.

The hybrids resulting from the cross, nullisomic-V (5B) tetrasomic-XVIII (5D) × euploid, could be expected to have 42 chromosomes and to be monosomic-V (5B) trisomic-XVIII (5D). They would



TEXT-FIG. 2.—The sequence of the test designed to determine which chromosomes are involved in the translocations which result from non-homologous pairing and recombination in the deficiency of chromosome V (5B).

also be heterozygous for any translocations arising from non-homologous pairing on the nullisomic-V (5B) tetrasomic-XVIII (5D) side of the parentage. Plants monosomic for chromosome V (5B) have normal meiotic behaviour, with twenty bivalents and one univalent, so that non-homologous pairing is prevented by chromosome V (5B) in single dose. Consequently there would be no further non-homologous recombination in the F_1 plants, or their derivatives, provided chromosome V (5B) was retained.

The planned procedure was to select translocation heterozygotes

in the F_1 generation, and to allow them to self-pollinate to obtain an F_2 in which a number of heterozygotes were available for checking. The F_2 plants would be either disomic, trisomic or tetrasomic for chromosome XVIII (5D) and either monosomic or disomic for chromosome V (5B). Individuals nullisomic for chromosome V (5B) would be expected to be very infrequent because pollen deficient for this chromosome rarely functions. However, the status of these two chromosomes could be ignored for the purpose of the test, except that plants completely deficient for chromosome V (5B) would have to be discarded because of the possibility of their giving rise to new non-homologous recombinants.

Translocation heterozygotes would be selected, on the basis of meiotic behaviour, in the F_2 generation and pollinated with the pollen of the lines in which each chromosome of the wheat complement was marked, in turn, by being telocentric. Translocation heterozygotes would again be selected, amongst the derivatives of these further crosses, and examined at meiosis to determine the behaviour of the telocentric chromosomes. If the telocentric was simply included in a bivalent, making a heteromorphic rod, and was never involved in a multivalent, then it could be concluded that the marked chromosome had not participated in a translocation. By contrast the incorporation of a telocentric in a multivalent would imply that the marked chromosome had been concerned in a translocation. The comparison of the behaviour of all the telocentric chromosomes, in a particular family, would show the translocated chromosomes which had at some time paired and recombined non-homologously in the nullisomic-V (5B) tetrasomic-XVIII (5D) stock.

7. THE DETERMINATION OF THE CHROMOSOMES INVOLVED IN TRANSLOCATIONS

(i) *Nullisomic-V (5B) tetrasomic-XVIII (5D) × euploid, F_1*

A single plant of the nullisomic-V (5B) tetrasomic-XVIII (5D) stock was pollinated with euploid pollen. A total of 31 seeds was obtained from this cross and all were grown. In order to obtain the maximum return of seeds, meiotic examination was confined to one inflorescence of each F_1 plant. Consequently, it was not always possible to study many first metaphase cells. However, there were 21 plants heterozygous for translocation differences which were clearly distinguishable by the presence of one or more quadrivalents in addition to the chromosome XVIII (5D) trivalent (plate I, fig. 2). Ten plants in which there were no additional multivalents must be presumed to have been structural homozygotes with no modification of the euploid chromosome pattern. The extraction of gametes with no translocations must mean that the nullisomic-V (5B) tetrasomic-XVIII (5D) parental plant was not homozygous for any structural differences relative to the euploid parent. However, it may have carried translocations, in the heterozygous condition, which had

resulted from non-homologous recombinations in an earlier generation. However, the critical feature of this generation was the demonstration of the clear possibility of extracting the products of non-homologous recombination from nullisomic-V (5B) tetrasomic-XVIII (5D) plants.

(ii) *Nullisomic-V (5B) tetrasomic-XVIII (5D) × euploid, F_2*

Ten F_2 progenies were grown from F_1 plants heterozygous for translocation differences. As many F_2 plants as possible were checked at meiosis to determine the segregation of the translocation differences (table 3). The majority showed quadrivalents at first metaphase, indicating heterozygosity for one or more translocation differences.

TABLE 3

The number of translocations heterozygous in the F_1, and their segregation in the F_2 of ten families of the cross T. æstivum *nullisomic-V (5B) tetrasomic-XVIII (5D) × euploid*

Family	No. translocations heterozygous in F_1	F_2 plants scored	Classification of F_2 plants on the number of translocations heterozygous			
			0	1	2	3
1	2	6	1	0	5	0
2	1	4	0	4	0	0
4	3	17	2	9	5	1
6	2	15	5	10	0	0
12	3	14	5	6	2	1
16	3	17	5	8	4	0
18	3	*	...	...	...	...
21	2	11	3	6	2	0
24	2	16	1	11	4	0
30	2	17	4	11	2	0

* No F_2 plants of Family 18 were checked at meiosis.

Except for Family 2 in which only one translocation had been heterozygous in the F_1, the F_2 families contained plants heterozygous for two, and occasionally for three, translocation differences. There was no evidence of multiple translocations involving more than two pairs of chromosomes.

Using, as female parents, individuals heterozygous for as many translocation differences as possible, crosses were made with the range of lines in which every chromosome was marked by being telocentric. No crosses were made with the line in which chromosome V (5B) was telocentric since the absence of this chromosome from the original nullisomic-V (5B) tetrasomic-XVIII (5D) parent precluded the possibility of its being concerned in non-homologous recombinations.

(iii) *(Nullisomic-V (5B) tetrasomic-XVIII (5D) × euploid F_2) × telocentric lines*

Five plants from the cross of each telocentric line with each F_2 family were scored at meiosis. Only those individuals with

quadrivalents, indicating translocation heterozygosity, were examined in detail to ascertain the behaviour of the telocentric chromosome.

