

CAUSES OF CHIASMA REPATTERNING DUE TO CENTRIC FUSIONS

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ABSTRACT

In several grasshopper species, centric fusions (Robertsonian translocations) have been reported to produce a repatterning of chiasmata. Proximal chiasmata are eliminated, chiasma formation shifts to distal ends and overall chiasma frequency is reduced in fusion trivalents and bivalents. In this paper, this repatterning is explained on the basis of evidence gathered from the grasshopper *Dichroplus pratensis*. It is assumed that the chromosomes enter meiosis with a Rab1 orientation and that chiasmata are formed preferentially in regions which include or are close to zones that pair early in prophase I and have the most protracted period of synapsis. Unfused telo-acrocentric chromosomes have both ends attached to the nuclear envelope and initiate pairing from either one or both ends, which would determine a basically proximal-distal chiasma distribution. In fused chromosomes, four original ends are replaced by two, the number of early pairing regions is reduced and these are shifted to the ends. This explains both the elimination of proximal chiasmata and the observed reduction in chiasma frequency brought about by the fusions.

INTRODUCTION

Chromosomal rearrangements usually have profound effects on chiasma frequency and localization. These effects may be intra- or interchromosomal. Typical cases are those of inversions and translocations (reciprocal and Robertsonian) (Hewitt, 1967, 1979; Hewitt and Schroeter, 1968; White, 1973; Arana *et al.*, 1980, 1987a,b; Parker *et al.*, 1982; Cabrero and Camacho, 1985; Sperlich and Pfriem, 1986; Colombo, 1987, 1988; Parker, 1987; Bidau and Mirol, 1988; Bidau, 1990, 1991).

Chiasma changes may be central to adaptation and speciation since production, maintenance and disruption of supergenes and linkage disequilibria can result from them (Bidau, 1990, 1991). Some models of speciation are based on these considerations (Sites and Moritz, 1987).

The mechanisms by which chromosomal rearrangements alter chiasma patterns are largely unknown. On the basis of observations on a system of Robertsonian translocations in the South American Acridid *Dichroplus pratensis*, I propose an explanation of the changes in chiasma frequency and distribution produced by centric fusions. It relies on current models of synapsis in Orthoptera (Moens, 1987; Moens *et al.*, 1989) and premeiotic chromosome disposition (Fussell, 1987).

The model proposes that the shift of chiasmata to distal segments of metacentric fusion chromosomes is due to the fact that telomeres of unfused telo-acrocentric chromosomes associate with the inner nuclear envelope determining points of pairing initiation. However in Robertsonian metacentrics, since telomeres near the centromeres have been deleted the association to the nuclear membrane is restricted to the remaining distal ends. These, having the most protracted period of pairing would form chiasmata more prone to the production of a basically distal distribution.

OBSERVATIONS AND INTERPRETATION

Populations of *D. pratensis* are polymorphic for up to three of seven centric fusions, involving the six L standard autosomes (L1-L6) (Bidau, 1984, 1986a,b; Bidau *et al.*, 1991). Previous studies (Bidau and Mirol, 1988; Bidau, 1990; Mirol, 1990; Mirol and Bidau, 1991, 1992) demonstrated that fusion heterozygotes and homozygotes for the seven fusions, have a significant modification of chiasma frequency and distribution in the chromosomes involved.

The standard telocentrics have a typical proximal-distal (P/D) chiasma distribution, interstitial chiasmata being rare. When fused chromosomes in any heterozygous or homozygous combination are analysed, the corresponding chromosome arms show an almost complete elimination of P chiasmata, a slight increase in I chiasmata and a highly significant increase of D ones. Total chiasma frequency per arm decreases significantly when compared to unfused telocentrics (Bidau, 1990). The change of chiasma pattern is similar in fusion trivalents and bivalents (Figure 1). These modifications are the basis of a model of chromosomal evolution in the species (Bidau, 1989, 1990, 1991; Bidau *et al.*, 1991). Similar repatterning occurs in simpler fusion systems (either polymorphic or fixed) of grasshoppers (Hewitt and Schroeter, 1968; John and Freeman, 1975; John, 1983; Colombo, 1987; 1988). No detailed chiasma analyses of fusion systems for other organisms are available but at least in one case (that of *Mus domesticus*), interracial Robertsonian hybrids seem to form less chiasmata than parental

