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Genetic Regulation of Chromosome Behaviour in Interspecific Hybrids of *Drosophila*

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Summary. When crossing *Drosophila virilis* females with *D. littoralis* males, the elimination of *D. littoralis* sixth chromosome (microchromosomes) was often observed. The absence of the sixth chromosome of *D. littoralis* was revealed when studying F_1 hybrids, because of the mosaic expression of the recessive gene *"gl"*, located in the sixth chromosome of *D. virilis*. In the reciprocal cross the elimination of the sixth chromosome of *D. littoralis* did not take place (Sokolov 1959).

Genetic analysis enabled the authors to conclude that the observed maternal effect on mitosis is controlled by recessive genes located on the second and fourth chromosome of *D. virilis*. The genes located on the second chromosome, differ from those on the fourth chromosome both in temperature sensitivity and in the time and/or the mechanism controlling the mitotic behaviour of the chromosomes.

By means of back-crosses a new stock was established where all chromosomes except the sixth belonged to *D. virilis*. The sixth pair (microchromosomes) in this line was represented by one *D. virilis* and one *D. littoralis* chromosome. It was shown that the sixth chromosome of *D. littoralis* might be eliminated or undergo non-disjunction in *D. virilis* germline but the frequency of such atypical behaviour was very low (about 2 %). Low temperature treatment was not effective for increasing the frequency of either elimination or non-disjunction of the *D. littoralis* sixth chromosome in *D. virilis* germ-line.

There is now no doubt that mitotic and meiotic behaviour of chromosomes are under genetic control. Many cases have been described leading to either elimination or non-disjunction of chromosomes in both meiosis and mitosis (Bridges 1925; Davis 1969; Baker and Carpenter 1972). The number and variability of meiotic mutants known for *D. melanogaster* enable one to conclude that chromosome behaviour is a very complex character. Highly coordinated, ordered firing of many genes is necessary to produce normal behaviour of chromosomes in the processes of meiosis and mitosis. It is quite clear that the abnormal behaviour of chromosomes often observed in plant and animal distant hybrids (Subrahmanyam and Kasha 1973) is due to imbalance in the genetic systems of parental species controlling different aspects of chromosome behaviour in the F_1 hybrids. A similar cause may be involved in chromosome elimination of the definite genome in mammalian somatic hybrids (Westerveld et al. 1971; Minna and Coon 1974).

A very peculiar case of chromosome behaviour was studied by Sokolov (Sokolov 1959); when crossing *Drosophila virilis* females to *D. littoralis* males the elimination or non-disjunction of the *D. littoralis* sixth chromosome (microchromosome) in F_1 hybrids took place with quite a high frequency. In reciprocal crosses the behaviour of both sixth chromosomes was normal. Moreover, Sokolov demonstrated (using substitutional back-crosses) that the ability of *D. virilis* cytoplasm to induce atypical behaviour of *D. littoralis* sixth chromosome in the early stages of F_1 hybrid development was due not to some "unknown" cytoplasmic factor but to the activity of the *D. virilis* genome itself. Thus maternal effect in the mitotic behaviour of chromosomes was demonstrated.

This report describes a partial analysis of the genetic system controlling the maternal effect on mitosis, including our attempts to study the behaviour of *D. littoralis* sixth chromosome in the germ line of *D. virilis*.

Materials and Methods

The two species used in the study, *D. virilis* and *D. littoralis*, belong to the so-called "virilis group" of *Drosophila* (Patterson and Stone 1952). *D. littoralis*, found and described in the USSR by Sokolov (Sokolov 1948), differs from *D. virilis* by six inversions including inversion in the sixth chromosome (microchromosomes) - Fig.1. Both species have six pairs of rod-like chromosomes. The species may be crossed under laboratory conditions and give fertile progeny, but not a single hybrid has been found in natural populations. To perform genetic analysis we used *D. virilis* flies (line 160) carrying recessive gene-markers in all autosomes: "broken" (b)-chromosome II; "gapped" (gp) - chromosome III; "cardinal" (cd) -

