The complex Robertsonian system of *Dichroplus pratensis* (Melanoplinae, Acrididae).

II. Effects of the fusion polymorphisms on chiasma frequency and distribution

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The effects of a complex series of Robertsonian polymorphisms on chiasma frequency and distribution were analysed in natural populations of the grasshopper *Dichroplus pratensis* which has a standard karyotype of $2n = 19$ (XO♂) telocentrics. Populations are usually polymorphic for one to three of seven distinct fusions between the six large (L_1 – L_6) autosomes. The study revealed that:

1. Standard males have an essentially proximal-distal pattern of chiasma distribution. Interstitial chiasmata are less frequent.
2. Fused males have significantly fewer total and proximal chiasmata than standards from the same population but show an increase in interstitial and distal chiasmata.
3. The former is due to the fact that centric fusions, either homozygous or heterozygous, produce a decrease in total chiasma frequency of the involved chromosomes and a redistribution of chiasmata resulting in a sharp reduction of proximal chiasmata and an increase in interstitial and distal ones. In this respect, there are no significant differences between fusion trivalents and corresponding fusion bivalents. The same chromosomes in the basic homozygous state, have a typical standard chiasma pattern.
4. The effects of each fusion are intrachromosomal and although the same chiasma repatterning occurs in all seven fusions, total reduction in chiasma frequency depends on the telocentrics involved since a highly significant positive correlation exists between telocentric length and chiasma frequency. Since all chromosome arms tend to have a minimum of one chiasma, the effects of a fusion are more marked in longer autosomes.
5. Comparisons of populations that differ for number and frequency of fusions, showed a highly significant negative correlation between mean number of different fusions per male (per population) ($\bar{F}$) and total chiasma frequency per cell (X_{ta}). The same type of correlation exists between $\bar{F}$ and proximal X_{ta} and $\bar{F}$ and between-cell variance of total X_{ta} frequency, while a positive correlation was found between $\bar{F}$ and mean interstitial chiasmata.
6. According to 5, intrachromosomal recombination within populations decreases as number and frequency of fusions increase. This effect is added to the instant reduction of interchromosomal recombination produced by the combination of two linkage groups into one.

These results suggest that redistribution of chiasma patterns is due to a direct effect of the rearrangements. Furthermore, the changes in chiasma patterns are discussed in relation to the maintenance of the polymorphisms since trivalents require the elimination of proximal and interstitial chiasmata for balanced orientation and segregation. This was corroborated by the finding of a population in which three fusions were fixed. Here, proximal and interstitial chiasmata in the fused chromosomes are significantly more frequent than expected. Finally, the modifications of recombination potential are discussed relative to the possible adaptive role of these widespread polymorphisms and to a model of chromosomal evolution for the species.

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INTRODUCTION

The effects of chromosomal rearrangements on chiasma frequency and localisation have been extensively studied and reviewed in animals and

plants. Instances of B chromosomes, interchanges, Robertsonian translocations, inversions and supernumerary heterochromatin affecting chiasmata and recombination, have been reported. Intra- and interchromosomal effects have been demonstrated (Hewitt, 1979; Parker *et al.*, 1982; Sperlich and Pfriem, 1986; White, 1973).

A distinction must be made however, between the effects of spontaneous and polymorphic rearrangements since in many cases, the survival and establishment of a stable polymorphic condition or conversely, its transience and the consequent elimination or fixation of a given karyomorph may depend on a reorganisation of the chiasma patterns in the involved chromosomes. Such is the case of centric fusions. In a small number of cases of spontaneous fusions studied in grasshoppers, no modifications of chiasma patterns were apparent in the resultant trivalents (Colombo, 1987; Kayano and Nakamura, 1960; López-Fernández *et al.*, 1984; Southern, 1967; Teoh and Yong, 1983). However, in the few cases of fusion polymorphisms studied in depth, the rearranged chromosomes showed modifications in chiasma frequency and localisation which allow stable convergent orientation and normal segregation of trivalents in heterozygotes (Bidau, 1984; Bidau and Hasson, 1984; Bidau and Mirol, 1988; Colombo, 1987, 1988; Hewitt and Schroeter, 1968). In some cases however, chromosomes may be pre-adapted to exist in a polymorphic state if they have low frequencies and distal localisation of chiasmata as in the Coleopteran *Chilocorus* (Smith and Virkki, 1978). However, this is not always so since trivalents of hybrids between *C. tricyclus* and *C. hexacyclus* show high frequencies of non-conver-

gent orientation despite strong distal localisation of chiasmata (Smith, 1966).

The modifications mentioned above have an additional secondary effect which is the reduction of intrachromosomal (as well as interchromosomal) recombination and this may be of evolutionary significance since it could allow the maintenance of adaptive supergenes.

The grasshopper *Dichroplus pratensis* Bruner offers a unique opportunity to study these effects. This South American melanopline is widespread in Argentina, Uruguay and Southern Brazil (Liebermann, 1963) and comprises several chromosomal races that differ with respect to number and frequency of at least seven different fusions that involve six pairs of large autosomes. With a single exception, all populations already sampled are polymorphic for one to three fusions. Karyotypes, geographic distribution of polymorphisms and meiotic behaviour of heterozygotes have already been described (Bidau, 1984, 1988; Bidau and Mirol, 1988).

In this paper the relationship of the fusion polymorphisms of *D. pratensis* to changes in chiasma frequency and localisation are studied in several Argentine populations.