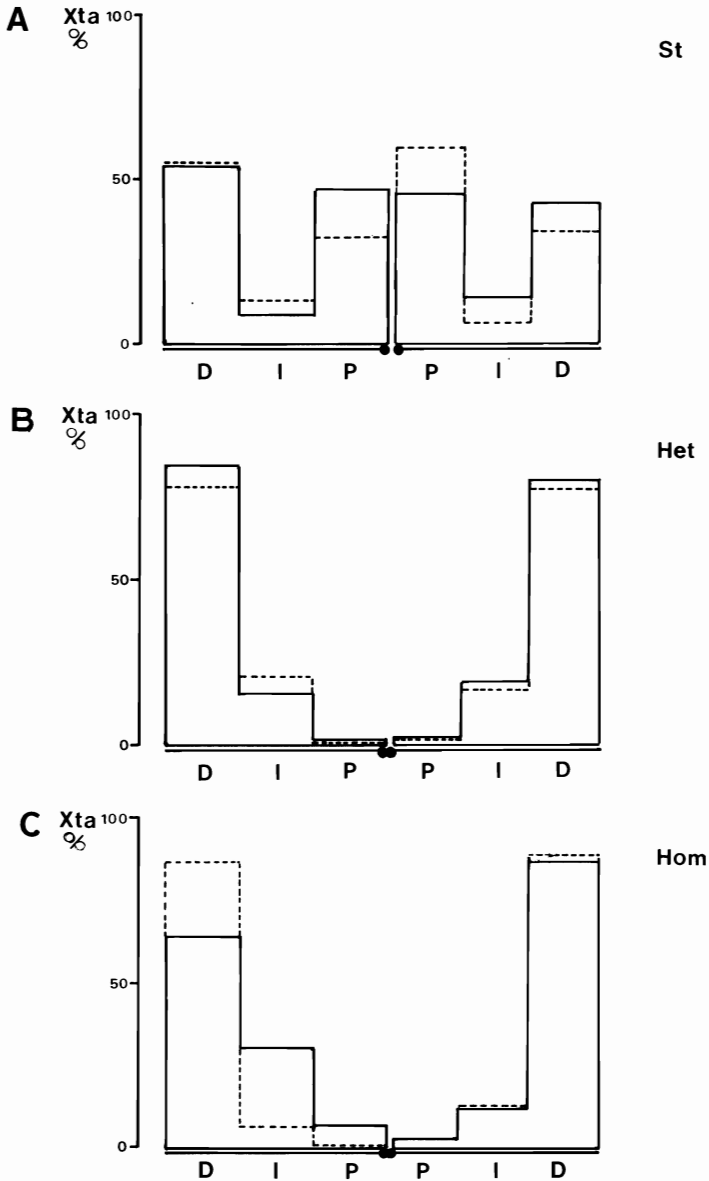


Figure 1 - Histograms representing the distribution of proximal (P), interstitial (I) and distal (D) chiasmata in four telocentric bivalents of *Dichroplus pratensis* and their centric fusion counterparts (*St*, standard bivalents; *Het*, fusion trivalents; *Hom*, fusion bivalents). Full-line histograms correspond to chromosomes (or chromosome arms) L5 and L6 and dotted-line ones, to L1 and L2. Data from the SV population (Bidau, 1990, 1991) which is polymorphic for both fusions. (Xta-chiasmata).

individuals (Capanna, 1982) and similar differences between telocentrics and fusion metacentrics occur in plants of the genus *Zebrina* (Mattson, 1972).

Cases of spontaneous fusions in grasshoppers (Southern, 1967; López-Fernández *et al.*, 1984; Teoh and Yong, 1983; Colombo, 1987) have been interpreted as proof that no direct effects of the rearrangement upon chiasma formation occur (Colombo, 1987; Bidau, 1990). However, a reexamination of these data shows that the evidence is not conclusive.