In the majority of plants the telocentric paired only with a single complete homologue, making a heteromorphic rod bivalent (plate I, fig. 3). Such a situation provided no evidence that the marked chromosome had participated in a translocation. Positive evidence

TABLE 4

The chromosomes involved in translocations in families of T. æstivum *derived from the cross, nullisomic-V (5B) tetrasomic-XVIII (5D) × euploid*

Family	No. of translocations	Chromosomes involved in translocations	Classification of translocated chromosomes into homœologous groups	
1	2	VI (6A), XIV (1A), XVII (1D), XIX (6D)	XIV (1A)-XVII (1D) VI (6A)-XIX (6D)	group 1 group 6
2	1	IV (4A), ?	IV (4A)	group 4
4	3	III (3B), VI (6A), XIV (1A), XVI (3D), XVII (1D), XIX (6D)	XIV (1A)-XVII (1D) III (3B)-XVI (3D) VI (6A)-XIX (6D)	group 1 group 3 group 6
6	2	VI (6A), XIX (6D), ?, ?	VI (6A)-XIX (6D)	group 6
12	3	II (2B), VI (6A), X (6B), XVII (1D), XX (2D), ?	XVII (1D) II (2B)-XX (2D) VI (6A)-X (6B)	group 1 group 2 group 6
16	3	I (1B), X (6B), XIV (1A), XIX (6D), XX (2D), ?	I (1B)-XIV (1A) XX (2D) X (6B)-XIX (6D)	group 1 group 2 group 6
18	3	III (3B), XII (3A), XIV (1A), XVII (1D), XX (2D), ?	XIV (1A)-XVII (1D) XX (2D) III (3B)-XII (3A)	group 1 group 2 group 3
21	2	III (3B), XIV (1A), XVI (3D), XVII (1D)	XIV (1A)-XVII (1D) III (3B)-XVI (3D)	group 1 group 3
24	2	I (1B), XIV (1A), ?, ?	I (1B)-XIV (1A)	group 1
30	2	I (1B), XIII (2A), XIV (1A), XX (2D)	I (1B)-XIV (1A) XIII (2A)-XX (2D)	group 1 group 2

? = unidentified chromosome.

of the involvement of a chromosome in a translocation was provided by the situation in which the appropriate telocentric was a component of a quadrivalent (plate I, fig. 4). These quadrivalents were always chains in which the telocentric was at one end of the chain of four chromosomes. Clearly, the formation of a ring of four was impossible because of the deficiency of one arm of the telocentric member. The chromosomes positively determined to be concerned in translocations are shown in table 4.

The chromosomes involved in translocations were fully ascertained

in Families 1, 4, 21 and 30; while only one chromosome remained undetected in Families 2, 12, 16 and 18. Two chromosomes in the translocations in Families 6 and 24 were not established.

Because the original F_1 plants, except that from which Family 2 was derived, were heterozygous for more than one translocation difference, it was not immediately possible to determine precisely the chromosomes between which translocations had occurred. In Family 2 both the translocated chromosomes were not determined, and in the other families it was impossible to assert which pairs had exchanged material when altogether four or six chromosomes were involved in translocations.

However, a remarkable distribution of translocated chromosomes became apparent when they were classified into homœologous groups, as in the final column of table 4. It was immediately apparent that the translocated chromosomes were not a random sample from the wheat complement. For in those families in which all were determined the translocated chromosomes always occurred in pairs in particular homœologous groups. Thus, in Family 1 two chromosomes, XIV (1A) and XVII (1D), were in group 1 and two others, VI (6A) and XIX (6D), were in group 6. Similarly, in Family 4 with three translocations, the six chromosomes concerned were distributed two to group 1, XIV (1A) and XVII (1D), two to group 3, III (3B) and XVI (3D), and two to group 6, VI (6A) and XIX (6D). The same pattern was present throughout, even in the incompletely assayed families. In Families 12, 16 and 18, with three translocations and one undetermined chromosome, four of the identified chromosomes were in two homœologous groups and the odd fifth chromosome in a third group.

The probability of obtaining such a distribution of chromosomes by chance is extremely slight. The implication must be that translocations had occurred entirely between homœologous chromosomes. Consequently it can also be concluded that the non-homologous recombinations, from which the translocations arose, had resulted from the meiotic pairing of homœologous chromosomes in the chromosome V (5B) deficient parental stock.

8. PROOF OF THE HOMŒOLOGOUS NATURE OF THE TRANSLOCATIONS

The results obtained from the first set of crosses with the telocentric lines indicated, with little room for doubt, that the translocations were between homœologues. Yet the proof was not absolute, so a further test was attempted in an effort to obtain the crucial evidence.

Plants in Family 4 which were heterozygous for translocation differences, and in which one of the chromosomes involved in the difference was already marked by being telocentric, were crossed with the lines ditelocentric, in turn, for each of the other five chromosomes concerned in translocations in the Family. The purpose of

these crosses was to obtain offspring which carried telocentrics for two chromosomes simultaneously and which were still heterozygous for translocation differences. The behaviour, at meiosis, of the two telocentrics relative to the translocation multivalents, would then show whether segments had been translocated between the two marked chromosomes.

The derivatives of the crosses were therefore selected initially, on the basis of their somatic chromosome constitutions determined from root-tip squashes, for the presence of two telocentric chromosomes. Table 5 shows that 11 of the 15 possible, double telocentric combinations were produced in the Family, in which chromosomes III (3B), VI (6A), XIV (1A), XVI (3D), XVII (1D) and XIX (6D) were involved in translocations.