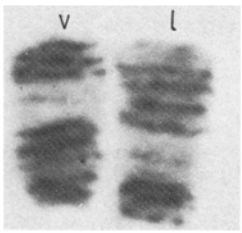

Fig. 1. *D. virilis* and *D. littoralis* sixth chromosome in hybrid condition (v and l letters indicate species index)

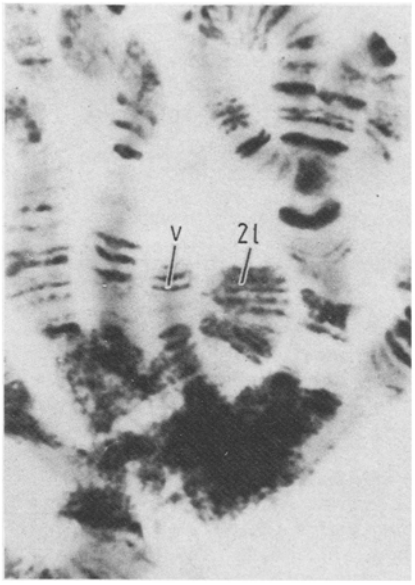

Fig. 2. Cytologically observed result of *D. littoralis* sixth chromosome non-disjunction

chromosome IV; "peach" (pe) - chromosome V: and "glossy" (gl) - chromosome VI. Since all autosomes of *D. virilis* were marked by recessive genes, it was possible to obtain lines with different combinations of *D. virilis* and *D. littoralis* chromosomes. In order to establish such stocks, we crossed mutant males (line 160) with wild type *D. littoralis* females (line 201). Hybrid males (F_1), heterozygous for all chromosomes, were back-crossed to *D. virilis* females (line 160). Among the FB_1 progeny we searched for males with the desired chromosome combinations and crossed them with *D. virilis* females (line 160) to establish the lines necessary for further analysis.

In this manner stocks were obtained where a definite chromosome was in the hybrid condition, i.e., was represented by one chromosome of *D. virilis* and another of *D. littoralis*, while all other chromosomes belonged to the *D. virilis* genome. Since we had no stock with hybrid X-chromosome, in order to obtain such females for genetic analysis we selected $\frac{\underline{b}\ \underline{gp}\ \underline{cd}\ \underline{pe}\ \underline{gl}}{\overline{b}\ \overline{gp}\ \overline{cd}\ \overline{pe}\ \overline{gl}}$ individuals from the FB_1 progeny.

Recently it has been shown by one of the authors that atypical behaviour of *D. littoralis* sixth chromosome (elimination and non-disjunction) takes place in F_1 hybrids (*virilis* × *littoralis*) in the process of synchronous mitotic divisions during cleavage (Sidorova 1974). Moreover, low temperature treatment applied at this stage increases the frequency of *D. littoralis* sixth chromosome elimination up to 100 %.

It is necessary to mention that the non-disjunction of *D. littoralis* sixth chromosome will give rise to cells with two *D. littoralis* sixth chromosomes and one sixth chromosome of *D. virilis*. Such cells (Fig. 2) are often observed when studying the salivary glands of F_1 hybrids (♀ *D. virilis* × ♂ *D. littoralis*). On the other hand, the absence of *D. littoralis* sixth chromosome in a cell, often observed in such mosaic glands, may be due to non-disjunction or elimination of this chromosome at early stages of hybrid embryo.

Since the recessive gene "glossy" (facettes structure) occurs in *D. virilis* sixth chromosome, the lack of *D. littoralis* sixth chromosome in F_1 hybrids was easily observed, not only in salivary gland nuclei but also in adults, through expression of the mutant phenotype. If *D. littoralis* sixth chromosome was eliminated at the first cleavage mitosis, F_1 individuals had both eyes glossy; in the cases where elimination (or non-disjunction) took place at later stages, spots of mutant tissue were observed on the surface of the eyes of F_1 progeny (mosaics). Thus the size of the eye region exhibiting mutant phenotype (gl) depends on the time of *D. littoralis* sixth chromosome elimination. In our experiments, all individuals exhibiting glossy phenotype among F_1 progeny were divided into the five following classes: 1 - both eyes - gl; II - an eye and a half - gl; III - one eye - gl; IV - half of an eye - gl; V - spots of gl tissue. The low temperature treatment (17° C) was applied when necessary to newly laid eggs for 24 hours. The eggs were obtained from mass matings of 5-10 females and 5-10 males per vial. To obtain information concerning *D. littoralis* sixth chromosome behaviour in *D. virilis* germ-line cells, we crossed individuals carrying hybrid sixth chromosome $\frac{gl}{+}$ (i.e. one sixth chromosome of such flies belonged to *D. virilis* and the other to *D. littoralis*) in the otherwise intact *D. virilis* genotype in the following combinations:

I ♀ *D. virilis* $\frac{gl}{+}$ × ♂ *D. virilis* $\frac{gl}{gl}$;

II ♀ *D. virilis* $\frac{gl}{gl}$ × ♂ *D. virilis* $\frac{gl}{+}$;

III ♀ *D. littoralis* × ♂ *D. virilis* $\frac{gl}{+}$.

Salivary gland chromosome analysis of the progeny from these crosses was performed. Salivary gland squash preparations were obtained as described elsewhere (Evgen'ev 1974).

Table 1. Elimination of *D. littoralis* sixth chromosome in reciprocals and back-crosses at 24° C and 17° C

Series of experiment		24° C			17° C		
		Number of flies		Elimination, % ± m	Number of flies		Elimination, % ± m
		total number of flies studied	number of flies exhibiting glossy phenotype		total number of flies studied	number of flies exhibiting glossy phenotype	
I	♀ *D. virilis* × ♂ *D. littoralis*	1729	728	42.3 ± 1.1	437	437	100
II	♀ *D. littoralis* × ♂ *D. virilis*	729	0	0	174	0	0
III	♀ F_1 (*virilis* × *littoralis*) × ♂ *D. littoralis*	767	1	0.1	205	8	3.9 ± 1.8

Table 2. Elimination of *D. littoralis* sixth chromosome different *D. virilis* chromosome being in hybrid condition (24° C)

Chromosome (in hybrid condition)	Number of flies		Elimination x ± m
	total number of flies studied	number of flies exhibiting glossy phenotype	
Control (♀ *D. virilis* $\frac{gl}{gl}$ × ♂ *D. littoralis*)	1719	728	42.3 ± 1.1
1	190	82	43.1 ± 3.6
2	2639	145	5.5 ± 0.4
3	2324	851	36.6 ± 1.0
4	1920	331	17.28± 0.9
5	1840	716	38.8 ± 1.1
6	595	228	38.3 ± 2.0
2 and 4	601	13	2.1 ± 0.6

Stock cultures were maintained at 24-25° C on standard medium supplemented with propionic acid to inhibit growth of mould.

Results and Discussion

As mentioned (see Materials and Methods), atypical behaviour of *D. littoralis* sixth chromosome in *D. virilis* cytoplasm may be registered by counting individuals exhibiting glossy phenotype among *D. virilis* × *D. littoralis* F_1 progeny. Table 1 summarizes the data on *D. littoralis* sixth chromosome elimination (atypical mitoses) in reciprocal crosses between *D. virilis* and *D. littoralis* (series I and II) and in the back cross (series III) at normal (24° C) and low (17° C) temperature. In this series of experiments we estimated the total number of flies exhibiting glossy phenotype among the progeny without discrimination into classes. It is evident (Table 1) that the elimination[1] of *D. littoralis* sixth chromosome took place only where *D. virilis* females were used in the crosses. Since the frequency of elimination was very low in FB_1 (series III), it might be concluded that the gene or genes of *D. virilis* providing "elimination" character (i.e. genes of mitoses) to *D. virilis* cytoplasm are practically recessive ones.

These data enabled us to perform experiments using the lines with different *D. virilis* chromosomes in "hybrid" condition (see Materials and Methods). In the combination where the *D. virilis* chromosome car-

[1] Here and elsewhere stated, "elimination" means the absence of *D. littoralis* sixth chromosome in the cells which may result from both elimination and non-disjunction of the chromosome mentioned.