I propose a hypothesis based on the mode of synapsis and its relation to chiasma formation. Two basic assumptions are necessary: 1) Homologous telomeres are attached to the nuclear envelope very near one another at early prophase I (see Moens *et al.*, 1989); 2) Chiasmata occur with a higher probability in regions that pair first and remain paired longer (Jones, 1987).

In the standard condition, at early prophase I both ends of each chromosome and its homologue are attached to the nuclear envelope and pairing starts at both ends. Even if synapsis is completed, the early pairing regions have an increased probability of recombination compared to interstitial ones. Thus chiasmata are more likely produced in proximal and distal portions in a telo-acrocentric bivalent. When two non-homologous telo-acrocentric chromosomes undergo centric fusion, the number of effective telomeres involved in synapsis is halved (either in the heterozygous or homozygous condition). Chiasmata will be formed preferentially in distal regions and proximal chiasmata will have a very reduced chance of being produced. A large pericentric region almost free of recombination would thus be created (Figure 2).

DISCUSSION

The modifications of crossing-over distribution produced by chromosomal rearrangements have been extensively documented (see Introduction) but few explanations have been put forward (Jones, 1987).

The model proposed in this paper makes sense if in the first place, premeiotic interphase chromosomes have a definite ordenation within the nucleus such as the Rabl orientation (Rabl, 1885) in which interphase chromosomes retain their telophase configuration so that all telomeres converge on a small region of the nuclear envelope, while centromeres are close to one another at the opposite side of the nucleus. Evidence for a Rabl orientation at mitotic interphase and prophase has been reviewed by Fussell (1987). It seems to be a rule that positions of telomeres are a function of arm length, thus chromosome arms of similar length have their telomeres attached to the nuclear membrane very close one to another if not in fixed positions, since at prometaphase chromosome movements would change the previous ordenation, producing a new Rabl orientation at each interphase (however, see below).