TABLE 5

The derivatives obtained with telocentrics of two different chromosomes in Family 4 (+ indicates the combination obtained)

Telocentric	Telocentric				
	VI (6A)	XIX (6D)	III (3B)	XVI (3D)	XIV (1A)
XVII (1D)	...	...	...	+	+
XIV (1A)	+	+	+	+	
XVI (3D)	...	+	+		
III (3B)	+	+			
XIX (6D)	+				

A range of patterns of pairing of the chromosomes involved in translocations was possible in the doubly telocentric derivatives, depending upon their precise constitution. Clearly, in respect of the chromosomes concerned in any translocation difference in the original stock, the gametes of the ditelocentric parents in the further crosses provided either two unmodified complete chromosomes or one unmodified complete and one telocentric chromosome. The parent heterozygous for a translocation difference and carrying a telocentric provided one telocentric plus either one of two reciprocally different translocated chromosomes or an unmodified chromosome. Only those offspring which had received a translocated chromosome were of further value so that when the doubly telocentric plants were examined at meiosis only translocation heterozygotes, in which a telocentric chromosome participated in the associated multivalent, were retained for further study. In those combinations involving

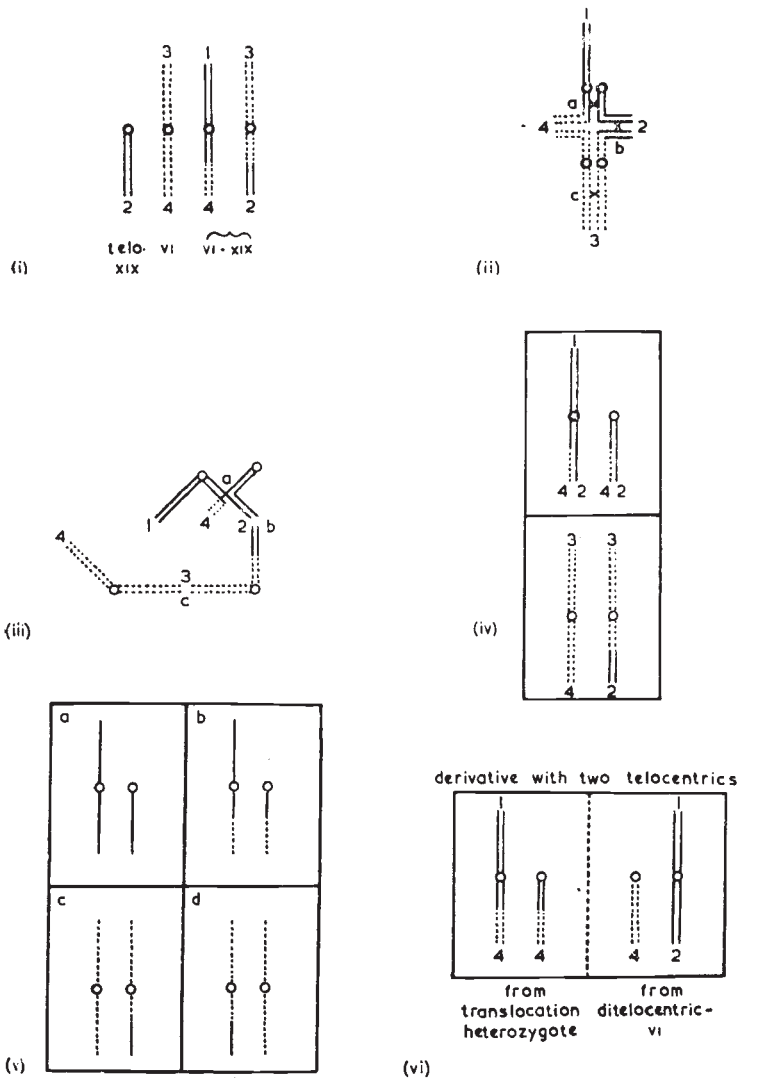
telocentric III (3B) with VI (6A), VI (6A) with XIV (1A) and XVI (3D) with XVII (1A) no plants heterozygous for translocation differences were obtained, so that no new evidence was produced.

The five combinations, in which the telocentric chromosomes were respectively III (3B) with XIV (1A), XIV (1A) with XVI (3D), III (3B) with XIX (6D), XIV (1A) with XIX (6D) and XVI (3D) with XIX (6D), gave unequivocal evidence that the two marked chromosomes were not involved in the same translocations. In all these combinations there were plants in which one telocentric chromosome participated in a quadrivalent while the other telocentric was in a heteromorphic rod bivalent.

Positive evidence that one translocation in Family 4 was between chromosomes XIV (1A) and XVII (1D) was obtained through the identification of cells in which the telocentrics for both chromosomes participated in the same trivalent (plate II, fig. 1). The trivalents were always chains, with the telocentrics at opposite ends of the chain. From this configuration one telocentric must have been homologous with the unmodified arm and the other homologous with the interchange arm of the translocated chromosome. It may be noted that chromosomes XIV (1A) and XVII (1D) are homœologous, both belonging to group 1 (table 1).