Table 3. Elimination of *D. littoralis* sixth chromosome different *D. virilis* chromosome being in hybrid condition (17° C)

Chromosome (in hybrid condition)	Number of flies		Elimination, % ± m	Haplo-6 individuals % ± m
	total number of flies studied	number of flies exhibiting glossy phenotype		
Control series (♀ *D. virilis* $\frac{gl}{gl}$ × ♂ *D. littoralis* $\frac{+}{+}$)	437	437	100	100
1	101	101	100	100
2	335	335	100	100
3	522	521	99.9 ± 0.1	99.8
4	527	517	98.1 ± 0.1	53.1
5	573	572	99.8 ± 0.1	99.1
6	111	109	98.2 ± 0.1	90.1
2 and 4	73	28	38.3	4.1

rying recessive "genes of mitoses" is represented by hybrid one, a decrease in elimination frequency (expressed as appearance of gl-mosaics) should be expected. Table 2 presents the data on the frequency of *D. littoralis* sixth chromosome elimination in series where *D. virilis* females carrying different chromosomes in hybrid condition were crossed to *D. littoralis* males. The frequency of individuals exhibiting gl phenotype among ♀ *D. virilis* $\frac{gl}{gl}$ × ♂ *D. littoralis* $\frac{+}{+}$ F_1 progeny was used as control one. The results in Table 2 clearly indicate that the hybrid condition of the second and fourth *D. virilis* chromosomes leads to a striking decrease in elimination frequency (5.5 and 17.2 %, respectively, against 42.3 % in the control series). In the series (last line) where both pertinent chromosomes in females were in the hybrid condition, the frequency of individuals lacking *D. littoralis* sixth chromosome, and thus exhibiting gl phenotype, among the F_1 progeny drops to 2.1 %.

The data of Table 2 allow the conclusion that major recessive genes controlling *D. littoralis* sixth chromosome atypical behaviour are located in the *D. virilis* second and fourth chromosomes.

When analysing the data of experimental series where low temperature treatment was applied at early stages of embryo development (see Materials and Methods), it becomes evident that in all crosses of the series except the last one, where both pertinent chromosomes were in hybrid condition, the frequency of individuals exhibiting mutant phenotype (gl) among F_1 offspring reaches 100 % (Table 3). However, the pattern (time) of *D. littoralis* sixth chromosome elimination is not by any means the same. In most cross combinations the individuals exhibiting mutant phenotype (gl) are represented mainly by haplo-6 flies, i.e. flies with both eyes glossy. The cytological analysis of salivary gland chromosomes of the offspring of the series proved that such haplo-6 flies really possess only one *D. virilis* sixth chromosome in all nuclei of a gland. However, in the combination where the fourth chromosome of the females was in hybrid condition the percentage of haplo-6 flies in the total number of offspring exhibiting glossy phenotype reached only 53 %.

Table 4 includes data on patterns of mosaics (different classes, see Materials and Methods) obtained in the crosses involving females carrying different chromosomes in the hybrid condition at normal temperature (24° C). The chi-square analysis showed that the patterns of mosaic distribution observed in all combinations except one were very similar. The only exception represented the progeny of females carrying hybrid fourth chromosome (i.e. only in the case where *D. littoralis* sixth chromosome elimination was determined by a gene or genes located on the second chromosome of *D. virilis*). In this cross combination point mosaics turned out to be the prevailing type (class V), see Table 4, Fig. 3.

From the data of Tables 3 and 4, it is plausible to conclude that "genes of mitoses" located on the second chromosome differ from those on the fourth chromo-

Table 4. Patterns of mosaics in the progeny of females carrying different chromosomes in hybrid condition