MATERIAL AND METHODS

This study is based on 297 males of *D. pratensis* collected by the author and collaborators at the localities shown in table 1. A much larger number of males has been cytologically studied, especially at Sierra de la Ventana, being the subject of forthcoming papers; however, some data of these are

Table 1 Origin of the populations whose chiasma characteristics are described in table VII. All populations are polymorphic for the involved fusions except C in which three fusions have become fixed. Populations K and SV belong to hybrid zones which result from the overlapping of chromosome races that differ for fusions with monobrachial homologies

Locality	Department	Province	Collection date	Centric fusions	Per cent standard males
Gaiman (G)	Biedma	Chubut	Jan '83	5/6	93.0
P. Madryn (PM)	Biedma	Chubut	Jan '83	1/4, 5/6	77.0
Km 784 (K)	Villarino	B. Aires	Feb '83	1/6, 3/4, 5/6	15.0
El Cóndor (EC)	A. Alsina	Río Negro	Jan '83	2/4, 5/6	4.0
Tortuguitas (T)	G. Sarmiento	B. Aires	Feb '82	1/6, 3/4	0.0
Necochea (N)	Necochea	B. Aires	Jan '85	1/6, 3/4	0.0
Balcarce (B)	Balcarce	B. Aires	Jan '85	1/6, 3/4	0.0
La Lobería (LL)	A. Alsina	Río Negro	Jan '83	2/4, 5/6	0.0
Tandil 1 (Ta 1)	Tandil	B. Aires	Jan '85	1/6, 3/4	0.0
Tandil 2 (Ta 2)	Tandil	B. Aires	Jan '85	1/6, 3/4	0.0
Sierra de la Ventana (SV)	Tornquist	B. Aires	Feb '83	1/2, 3/4, 5/6, 1/6	0.0
La Florida (LF)	Pringles	San Luis	Jan '84	1/6, 3/4, 2/5	0.0
Monte Hermoso (MH)	C. Dorrego	B. Aires	Jan '83	1/2, 3/4, 5/6	0.0
Cerro (C)	Tornquist	B. Aires	Jan '86	1/2, 3/4, 5/6	0.0

incorporated in this paper. All males were processed in the field. Testes were fixed in 3:1 alcohol-acetic and squashed in lacto-propionic orcein.

Chiasmata were scored at MI since orientation of bivalents and trivalents at this stage allows easy identification of chiasma position. Ten cells were scored per male and chiasmata classified as proximal (P), interstitial (I) and distal (D) according to their location in the first (proximal), second or third portion of the chromosome or chromosome arm when the latter are divided in equal parts.

RESULTS

The karyotype and fusion polymorphisms of D. pratensis

The Robertsonian system of the species has already been described (Bidau, 1984, 1986, 1988). The karyotype comprises in its standard form, six pairs of large telocentric autosomes (L_1 – L_6), three small telocentrics (S_7 – S_9) of which S_7 is the megameric bivalent and S_8 carries the single standard NOR, and one (δ) or two (φ) medium-sized telocentric X chromosomes. L_1 – L_6 chromosomes can be unambiguously recognised by distinctive length. Only L_6 can be identified by heterochromatin content since it usually has a C-positive heterochromatic block at its telomeric end. The six L autosomes are involved in fusions and seven different fusions have been identified (1/2; 1/4; 1/6; 2/4; 2/5; 3/4; 5/6). Some populations are polymorphic for a single fusion, some for two and some for three although not necessarily the same ones since the same telocentric is involved in different fusions. Hybrid zones between chromosomal races have been identified and within them, populations may be polymorphic for four fusions with monobrachial homologies (Bidau, 1988).

Chiasma frequency and localisation in standard and fused males

Until the present, no completely standard (*st*) population has been found in the sampled areas. Indeed, *st* individuals are very rare (Bidau, 1988) due to the numbers and frequencies of the fusions present. Only two populations showed high frequencies of *st* males: Puerto Madryn (PM) and Gaiman (G) (table 1), both from Chubut and about 80 km apart. The first one is polymorphic for fusions 1/4 and 5/6. In Gaiman, a single 5/6 heterozygote was found among 14 males sampled. The standard individuals from these populations were assumed to display the typical chiasma pat-

terns of non-fused individuals of all populations studied although variations between populations probably do occur. Nevertheless, *st*'s from PM and G were very similar regarding chiasma frequency and localisation (table 2) (see also Bidau, 1984).

Fig. 1 shows chiasma patterns of several distinct fusion karyomorphs. The S bivalents never form more than one chiasma that may be P, I or D although the latter predominante (fig. 1 (a)–(h)). Telocentric L bivalents never form more than two chiasmata (fig. 1(a)–(c), (f), (h)). Monochiasmate L bivalents usually have a P or a D chiasma (fig. 1(a)–(c), (f), (h)), seldom an I one (fig. 1(b)). Bichiasmate telocentric L bivalents are very frequently P/D (fig. 1(a), (b), (h)), sometimes I/D (fig. 1(f)) and only rarely P/I. A summary of chiasma frequencies and distribution in telocentric L bivalents of standard males is given in table 2. Chiasma conditions are radically altered in meta-centric fused chromosomes as discussed below (fig. 1(c)–(h)). There is a highly significant correlation between chiasma frequency per bivalent and chromosome length (fig. 2; table 3) within the L group. The correlation does not hold for the S bivalents since there must always be a chiasma present for proper segregation.

Frequencies of total (T), P, I and D chiasmata in 47 *st* males from PM are shown in fig. 3(a)–(d). These are not significantly different from those of the *st*'s from G. That is, standards have a mainly P/D distribution, I chiasmata being rare (Bidau, 1984). In PM, 15 males carrying fusions (all of them heterozygotes) were found: nine had the 1/4 fusion, five the 5/6 fusion and the remaining one was a double 1/4, 5/6 heterozygote. These males, when considered jointly showed significantly fewer total chiasmata than the *st* males from the same population (fig. 3(a)). This was mainly due to a significant decrease in P chiasmata (fig. 3(b)). D and I chiasmata were, on the contrary, higher in heterozygotes (fig. 3(c)–(d)). Chiasma frequencies and distribution of individual 1-1.4.4 and 5-5.6-6 trivalents are summarised in table 4.