From the information available about the behaviour of the doubly telocentric plants described above, it was already clear that chromosome XIX (6D) was not involved in a translocation with chromosomes III (3B), XIV (1A) or XVI (3D). Moreover, the demonstration that the translocation in which chromosome XVII (1D) participated was with chromosome XIV (1A) showed that XVII (1D) had not undergone translocation with XIX (6D). Consequently four of the five possible chromosomes with which XIX (6D) might have exchanged segments could be eliminated, leaving only one unaccounted for, namely, chromosome VI (6A). There was, thus, from the crosses already described, evidence of a translocation between chromosomes VI (6A) and XIX (6D).

Supporting evidence for this conclusion came from the only plant which was heterozygous for a translocation and carried chromosomes VI (6A) and XIX (6D) as telocentrics. In this plant there were many cells with multivalents in which the two telocentrics participated. There were cells with triradial trivalents involving two telocentrics and with quadrivalents which included two complete and two telocentric chromosomes. In the latter, chiasmata on both sides of their centromeres associated the two complete chromosomes, and the chiasmata associating the two telocentric with the two completed chromosomes had terminalised towards each other (plate II, fig. 2). In addition there were " panhandle " trivalents involving one telocentric and two complete chromosomes, as well as cells with two heteromorphic rod bivalents each including one telocentric chromosome (plate II, fig. 4). However, the most critical cells were those



TEXT-FIG. 3.—A diagram to illustrate a possible mode of origin by recombination of the relevant chromosome structures of the plant obtained, in Family 4, in which the telocentric of chromosome VI (6A) could pair, at meiosis, with a telocentric derived from telocentric-XIX (6D). (i) The chromosome arrangement of the original plant heterozygous for a VI (6A)-XIX (6D) translocation and carrying the telocentric of XIX (6D). (ii) A possible pattern of pairing, at prophase, of the chromosomes in the VI (6A)-XIX (6D) translocation with chiasmata at *a*, *b* and *c*. (iii) A possible first metaphase orientation of the chromosomes so paired. The chiasma *a* has resulted in the transference of the translocation structure to one of the chromatids of the telocentric. (iv) The first anaphase segregation of these chromosomes. (v) The second anaphase segregation necessary to produce a gamete (vb) in which the same translocation structure is carried by both the telocentric and the complete chromosome. (vi) The structure of the derivatives of chromosomes VI (6A) and XIX (6D) in the doubly telocentric plant extracted from the cross, translocation heterozygote carrying telocentric XIX (6D) × ditelocentric VI (6A). All the observed configurations could be produced by a plant with the chromosome structure illustrated in (vi).

in which the two telocentric chromosomes paired together to form a bivalent (plate II, fig. 3).

Since the ditelocentric parent of this plant contributed an unmodified chromosome XIX (6D) and a telocentric chromosome VI (6A), the structure of the derivative was explicable in two ways. According to one explanation there could have been misdivision, in the parent heterozygous for the translocation, such that a new telocentric was derived from the arm of a translocated chromosome which included segments of both VI (6A) and XIX (6D). The new telocentric must then have been transmitted together with the complete chromosome carrying the reciprocal translocation structure.

Although all the observed configurations could have resulted from the presence of a new telocentric originating in the way described, an alternative explanation appears the more likely. According to this explanation the translocation heterozygote must have transmitted a gamete in which the translocation structure had been transferred to the telocentric chromosome as a result of normal meiotic recombination. That is to say the gamete was one in which there had been recombination between a translocated chromosome and the telocentric of XIX (6D) in the region between the centromere and the exchange point (text-fig. 3). If this were so, the observed configurations would also imply that the complete chromosome, also involved in this particular translocation and transmitted by the same parent, carried on one arm the same translocation pattern as the telocentric. Both postulated mechanisms provide for the prime requirements of the observations, namely that the two telocentrics were able to pair and that the two complete chromosomes had homologous regions on both sides of their centromeres.

That the translocation-bearing telocentric, derived from the telocentric of chromosome XIX (6D), could pair with the unmodified telocentric of chromosome VI (6A)—either directly or indirectly through a common third chromosome—confirms the conclusion, reached by indirect evidence, that there had been a translocation between the two chromosomes. It may be noted that chromosomes VI (6A) and XIX (6D) are homœologous, both belonging to group 6 (table 1).

Since the chromosomes concerned in two of the three translocations carried by Family 4 had been identified, the other translocation must have involved the remaining two translocated chromosomes, III (3B) and XVI (3D). Direct evidence of this could not be obtained from the plants in which both were telocentric because of the consistent formation of two heteromorphic rods bivalents each including one telocentric. However, the indirect evidence permits no other conclusion than that these two chromosomes had exchanged segments.

It may be noted that chromosomes III (3B) and XVI (3D) are homœologous, both belonging to group 3 (table 1). Consequently all three translocations carried by Family 4 were between homœologous

chromosomes, so there was clear evidence that the non-homologous pairing and recombination, in the absence of chromosome V (5B), was homœologous.

9. NON-HOMOLOGOUS RECOMBINATION IN THE DEFICIENCY OF CHROMOSOME V (5B)

(i) *Chromosome pairing*

It is clear that the numerous translocations states that could be extracted from the nullisomic-V (5B) tetrasomic-XVIII (5D) parent must have resulted from the non-homologous pairing by which its meiosis is characterised. Moreover, nullisomic-V (5B) plants of *T. æstivum* typically display similar non-homologous pairing, whereas plants tetrasomic for chromosome XVIII (5D) do not. Consequently, the non-homologous pairing can be ascribed solely to the absence of a control, normally exercised by chromosome V (5B), which confines pairing to fully homologous partners.

The ultimate resolution of the translocations in Family 4 demonstrated that they were entirely between homœologous chromosomes, III (3B) with XVI (3D), VI (6A) with XIX (6D) and XIV (1A) with XVII (1D). This confirmed the inference, drawn from the occurrence of pairs of translocated chromosomes in each of two or three homœologous groups in the other families (table 4), that the translocations were homœologous.

