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CHROMOSOMA

Chiasma Interference and Centromere Co-orientation in a Spontaneous Translocation Heterozygote of *Euchorthippus pulvinatus gallicus* (Acrididae; Orthoptera)

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Abstract. The meiosis of an individual of the species *Euchorthippus pulvinatus gallicus* heterozygous for a reciprocal translocation involving chromosomes 3 and 6 has been analysed using the Giemsa C-banding technique. It is concluded that: (i) Chiasma interference in the quadrivalent seems to act only at the arm level. There is no interference across the translocation break point. No interchromosomal chiasma interference could be demonstrated. (ii) The results concerning the co-orientation of the quadrivalent suggest that the length of the chromosomal segments between two adjacent centromeres at metaphase I is related with their orientation behaviour.

Introduction

From the genetic point of view, crossing-over and centromere co-orientation are the two phenomena leading to the most important events taking place during the first meiotic division, namely, genetic recombination and chromosome number reduction.

Translocation heterozygotes in grasshoppers are a very favourable material for the study of some aspects of both phenomena. In several instances the analysis of interchromosomal effects in chiasma frequency and of co-orientation has been carried out using these interchange heterozygotes (Sarkar, 1955; Kayano and Nakamura 1960; Lewis and John, 1963; John and Hewitt, 1963; Hewitt and John, 1965; Hewitt, 1967; Southern, 1967b; Wise and Rickards, 1977; Sannomiya, 1978).

The Giemsa C-banding technique offers the possibility of recognizing the different multivalent arms as well as the location of centromeres of such multivalents and thus provides a basis for an accurate analysis.

In the present work we have studied the meiosis of a spontaneous translocation heterozygote of the grasshopper *Euchorthippus pulvinatus gallicus* using the Giemsa C-banding technique. The effect of this reciprocal translocation in intra and interchromosomal chiasma interference, as well as the relationship

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between chiasma location (affecting the shape of the quadrivalent at metaphase I) and centromere co-orientation have been analysed.

Material and Methods

The reciprocal translocation appeared in one male among 100 individuals examined of a wild population of *E. pulvinatus gallicus* collected near Calatayud, Zaragoza, Spain, during July 1978. Mitotic metaphases were obtained from female gut caeca fixed in acetic alcohol 1:3, 4h after injection with 0.25% colchicine in insect saline. Testes of males were fixed without previous treatment in acetic alcohol 1:3.

Squash preparations of the fixed material were stained following the Giemsa C-banding technique described previously (Santos and Giraldez, 1978).

Results

I. The Nature of the Translocation

Euchorthippus pulvinatus gallicus has 17 chromosomes (16+X) in the male and 18 chromosomes (16+XX) in the female. Three pairs of autosomes are long

