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Cytogenetic studies in *Sinipta dalmani* Stål (Orthoptera: acrididae). II. Effects of centric fusions on chiasma frequency and distribution

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Summary – Spontaneous and polymorphic centric fusions were detected in a population of *Sinipta dalmani* ($2n: 23, XO$ male/ XX female) from Entre Ríos Province (Argentina). The spontaneous rearrangement affects 2 autosomes (M_6 and M_7) while the polymorphic one involves the sex chromosome and the fifth member of the complement. The former has irregular behaviour presenting a high frequency of non disjunctional orientation during metaphase I. This mutation does not affect either the frequency or the distribution of chiasmata in the bivalents involved. However, the polymorphic fusion has a significant influence on chiasma distribution, since an increment in the distal chiasma frequency in the affected bivalent was observed. These results indicate that the polymorphic mutation has an effect on intrachromosomal recombination, which would have adaptive significance, in contrast with the situation of spontaneous fusion which rarely persists in the population.

orthoptera / chiasma / centric fusion

Résumé – Etudes cytogénétiques chez la sauterelle *Sinipta dalmani* Stål (Orthoptera: acrididae). II. Effets des fusions centriques sur la fréquence et la distribution des chiasmas. Des fusions centriques spontanée et polymorphe ont été détectées dans une population de *Sinipta dalmani* ($2n=23$, mâles XO /femelles XX) de la province d'Entre Ríos (Argentine). Le réarrangement spontané affecte 2 autosomes (M_6 et M_7), tandis que la fusion polymorphe implique le chromosome sexuel et le 5^e autosome (M_5). La première fusion présente un comportement irrégulier où le chromosome fusionné M_{6-7} accompagne fréquemment en métaphase I l'un des 2 chromosomes acrocentriques M_6 ou M_7 . La fréquence et la distribution des chiasmas ne sont pas modifiées dans les bivalents correspondants. En revanche la fusion polymorphe a un effet significatif sur la distribution des chiasmas, avec un accroissement de fréquence des chiasmas distaux dans les bivalents observés. Ces résultats indiquent que la mutation polymorphe a un effet sur la recombinaison intrachromosomique, qui aurait une signification adaptative, contrairement à la situation de la fusion spontanée qui se maintient rarement dans la population.

orthoptère / chiasma / fusion centrique

INTRODUCTION

In wild populations, chromosome mutations can be present either in single individuals, constituting examples of spontaneous rearrangements, or in several ones producing polymorphic or polytypic situations. The meiotic behaviour of such mutations affects, to a great extent, their maintenance in the population. In particular, a centric fusion may survive in a population according to the orientation in the spindle of the trivalent during metaphase I and the regular segregation at first anaphase. In general, the orientation of the multivalent is affected by the size of the chromosomes involved, the chiasma distribution and the centromere reorientation (Sybenga, 1975; Arundhati *et al*, 1986).

Spontaneous centric fusions are rarely found in Orthoptera. Generally, they present a low rate of alternate orientation and thus probably fail to be maintained in a polymorphic state (Teoh and Yong, 1983; Lopez Fernandez *et al*, 1984; Colombo, 1987). This fact may largely explain the limited number of polymorphisms for centric fusions found in natural populations of this group. In general, when this situation occurs, changes in chiasma position and frequency, that insure the regular multiple orientation and segregation, are observed (Hewitt, 1979; Bidau, 1984; Colombo, 1987).

In the grasshopper *Sinipta dalmani*, spontaneous and polymorphic centric fusions have been detected in a population from Entre Ríos Province (Argentina). In the present paper, meiotic behaviour and effects on chiasma conditions are studied in order to analyse the influence of the different kinds of mutations.

MATERIALS AND METHODS

In the present study, 30 and 38 adult males of *Sinipta dalmani* Stål, collected from Arroyo Los Loros (LL) (National Park El Palmar, Entre Ríos Province) in December 1986 and 1987, respectively, were analysed. Testes were dissected and immersed for 10 min in a hypotonic solution (KCl 0.5%). The material was fixed in 3:1 (absolute ethanol: glacial acetic acid) and stored at 4 °C until use. Staining was carried out on the slides in 1 or 2 drops of acetic orcein (2%) for 5 min. After this time, temporal preparations were made by squash.

RESULTS

The standard complement of *S. dalmani* consists of 23 acrocentric chromosomes in males with an XO/XX sex-determining mechanism. The autosomes may be grouped in 3 large (L₁-L₃), 5 medium (M₄-M₈) and 3 small (S₉-S₁₁) chromosome pairs (Bidau, 1984; Remis, 1989).