These results demonstrate that the modified meiotic behaviour, which occurs when chromosome V (5B) is deficient from *T. æstivum*, is due to the operation of homœologous, as well as the usual homologous, pairing. This confirms the hypothesis originally proposed by Riley and Chapman (1958) when the abnormal meiotic behaviour was first discovered. The normal restriction of association to complete homologues, in the presence of chromosome V (5B), means that the activity of this chromosome limits the specificity of pairing. This occurs despite the demonstrable similarity of homœologues in genetic activity.

This situation has an obvious significance for the understanding of the cytogenetic structure and evolution of *T. æstivum* and of all polyploids. The control exercised by chromosome V (5B) illustrates how high fertility, and the genetic stability which stems from disomic inheritance, can be achieved in an organism with considerable levels of genetic duplication or triplication.

In addition, an appreciation of the wheat situation may assist in the assessment of the general problem, as yet virtually unexplored, of the specificity of chromosome pairing. For this purpose it may be useful to attempt to define the probable differences between homologous and homœologous chromosomes. Homœologues are chromosomes of common origin tracing back to the same chromosome of some remote ancentral diploid. They have been long isolated from recombination with each other, first in distinct diploid species and subsequently,

after their inclusion in polyploid wheat, by the action of chromosome V (5B). As a result they have probably diverged from each other through the accumulation of mutations which removed, or changed, the functions of loci. There may also have been minor internal modifications of structure. Presumably these changes are distributed at random along the chromosomes. By contrast, exposed to the equalising effects of recombination, homologues have not diverged to the same extent.

If the assumption that the primary distinction between homologues and between homœologues, in wheat, resides in differences in the sum and continuity of genetically distinct regions, then it must be upon these factors that the specificity of synapsis depends. The effect of the activity of the chromosome V (5B) mechanism is so to shift the threshold values for these factors that homologues but not homœologues are sufficiently alike to pair.

It may then follow that the absence of non-homologous pairing in normal diploid organisms has a similar basis, since it seems inevitable that non-homologous chromosomes in diploids must possess, even if only at the level of sequences of nucleotide triplets, structurally and genetically similar regions. However, on the model derived from the behaviour of wheat, these would not lead to non-homologous pairing if below a critical continuity of extent or total. Thus, while synapsis is locus specific, the initiation of pairing may depend upon the extent of the equivalent regions that chromosomes have in common. There is little experimental access to the problem of the specificity of chromosome pairing in diploids so it may be that the present hypothesis, deriving from the relationships between homologues and homœologues in wheat, will provide an acceptable model.

(ii) *The distribution of homœologous recombination*

In view of the evidence of homœologous pairing in Family 4, it can be safely assumed that the pairs of translocated chromosomes in the same homœologous groups in the other families represent the precise chromosomes between which exchanges had occurred (table 4). These were, therefore, the chromosomes which underwent homœologous meiotic recombination. Consequently, it is now possible to consider the evidence on the distribution of homœologous pairing amongst groups and between genomes.

In all, 23 translocations were studied, of which six were incompletely analysed (table 4). Where the same two chromosomes were involved in translocations in more than one family it was impossible to determine whether the same translocation was present in each family, or whether there were different translocations. Thus the four families, Families 1, 4, 18 and 21, in which there were exchanges between chromosomes XIV (1A) and XVII (1D), might all have carried equivalent products of the same homœologous recombinational event. If the recombination had happened at an earlier meiosis, the immediate nullisomic-V (5B)

tetrasomic-XVIII (5D) parental plant would have been heterozygous for the resulting translocation difference. Alternatively some, or all, of the XIV (1A)-XVII (1D) exchanges might have been different deriving from separate recombinations in the last nullisomic-V (5B) tetrasomic-XVIII (5D) meioses.

Similar arguments apply to the I (1B)-XIV (1A) exchanges carried by Families 16, 24 and 30; to the III (3B)-XVI (3D) exchanges carried by Families 4 and 21; as well as to the VI (6A)-XIX (6D) exchanges carried by Families 1, 4 and 6 (table 4). The nullisomic-V (5B) tetrasomic-XVIII (5D) parental plant may have been heterozygous for any of these translocations. However, the evidence of the derivation of structural homozygotes in its first generation products,

TABLE 6

The distribution of the chromosomes involved in recombination-translocation in the derivatives of T. æstivum *nullisomic-V tetrasomic-XVIII. (In brackets are indicated the numbers of separate families in which the two chromosomes were in translocations)*

Homœologous groups	Genomes		
	A-B	A-D	B-D
1	XIV-I (3)	XIV-XVII (4)	...
2	...	XIII-XX (1)	II-XX (1)
3	III-XII (1)	...	III-XVI (2)
4	...	...	...
5	...	...	...
6	VI-X (1)	VI-XIX (3)	X-XIX (1)
7	...	...	...

as well as the absence of a translocation common to all ten families examined in detail, shows that it was not homozygous for any translocation state relative to the euploid.

It seems safer to assume that all exchanges between the same two chromosomes relate to the same recombinational event. If this is so, nine clearly distinct recombinations between different homœologues have been revealed in the present analysis (table 6). All three possible interchromosomal exchanges occurred in homœologous group 6, while two of the three occurred in groups 1, 2 and 3. No recombinants were isolated in groups 4, 5 and 7; although in the incompletely ascertained translocation in Family 2 one chromosome involved was in group 4. The absence of homœologous pairing in group 5 may relate to its disturbed balance in the parental material from which chromosome V (5B) was deficient while chromosome XVIII (5D) was tetrasomic.