Chromosome in hybrid condition	Total number of mosaics	Classes of mosaics				
		1	2	3	4	5
1	82	5.0 ± 2.4	2.5 ± 1.7	19.5 ± 4.4	12.2 ± 3.6	62.2 ± 4.8
2	145	1.4 ± 0.8	1.4 ± 0.8	17.9 ± 3.1	5.5 ± 1.8	75.6 ± 3.5
3	743	2.1 ± 0.5	1.2 ± 0.3	14.6 ± 1.3	9.8 ± 1.1	73.3 ± 1.5
4	331	1.2 ± 0.6	0	3.3 ± 0.9	3.3 ± 0.9	92.2 ± 1.4
5	715	2.2 ± 0.5	0.3 ± 0.2	7.5 ± 0.9	9.3 ± 1.0	80.5 ± 1.4
6	202	2.9 ± 1.1	0.5 ± 0.4	10.9 ± 2.2	8.9 ± 2.0	76.7 ± 2.9
Control series (♀ *D. virilis* $\frac{gl}{gl}$ × ♂ *D. littoralis* $\frac{+}{+}$)	815	2.5 ± 0.5	1.7 ± 0.4	13.1 ± 1.2	10.5 ± 1.0	72.2 ± 2.2

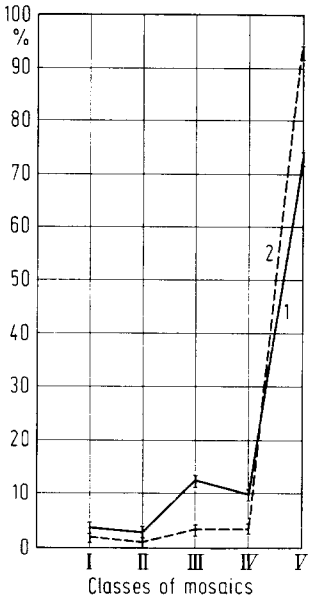

Fig. 3. The distribution of mosaics by classes in control series (I) (F_1 *virilis* × *littoralis*) and in the series where parental females carried hybrid chromosome 4 (2)

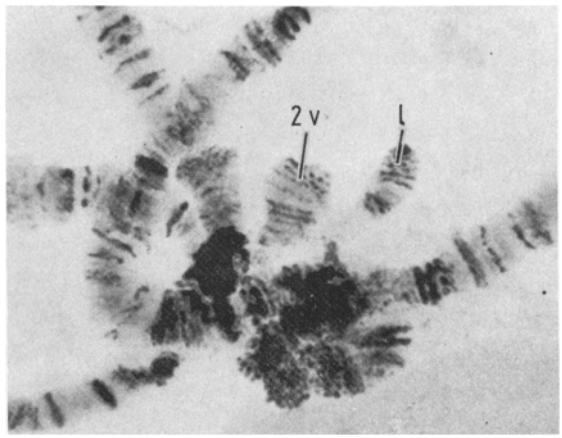

Fig. 4. Cytologically observed results of sixth chromosomes non-disjunction in germ-line cells of *D. virilis*

some both in temperature sensitivity and in the time (or mechanism) controlling mitotic behaviour of the chromosome.

Postulating the existence of the genes, products of which take part in the regulation of mitotic behaviour of chromosomes during cleavage, it is interesting to investigate whether these genes act in the germ-line cells.

In order to answer this question, a special line was established (see Materials and Methods) where all chromosomes but the sixth one belonged to *D. virilis*. The results of experiments using this stock are presented in Table 5. As cytological analysis of salivary gland chromosomes showed in the first two crosses (I, II) involving this line, exceptions were individuals carrying two chromosomes of *D. virilis* and one chromosome of *D. littoralis* (2vl1) - Fig. 4 - and haplo-6 individuals (Iv). Haplo-6 individuals (Iv) may result from the elimination of *D. littoralis* sixth chromosome either in germ cells of *D. virilis* $\frac{gl}{+}$ flies or in the process of cleavage mitoses of the F_1 embryo. On the other hand, the occurrence of 2v Il flies among the

Table 5. Cytological analysis of salivary gland chromosomes of progeny from crosses I-IV

Crosses	Chromosome combinations encountered in the progeny of crosses studied						
	2v	21	1v1l	1v	1l	2v1l	2l1v
I ♀ *D. virilis* $\frac{gl}{+}$ × ♂ *D. virilis* $\frac{gl}{gl}$	107	-	54	1	-	1	-
II ♀ *D. virilis* $\frac{gl}{gl}$ × ♂ *D. virilis* $\frac{gl}{+}$	799	-	586	40	-	12	-
III ♀ *D. littoralis* $\frac{+}{+}$ × ♂ *D. virilis* $\frac{gl}{+}$	-	153	182	-	5	-	1
IV ♀ *D. virilis* $\frac{gl}{gl}$ × ♂ F_1(♀ *D. littoralis* $\frac{+}{+}$ × ♂ *D. virilis* $\frac{gl}{gl}$)	452	-	263	19	-	-	-

offspring of these crosses may be due only to the non-disjunction of sixth chromosomes in germ-line cells of *D. virilis* $\frac{gl}{+}$ individuals.