A pericentric polymorphic inversion in the M₄, which changes the chromosome morphology from being acrocentric to submetacentric, was detected in both 1986 (Remis, 1989) and 1987 (unpublished data) samples.

The spontaneous centric fusion

One out of 30 males of the LL population (1986 sample), a heterozygote for the pericentric inversion, was a complete germ line mutant for a spontaneous centric fusion between the M_6 and M_7 chromosomes (figs 1,2). The rearrangement does not apparently produce a reduction in chromosome size and no free fragment was observed.

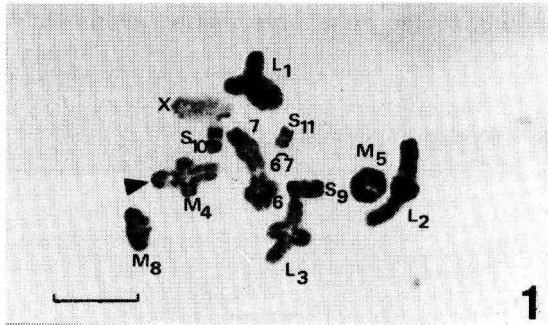


Fig 1. First metaphase showing the fusion trivalent (6-6 7-7) with linear orientation.

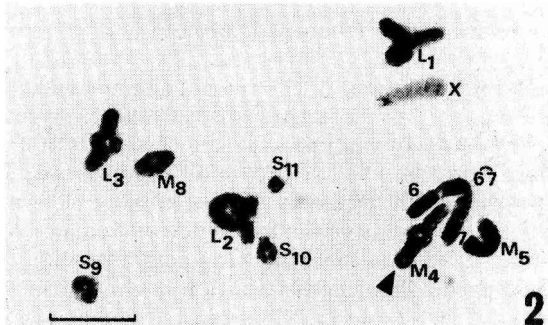


Fig 2. First metaphase showing the fusion trivalent (6-6 7-7) with alternate orientation.

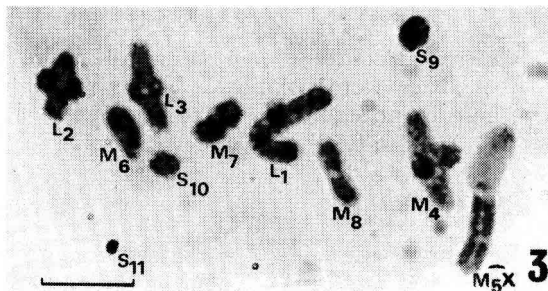


Fig 3. Metaphase I showing the noe XY bivalent (M_5X). Arrowhead indicates the heteromorphous bivalent for pericentric inversion. Bar: 10 μ .

During diplotene and metaphase I, a trivalent maintained by 2 chiasmata was always observed (figs 1,2). At first metaphase, the trivalent can adopt 2 different orientations which are expected to have different consequences for the production of balanced gametes (table I). The predominant class was the linear orientation where the metacentric (M_{6-7}) is oriented to the same pole with one M_6 or M_7 acrocentric chromosome (fig 1). In the alternate orientation the fused chromosome is co-oriented with regard to the M_6 and M_7 chromosomes (fig 2). However, there are virtually equal frequencies of balanced and unbalanced products at second metaphase, which represent highly significant differences with regard to the expected frequency of balanced cells according to the metaphase I orientations (table I) ($\chi^2 = 10.17$, $P = 0.001$).

Table I. Frequencies of the different orientations of the trivalent at metaphase I and chromosome combinations at metaphase II.

<i>Chromosome combinations</i>	<i>Metaphase I</i>	<i>Metaphase II</i>
$M_{6-7}+M_6/M_7$		
$M_{6-7}+M_7/M_6$	78 (77%) (linear)	18 (51%)
$M_{6-7}+M_6/M_7$	23 (23%) (alternate)	17 (49%)

Influence of the spontaneous fusion on chiasma distribution

With the aim of studying the effects of the rearrangement on chiasma distribution, the spontaneous mutant and 5 other individuals (also heterozygotes for the pericentric inversion) were exhaustively analysed. In each case, cells at first metaphase were studied and chiasmata were classified as proximal (P), interstitial (I) and distal (D) according to their position with regard to the centromere. The results suggest that the spontaneous fusion does not alter the frequency of chiasmata at first metaphase since the trivalent presents 2 chiasmata and the corresponding non-fused (M_6 and M_7) form one chiasma each. Chiasma distribution in the trivalent varies depending on the different orientations (table II). The most frequent class had 2 distal chiasmata in the alternate orientation and 1 distal and 1 interstitial chiasma in the linear one. Thus, chiasma distribution in the multivalent affects the orientation in the spindle.

