

Cytological Evidence for Preferences of Identical Over Homologous but Not-identical Meiotic Pairing

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Abstract. A spontaneous tetraploid/diploid chimera involving meiotic cells of a male individual of *Euchorthippus pulvinatus gallicus* was heterozygous for the C-banding pattern in chromosome pair 8. This allowed the study of the possible existence of competition in meiotic pairing between identical and homologous but not-identical chromosomes. The results suggest the existence of such a competition. An excess of bivalents formed by identical chromosomes was observed. It is suggested that during the pairing process slight specificity or activity differences between chromosomes with a high degree of resemblance would be responsible for the pairing preferences found.

Introduction

Under favourable conditions synapsis and crossing over can take place between chromosomes which are not strictly homologous. Non-homologous pairing in some haploids and homoeologous pairing in hybrids between related species are examples.

When more than two potential partners are available a situation of competition is produced, and pairing preferences (depending on the similarities between the chromosomes involved) can be studied. In these competitive pairing situations three degrees of resemblance between chromosomes have been studied up to date, namely, non-homology, homoeology and homology. The degree of resemblance between two chromosomes can be, however, greater than homology. In autotetraploid chimeras appearing in diploid individuals each chromosome is accompanied by one identical and two homologous but not necessarily identical chromosomes in the same cell. In these situations there could be a competition in pairing between identical and homologous chromosomes. Difficulties in distinguishing between identical and merely homologous chromosomes can be solved if differences in C-banding pattern between homologous chromosomes exist.

Competition in meiotic pairing between identical and homologous but not strictly identical chromosomes has been analysed in a tetraploid chimera of *Euchorthippus pulvinatus gallicus* (Acrididae, Orthoptera).

Material and Methods

The tetraploid cells analysed appeared spontaneously in the testes of one male among 100 individuals examined of a wild population of *E. pulvinatus gallicus* collected near Valdemoro, Madrid, Spain, in July 1979.

The testes were fixed in acetic alcohol 1:3, squashed and stained following the Giemsa C-banding technique described previously (Santos and Giraldez, 1978).

Results

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 and submetacentric, whereas the remaining five pairs are of medium to small size and telocentric or subtelocentric. All chromosomes except 1 and 2 can be distinguished at meiosis when C-banded. This species shows a polymorphism for the banding pattern of chromosomes 7 and 8 (Arana et al., 1980). The individual analysed was heterozygous for the banding pattern of chromosome 8, one of the members of this pair having an interstitial band near the centromere, the other not (Fig. 1). One of the tubules of the testes showed more than a hundred tetraploid late metaphase I and anaphase I cells at a short distance from one another, indicating that the polyploidy affected a complete cyst (128 cells).

Sixty four polyploid metaphase I cells could be analysed in detail, although the changes in chromosome morphology due to the formation of multivalents did not allow the distinction between chromosomes 1, 2 and 3 nor between chromosomes 4 and 5 in all cases.

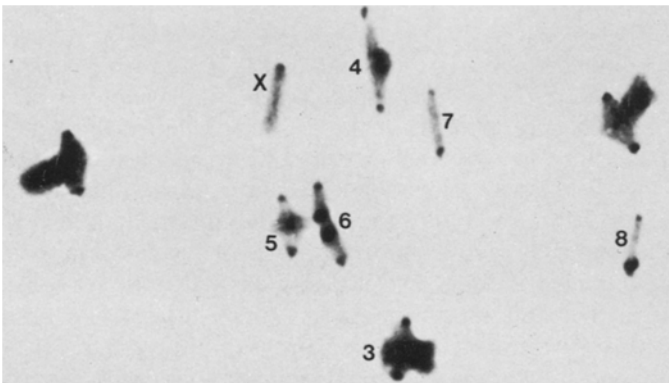


Fig. 1. Diploid metaphase I cell. The two chromosomes forming bivalent 8 show a different banding pattern

Table 1. The frequency of the different polyploid cells according to the number and type of chromosome association

Chromosome	Configurations observed per cell			
	IV	II	I	Frequency
1+2+3	3	-	-	9
	2	2	-	21
	1	4	-	31
	-	6	-	3
4+5	2	-	-	1
	1	2	-	18
	-	4	-	45
6	1	-	-	0
	-	2	-	64
7	1	-	-	0
	-	2	-	64
8	1	-	-	0
	-	2	-	61
	-	1	2	3

Table 1 shows the frequency distribution of number and type of chromosome association. Only chromosomes 1, 2, 3, 4 and 5 were able to form quadrivalents, the remaining medium and short chromosomes (6, 7 and 8) formed bivalents in all cases except in three cells in which two univalents formed by the smallest member of the complement were observed. The two X chromosomes were invariably univalent.

Two types of bivalent sets of chromosome 8 could be distinguished in respect to the banding pattern:

i) Two bivalents formed by identical chromosomes, i.e., one of the bivalents formed by two chromosomes with the interstitial heterochromatic band and the other by chromosomes without the band (Fig. 2a).

ii) Two bivalents formed by homologous but not-identical chromosomes, i.e., each bivalent contained one chromosome with the interstitial band and one without (Fig. 2b).