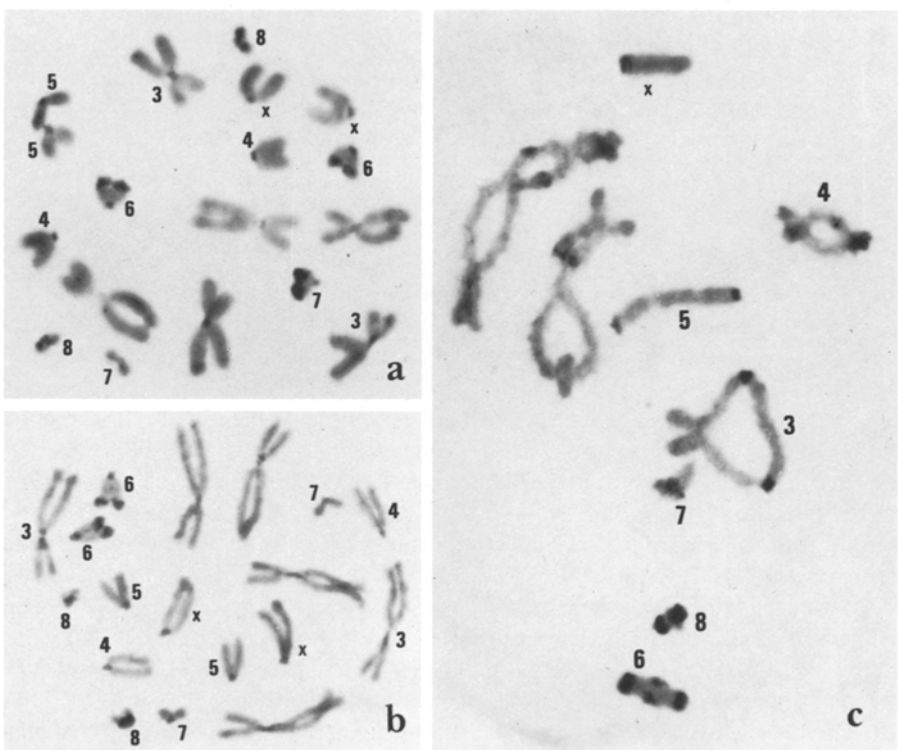

Fig. 1 a–c. C-banded chromosomes. **a and b.** Mitotic metaphases of two different females of *Euchorthippus pulvinatus gallicus*. **c** Diplotene cell of a male showing the same banding pattern than the translocation heterozygote for chromosomes 7 and 8

and submetacentric, whereas the remaining five pairs are of medium to small size and telo or subtelocentric. All chromosomes except 1 and 2 can be cytologically distinguished at mitotic metaphase as well as at meiosis (Fig. 1), especially when C-banded.

In addition to the C-heterochromatin which is present in the centromere region of all chromosomes, chromosome 6 shows a C-heterochromatic band located subterminally and, in the population studied, chromosomes 7 and 8 showed a polymorphism for their banding pattern (Fig. 1). Chromosome 7 can have a thick interstitial band near the telomere and chromosome 8 can have a thin interstitial band near the centromere (centromeric heterochromatin appearing in such cases as forming two bands).

The observations of C-banded cells at diplotene in the individual heterozygous for the translocation indicated that chromosomes 3 and 6 were involved in the reciprocal translocation, the points of interchange being located in the short arm of chromosome 3 and in the euchromatic proximal region of chromosome 6. In addition, this individual was homozygous for the chromosome 8 type having the interstitial heterochromatic band and homozygous for the chromosome 7 type without the subterminal band (Figs. 3a and 4a).

Figure 2 shows diagramatically the nature of the translocation, as well as the expected pachytene pairing configuration of the quadrivalent.

II. Chiasma Interference

The Giemsa C-banding technique allowed an identification of the four arms of the quadrivalent. In these four arms, five different positions of chiasmata could be distinguished (Fig. 2):

Region I, between the break point and the telomere of the short arm of chromosome 3.

Region II, the long arm of chromosome 3.

Region III, between the C-heterochromatic band and the telomere of chromosome 6.

Region IV, between the break point and the C-heterochromatic band of chromosome 6.

Region V, between the break point and the centromere of chromosome 6.

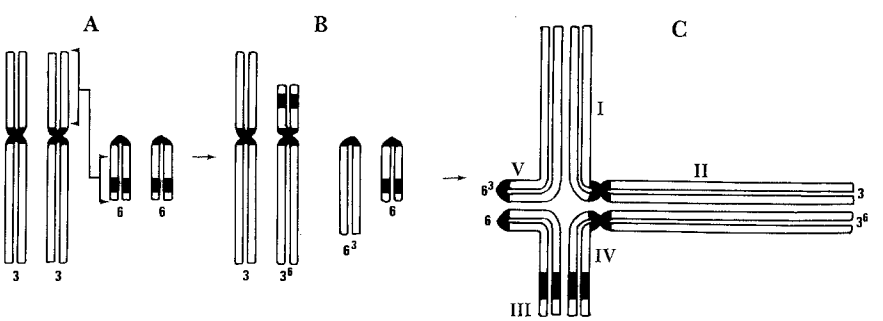

Fig. 2A–C. A diagram of the reciprocal translocation. **A** The normal chromosomes 3 and 6. **B** The two normal and two rearranged chromosomes. **C** The expected pairing configuration of the quadrivalent at pachytene