To determine whether the fusion does or does not affect the pattern of chiasma distribution, their frequencies were compared between trivalent and standard bivalents (table III). There are no significant differences in the chiasma distribution, either in the M_6 ($\chi^2 = 1.53$, $P = 0.89$) or in the M_7 pairs ($\chi^2 = 3.71$, $P = 0.16$).

Sex chromosome polymorphism

A polymorphic centric fusion, which involves the sex chromosome, was detected in the 1986 and 1987 samples of the LL population. A comparison of the relative length between the standard complement and the neo XY form indicates that the M_5 autosome participates in this rearrangement (fig 3).

Table II. Frequencies of the chiasma distribution in the trivalent according to the metaphase I orientations.

Chiasma Distribution		Alternate	Linear
M ₆	M ₇		
I	D	3 (19%)	21 (38%)
D	I	1 (6%)	18 (32.5%)
D	D	11 (69%)	12 (22%)
D	P	0	1 (2%)
P	D	0	2 (3.5%)
I	I	1 (6%)	1 (2%)

P: proximal, I: interstitial, D: distal.

Table III. Frequencies of chiasma distribution in the different kinds of bivalents (II) and in the trivalent (III) according its chiasma distribution at metaphase I.

	II		III	
	M ₆	M ₇	M ₆	M ₇
P	5 (7%)	9 (12%)	3 (4%)	2 (3%)
I	19 (25 %)	24 (31.5 %)	23 (34%)	20 (30%)
D	52 (68%)	43 (56.5%)	42 (62%)	45 (67 %)

P: proximal, I: interstitial, D: distal.

According to White (1973), the portion of the neo X which corresponds to the original X chromosome is termed X_L , while the remaining one is labelled X_R . The X_L component maintains the allocyclic behaviour while the X_R is euchromatic. The neo Y is euchromatic and presents the same size as X_R .

The frequency of this rearrangement in the males was higher in the second year (table IV), though the difference was not significant ($\chi^2 = 2.01$, $P = 0.16$).

Table IV. Karyomorph and fusion (q) observed frequencies in males of Los Loros population in 2 consecutive years.

	XO	neo XY	q
1986	29	1	0.033 3
1987	33	5	0.13 57

Effects of the polymorphic fusion on chiasma formation

In order to analyze the effect of the chromosome polymorphism on chiasma frequency, 4 neo XY males (2 basic homozygotes and 2 heterozygotes for the peri-

centric inversion) and 20 *XO* males (10 individuals of each inversion karyomorph) were studied.

The results of the analyses of the 1986 sample indicated that the pericentric inversion affects the interstitial chiasma (X_i) frequency in the homozygous conditions (Remis, 1989). However, the X_i frequency within each fusion karyomorph was compared between carriers and non carriers of the inversion, through analysis of variance, in the 1987 sample (tables V and VI). No significant differences between basic homozygotes and heterozygotes for inversion, either in *XO* or neo *XY* individuals were found ($F = 0.89$, $P = 0.36$; $F = 2.84$, $P = 0.23$). This corroborates the results obtained and indicates that there are no interactions between the analyzed rearrangements.

Table V. Interstitial chiasma frequencies (\bar{X}_i) and number of studied cells in basic homozygotes for the pericentric inversion with different fusion karyomorph.

	<i>neo XY</i>			<i>XO</i>										
<i>Specimen</i>	9	13	<i>Total</i>	24	19	14	26	8	27	12	18	6	2	<i>Total</i>
<i>No of cells</i>	25	25	50	10	14	13	18	12	12	10	12	10	12	123
\bar{X}_i	3.24	3.22	3.23	4.2	2.8	5.4	3.8	3.6	4.5	3.7	4.2	3.9	3.7	3.966

Table VI. Interstitial chiasma frequencies (\bar{X}_i) and number of studied cells in heterozygotes for the pericentric inversion with different fusion karyomorph.