In these polyploid cells each chromosome has one identical and two homologous partners. Then, if pairing (and crossing over) between the four partners were at random one would expect the number of bivalents formed by homologous not-identical chromosomes to be double the number of bivalents formed by identical ones. Among the cells analysed only 4 showed a pair of bivalents 8 formed by homologous not-identical chromosomes, the remaining 60 cells having the two bivalents formed by identical partners (the three cells with two univalents had one bivalent formed by the two chromosomes with the interstitial band). A highly significant departure from random was thus observed, an excess of bivalents formed by identical chromosomes being produced.

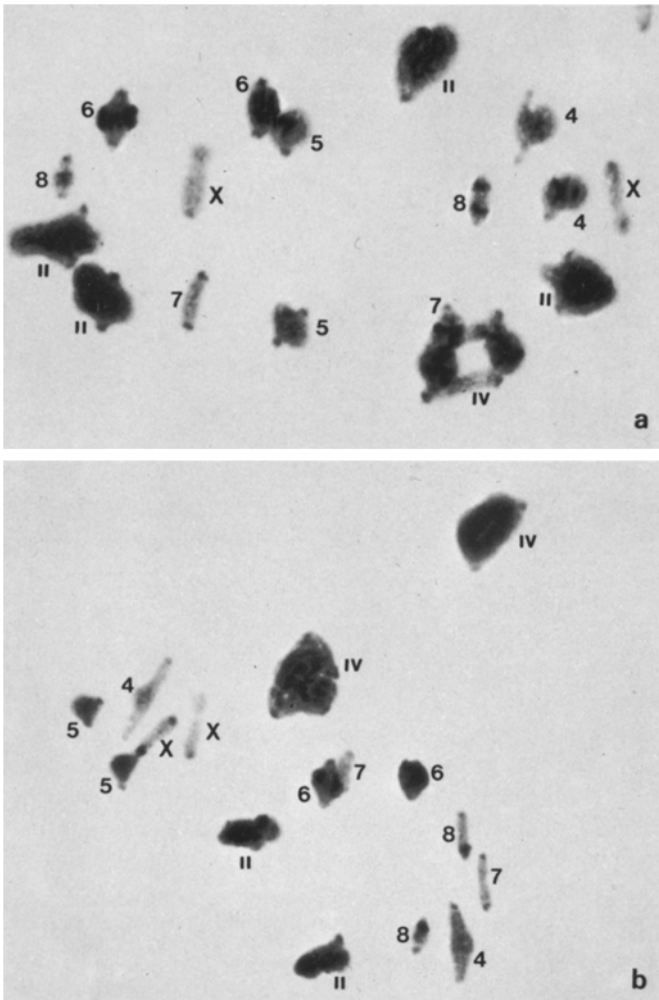


Fig. 2a and b. Tetraploid metaphase I cells. **a** The two bivalents 8 are formed after the pairing of identical chromosomes. **b** The two bivalents 8 are formed after the pairing of homologous, not strictly identical chromosomes

Discussion

John and Henderson (1962) made a comparative study of multivalent and chiasma formation in diplotene polyploid cells of several species of Acrididae and concluded that the number of quadrivalents formed by each chromosome of the complement is predominantly a function of the relative chromosome length and the diploid chiasma frequencies of the bivalent concerned; short chromosomes rarely formed quadrivalents and even appeared in some cases as univalents. Although in the present work the polyploid cells were at metaphase I, the results shown in table 1 agree with these findings, indicating that the possibili-

ty of chiasma loss as the origin of the bivalents and univalents formed by the shortest chromosomes of the complement can be excluded.

As pairing is necessary for chiasma formation and these short bivalents also in diploid cells have only one chiasma, the excess of bivalents 8 formed by identical chromosomes can be interpreted to be a reflection of pairing preferences.

There are some cases in which a restriction of pairing to molecularly identical copy chromosomes has been reported (Driscoll et al. 1967; Shaw and Wilkinson, 1978). In such cases polyploidy was induced in the last premeiotic mitosis. Then, the pairing preferences were accounted for in terms of the close proximity of the recently formed identical chromosomes when the pairing process was initiated. In the present case, extended premeiotic pairing might condition a preference for association of chromosomes originally close together, which would preclude regular formation of multivalents. These, however, have been found. The number and the location of the polyploid cells analysed indicate that a complete cyst (128 cells) was affected by the polyploidy. This strongly suggest that chromosome doubling occurred at least in the original cell from which the whole cyst was formed. Then, the cell in which polyploidy arose underwent at least seven premeiotic mitoses before the resulting cells entered meiosis.

These reasons make it improbable that high proximity between identical chromosomes is a major cause of the pairing preferences found.

According to Sybenga (1976), pairing preferences could be explained not only by specificity but by efficiency or activity differences between chromosomes. In the first case, the small differences between related chromosomes would be recognised during the pairing process. In the second case, for instance, one of the chromosome types would be more effective in pairing than the other, or start pairing earlier, and there will be a preference for the most active ones to find each other. The other two will follow, and may still be in time to complete pairing and crossing over.

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