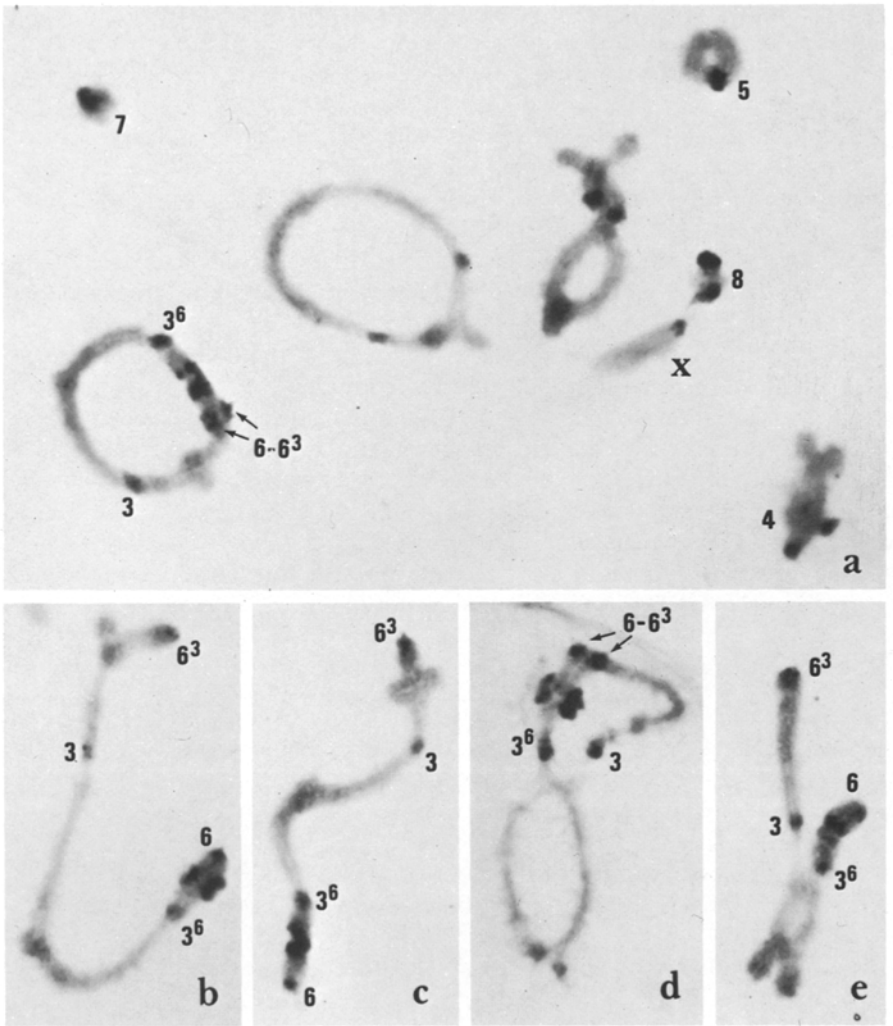

Fig. 3a–e. C-banded diplotene quadrivalents in which different number and positions of chiasmata can be observed. **a** Diplotene cell showing a ring quadrivalent with one chiasma in each of the regions I, II, III and V. **b** A chain quadrivalent having one chiasma in the regions I, II and IV. **c** A chain quadrivalent with one chiasma in the regions I, II and III. **d** A ring quadrivalent with two chiasmata in region II and one chiasma in the regions I, IV and V. **e** A chain quadrivalent with two chiasmata in region II and one chiasma in the regions I and III

In the region between the break point and the centromere of chromosome 3 chiasmata were never observed, indicating that this segment must be very short.

Figure 3 shows C-banded diplotene quadrivalents in which different numbers and positions of chiasmata can be observed.

Table 1 shows the frequencies of the different quadrivalents according to the numbers and positions of chiasmata at diplotene. The variation in chiasma

Table 1. The frequency of the different quadrivalents according to the number and positions of chiasmata at diplotene

Quadrivalent region (see Fig. 2) and number of chiasmata formed					Configuration	Frequency
I	II	III	IV	V		
1	1	–	1	1	ring	6
1	2	–	1	1	ring	2
1	1	1	–	1	ring	17
1	2	1	–	1	ring	10
1	1	–	1	–	chain	9
1	2	–	1	–	chain	2
1	3	–	1	–	chain	1
1	1	1	–	–	chain	19
1	2	1	–	–	chain	14

Table 2. The independence tests for Chiasma frequency at diplotene between the three pairs of adjacent regions II–IV, III–IV an V–IV (see Fig. 2)

Quadrivalent region						
IV	II		III		V	
Number of chiasmata	1	2 or +	0	1	0	1
0	36	24	–	60	33	27
1	15	5	20	–	12	8
Contingency χ^2	1.460 $0.3 > p > 0.2$		coincidence = 0		0.152 $0.7 > p > 0.6$	