In order to test for possible interchromosomal effects, mean cell chiasma frequencies ($\bar{X}$) excluding chromosomes 1 and 4 in one case, and 5 and 6 in the other, were calculated in ten randomly chosen non-fused males. The same was done with nine 1/4 and five 5/6 heterozygotes. The chiasma frequencies thus calculated were not significantly different in both cases (non fused, $\bar{X} = 7.86$ vs. 1/4, $\bar{X} = 7.71$; $F_{1,189} = 1.56$; $P > 0.05$; non-fused, $\bar{X} = 8.30$ vs. 5/6, $\bar{X} = 8.56$; $F_{1,149} = 1.92$; $P > 0.05$). These results suggest that the effect of the fusions on chiasma frequency are exerted solely upon the

Table 2 A summary of chiasma frequencies and distribution in the L bivalents of standard ($2n = 19$) males of *Dichroplus pratensis*. Data of each L bivalent (L1-L6) are given for the G (upper row) and PM (lower row) populations. X_t , X_p , X_i and X_d are mean numbers of total, proximal, interstitial and distal chiasmata per bivalent, respectively. Percentages are given in parentheses. The right part of the table represents the distribution of bivalents with different localisation of 1 and 2 chiasmata

Chiasma frequencies				Bivalents with n chiasmata								Total II's	
				1				2					
X_1	X_p	X_i	X_d	P	I	D	t	P/D	I/D	P/I	t		
1	1.5538	0.5538	0.0308	0.9692	2 (1.54)	2 (1.54)	54 (41.54)	58	70 (53.84)	2 (1.54)	0	72	130
	1.6063	0.6271	0.0646	0.9146	30 (6.30)	11 (2.30)	148 (30.80)	189	271 (56.50)	20 (4.20)	0	291	480
2	1.4835	0.5462	0.0923	0.8000	14 (10.80)	12 (9.20)	47 (36.20)	73	57 (43.80)	0	0	57	130
	1.4667	0.6646	0.1188	0.6833	117 (24.40)	32 (6.70)	107 (22.30)	256	199 (41.50)	22 (4.60)	3 (0.60)	224	480
3	1.3692	0.6154	0.0846	0.6462	35 (26.90)	8 (6.10)	39 (30.00)	82	45 (34.60)	3 (2.30)	0	48	130
	1.2833	0.6063	0.1458	0.5313	170 (35.40)	52 (10.80)	122 (25.40)	344	118 (24.60)	15 (3.10)	3 (0.60)	136	480
4	1.2615	0.6077	0.1385	0.5154	49 (37.70)	14 (10.80)	33 (25.40)	96	30 (23.10)	4 (3.10)	0	34	130
	1.1833	0.5125	0.1313	0.5396	169 (35.20)	48 (10.00)	175 (36.50)	392	73 (15.20)	11 (2.30)	4 (0.80)	88	480
5	1.1615	0.6538	0.0692	0.4385	65 (50.00)	8 (6.20)	36 (27.70)	109	20 (15.40)	1 (0.80)	0	21	130
	1.1521	0.5167	0.0333	0.6021	176 (36.70)	15 (3.10)	216 (45.00)	407	72 (15.00)	1 (0.20)	0	73	480
6	1.1154	0.7308	0.0308	0.3538	80 (61.50)	4 (3.10)	31 (23.90)	115	15 (11.50)	0	0	15	130
	1.0917	0.6000	0.0313	0.4604	244 (50.80)	15 (3.10)	177 (36.90)	436	44 (9.20)	0	0	44	480

involved chromosomes. The same type of comparison was made for P, I and D chiasmata and again, differences were not statistically significant. The other fusions studied produce similar effects on chiasma frequency and distribution (see for example, table 6).

Furthermore, these results indicate that the two fusions affect chiasma frequency differently. This is expected since in *st* males, chromosomes 1 and 4 have on average more chiasmata than 5 and 6 (table 3; fig. 2). This is corroborated by the following: (a) while mean cell chiasma frequency of *st*'s is 10.75, that of 1/4 heterozygotes is 9.83 ($F_{1,559} = 42.30$; $P < 0.01$) and that for 5/6 heterozygotes, 10.52 ($F_{1,519} = 1.46$; $P > 0.05$); (b) when unfused chromosomes 1 and 4 or 5 and 6 are compared

with their fusion counterparts as in fig. 4(a), (b) it is obvious that in both cases, chiasma frequency is reduced in the fused chromosomes though the effect is less marked in the 5/6 fusion as expected; (c) when 1/4 and 5/6 heterozygotes were compared with respect to total chiasma frequency, the difference was highly significant ($F_{1,139} = 18.26$; $P < 0.01$) but the reduction in proximal chiasmata is similar ($F_{1,139} = 0.31$; $P > 0.05$).

It was considered relevant to compare fusion heterozygotes and homozygotes regarding chiasma frequency. Since males differing karyotypically only for the fusion in question are difficult to find in sufficiently large numbers owing to the nature of the polymorphisms, comparisons were made solely between the trivalent and the corresponding

Figure 1 Chiasma distribution at MI in *Dichroplus pratensis* males. (a), (b). Two cells from a standard male ($2n = 19$). (c) Hom 1/6, Het 3/4 ($2n = 16$). (d) Triple 2/5, 3/4, 1/6 Het; the 1/6 trivalent is linearly oriented; note distal localisation of chiasmata ($2n = 16$). (e) Het 1/6, Hom 2/5, 3/4 ($2n = 14$). (f) Het 1/6, Hom 3/4 ($2n = 16$). (g) Double 1/6, 3/4 Het, 2/5 Hom ($2n = 15$); note exceptional proximal chiasma in bivalent 2/5 (left). Het 1/6, Hom 3/4. References: P (proximal), I (interstitial), D (distal). Bar = 10 μ m.