	<i>neo XY</i>			<i>XO</i>										
<i>Specimen</i>	1	20	<i>Total</i>	B	17	28	15	22	3	30	10	5	7	<i>Total</i>
<i>No of cells</i>	20	20	40	10	10	10	10	10	10	10	10	10	10	100
\bar{X}_i	3.3	3.5	3.4	4.3	3.7	4.1	5.4	4.1	5.5	3.7	3.5	4.8	4.0	4.31

Thus, to study the influence of the centric fusion alone, the chiasma frequency of 4 neo *XY* and 8 *XO* individuals was studied (table VII). The results indicate a slight increment in the X_i frequency in the individuals with the standard complement. An analysis of variance revealed that this difference is statistically significant ($F = 5.80$, $P = 0.037$).

Table VII. Mean interstitial chiasma frequencies (\bar{X}_i) and number of analyzed cells in neo *XY* and *XO* individuals.

	<i>neo XY</i>	<i>XO</i>
<i>No of cells</i>	90	80
\bar{X}_i	3.31	4.2

With the aim of determining whether this results is due to intra or interchromosomal effect, the pattern of chiasma distribution in the involved bivalent was studied. Since the pericentric inversion produces a significant decrease in the X_i frequency in heterozygotes and homozygotes in the M_5 - M_8 pairs (Remis, 1989), the chiasma distribution of 18 XO and 4 neo XY individuals within each karyomorph for inversion were compared. In each case, a minimum of 10 cells were studied (table VIII). The fusion carriers present no chiasma in proximal position and a decrease in the percent of interstitial chiasmata. When the numbers of chiasmata in distal and interstitial position are compared through χ^2 contingency test, a highly significant increase in the former in neo XY individuals, in both homozygotes and heterozygotes for the inversion, was found (table VIII) ($\chi^2 = 26.98$, $P \cong 0$; $\chi^2 = 20.22$, $P \cong 0$).

Table VIII. Chiasma distribution in the M_5 pair of neo XY and XO individuals and number of analyzed cells within each inversion karyomorph.

	<i>Basic homozygotes</i>		<i>Heterozygotes</i>	
	<i>XO</i>	neo <i>XY</i>	<i>XO</i>	neo <i>XY</i>
<i>No of cells</i>	109	103	94	45
P	1%	—	3%	—
I	49%	15%	39.5%	2%
D	50%	88%	57.5%	98%

P: proximal, I: interstitial, D: distal.

Within neo XY individuals the heterozygotes for the inversion show a lower percent of X_i than does the basic homozygote. It is possible that the inversion heterozygotes have in the M_5 pair a decrease of this variable owing to the simultaneous presence of the fusion and the inversion (table VIII).

In order to determine if this significant decrease in the neo XY individuals is produced by a redistribution of chiasmata in the bivalent involved, the results excluding the data of the M_5 bivalent were analyzed (table IX). In this case, there are no significant differences in the fusion carriers ($F = 4.06$, $P = 0.07$). Thus, the centric polymorphic fusion shows only an intrachromosomal effect on chiasma distribution.

Table IX. Mean chiasma frequencies (\bar{X}_i) and number of analyzed cells in the neo XY and XO individuals without the data of M_5 pair.

	neo <i>XY</i>	<i>XO</i>
<i>No of cells</i>	90	87
\bar{X}_i	3.22	3.85

DISCUSSION

Centric fusions are detected in natural populations of Orthoptera (Hewitt, 1979; John, 1983). These rearrangements may involve 2 non homologous chromosomes, either 2 autosomes or 1 autosome and the sex chromosome. Spontaneous mutants for this rearrangement are rarely found in this group (Hewitt, 1979; John, 1983). In these situations, the fusion trivalent may have different frequencies of alternate and linear orientations. In *Chortippus jucundus* a centric fusion between acrocentrics of different size presents 28% of alternate orientation (Lopez Fernandez *et al*, 1984). Teoh and Yong (1983) described in *Valanga nigrocornis* a fusion between autosomes M_8 and M_9 which had about equal proportions of alternate and linear orientations. On the other hand, in *Leptysma argentina* the orientation of the fusion trivalent was less irregular (64% alternate orientation) (Colombo, 1987). In the species studied here, the spontaneous mutant presents a low rate of alternate orientation (25%). Thus, it is expected that it produces a concomitant decrease in the carrier fertility. However, in *Myrmeleotettix maculatus* a spontaneous fusion mutant apparently has not affected the production of normal gametes in spite of non disjunctional orientation observed in metaphase I (Southern, 1967). Similarly, *S dalmani* presents an increment in the frequency of balanced products of second division with respect to the percentage of observed linear orientation. This result suggested instability for linear orientations. The trivalent may undergo a reorientation in the spindle before anaphase I separation (Southern, 1967; Sybenga, 1975; Arrundhati *et al*, 1986). Thus, the frequency of balanced gametes of a spontaneous fusion carrier may be higher than that expected on the basis of the recorded metaphase trivalent orientation.