Some significance may be attached to the distribution of recombinants between groups, since it may reflect differences in the affinities of homœologues. It is interesting to note that the homœologous

recombinants extracted most frequently by Okamoto and Sears (1962), from haploid wheats, were between chromosomes VI (6A) and XIX (6D) in group 6, and that group 6 recombinations were common in the present work. Of the three other types of homœologous recombinants in haploids observed by Okamoto and Sears, one, between chromosomes II (2B) and XX (2D), was also detected in the present work. However two others, between chromosomes XII (3A) and XVI (3D) and between XI (7A) and XXI (7D), were not detected.

As will be seen from table 6, three homœologous recombinations each took place respectively between the A and B, the A and D and between the B and D genomes. This distribution contrasts with the preponderance of A and D genome homœologous recombinants extracted by Okamoto and Sears (1962) from haploids. Indeed the results at present available provide no evidence that in the absence of chromosome V (5B) homœologous pairing takes place more commonly between the chromosomes of particular genomes. By contrast there may well be some distinction between the freedom with which homœologous pairing takes place within different groups.

10. SUMMARY

1. The deficiency of chromosome V (5B) from the common wheat of agriculture, *Triticum æstivum* ($2n = 6x = 42$), leads to the occurrence of non-homologous meiotic pairing. The purpose of the present investigation was to determine the relationships of the chromosomes that paired non-homologously.

2. Non-homologous pairing and recombination lead to the formation of translocations relative to the original chromosome structure. Consequently, the determination of the chromosomes which had participated in translocations originating in plants deficient for chromosome V (5B) would also lead to the ascertainment of the chromosomes which had paired and recombined non-homologously.

3. A test depending upon this principle was conducted in the first stage of which translocation heterozygotes were extracted in the F_1 generation of the cross, nullisomic-V (5B) tetrasomic-XVIII (5D) $\times$euploid. Individuals heterozygous for translocation differences, in the F_2 generation, were crossed with the lines in which each chromosome of the wheat complement was marked, in turn, by being disomic telocentric.

4. The behaviour of the telocentric chromosomes was examined at meiosis in the translocation heterozygotes derived from these crosses. Evidence of the participation of a particular chromosome in a translocation was afforded by the occurrence of its telocentric in a translocation mutivalent. Families obtained from ten of the original F_1 plants were studied in this way and most of the chromosomes involved in translocations were identified.

5. All the families, except one which was incompletely ascertained, carried more than one translocation so that it was not clear between

Plate I

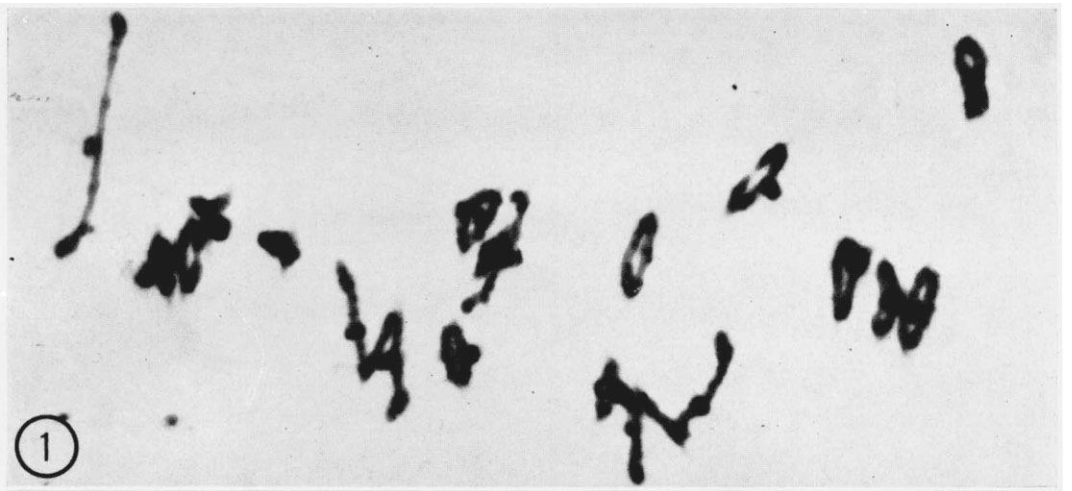
Photomicrographs of first metaphase of meiosis in pollen mother cells, stained with Feulgen and propionic orcein, of derivatives of *T. æstivum* var. Chinese Spring. × 1700.

FIG. 1.—Nullisomic-V (5B) tetrasomic-XVIII (5D) showing 17 bivalents and two quadrivalents. One of the quadrivalents is probably ascribable to the tetrasomy of chromosome XVIII (5D), the other is the product of non-homologous pairing.

FIG. 2.—Nullisomic-V (5B) tetrasomic-XVIII (5D) × euploid F_1, in which chromosome V (5B) was monosomic and XVIII (5D) trisomic. There are 17 bivalents, one trivalent, one quadrivalent and one univalent. The trivalent, at the left-hand end of the plate, is ascribable to the trisomy of XVIII (5D) and the univalent (right) to the monosomy of V (5B). The quadrivalent is indicative of translocation heterozygosity.