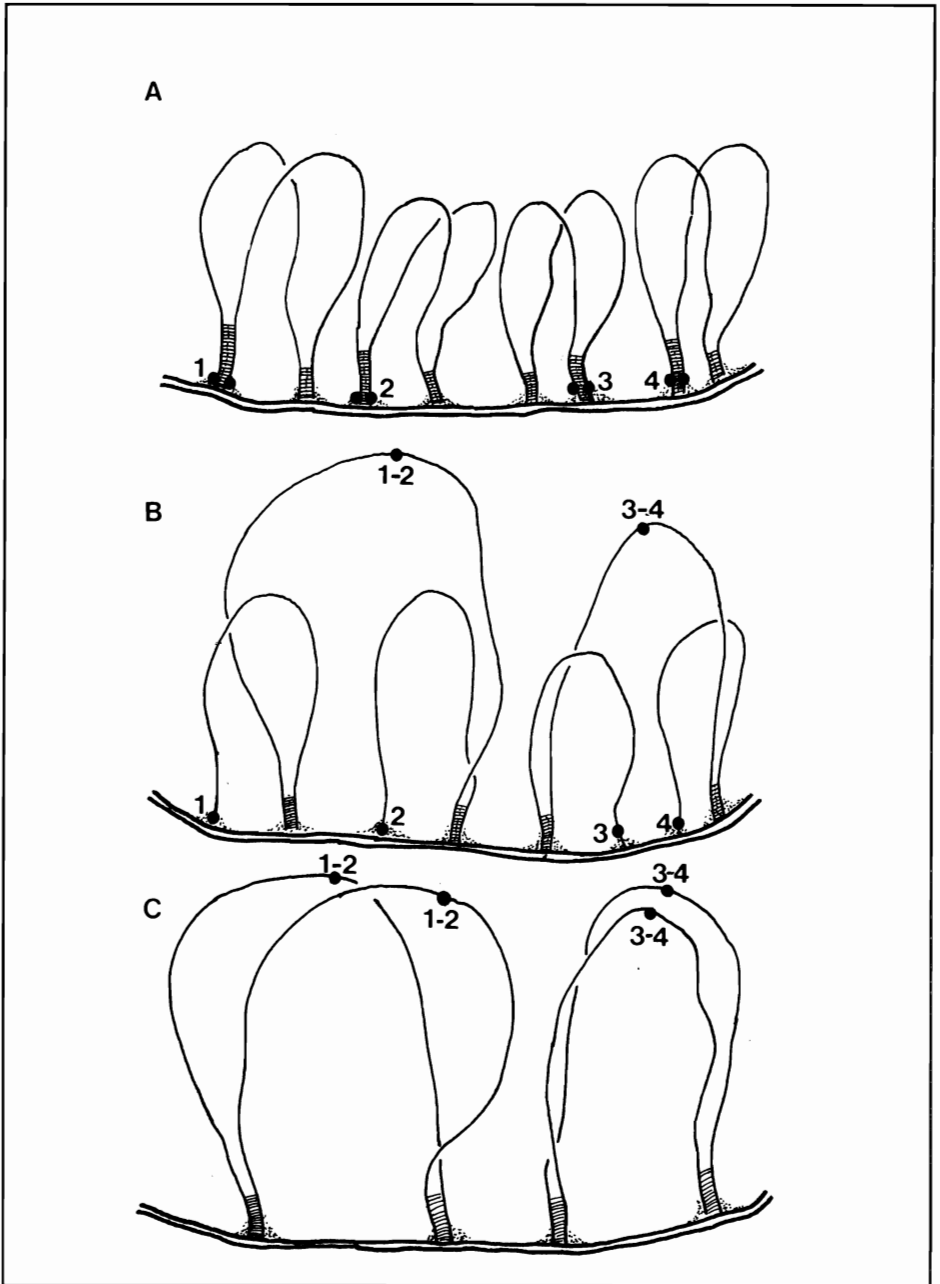


Figure 2 - A schematic representation of the beginning of synapsis according to the model put forward in this paper. (A) Four telocentric bivalents. (B) Two fusion trivalents. (C) Two fusion bivalents.

Fussell (1987) proposed that if a Rabl orientation occurs at premeiotic interphase, synapsis at zygotene would be facilitated due to proximity of homologous ends within the nucleus. The usual bouquet arrangement would have its origin in the Rabl orientation by the sliding of the telomeres on the inner nuclear envelope.

In many grasshoppers, pairing starts at the ends of chromosomes attached to the nuclear membrane (Jones, 1987; Moens *et al.*, 1989). Proximity of homologous ends would allow recognition for pairing initiation. Furthermore, there are reports on non-random and constant spatial configurations (including somatic pairing) at metaphase (Avivi and Feldman, 1980; Bennett, 1982, 1983) that argue in favour of the same arrangement in different mitoses. Thus, if homologous chromosomes tend to be close together during the cell cycle they will probably be grouped at premeiotic interphase and their ends attached to the nuclear envelope, not just in the same general area due to arm length, but also non-randomly clustered.

The model thus explains satisfactorily the changes in chiasma patterns produced by centric fusions. A quantitative relationship exists between pairing behavior and chiasma distribution. Also, chiasma formation in a given region could depend on the duration and extent of pairing (Rhoades, 1968). Thus chiasmata would form in regions that pair first and remain paired longer; then they would have to be closely associated to sites of pairing initiation. This view is supported by studies of chiasma distribution in normal bivalents and structurally rearranged chromosomes (Jones, 1987).

In species where pairing starts at the ends of chromosomes and progresses sequentially, proximal (P)-distal (D) chiasma distributions usually occur although pairing is complete. A P-D distribution implies that most bivalents have a P or a D chiasma, or both. The standard telocentric L bivalents of *D. pratensis* are a good example of the former (Bidau, 1990) and offer an opportunity to test some predictions of the model. First, it is assumed that pairing begins simultaneously at both ends and progresses at the same rate in both directions. If chiasmata are directly related to regions that pair first and a maximum of two chiasmata per bivalent is assumed (which is common for most telo-acrocentric bivalents of Acrididae except S chromosomes) it can be predicted that the majority of bivalents will show two chiasmata (one P and the other, D), irrespective of bivalent length. To test this prediction, the percentage of P/D bivalents was calculated for the six L pairs of *D. pratensis*, and plotted against relative length. A significant positive correlation was found (Tables I, III; Figure 3), showing that longer bivalents form with a greater probability a P and a D chiasma forming simultaneously.