Figure 2 Relationship between relative L chromosome length (RL) and chiasma frequency per chromosome or chromosome arm in ten standard males (*), ten randomly chosen males from a polymorphic population for fusions 1/2, 3/4 and 5/6 (○) and ten males from a population with the same fusions fixed (●). Regression equations and their significance are given in table 3.

fusion bivalent. The fact that no interchromosomal effects have been detected (see above) was considered. The comparisons were made using individuals from the SV, LF and EC populations. As can be seen in tables 5 and 6, no significant differences between Hets. and Homs. are apparent (interstitial chiasmata are however, more frequent in fusion bivalents than in trivalents).

These results suggest that the recombination capacity of a given population (hence its potential ability for the liberation of genetic variability) depends on the quality, number and frequency of the fusions present.

Inter-population comparisons

It is worth noting that interchromosomal recombination is instantly reduced as a consequence of a centric fusion. Two independent linkage groups

are combined into one thus reducing the number of elements that are randomly transmitted to the gametes. Chiasma frequency reduction is added to this effect producing a generalised decrease in recombination.

To test this prediction, the mean number of different fusions per individual ($\bar{F}$) was calculated for each population (table 7). Mean cell total, proximal, interstitial and distal chiasma frequency and inter cell variance of total chiasma frequency, were plotted against $\bar{F}$. The results of the regression analyses (figs. 5 and 6) show that T, P and I chiasma frequency and inter-cell variance depend significantly upon $\bar{F}$.

A further confirmation of this effect was obtained when populations SV, PM and C were compared for chiasma frequency on each L chromosome or chromosome arm. Ten males from each sample were considered: ten *st*'s from PM, ten triple homozygotes (1/2, 3/4, 5/6) from C and

Table 3 Chiasma frequency per L chromosome or chromosome arm based on ten randomly chosen standard males (a) from PM population, ten from a polymorphic population (b) (SV population polymorphic for 1/2, 3/4 and 5/6 fusions) and ten from a monomorphic population (c) (C population; fusions 1/2, 3/4 and 5/6 fixed)

		L chromosome or chromosome arm					
		1	2	3	4	5	6
Mean relative length (RL)		17.85	14.67	13.68	12.20	10.93	9.72
Mean chiasma frequency per L chromosome or chromosome arm ($\bar{X} \pm \text{SE}$)	(a)	1.49 $\pm$ 0.05	1.40 $\pm$ 0.05	1.25 $\pm$ 0.04	1.20 $\pm$ 0.04	1.15 $\pm$ 0.04	1.05 $\pm$ 0.02
	(b)	1.33 $\pm$ 0.05	1.26 $\pm$ 0.04	1.12 $\pm$ 0.03	1.03 $\pm$ 0.02	1.18 $\pm$ 0.04	1.06 $\pm$ 0.02
	(c)	1.08 $\pm$ 0.03	1.02 $\pm$ 0.02	1.04 $\pm$ 0.02	0.98 $\pm$ 0.03	0.95 $\pm$ 0.03	0.94 $\pm$ 0.03

(a) RL vs. $\bar{X}$. $Y = 0.54 + 0.055X$; $F(1, 4) = 93.70$; $P < 0.01$.

(b) RL vs. $\bar{X}$. $Y = 0.74 + 0.032X$; $F(1, 4) = 6.96$; $P < 0.01$.

(c) RL vs. $\bar{X}$. $Y = 0.76 + 0.018X$; $F(1, 4) = 78.86$; $P < 0.01$.

Figure 3 Distribution of the number of (a) total (T), (b) proximal (P), (c) distal (D) and (d) interstitial (I) chiasmata in standard (open histograms) and fused (shaded histograms) males of the PM population. Means are indicated. Results of the respective analyses of variance are: (a) $F_{1,168} = 32.5$; $P < 0.001$; (b) $F_{1,168} = 134.6$; $P < 0.001$; (c) $F_{1,168} = 12.3$; $P < 0.001$; (d) $F_{1,168} = 5.4$; $P < 0.001$.

ten randomly chosen males (including individuals with 1, 2 and 3 fusions) from the highly polymorphic SV population. From fig. 2 it can be seen that the relationship between chromosome length and chiasma frequency varies according to the number of fusions present (table 3).

DISCUSSION

The presence of chromosomal polymorphisms in natural populations is frequently associated with

profound effects on intra- and/or interchromosomal recombination. Examples can be found in different organisms and include inversions in *Drosophila* and some grasshoppers (Confalonieri, 1988; Confalonieri and Colombo, 1989; Goñi *et al.*, 1985; Hewitt, 1979; Sperlich and Pfriem, 1986; Weissman, 1976; White and Morley, 1955), supernumerary segments in many Orthoptera (Hewitt, 1979; John, 1983; Riva *et al.*, 1984), B chromosomes (Jones and Rees, 1982), etc. The mechanism by which recombination is modified depends on the rearrangement involved and may imply vari-

Table 5 A summary of chiasma frequency and distribution of different fusions of *Dichroplus pratensis* in the homozygous, heterozygous and standard states. Only those chiasma configurations that were observed at least once, are included. The configurations for the fusions in the standard form result from the combination of the chiasma patterns of both telocentric bivalents from the same cell; the same applies for standard chiasma frequencies