Table 3. Correlation of chiasma frequencies between the quadrivalent and the six non translocation bivalents within diplotene cells. In brackets: numbers expected under the independence hypothesis

	Number of chiasmata formed by the bivalents							Totals	Mean
	8	9	10	11	12	13	14		
Number of chiasmata in the quadrivalent									
3	–	–	8 (6.3)	9 (8.4)	8 (7.4)	2 (2.1)	1 (0.4)	28	11.250
4	–	6 (4.4)	8 (8.8)	13 (11.7)	9 (10.2)	3 (2.9)	–	39	10.872
5	1 (0.2)	3 (1.5)	2 (2.9)	2 (3.9)	4 (3.4)	1 (1.0)	–	13	10.615
	1	9	18	24	21	6	1	80	

$\chi^2_2 = 0.923$ $(0.7 > p > 0.5)$ (classes < 5 excluded)

Regression coefficient of mean number of chiasmata in the bivalents on number of chiasmata in the quadrivalent, $b = 0.3173$ $(t = 9.009;\ 0.1 > p > 0.05)$

Table 4. The chiasma frequency of each bivalent in normal individuals of the population (8 individuals, 30 cells each), compared with that of the corresponding karyotype regions in the translocation heterozygote. All individuals had the same c-banding pattern for chromosomes 7 and 8

	Number of chiasmata per bivalent												
	Bivalents 1+2					Bivalent 3[a]					Bivalent 4			
	1	2	3	4	Mean	1	2	3	4	Mean	1	2	3	Mean
Translocation heterozygote	1	32	95	32	2.988 ±0.04	–	51	28	1	2.375 ±0.05	30	49	1	1.638 ±0.05
Normal individuals	1	115	316	48	2.856 ±0.02	1	149	90	–	2.371 ±0.03	123	117	–	1.488 ±0.03
Contingency χ^2	11.026 (0.05 > p > 0.01)					0.040 (0.95 > p > 0.90)					4.546 (0.05 > p > 0.01)			

	Bivalent 5			Bivalent 6[a]			Bivalent 7			Bivalent 8	
	1	2	Mean	1	2	Mean	1	2	Mean	1	Mean
Translocation heterozygote	61	19	1.238 ±0.04	45	35	1.438 ±0.05	75	5	1.063 ±0.02	80	1.000 ±0.00
Normal individuals	226	14	1.058 ±0.01	240	–	1.000 ±0.00	240	–	1.000 ±0.00	240	1.000 ±0.00
Contingency χ^2	20.824 (0.001 > p)			–					–		

[a] Chromosomes 3 and 6 were involved in the reciprocal translocation. Regions I and II of the quadrivalent correspond to bivalent 3 and regions III, IV and V correspond to bivalent 6

frequency shown by regions II, III, IV and V allows an analysis of chiasma interference between adjacent regions. The quadrivalent regions II and IV are separated by the break point and the centromere of chromosome 3. The regions III and IV belong to the same quadrivalent arm, separated only by the heterochromatic band of chromosome 6. The regions IV and V belong to normal chromosome 6 and are separated by the break point.

If there is no chiasma interference, the probabilities of chiasmata in two adjacent regions will be independent. Table 2 shows the results of the independence tests for the three pairs of adjacent regions described above. These results indicate that there is no chiasma interference between regions II and IV nor between regions IV and V, whilst between regions III and IV the interference equals 1 (coincidence = 0).

The analysis of independence between the non adjacent regions II and V, III and V, and II and III shows the χ^2 values: 0.104 ($0.80 > p > 0.70$); 0.152 ($0.7 > p > 0.6$) and 0.146 ($0.3 > p > 0.2$) respectively, i.e., there is independence between these three pairs of segments.

In order to investigate the existence of interchromosomal chiasma interference, an approach similar to that described by Sybenga (1975) was used. Table 3 shows the correlation of chiasma frequencies between the quadrivalent and the six non translocation bivalents within diplotene cells. Although a tendency towards a decrease of the mean number of chiasmata in the bivalents with increasing numbers of chiasmata in the quadrivalent could be observed, the results are not significantly different from those expected under the independence hypothesis. No interchromosomal chiasma interference could be demonstrated.