This is an indirect indication that interference plays a role in chiasma distribution. If this is true, the analysis of the frequency of P and D chiasmata could be an indication that, although pairing starts at both ends, either the onset of pairing or the rate of its progress are differential. When the percentage of total P chiasmata in L-bivalents was plotted against relative length a significant negative correlation was

Table I - Percent of proximal (P) and distal (D) chiasmata (Xta) per telocentric L-bivalent and percent of P/D bivalents in a sample of 61 standard males of *Dichroplus pratensis*^a.

LN ^b	RL ^c	Total II's	Total Xta	% Xta per II		% P/D II's
				P	D	
1	17.85	610	973	38.3	58.1	55.9
2	14.67	610	891	43.8	48.5	42.0
3	13.68	610	794	46.7	43.1	26.7
4	12.20	610	732	44.4	44.5	16.9
5	10.93	610	704	47.3	49.2	15.1
6	9.72	610	669	57.3	39.9	9.7

^a Ten metaphase I cells were scored per male in conventional lacto-propionic orcein squashes. Forty-eight males belonged to the Puerto Madryn population and the remaining 13, to the Gaiman population, both described in Bidau (1990) and Bidau *et al.* (1991).

^b L-bivalent number.

^c Relative length of L-chromosomes expressed as percent of total haploid genome length.

found (Tables I, III; Figure 3). Thus, shorter bivalents form more P chiasmata than longer ones. The reverse occurs with D chiasmata (Tables I, III; Figure 3). These results suggest that pairing starts asynchronously at both ends, or else it progresses faster from the centromeric end so that P chiasmata are readily formed. The decrease in D chiasmata in shorter bivalents could be due to increasing interference.

The same comparisons were made between the L-chromosomes in the fusion (heterozygous or homozygous) condition and relative length. In this case, a majority of D chiasmata is expected irrespective of chromosome arm length and combination. That is, the frequency of D chiasmata will be similar and that of P/D per arm, very low. The results (Tables II, III; Figure 4) support this view. None of the correlations were statistically significant. Furthermore, the most common bivalent and trivalent configuration in seven different fusions was a D-D one (Bidau, 1990).

As noted above, some cases of spontaneous fusions in grasshoppers were considered as proof of a lack of instantaneous effects of the rearrangement on chiasma formation (Colombo, 1987). The present model does predict such intrachromosomal repatterning in the heterozygous mutants. There are some points worth considering before discussing these cases: first, the spontaneous fusions studied are very few; second, in only one case chiasma frequency *and* distribution were analyzed in detail

Table II - Percent of proximal (P) and distal (D) chiasmata (Xta) per chromosome arm and percent of P/D chromosome arms in heterozygous and homozygous centric fusions in a sample of 46 males of *Dichroplus pratensis* from a polymorphic population^a.

Chromosome arm	Fusion status	Total configurations ^b	Total Xta	% Xta per configuration		% P/D configurations
				P	D	
1	Het 1/2	130	150	0.9	77.9	0.8
	Het 1/6	110	120	0.9	84.6	1.0
	Hom 1/2	40	44	0.9	86.7	2.5
	Hom 1/6	30	30	0.9	80.2	0.0
2	Het 1/2	130	140	1.9	75.9	1.5
	Hom 1/2	40	41	0.0	88.1	0.0
3	Het 3/4	150	163	1.8	76.1	1.3
	Hom 3/4	310	344	1.4	79.5	0.7
4	Het 3/4	150	156	0.0	82.7	0.0
	Hom 3/4	310	311	0.3	92.7	0.3
5	Het 5/6	110	112	1.0	84.3	0.0
	Hom 5/6	40	47	6.4	63.3	2.5
6	Het 1/6	110	112	1.0	81.4	0.0
	Het 5/6	110	115	1.9	79.1	0.9
	Hom 1/6	30	31	0.0	96.8	0.0
	Hom 5/6	40	42	2.4	85.7	0.0

^a The SV population in Bidau (1990, 1991). This population is part of a hybrid zone and is polymorphic for fusions 1/2, 3/4, 5/6 and 1/6.