FIG. 3.—A derivative of Family 4 (nullisomic-V (5B) tetrasomic-XVIII (5D) × euploid, F_2) × ditelocentric for chromosome I (1B), with 15 normal bivalents and one heteromorphic rod bivalent which includes the telocentric of chromosome I (1B), one trivalent and two quadrivalents. Since there are 43 chromosomes and a trivalent (centre) without a univalent this plant must have been trisomic-XVIII, while the two quadrivalents indicate heterozygosity for two translocation differences. There is no evidence that chromosome I (1B) is involved in a translocation.

FIG. 4.—A derivative of Family 4 (nullisomic-V (5B) tetrasomic-XVIII (5D) × euploid F_2) × ditelocentric for chromosome III (3B), with 19 bivalents and one quadrivalent. The telocentric of chromosome III (3B) is a component of the quadrivalent, indicating that this chromosome is involved in a translocation in the Family.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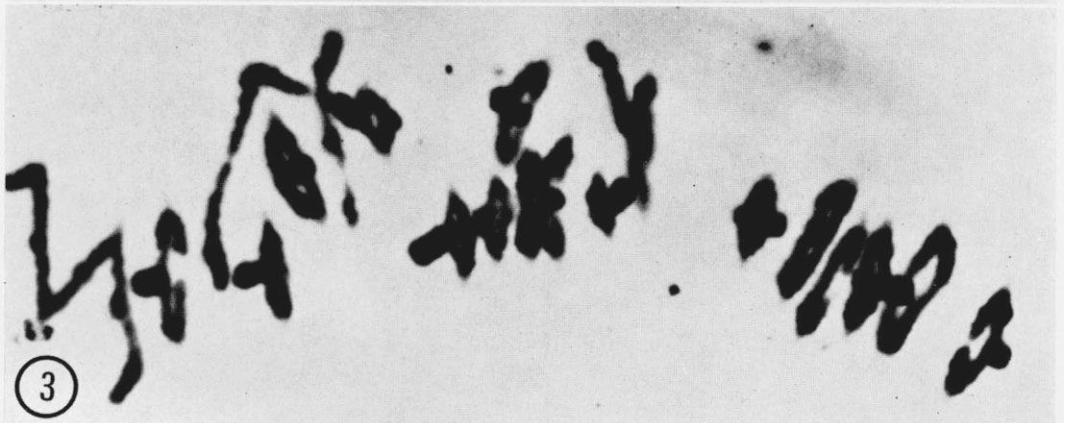
③

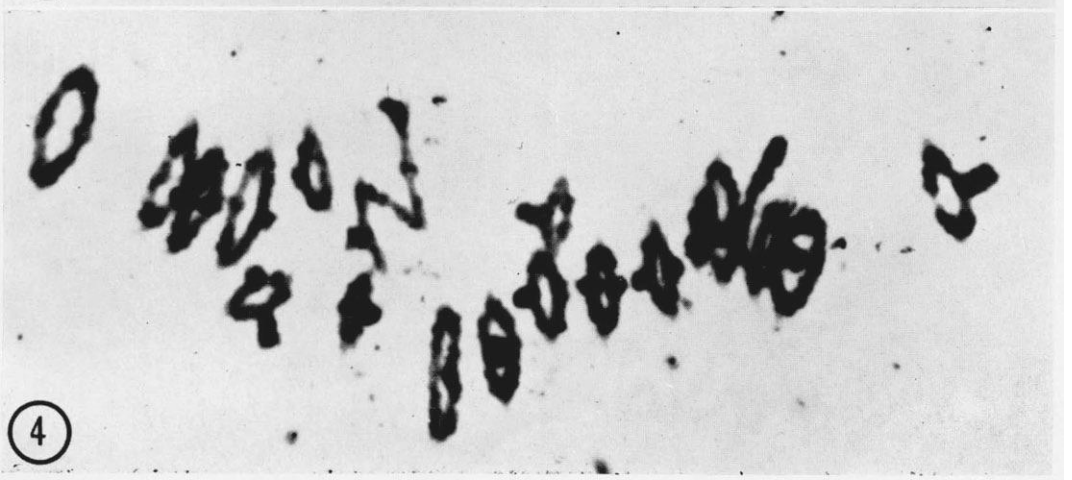
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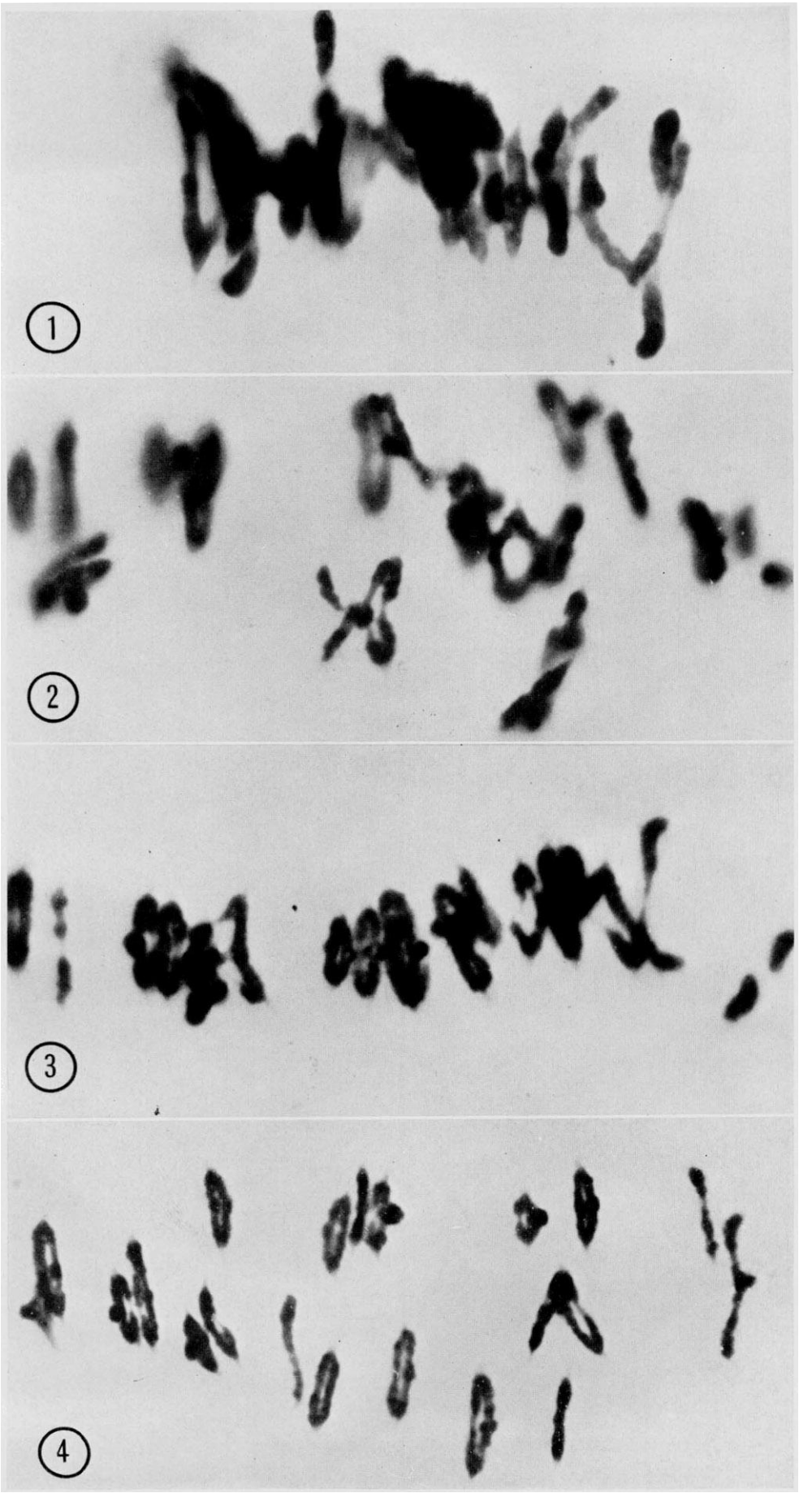
Plate II