III. Chiasma Frequency

Table 4 shows the comparison between the chiasma frequency at diplotene of each bivalent in normal individuals of the population (8 individuals having the same banding pattern for chromosomes 7 and 8, 30 cells each) and that of the corresponding regions in the translocation heterozygote. Chiasma fre-

Table 5. The comparison between the distributions of chiasmata per cell at diplotene (considering all chromosomes and only the chiasmata formed by the chromosomes not involved in the reciprocal translocation) in the normal individuals and in the translocation heterozygote

	Chiasmata per cell (considering all chromosomes)									Chiasmata per cell formed by the chromosomes not involved in the reciprocal translocation							
	11	12	13	14	15	16	17	18	Mean	8	9	10	11	12	13	14	Mean
Translocation heterozygote	–	–	15	20	23	13	8	1	14.77 ±0.14	1	9	18	24	21	6	1	10.96 ±0.14
Normal individuals	7	28	83	68	44	8	2	–	13.61 ±0.07	10	37	102	70	18	3	–	10.24 ±0.06
Contingency χ^2	49.374 $0.001 > p$									35.104 $0.01 > p > 0.001$							

quency is significantly higher in most karyotype regions of the translocation heterozygote by comparison with the pooled normal individuals. However, in the long chromosomes (1+2 and 3) some of the individuals have a chiasma frequency higher than that of the translocation heterozygote. In the chromosomes 4, 5, 6 and 7 the individual carrying the reciprocal translocation shows the highest chiasma frequency and in chromosome 8 there is no variation.

Table 5 shows the comparison between the distributions of chiasmata per cell at diplotene in the translocation heterozygote and in normal individuals considering all chromosomes and considering only the chiasmata formed by the chromosomes not involved in the interchange. In both cases a significantly

