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Non-mendelian female sterility in *Drosophila melanogaster*: variations of chromosomal contamination when caused by chromosomes of various inducer efficiencies

By ALAIN PÉLISSON

Laboratoire de Génétique, Université de Clermont-Ferrand II, B.P. 45, 63170 Aubière, France

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SUMMARY

A quite specific kind of sterile F_1 female, called *SF* females, arises only when females of strains denoted reactive are crossed with males of the other class (inducer). It was previously shown that this sterility results from a nucleocytoplasmic interaction between the maternal reactive cytoplasm and a factor, called *I*, which may be born by any one of the paternal chromosomes. In *SF* females, but not in their brothers, a varying proportion of reactive chromosomes are able to acquire irreversibly the *I* factor, independently of any classical genetic recombination with the inducer chromosome(s). During this process, called chromosomal contamination, the contaminating chromosome(s) do not undergo any apparent change. The present paper deals with the efficiency of both original inducer and contaminated chromosomes to yield a more or less intense *SF* sterility. The *Otanu* inducer laboratory strain contains at least two types of *X* chromosomes (called *strong* and *weak*) which differ genetically with respect to their inducer efficiency. Reactive third chromosomes were contaminated by these *strong* or *weak X* chromosomes and their inducer efficiencies compared. Results show that they are on average *stronger* when they have been contaminated by *strong X* chromosomes than when contaminated by *weak* ones. Such a correlation favours the hypothesis that chromosomal contamination is due to the insertion of some genetic element(s) into reactive chromosomes.

1. INTRODUCTION

Systematic crosses between various strains of *Drosophila melanogaster* lead in some cases to F_1 females that exhibit a more or less reduced fertility. On the basis of this fertility, all strains fall into three classes: reactive, inducer and neutral; sterile F_1 females (*SF* ♀) arise only when reactive females are crossed with inducer males; the reciprocal cross and the seven other possible crosses yield normally fertile daughters (Picard *et al.* 1972). A survey of 171 strains has indicated that the inducer condition is apparently the only one to be found in the wild, whereas

the three classes of strains have been found among the *D. melanogaster* stocks in several European and American laboratories (Picard *et al.* 1976).

The following features characterize this quite specific kind of sterility (Picard *et al.* 1977): (1) it results from the failure of some eggs to complete embryonic development; (2) all the eggs that hatch successfully give flies which do not exhibit any conspicuous aberration; (3) the hatchability of eggs laid by *SF* females does not depend on the genetic origin of their mates; (4) hatchability increases regularly when *SF* females age, often reaching normal values before the end of their life.

Even when assayed on a sample of the first-laid eggs, the fertility of *SF* females varies within broad limits, according to the choice of both reactive and inducer parental strains (Bucheton *et al.* 1976). Among reactive strains there is considerable variation of efficiency in producing *SF* females with a more or less reduced fertility. A complete range of reactive efficiencies can be found, from the *weakest* reactive strains which give *SF* females showing almost normal fertility, to the *strongest* which, with the same mates, breed sterile or very poorly fertile *SF* females. Similar variations are observed among inducer strains, with respect to their inducer efficiency.

The efficiency of a reactive strain, also called its reactivity, is a quantitative trait with a complex hereditary transmission (Bucheton, 1973; Bucheton & Picard, 1975, 1978). It is mainly transmitted by the maternal cytoplasm but is subject, in the long run, to chromosomal control.

The sterility of an *SF* female is the outcome of an interaction between this reactive cytoplasm and a paternal chromosome-linked factor, called the *I* factor. When reactive females are crossed with heterozygous males bearing chromosomes of both inducer and reactive origins, *SF* sterility is only observed among daughters which have received at least one chromosome of inducer origin. A chromosome able to induce the *SF* sterility is considered as carrying the *I* factor and is called an inducer chromosome (i^+). Any one of the three major chromosomes (Picard, 1976) and even the small fourth (Pélisson, 1977; Picard & Pélisson, 1979), may be an i^+ chromosome. The other chromosomes of inducer origin which are not able to give rise to *SF* females when introduced by a paternal gamete into a reactive oocyte are called non-inducer chromosomes (i^o). Picard (1976) has reported that these i^o chromosomes may co-exist in inducer strains with homologous i^+ chromosomes. Kearsey *et al.* (1977), in a study which dealt probably with the same kind of sterility, presented similar observations. The characterization of these non-inducer chromosomes originating from inducer strains is reported elsewhere (Picard & Pélisson, 1979). Results reported in the present paper provide evidence for a polymorphism between the i^+ chromosomes themselves: within the same inducer strain, at least two types of i^+X chromosomes which differ in their inducer efficiencies have been found.