			1			2							
Fusion			D-O O-D	P-O O-P	I-O O-I	D-D	D-I I-D	D-P P-D	I-I	I-P P-I	P-P	P/D-O O-P/D	I/D-O O-I/D
1/2	SV	Hom	—	—	—	70.0	17.5	—	2.5	—	—	—	—
		Het	—	—	—	54.0	21.0	—	4.0	—	—	—	—
		St	—	—	—	4.4	—	14.4	—	1.1	1.1	—	—
3/4	SV	Hom	0.7	—	0.3	72.4	10.3	0.3	3.1	—	—	—	0.3
		Het	—	—	—	58.0	27.3	0.7	1.3	—	—	—	—
3/4	LF	Hom	—	—	—	86.7	8.3	—	—	—	0.8	—	—
		Het	—	—	—	76.2	20.0	1.2	—	—	—	—	1.2
		St	—	—	—	30.0	—	30.0	—	—	10.0	—	—
5/6	EC	Hom	5.0	—	1.0	71.0	17.0	2.0	3.0	—	1.0	—	—
		Het	—	—	—	74.6	20.0	3.6	1.8	—	—	—	—
		St	—	—	—	2.5	5.0	12.5	5.0	7.5	30.0	—	—
		Hom	—	—	—	57.5	20.0	2.5	—	—	—	—	—
5/6	SV	Het	—	—	—	68.2	20.9	0.9	2.7	1.8	—	—	—
		St	—	—	—	15.8	1.7	27.5	0.8	4.2	4.2	—	—
1/6	LF	Hom	7.1	1.4	2.9	32.9	32.9	1.4	4.3	1.4	—	1.4	—
		Het	2.3	—	—	68.5	14.5	0.8	4.6	—	—	—	—
		St	—	—	—	—	—	20.0	—	—	20.0	—	—
1/6	SV	Hom	—	—	—	93.4	3.3	—	—	—	—	—	—
		Het	—	—	—	70.0	18.2	0.9	0.9	—	—	—	—
		St	—	—	—	22.5	2.5	25.0	—	—	2.5	—	—
2/5	LF	Hom	1.0	—	—	60.0	23.0	—	2.0	3.0	—	1.0	—
		Het	—	—	—	80.0	11.4	—	—	—	—	—	—
		St	—	—	—	2.5	2.5	5.0	—	5.0	40.0	—	—
2/4	EC	Hom	6.0	2.0	—	60.0	28.0	—	4.0	—	—	—	—
		Het	—	—	—	50.0	41.0	—	7.0	—	—	—	—
		St	—	—	—	—	2.9	11.4	2.9	8.6	22.9	—	—
3													
Fusion			P/D-P P-P/D	P/D-I I-P/D	P/D-P D-P/D	I/D-P P-I/D	I/D-I I-I/D	I/D-D D-I/D	P/I-P P-P/I				
1/2	SV	Hom	—	—	2.5	—	—	5.0	—				
		Het	—	—	3.0	—	1.0	17.0	—				
		St	10.0	4.4	33.3	4.4	—	1.1	1.1				
3/4	SV	Hom	0.3	0.3	0.3	—	0.3	11.0	—				
		Het	1.3	—	—	—	—	11.3	—				
3/4	LF	Hom	—	—	—	—	0.8	2.5	—				
		Het	—	—	—	—	—	1.2	—				
		St	—	10.0	20.0	—	—	—	—				
5/6	EC	Hom	—	—	—	—	—	—	—				
		Het	—	—	—	—	—	—	—				
		St	22.5	7.5	7.5	—	—	—	—				
5/6	SV	Hom	—	—	2.5	—	2.5	12.5	—				
		Het	—	—	—	—	1.8	3.6	—				
		St	15.0	5.8	15.0	0.8	—	3.3	—				
1/6	EC	Hom	—	—	—	—	2.9	11.4	—				
		Het	—	—	0.8	—	2.3	6.2	—				
		St	10.0	—	30.0	—	—	—	—				
1/6	SV	Hom	—	—	—	—	—	3.3	—				
		Het	—	—	—	—	0.9	8.2	—				
		St	22.5	—	7.5	5.0	2.5	2.5	5.0				
2/5	LF	Hom	—	1.0	1.0	—	1.0	6.0	1.0				
		Het	—	—	—	—	—	8.6	—				
		St	25.0	2.5	7.5	—	—	—	—				
2/4	EC	Hom	—	—	—	—	—	—	—				
		Het	—	2.0	—	—	—	—	—				
		St	31.4	7.1	8.6	—	—	—	—				

Table 5 continued

			4								
Fusion			I/D-I/D	P/D-I/D I/D-P/D	P/D-P/D	P/I-P/D P/D-P/I	N	Xt	Xp	Xi	Xd
1/2	SV	Hom	2·5	—	—	—	40	2·13	0·03	0·33	1·77
		Het	—	—	—	—	100	2·21	0·03	0·48	1·70
		St	—	7·8	14·4	2·2	90	3·03	1·23	0·22	1·58
3/4	SV	Hom	—	—	—	—	290	2·12	0·02	0·29	1·81
		Het	—	—	—	—	150	2·13	0·02	0·41	1·70
3/4	LF	Hom	—	—	—	—	120	2·03	0·02	0·13	1·88
		Het	—	—	—	—	80	2·01	0·01	0·23	1·77
		St	—	—	—	—	10	2·30	0·80	0·10	1·40
5/6	EC	Hom	—	—	—	—	100	1·94	0·04	0·24	1·66
		Het	—	—	—	—	110	2·00	0·04	0·24	1·72
		St	—	—	—	—	40	2·38	1·40	0·38	0·60
5/6	SV	Hom	2·5	—	—	—	40	2·23	0·05	0·43	1·75
		Het	—	—	—	—	110	2·05	0·03	0·35	1·67
		St	—	0·8	7·5	—	120	2·53	1·02	0·18	1·33
1/6	LF	Hom	—	—	—	—	70	2·03	0·06	0·63	1·34
		Het	—	—	—	—	130	2·07	0·02	0·35	1·70
		St	—	10·0	10·0	—	10	2·80	1·40	0·10	1·30
1/6	SV	Hom	—	—	—	—	30	2·03	0·00	0·07	1·96
		Het	—	0·9	—	—	110	2·11	0·02	0·31	1·79
		St	—	—	2·5	—	40	2·50	1·03	0·20	1·27
2/5	LF	Hom	—	—	—	—	100	2·09	0·07	0·35	1·67
		Het	—	—	—	—	70	2·09	0·00	0·20	1·89
		St	—	2·5	7·5	—	40	2·55	1·68	0·13	0·74
2/4	EC	Hom	—	—	—	—	50	1·92	0·02	0·36	1·54
		Het	—	—	—	—	100	2·02	0·02	0·57	1·43
		St	—	—	4·3	—	70	2·56	1·53	0·24	0·79