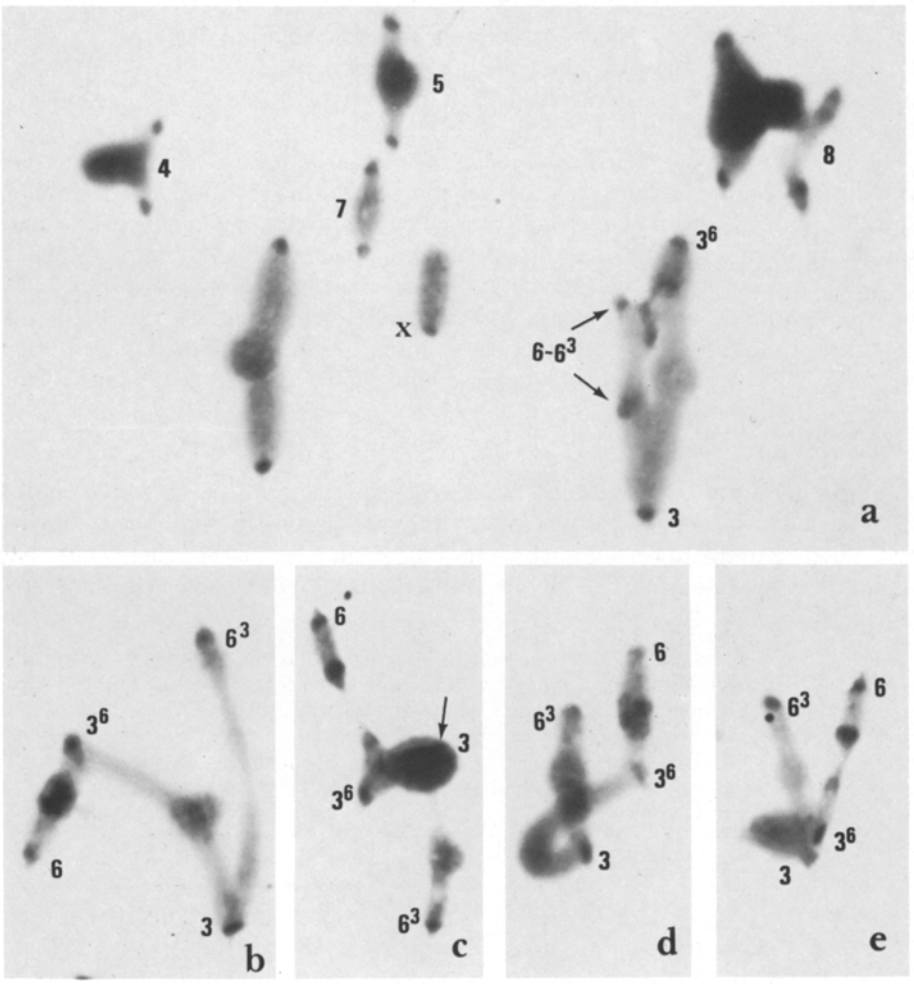

Fig. 4a–e. The different types of quadrivalent co-orientation at metaphase I. **a** Metaphase I cell showing a ring quadrivalent with alternate or adjacent I co-orientation. **b** Alternate chain quadrivalent with a single chiasma in region II. **c** Alternate chain quadrivalent with two chiasmata in region II. **d** Adjacent II chain quadrivalent with a single chiasma in region II. **e** Adjacent II chain quadrivalent with two chiasmata in region II

higher chiasma frequency occurred in the translocation heterozygote by comparison with the pooled normal individuals. Only one individual showed a higher chiasma frequency in the chromosomes not involved in the reciprocal translocation when compared with the heterozygote.

IV. Co-orientation

Figure 4 shows the different types of quadrivalent configurations found in 150 late metaphase I cells of the translocation heterozygote. In all cases a 2:2 orientation was observed. In the ring quadrivalents (i.e., having a chiasma in region V) the centromeres of chromosomes 6 and 6^3 were always oriented to opposite poles ($6–6^3$ 3 / $6–6^3$ 3^6, Fig. 4a), whereas in chain quadrivalents (i.e., without chiasmata in region V) only alternate (6 3 / 6^3 3^6, Figs. 4b and 4c) and adjacent II (6 6^3 / 3 3^6, Figs. 4d and 4e) configurations were observed. Chain quadrivalents having one or two chiasmata in the long arm of chromosome 3 (region II) could be distinguished and were scored separately.

The chromosome segregation types found at anaphase I were those corresponding to the quadrivalent configurations observed at metaphase I (Fig. 5). Table 6 shows the frequencies of the different types of quadrivalent at metaphase I as well as the frequencies of the different types of anaphase I segregations. Although no valid statistical test could be made due to the small number of anaphase I cells observed, it can be concluded that there is a good correspondence between anaphase I and metaphase I results. On the other hand, the

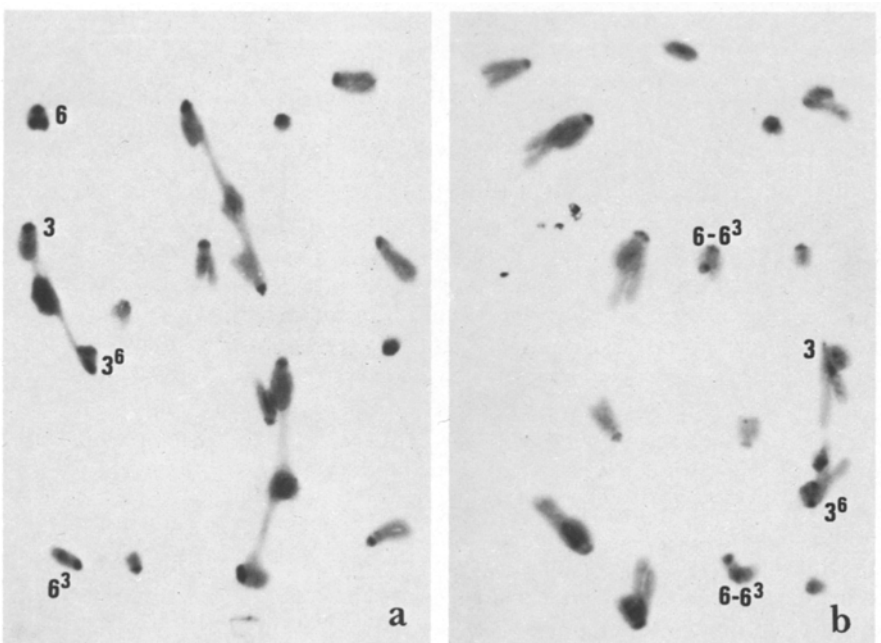

Fig. 5a and b. C-banded anaphase I cells. **a** Chromosome segregation resulting from a chain quadrivalent with alternate co-orientation. **b** Chromosome segregation resulting from a ring quadrivalent with alternate or adjacent I co-orientation