The mendelian behaviour of the *I* factor is maintained only through male meiosis. In females heterozygous for chromosomes of both origins, either a chromosome of reactive origin (*r* chromosome) or an i° chromosome (Picard & Pélisson, 1979) may acquire the *I* factor, independently of any classical genetic

recombination with an i^+ chromosome. This phenomenon, called chromosomal contamination, takes place even between heterologous chromosomes. In some circumstances it may reach a frequency of 100% (Picard, 1976). Picard (1979) recently reported the two following observations: (1) contamination does not involve any apparent change in the contaminating i^+ chromosome(s); (2) chromosomal contamination involves an irreversible change and a contaminated chromosome retains its i^+ character when transmitted together with r chromosomes through several generations of males.

With the available data, two main hypotheses about chromosomal contamination may be suggested: it may result either from the insertion of some genetic element(s) into r chromosomes or from some regulation mechanism derepressing genes carried by all chromosomes but active only on i^+ (Picard, 1979). In order to choose between these two hypotheses, it is necessary to know whether there is any correlation between the characteristics of a contaminating chromosome and those of the corresponding contaminated ones. The experimental data reported in the present paper show that the inducer efficiency of a contaminated chromosome depends on the efficiency of the one that contaminated it, and thus favour the insertion hypothesis.

2. MATERIALS AND METHODS

Genetic symbols are those used by Lindsley & Grell (1968). All flies were bred at 20 °C in vials containing the axenic food described by David (1959).

(i) *Strains of* Drosophila melanogaster

Otanu is a wild-type laboratory inducer strain. It was supplied in 1973 by the Zoology Laboratory of Paris VI University (France). *M-5* is an inducer stock coming from the Department of Genetics of Birmingham University (stock no. 25 in *Dros. Inf. Serv.* 46). The following reactive strains derive by selection from our own original reactive strains, following the method described by Picard *et al.* (1972): LH_{23} comes from the *LH* strain (genotype *M-5 M-5*; *Cy/Pm*; *Sb/H*). All its chromosomes are dominant-marked, but only *M-5* and *Cy* are crossing-over inhibitors. seF_8 and e_{st28} were obtained by selection from original strains homozygous for the *sepia* and *ebony* mutations.

(ii) *Procedures used for extracting* X *chromosomes*

Single X chromosomes were extracted from *Otanu* males and made homozygous with the standard *M-5* technique, using the inducer *M-5* strain. Of 31 separate extractions, 9 were i^o X chromosomes the study of which will be reported elsewhere; only the 22 clones derived from an i^+ X chromosome were used in the following experiments.

(iii) *Fertility measurement of individual females*

Females were allowed to be fertilized by their brothers since it had been previously shown that the hatching percentage of the eggs laid by *SF* females does not depend on the choice of their mates (Picard *et al.* 1977). Eggs of individual

2-day-old females were collected during about 3–4 days; 30–48 h later the percentage of hatched eggs was determined on a sample of about 40 eggs. The effect of ageing on the female fertility was studied similarly by collecting successive layings.