somes or else, that the loss in fertility is sufficiently compensated by some selective advantage that the heterozygote might possess.

In the case of fusions, one condition that ensures proper orientation and segregation of trivalents is the absence of proximal chiasmata which, when present, frequently determine linear orientation. For the maintenance of a fusion polymorphism it is then necessary that proximal chiasmata are eliminated either through a direct effect

of the rearrangement or by selection against proximal chiasma formation (unless preadaptation in the form of strong distal localisation in telo/acrocentrics occurs).

When considering the multiple fusion polymorphisms of *D. pratensis* two points are then worthy of discussion; first, the initial establishment of the polymorphisms and second, the possible adaptive significance of the fusions themselves and the modifications on recombination. Both points are, however, intimately related.

In the three thoroughly studied cases of fusion polymorphism in Acrididae, those of *Oedaleonotus enigma* (Hewitt and Schroeter, 1968), *Leptysmia argentina* (Bidau and Hasson, 1984; Colombo, 1987, 1988) and *D. pratensis* (Bidau, 1984, 1986, 1988; Bidau and Mirol, 1988; Tosto *et al.*, 1987; this paper), a marked reduction in proximal chiasmata accompanying a general redistribution of chiasmata in the involved chromosomes of heterozygotes was observed. In all three cases, trivalents show fairly regular orientation and segregation. Indeed, in *D. pratensis* non-convergently oriented trivalents have on average more proximal

Table 6 Comparison between chiasma frequencies of different L chromosome combinations in the heterozygous (Het) and homozygous (Hom) states

Fusion	$\bar{X}$ Het	$\bar{X}$ Hom	F	d_f	P
1/2	$n = 100$ 2.25 ± 0.04	$n = 40$ 2.10 ± 0.05	3.97	1, 138	0.05-0.01
3/4	$n = 100$ 2.12 ± 0.03	$n = 100$ 2.19 ± 0.04	0.87	1, 198	>0.05
5/6	$n = 100$ 2.08 ± 0.03	$n = 50$ 2.18 ± 0.07	2.95	1, 148	>0.05
1/6	$n = 110$ 2.10 ± 0.03	$n = 30$ 2.10 ± 0.06	0.00	1, 138	>0.05

Table 7 Chiasma characteristics of 14 natural populations of *D. pratensis* (for references see table 1)

Population	N	$\bar{F}$	$\bar{X}_t$	$\bar{X}_p$	$\bar{X}_i$	$\bar{X}_d$	S_i^2
G	14	0.07 ± 0.07	10.76 ± 0.11	3.57 ± 0.13	0.77 ± 0.07	6.47 ± 0.11	1.674
PM	62	0.26 ± 0.06	10.59 ± 0.05	3.45 ± 0.06	0.77 ± 0.03	6.37 ± 0.06	1.555
K	20	1.20 ± 0.17	9.84 ± 0.07	2.26 ± 0.09	0.92 ± 0.07	6.67 ± 0.09	0.939
EC	24	1.54 ± 0.12	9.92 ± 0.05	3.42 ± 0.09	1.09 ± 0.06	5.41 ± 0.10	0.706
T	13	1.57 ± 0.14	9.55 ± 0.06	2.01 ± 0.12	0.94 ± 0.08	6.61 ± 0.14	0.529
N	5	1.80 ± 0.20	9.54 ± 0.10	2.20 ± 0.15	1.06 ± 0.13	6.28 ± 0.20	0.539
B	10	1.80 ± 0.13	9.43 ± 0.06	2.34 ± 0.11	1.39 ± 0.13	5.68 ± 0.14	0.389
LL	6	1.83 ± 0.17	10.03 ± 0.09	2.63 ± 0.13	1.17 ± 0.12	6.23 ± 0.17	0.440
Ta2	15	1.87 ± 0.09	9.50 ± 0.07	2.01 ± 0.10	1.52 ± 0.10	5.97 ± 0.12	0.681
Ta1	18	2.00 ± 0.00	9.56 ± 0.07	1.63 ± 0.07	1.23 ± 0.09	6.70 ± 0.09	0.837
SV	46	2.33 ± 0.15	9.91 ± 0.04	1.33 ± 0.05	1.31 ± 0.05	7.27 ± 0.06	0.780
LF	21	2.71 ± 0.10	9.29 ± 0.05	0.91 ± 0.06	1.16 ± 0.07	7.21 ± 0.09	0.454
MH	6	3.00 ± 0.00	9.03 ± 0.06	0.73 ± 0.13	1.62 ± 0.13	6.68 ± 0.15	0.236
C	16	3.00 ± 0.00	9.04 ± 0.06	0.58 ± 0.06	1.96 ± 0.12	6.54 ± 0.13	0.489