Several factors may play a role in the variation of the frequencies of multiple orientation. Two of them are the size of the chromosomes involved and the location of chiasmata. In *Chortippus jucundus* the unequal chromosome size may be the principal factor to affect the relative frequency of linear arrangement since the chiasma distribution is heterogeneous in both orientations (Lopez Fernandez *et al*, 1984). In *S dalmani*, the size of the chromosomes involved is similar. However, according to the data presented here, the chiasma distribution may have an important influence on the orientation of the trivalent. The linear orientation presents a high frequency of interstitial chiasmata in 1 or in both arms of combined chromosomes while the alternate is associated with two distal chiasmata. Colombo (1987) found that the linear arrangement presented a higher proximal chiasma frequency in *Leptysma argentina*. These results indicate that the disjunctional orientations are associated with chiasmata at considerable distances from the centromere in the 2 arms of a fused chromosome.

Generally, chromosome rearrangements are accompanied by influence on chiasma conditions (Hewitt, 1979; John, 1983). However, in most of the reported cases, spontaneous fusions do not affect this variable in the 2 combined chromosomes (Southern, 1967; Teoh and Yong, 1983; Colombo, 1987). In agreement with this, in *S dalmani*, the spontaneous fusion does not show any intrachromosome effect on chiasma frequency and distribution. Thus, the results indicate that any effect of polymorphic chromosome mutation on chiasma condition may not be a direct consequence of the fusion itself.

In wild populations of Orthoptera, centric fusions may also be present in several individuals creating intra or interpopulation variation. However, the frequency of this rearrangement in polymorphic state is low (Hewitt, 1979; John, 1983). Moreover, no polymorphism for centric fusion involving the sex chromosome had been described (John, 1983). The most exact reported example is that of *Podisma pedestris* (John and Hewitt, 1970; Hewitt and John, 1972). This species is distributed across Russia, Siberia, Mongolia and Western Europe. The populations of Europe are of 2 classes, XO/XX or neo XY /neo XX . It appears to be a polytypic situation in which the polymorphic region is limited to a narrow hybrid zone (John, 1983).

S. dalmani is distributed across east, West, Central and South Argentina. At present, 2 populations of El Palmar National Park 3 km apart were studied. One of them has an XO/XX sex chromosome system (Remis, 1989) while in the other (the present study), XO and neo XY forms are present. The Gualaguaychú population, located south of the National Park (Remis, unpublished data) and a population situated at km 1058 of Ruta Nacional No 3 (Río Negro) (Bidau, 1984) were also analyzed. So far, no population possessing neo XY forms has been observed. Thus, the detected intrapopulation variation may be considered as a polymorphic situation. The frequency of the fusion in the first year of collection was a quarter of the value of the second one (0.0333 vs 0.1316). There is a noticeable increase (although it is not statistically significant), in the frequency of the rearrangement which does not allow this polymorphism to be considered stable with any certainty. Therefore, the results presented here constitute an interesting example for determination of whether this population will ever reach a stable polymorphism, or whether there will be a tendency to fixation of either form of sex chromosome.

The main consequence of centric fusions is the alteration in the pattern of interchromosome recombination since it reduces the number of independent linkage groups. Moreover, this mutation may modify the pattern of intrachromosome recombination, affecting chiasma frequency and distribution (Hewitt, 1979; Bidau, 1984; Colombo, 1987; Hewitt and Schroeter, 1988). In *Podisma pedestris* a considerable restriction in the frequency of proximal chiasmata in the X_R arm of the neo XY was observed (John and Hewitt, 1970). In *Sinipta dalmani* the neo XY individuals show a significant increase in the percent of distal chiasmata in the M_5 pair. This effect may have an adaptive significance since it reduces the intrachromosome recombination, restraining the occurrence of chiasmata in proximal and interstitial positions.

Finally, the polymorphic fusion is associated with effects on chiasma conditions, which would have evolutionary consequences, in contrast with the situation of the spontaneous fusions which rarely persist in the population.

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