Photomicrographs of first metaphase of meiosis in pollen mother cells, stained with Feulgen and propionic orcein, in the doubly telocentric derivatives of Family 4. × 1700.

FIG. 1.—A derivative from the cross of a translocation heterozygote carrying a telocentric of chromosome XIV (1A) × ditelocentric XVII (1D). The telocentrics are at opposite ends of a chain trivalent (right), so that chromosome XIV (1A) and XVIII (1D) are involved in the same translocation in Family 4.

FIGS. 2, 3, and 4.—Cells of a derivative from a cross of a translocation heterozygote carrying a telocentric of chromosome XIX (6D) × ditelocentric VI (6A). Fig. 2. Both telocentrics in a quadrivalent (centre). Fig. 3. The telocentrics paired together to form a bivalent (second bivalent from the left). Fig. 4. Each telocentric in a separate heteromorphic rod bivalent.

These configurations demonstrated the presence of a VI (6A)-XIX (6D) translocation and imply the occurrence of some modification of the XIX (6D) telocentric.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which precise chromosomes translocations had taken place. However, when the chromosomes involved in any family were classified, on the basis of the homœologous groups in which they occurred, they fell two into each of the same number of groups as there were translocations. This was very suggestive of the homœologous nature of the translocations, implying that the translocations were between genetically equivalent chromosomes of the different wheat genomes.

6. In order to obtain the final proof, one family, in which there were three translocations, was used in further crosses. Translocation heterozygotes, with one of the chromosomes involved in the translocation difference marked by being telocentric, were crossed with plants ditelocentric for the remaining chromosomes in translocations in the same family. The behaviour of the two telocentrics relative to each other was compared at meiosis in doubly telocentric derivatives of the crosses. The occurrence of both telocentrics in the same multivalent showed that the two marked chromosomes were involved in the same translocation. By contrast the occurrence of one telocentric in a quadrivalent and the other in a bivalent showed that the two marked chromosomes were not involved in the same translocation. The results demonstrated that all three translocations were between homœologous chromosomes.

7. It was thus clear that the non-homologous meiotic pairing and recombination, from which all the translocations studied had arisen in the deficiency of chromosome V (5B) of *T. æstivum*, were between homœologous chromosomes. That is, non-homologous pairing was between equivalent chromosomes of the three genomes of which the wheat complement is composed. Thus the effect of the normal activity of chromosome V (5B) is to suppress meiotic affinity between corresponding chromosomes derived from the different diploid parents of the hexaploid—chromosomes which presumably had a common origin in an original prototype diploid from which the parental diploids had diverged.

8. The implications of the present results for theories of the specificity of meiotic chromosome pairing, and for the understanding of the evolution of wheat, are discussed. It is now certain that the activity of chromosome V (5B) is responsible for the diploid-like meiotic behaviour and the disomic inheritance of polyploid wheat.

Acknowledgment.—The financial assistance of the Government of Mysore (India) to one of us (C. K.) is gratefully acknowledged. It is a pleasure to acknowledge the considerable help of our colleague, Mr Victor Chapman. Valuable technical assistance was given by Mr T. E. Miller and Mr H. A. Torrens.

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