Table 6. The frequency of the different types of co-orientations in chain and ring quadrivalents at late metaphase I and the frequency of the corresponding anaphase I segregations

Type of co-orientation	Quadrivalent configuration at metaphase I			Anaphase I segregation
	Chain		Ring	
	1 chiasma in region II	2 chiasmata in region II		
Alternate ($6\,3 / 6^3\,3^6$)	23	27	–	7
Adjacent II ($6\,6^3 / 3\,3^6$)	24	6	–	2
Alternate or Adjacent I ($6\text{–}6^3\,3 / 6\text{–}6^3\,3^6$)	–	–	70	8

Contingency χ^2 test for independence between number of chiasmata in region II and co-orientation type: $\chi^2 = 8.944$ $0.01 > p > 0.001$

contingency χ^2 test for independence between number of chiasmata in the long arm of chromosome 3 (region II) and configuration type at metaphase (alternate or adjacent II) within the chain quadrivalents showed a significant deviation. An excess of alternates with two chiasmata in region II was found.

Discussion

I. Chiasma Interference

Chiasma interference in the Acrididae was first cytologicaly analysed by Henderson (1963) and later by Fox (1973) in *Schistocerca gregaria.* In both cases the existence of chiasma interference was demonstrated. The same phenomenon was found by Southern (1967a) in several species of Truxaline grasshoppers, who, in addition, concluded that the centromere acts as a barrier to interference. There are many cases in which both positive and negative interference between the regions adjacent to the translocation break point have been found (Sybenga, 1975). The explanation of this phenomenon is given by this author in terms of pairing difficulties in these regions. Analysing the data of Sannomiya (1968) on a translocation heterozygote of *Acrida lata,* Sybenga (1975) concludes that they were in agreement with the expectation of independence in chiasma formation across the translocation break point, the absence of interference being attributed to the completion of pairing around the break point due to the special characteristics of the interchange.

In agreement with these findings, the present results (Table 2) indicate that there is chiasma interference within the same quadrivalent arm, whereas between zones belonging to different quadrivalent arms chiasmata form randomly (i.e., there is no chiasma interference across the translocation break point). These facts are especially apparent in the comparison between the behaviour of chromosome 6 in the translocation heterozygote and in the normal individuals:

(i) in normal individuals only one chiasma was always formed, which could

be proximally (between the heterochromatic band and the centromere) or distally (between the heterochromatic band and the telomere) located. Then, the heterochromatic band marks the separation between two chromosome segments, the proximal one corresponding to quadrivalent regions IV and V, and the distal one corresponding to quadrivalent region III. A complete interference (coincidence = 0) between these two segments is always found in normal individuals.

(ii) In the translocation heterozygote the behaviour of chromosome 6 is different. Two chiasmata are formed in a 56% of the cells; complete interference is maintained between regions III and IV (belonging to the same quadrivalent arm) but chiasma formation in these two regions is independent of that of region V (separated from the rest of the chromosome by the translocation break point). The absence of interference between the segments adjacent to the translocation break point could be a consequence of the special characteristics of this interchange. As in the case studied by Sannomiya (1968) pairing in these regions would not be as drastically affected as to show the secondary effects described by Sybenga (1975) on rye and other plant species.

It is interesting to note that, although chiasmata do not form in heterochromatin, the heterochromatic band located in chromosome 6 does not affect chiasma interference. Then, it seems reasonable to conclude that the barrier to interference marked by the centromere is not related with the presence of heterochromatin in the centromeric region. The reason why, in the Acrididae, chiasma interference seems to act only at the arm (multivalent or bivalent arm) level could be a structural one. Both centromere and translocation break point could represent a discontinuity in the physical structure necessary for the maintenance of chiasma interference.

II. Chiasma Frequency

The results shown in Tables 4 and 5 indicate that the translocation heterozygote has a higher chiasma frequency than the normal individuals not only in the quadrivalent but also in the chromosomes not involved in the interchange. The higher chiasma frequency in the quadrivalent can be explained by the above indicated modification of the chiasma interference in chromosome 6 (in chromosome 3 the differences in chiasma frequency between the structural heterozygote and the normal individuals are not significant). It is worth mentioning that this increase in chiasma frequency is very low, being more apparent in chromosomes 4, 5 and 7, since in the translocation heterozygote these chromosomes form two chiasmata with a higher frequency than in the normal individuals (two chiasmata were never observed in chromosome 7 of normal individuals).