(1) $\bar{F}$ vs. $\bar{X}_t$. $Y = 10.65 - 0.53X$; $F(1, 12) = 51.94$; $P < 0.01$. $r = -0.9014$; $t(12) = 7.21$; $P < 0.001$

(2) $\bar{F}$ vs. $\bar{X}_p$. $Y = 3.90 - 1.02X$; $F(1, 12) = 55.88$; $P < 0.01$. $r = -0.9071$; $t(12) = 7.17$; $P < 0.001$

(3) $\bar{F}$ vs. $\bar{X}_i$. $Y = 0.64 + 0.32X$; $F(1, 12) = 25.84$; $P < 0.01$. $r = 0.8257$; $t(12) = 5.07$; $P < 0.001$

(4) $\bar{F}$ vs. $\bar{X}_d$. $Y = 6.13 + 0.17X$; $F(1, 12) = 1.13$; $P > 0.05$. $r = 0.2931$; $t(12) = 1.06$; $0.3 < P < 0.04$

(5) $\bar{F}$ vs. S_i^2 . $Y = 1.47 - 0.41X$; $F(1, 12) = 32.87$; $P < 0.01$. $r = 0.8569$; $t(12) = 5.76$; $P < 0.001$

(6) $\bar{X}_p$ vs. $\bar{X}_i$. $Y = 4.71 - 2.18X$; $F(1, 12) = 14.77$; $P < 0.01$. $r = -0.7430$; $t(12) = 3.85$; $P < 0.01$

(7) $\bar{X}_t$ vs. $\bar{X}_p$. $Y = -13.83 + 1.64X$; $F(1, 12) = 14.31$; $P < 0.01$. $r = 0.8493$; $t(12) = 5.57$; $P < 0.001$

and interstitial chiasmata than correctly oriented ones (Bidau and Mirol, 1988). It is relevant to note however, that the same modifications occur in fusion homozygotes, where the restrictions imposed by chiasmata do not apply. Furthermore, non-fused telocentrics remain unaffected (see table 5).

It is interesting however, to note the following: while a pronounced reduction in chiasma frequency (especially of the proximal type) is expected in polymorphic populations due to the "need" of stabilising trivalent orientation, this restriction need not operate in populations where the fusions are fixed. Since only one population in which three fusions were fixed was obtained, a comparison was made between the former and a related population (SV) in which males homozygous for the same three fusions were considered. Although males from the monomorphic population had on average fewer total chiasmata than those from the polymorphic one, the former had more proximal chiasmata and the difference was statistically significant (table 8).

When considering these facts, one is confronted with two alternative hypotheses about the chiasmata modifications produced by the polymorphisms, as stated above. Colombo (1987), on the basis of his observations of a spontaneous fusion 5/7 heterozygote in *L. argentina* suggested that, since no redistribution of chiasmata occurred in chromosomes 5 and 7 in the mutant as compared with

Table 8 Comparisons of mean cell total ($\bar{X}_t$) and proximal ($\bar{X}_p$) chiasma frequencies between 16 males of the monomorphic C population (all homozygous for fusions 1/2, 3/4 and 5/6) and 11 males from a polymorphic population (SV) also homozygous for the same three fusions

Population	n	$\bar{X}_t$	F(1, 268)	$\bar{X}_p$	F(1, 268)
C	160	9.04	32.17 $P < 0.01$	0.58	52.47 $P < 0.01$
SV	110	9.54		0.37	

standard individuals, the modifications in the widespread polymorphic 3/6 fusion are the result of a later adaptation to the polymorphic condition. This author also discusses the evidence provided by observations on other spontaneous fusions in Acrididae (Kayano and Nakamura, 1960; López-Fernández *et al.*, 1984; Southern, 1967; Teoh and Yong, 1983) where no redistribution of chiasmata was reported. It is not safe however, to *a priori* accept this hypothesis solely on the tenuous grounds derived from observations on spontaneous mutants (a scanty amount indeed). In the first place, the studied fusion polymorphisms (very few in fact) are undoubtedly not a random sample of all fusions that occur spontaneously in nature. This is certainly true of other rearrangements (*i.e.* inversions; Sperlich and Pfiem, 1986). Therefore, the successful extant polymorphisms may be simply those which originally survived owing to an instantaneous modification of the cross-over

Figure 5 Relationship between mean number of different fusions per male ($\bar{F}$) and mean (a) total ($\bar{X}_t$), (b) proximal ($\bar{X}_p$), (c) interstitial ($\bar{X}_i$) and distal ($\bar{X}_d$) chiasmata per cell in 14 populations of *D. pratensis*. Regression equations and their significances are given in table 7.

pattern in heterozygous mutants. Extensive chiasma modifications certainly do occur in mutants heterozygous for interchanges or fissions (Arana *et al.*, 1980; Hewitt, 1967; Parker, 1987; Parker *et al.*, 1982) and these are obviously a result of the rearrangement itself. Second, comparisons have been made between different chromosomes which do not necessarily respond equally to the rearrangement. Ideally, comparisons should involve the same fusion, polymorphic in one population and spontaneous in another.

Perhaps more relevant is the fact that it is difficult to envisage a selective process by which proximal chiasmata are eliminated in the fusion chromosomes without a concomitant elimination in the corresponding telocentrics of standards, unless genes responsible for chiasma control are

tightly linked with the metacentric fusion chromosome. The latter is improbable since in *D. pratensis* all seven fusions behave equally: in all cases telocentrics have high proximal chiasma frequencies (see the results section) and besides, control of chiasma frequency is probably polygenic (Shaw, 1972).