In the progeny of cross III, where *D. littoralis* females were used and thus no elimination or non-disjunction of sixth chromosome in the process of cleavage could occur, both exceptions, namely 21 Iv and II, may appear only as a result of *D. littoralis* sixth chromosome atypical behaviour in germ-line cells of *D. virilis* $\frac{gl}{+}$ males. As can be seen from Table 5, in all three crosses we observed exceptional individuals, which may be only of germ-line origin.

The sixth chromosomes of *D. virilis* and *D. littoralis* differentiated by species specific inversion never conjugate in salivary gland nuclei and may behave in the same manner in meiosis (Evgen'ev 1971a, 1971b). Thus the occurrence of exceptions in these crosses may be due to the unconjugated state of these chromosomes and not to the action of "genes of mitoses" located in *D. virilis* genome. To check this possibility we studied cytologically the progeny of ♂ F_1 (♀ *D. littoralis* × ♂ *D. virilis*) to ♀ *D. virilis* $\frac{gl}{gl}$ (IV series). In the latter cross, where both sixth chromosomes also never conjugate, no exceptions of clear cut germ-line origin were registered.

Since the frequency of germ-line origin exceptions was very low in all three series of experiments (I, II, III), recently we attempted to increase the frequency of *D. littoralis* sixth chromosome elimination in *D. virilis* females carrying *D. littoralis* sixth chromosome in the heterozygous condition using low-temperature treatment. In these experiments (Evgen'ev and Sidorova, in press) we applied low-temperature treatment (17°C) either to stages (till pupae) where only oogonial divisions take place (Whittinghill and Davis 1961) or to mature oocytes at the stage of meiotic prophase (Tokunaga 1970a, b). In both series we failed to increase significantly the frequency of *D. littoralis* sixth chromosome elimination or non-disjunction in germ cells of *D. virilis* $\frac{gl}{+}$ females. Thus, on the one hand, we observe a marked increase of *D. littoralis* sixth chromosome elimination frequency (up to 100 %) after low temperature applied at the early stages of embryogenesis of F_1 (*virilis* × *littoralis*) progeny while, on the other hand, low temperature treatment was not an effective tool to increase *D. littoralis* sixth chromosome elimination in germ-line cells of *D. virilis*.

To explain these contradictory results we propose that replication asynchrony may be involved in the process of sixth chromosome atypical behaviour studied.

In investigations of mammalian somatic hybrids it has been shown that chromosomes of one definite par-

ental species are often continuously eliminated from hybrid cells. Moreover, late replicating chromosomes are usually subject to elimination (Marshall and Graves 1972; Johnson and Rao 1972).

Studying replicative behaviour of sixth chromosomes in *virilis* × *littoralis* F_1 hybrids in salivary gland nuclei, we showed that the *D. littoralis* sixth chromosome is late replicating in comparison with the *D. virilis* homeologue (Evgen'ev and Gubenko, in press). If these chromosomes preserve such a replicative pattern in the process of cleavage (where *D. littoralis* sixth chromosome elimination and non-disjunction take place), this asynchrony may be the main cause of sixth chromosome atypical mitotic behaviour. Low temperature treatment applied at this stage may increase asynchrony leading to a parallel increase in elimination frequency. On the other hand, replicative asynchrony playing an important role at very fast synchronous mitotic divisions in the process of cleavage may be not so essential at long lasting germ-line mitotic and meiotic divisions.

Current investigations will check the hypothesis and show whether "genes of mitoses" located by us in the second and fourth chromosomes of *D. virilis* influence the pattern of sixth chromosome replication.

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