^b Configurations: arm pairs scored for chiasmata.

(López-Fernández *et al.*, 1984); third, the modifications in chiasma pattern will obviously depend on the previous chiasma characteristics of the chromosomes involved.

In *Valanga nigricornis*, Teoh and Yong (1983) described a germ-line mosaic male mutant for a fusion between M8 and M9 autosomes. The fusion seems to have an

Table III - Regression equations, correlation coefficients and their statistical significance, of the data shown in Tables I and II (lines 1-3 and 4-5 respectively). The chiasma data, expressed as percentages in Tables I and II, was corrected for normality using the *arcsin* transformation (angle = arcsin percentage).

1. $\bar{X}P$ vs RL	$Y = 57.62 - 1.12X; t(4) = 4.15$	$0.01 < P < 0.025$	$r = -0.87; t(4) = 3.48$	$0.025 < P < 0.05$
2. $\bar{X}D$ vs RL	$Y = 30.62 + 0.97X; t(4) = 2.43$	$0.05 < P < 0.10$	$r = 0.80; t(4) = 3.20$	$0.025 < P < 0.05$
3. $\bar{X}P/D$ II's vs RL	$Y = -20.00 + 3.86X; t(4) = 8.21$	$0.001 < P < 0.005$	$r = 0.98; t(4) = 9.90$	$P < 0.001$
4. $\bar{X}P$ vs RL	$Y = 7.37 - 0.13X; t(14) = 0.42$	$P < 0.5$	$r = -0.11; t(14) = 0.41$	$P < 0.5$
5. $\bar{X}D$ vs RL	$Y = 61.98 + 0.27X; t(14) = 0.53$	$P < 0.5$	$r = 0.13; t(14) = 0.26$	$P < 0.5$
6. $\bar{X}P/D$ II's vs RL	$Y = -1.70 + 0.39X; t(14) = 1.44$	$0.1 < P < 0.2$	$r = 0.35; t(14) = 1.40$	$0.1 < P < 0.2$

interchromosomal effect reducing chiasma frequency in the L and M chromosome groups when cells from testis follicles carrying the fusion were compared to those from normal follicles. It is not clear however if cells within each group (only seventeen) belong to one or several follicles and if interfollicular variation occurs. The cells with the fusion had a lower chiasma frequency (14.94) than nine standard males, but this difference is not necessarily relevant since chiasma frequency in the latter ranged from 16.63 to 22.56 revealing considerable interindividual variation, and cells without the fusion in the mutant had a mean of 16.0, showing that this male already had a low chiasma frequency. Furthermore, the fusion trivalent was not analysed individually and compared to the M8 and M9 bivalents, so that it is not possible to know if chiasma reduction in the M group is a general one, or occurs solely in the chromosomes involved (which is unlikely since M8 and M9 are small autosomes and their individual chiasma frequencies are probably not much higher than 1.0). Nevertheless, *there is* a suggestion that chiasma location is altered in the trivalent. The authors state that the M8 and M9 limbs of the trivalent "frequently" form interstitial chiasmata and these "terminalize completely" by metaphase I in one or both arms. Their figures are not clear in this respect and since terminalization is unlikely to occur in grasshoppers (Jones, 1987), the fact that the trivalent invariably forms two mainly distal chiasmata supports the model.

Colombo (1987) studied a complete germ-line mutant of *Leptysma argentina*. This case is interesting since the mutant was also heterozygous for the polymorphic 3/6 fusion (Bidau and Hasson, 1984) which shows a typical repatterning of chiasmata according to the present model. The spontaneous 5/7 trivalent however, does not show a reduction in chiasma frequency when compared to normal 5 and 7 bivalents. Nevertheless, although the author claims that a repatterning does not occur either, this cannot be concluded directly from the data since in the comparisons, P and I chiasmata were not scored separately.