There are only a few reports in which changes in chiasma frequency produced by structural heterozygosity in grasshoppers have been cytologically studied. Such effects have not been demonstrated in all cases. Schroeter (1967) in a pericentric inversion heterozygote of *Trimerotropis helferi,* White (1963) in a translocation heterozygote of *Moraba scurra* and Hewitt (1967) in a translocation heterozygote of *Cibolacris parviceps* observed a significant increase in chiasma frequency. However, Hewitt and John (1965) in *Chorthippus brunneus* did not find significant differences in chiasma frequency between a translocation hetero-

zygote and normal individuals. As pointed out by Lucchesi and Suzuky (1968), structural heterozygosity itself could be the reason for the differences found. However, in all cases including the present work the comparison was made between a single structural heterozygote and a series of normal individuals. Then, although an association between structural heterozygosity and increase of chiasma frequency has been observed in most cases, the possibility of such differences being caused merely by genetic variation cannot be excluded.

III. Co-orientation

Three remarkable facts can be observed concerning the co-orientation of the quadrivalent (Table 6), namely, the absence of adjacent II configurations in ring quadrivalents, the absence of adjacent I configurations in chain quadrivalents and the excess of alternate configurations in chains having two chiasmata in the long arm of chromosome 3 (region II).

These facts could be explained under the hypothesis that the distance between two adjacent centromeres at metaphase I is related with their orientation behaviour; the shorter the distance, the higher the probability for these centromeres to orientate to opposite poles:

(i) Ring quadrivalents are formed when a chiasma is produced in the interstitial region V. Then, the distance between the two centromeres 6 and 6^3 at metaphase I is very short. The absence of adjacent II co-orientations can be explained in terms of the high probability of orientation of these centromeres to opposite poles. In several instances it has been found that when chiasmata are formed in the interstitial segments of a quadrivalent the homologous centromeres always pass to opposite poles (Burnham, 1950, 1956; Lewis and John, 1963; Wise and Rickards, 1977). The validity of the hypothesis expressed above is supported by these findings, since one can infer that in most reciprocal translocation heterozygotes a chiasma in an interstitial region results in a short distance between two of the homologous centromeres at metaphase I.

(ii) In chain quadrivalents the distances between adjacent centromeres at metaphase I depends on the positions of chiasmata in each quadrivalent arm. The distance between centromeres 6–3^6 and 6^3–3 could be always short enough to lead to an orientation of the two members of these pairs of centromeres to opposite poles. This can explain the absence of adjacent I co-orientations in this quadrivalent type.

The distance between centromeres 3 and 3^6 is subject to a higher variation than that between the other centromere pairs. When only one chiasma is formed in region II, this chiasma, usually distal, will result in a long distance between these centromeres, whereas when two chiasmata are formed in this region the two centromeres would be at a shorter distance. Then, under the hypothesis indicated above, one can expect that in chain quadrivalents having two chiasmata in region II centromeres 3 and 3^6 will orient to opposite poles with a higher probability than to the same pole. Assuming that each centromere is interacting simultaneously with its two adjacent ones, centromeres 3 and 3^6 will also co-orient with centromeres 6^3 and 6 respectively, and this can explain the excess

of alternate configurations in chain quadrivalents having two chiasmata in region II.

In chain quadrivalents having one chiasma in region II the long distance between centromeres 3 and 3^6 would allow their random behaviour.

It has been established that during metaphase I the centromeres move until a stable co-orientation is produced, physical tension being necessary for the stability of such co-orientation (Bauer et al., 1961; Nicklas and Koch, 1969; Henderson and Koch, 1970). Then, it can be supposed that between two centromeres at a short distance (at metaphase), a stronger tension will be obtained than between centromeres separated by a long chromosomal segment. In some cases anaphase can start before the centromeres, being far apart, have acquired their stability. This agrees with the fact that in the cases in which a 3:1 segregation of chromosomes of the quadrivalent formed by translocation heterozygotes of grasshoppers has been found (Carothers, 1931; Sarkar, 1955; Kayano and Nakamura, 1960; Wise and Rickards, 1977) at least one of the chromosomes involved in the quadrivalent has its centromere at a long distance from the others at metaphase I. If the tension between this centromere and the rest of the quadrivalent is not acquired before anaphase I a 3:1 segregation can be produced.

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