It is then more plausible that the fusions exert some direct restrictions on proximal chiasma formation at the heterozygous and homozygous conditions through for example, modifications of synapsis. A possible model is the following: if chiasmata are formed preferentially in regions which include or are close to zones of pairing initiation which are paired early in prophase I and have the most protracted period of synapsis, the chance of chiasma formation in these regions may

Figure 6 Relationship between (a) $\bar{F}$ and mean between-cell variance of total chiasmata (S_t^2) in 14 populations of *D. pratensis* and (b) mean frequency of interstitial ($\bar{X}_i$) and proximal ($\bar{X}_p$) chiasmata in the same populations. Regression equations and their significance are given in table 7.

well be increased. Then, if unfused telocentrics have both ends attached to the nuclear membrane, they can initiate pairing from either or both ends, which could explain the P/D chiasma distribution. In fused chromosomes however, four original ends are replaced by two and the number of early pairing regions is consequently reduced and shifted to distal ends only. This would explain both the reduction in total chiasma frequency and the reduction in proximal chiasmata in fusion heterozygotes and homozygotes.

Turning to the possible adaptive significance of the *D. pratensis*'s polymorphisms one is tempted to relate their maintenance to the restrictions imposed upon recombination. Fusions are not as effective suppressors of recombination as inversions but a fusion instantly reduces interchromosomal recombination by bringing together two formerly independent linkage groups, usually accompanied by a suppression of chiasmata in proximal portions of chromosomes as discussed above. These facts could allow the conservation of coadapted supergenes partially or completely protected from recombination. Thus the maintenance of the polymorphisms would become adaptive since fixation could, by eliminating the segregation restrictions of heterozygotes, result in an increase in crossing-over in regions previously protected (as in the C population described in Results) and the disruption of supergenes.

Two hypotheses relate polymorphic rearrangements and supergenes, the postadaptation and the preadaptation hypotheses (Sperlich and Pfriem, 1986). In the first case, the newly arisen fusion

could be initially successful because of favourable position effects. The need for stabilising segregation in heterozygotes could then, by restricting chiasma formation, allow the surging of supergenes. That is, the decrease in recombination being a byproduct of the establishment of the polymorphism would not be the initial cause of its maintenance. In the second case one could envisage a situation in which some coadaptation already exists and any fusion that involves such gene arrangements should be favoured since it would protect them from recombination.

A model proposed for the chromosomal evolution of *D. pratensis* (Bidau, 1984, 1988) can be expanded when the effects of the fusions on recombination are considered. It proposes that range expansion of the species occurred mainly in the monomorphic standard form since these populations have more recombination potential and thus, a greater capacity for liberating genetic variability which allows the production of more gene arrangements to be selected for in order that the population becomes adapted to a new environment. Once a new colony adapts successfully to its new habitat, the fortuitous appearance of one or more fusions that include the adaptive gene combinations would generate the polymorphic condition to preserve them as explained above.

It is possible to relate this model to the central-marginal model of evolutionary biology as it has been applied for example to *Drosophila* (Brussard, 1984; Sperlich and Pfriem, 1986). The model assumes that populations belonging or near to the centre of a species' range, have certain characteris-

tics such as high density, high levels of genetic and phenotypic variation, etc. In contrast, peripheral populations are isolated, sparse, have low levels of chromosomal polymorphism, etc. A number of hypotheses concerning the inversion polymorphisms in *Drosophila* as related to this model have been put forward (Brussard, 1984).

When considering the distribution of fusion polymorphisms in *D. pratensis* it was shown that, at least in the sampled area, no clear pattern is evident (Bidaú, 1988). Certainly, some fusions are widespread and others restricted to particular localities, and populations are generally very polymorphic. Exceptions however, do exist; two Patagonian populations have exceptionally high frequencies of standard individuals (PM and G) and are consequently the less polymorphic ones and those with the highest recombination indexes. Despite the wide ecological tolerance displayed by the species, these populations are the best candidates for being considered marginal (in the ecological sense) since environmental conditions in these areas are certainly more strenuous (see Bidaú, 1984).

These populations, having more recombination potential, could liberate more genetic variability (if available) that would be of advantage in a new, unexploited environment. The PM and G populations would then agree with Carson's (1959) model in having low polymorphism and high recombination. It is however relevant to discuss some morphological data of *D. pratensis* (Bidaú and Tosto, 1986). Although the putative marginal populations seem to be phenotypically more variable than those presumed to be central (or optimal in the ecological sense), no statistically significant correlation was found between degree of polymorphism and morphological variability. This is in contrast with the report of Westerman (1983) on *Phaulacridium* in which a negative correlation between recombination potential and phenotypic variability was demonstrated. He produced a very apt explanation: those populations with high cross-over frequencies liberate much genetic variability which is subjected to selection very rapidly and consequently, rapidly lost. Populations with a lower recombination potential would preserve the extant genetic variability. In Westerman's (1983) case however, low recombination populations were the peripheral ones. A further case of a central-marginal distribution of a fusion polymorphism in a grasshopper was reported by Colombo (1988).

The case of *D. pratensis* is puzzling. On the one side, polymorphism is lower and recombina-

tion higher in marginal populations; on the other, phenotypic variation shows no significant differences. The latter could be related to the fact that allozyme variability is not correlated with chromosomal variability (Brussard, 1984). It is relevant however to note that although central populations may be chromosomally more polymorphic, the type of polymorphism conditions the propositions of the central-marginal model: central populations may be highly polymorphic for B chromosomes which raise chiasma frequency, or inversions or fusions that decrease it. Hence, the chromosomal situation is possibly related not only to modifications of recombination but to other effects due to the rearrangements themselves.

The hypothesis that the PM and G populations are recent invaders is appealing but by no means definitive.

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