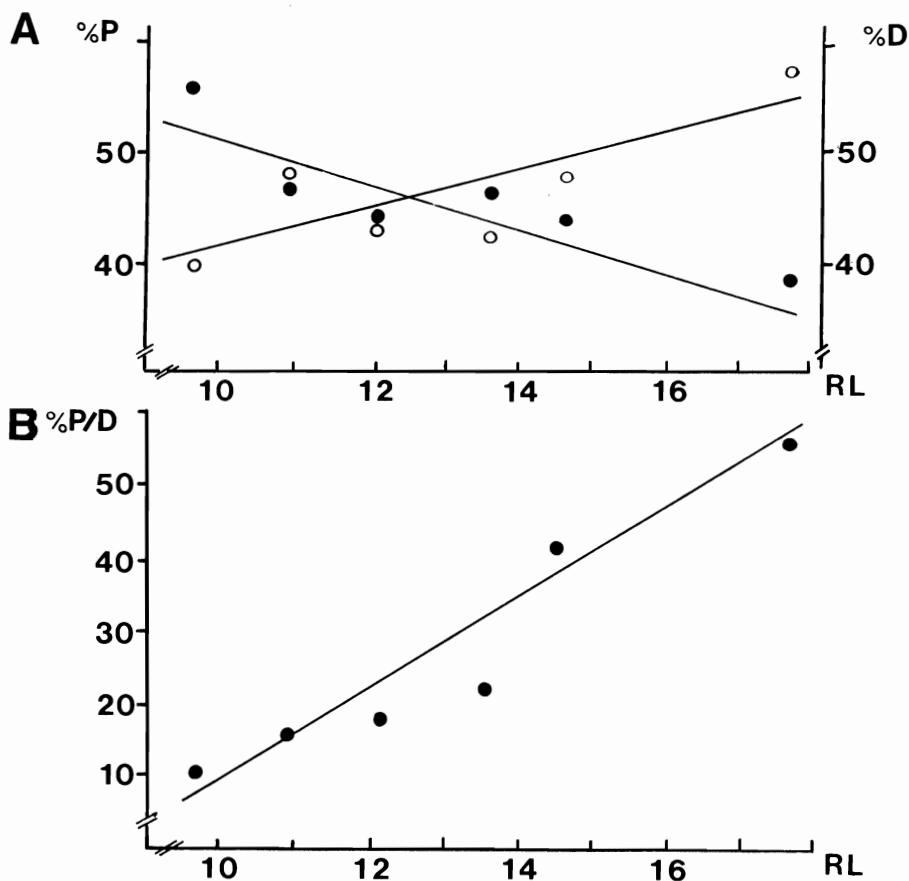


Figure 3 - (A) The relationship between percent proximal (%P; ●) and distal (%D; ○) chiasmata per telocentric L-chromosome and relative length (RL). (B) The relationship between percent P/D bivalents and relative length in the same standard individuals. For the purposes of the analyses percentages were converted to angles using the *arcsin* transformation (see Table III).

The case reported by López-Fernández *et al.* (1984) is the clearest one. A male of *Chorthippus jucundus* carried a spontaneous fusion between M5 and S8, which is very asymmetric since M5 is twice the size of S8. A repatterning of chiasmata occurs in S8, shifting the single chiasma to distal positions, but not in M5, which retains the same distribution of the standard M5, including a moderate proportion of P chiasmata. The change in S8 agrees with the model; the lack of change in M5 does not disagree either,

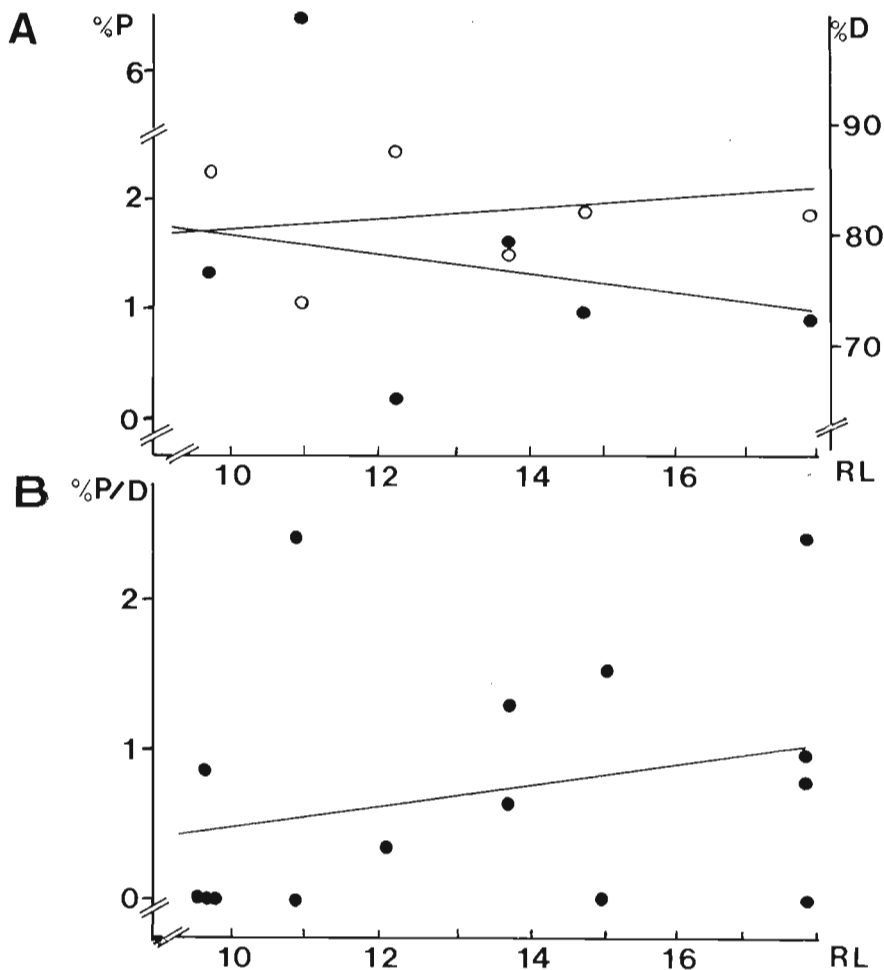


Figure 4 - The relationship between percent proximal (%P; ●) and distal (%D; ○) in arms of fusion trivalents/bivalents and relative length (RL). (B) The relationship between percent P/D configurations and relative length in the same individuals. For the purposes of the analyses percentages were converted to angles using the *arcsin* transformation (see Table III).

considering the length difference between the chromosomes and assuming no interference through the centromere. Thus, the distance between the S8 early pairing end and the centromere is very short and probability of P chiasma formation in M5 is not necessarily diminished.

The model discussed here is applicable to centric fissions (homozygous) but no supporting evidence from grasshoppers is available. Parker (1987) and Parker *et al.* (1982) observed an increase in chiasma frequency in a fission of *Hypochoeris radicata*, but the effect is equally expressed in hetero- and homozygotes. However, pairing and chiasma formation patterns are not necessarily alike in animals and plants and other factors may be involved.

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RESUMO

Em várias espécies de gafanhoto tem sido reportado que as fusões cêntricas (translocações Robertsonianas) produzem uma reorganização dos quiasmas. Os quiasmas proximais são eliminados, a formação de quiasmas se desloca até os pontos distais e a frequência geral de quiasmas é reduzida nos trivalentes e bivalentes de fusão. Neste trabalho, esta reorganização é explicada baseada na evidência colhida do gafanhoto *Dichroplus pratensis*. Presume-se que os cromossomos entrem em meiose com uma orientação de Rab1 e que os quiasmas se formam preferencialmente em regiões que incluem ou estão próximas às zonas que se pareiam precocemente em profase I e têm um período mais prolongado do sinapse. Os cromossomos telo-acrocêntricos não fusionados, possuem suas duas extremidades ligadas ao envelope nuclear e iniciam pareamento a partir de um ou ambos extremos, o que determinaria uma distribuição de quiasmas basicamente proximal-distal. Em cromossomos fusionados, quatro pontos originais são substituídos por dois, o número de regiões de pareamento precoce é reduzido pela metade e estes são deslocados para as extremidades. Isto explica tanto a eliminação dos quiasmas proximais como a redução observada na frequência de quiasmas produzidas pelas fusões.

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