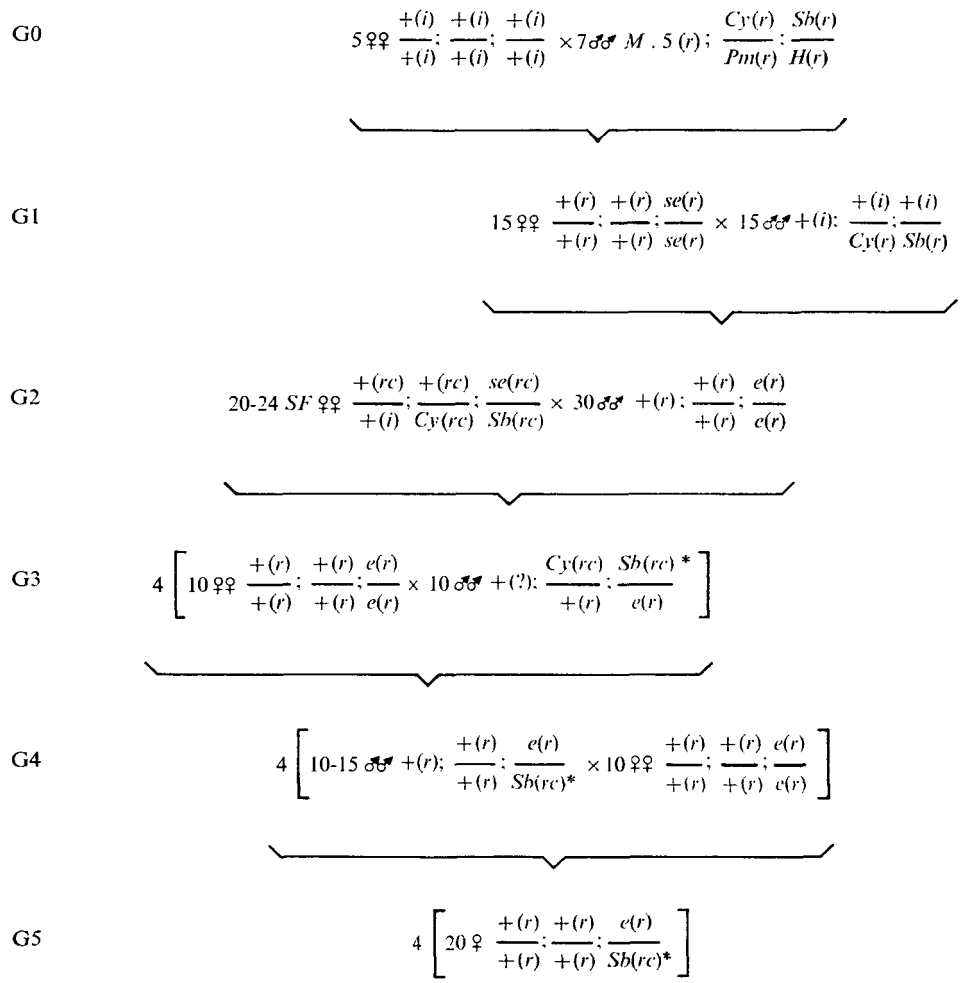

Fig. 1. Mating scheme for one of the *Otanu X* clones assayed in experiments *A* and *B*. G0–G5 represent successive generations in the mating scheme. (*i*) denotes a chromosome coming from a sample of five G0 females taken in this clone at the generation no. 1, 4, 16, 17 (experiments *A*) or 9 (experiments *B*). In experiments *A*, only the two first matings were made and the fertility of 5–10 individual G2 females measured. (*r*) denotes a chromosome coming from one of the following reactive strains: LH_{23} (G0 males), seF_8 (G1 females) and e_{st28} (G2 males, G3 and G4 females). (*rc*) denotes a reactive chromosome which may have been contaminated in G2 females. * The *Sb* chromosome is possibly a recombinant one. Chromosomes *4* are not figured. Using G0 females of the reactive e_{st28} strain instead of an *Otanu X* clone, similar matings were carried out as control experiments.

Table 1. *Fertility of the G2 females bred from the* Otanu X *clones* (*Experiments* A)

Clone no.	Generation no. sampled: 1 p ± S.E. (× 100)	4 p ± S.E. (× 100)	16 p ± S.E. (× 100)	17 p ± S.E. (× 100)	4 generations pooled, $\bar{p}$ ± S.E. (× 100)	
27	0 ± 1	0·2 ± 0·2	0·2 ± 0·2	0·4 ± 0·4	0·2 ± 0·1	Group Ia
18	3 ± 1	0·8 ± 0·9	6 ± 5	4 ± 2	4 ± 2	
29	0·9 ± 0·6	3 ± 1	9 ± 3	7 ± 3	5 ± 1	
20	2 ± 1	6 ± 2	4 ± 2	17 ± 8	7 ± 2	
38	19 ± 9	0·7 ± 0·3	—	—	8 ± 4	
30	13 ± 7	13 ± 3	6 ± 2	23 ± 7	14 ± 2	Group Ib
40	22 ± 5	6 ± 2	16 ± 11	18 ± 11	16 ± 4	
13	28 ± 3	14 ± 5	26 ± 7	6 ± 1	18 ± 3	
69	26 ± 7	30 ± 5	37 ± 6	31 ± 4	31 ± 3	Group II
74	33 ± 4	33 ± 3	35 ± 4	21 ± 4	31 ± 2	
84	43 ± 6	20 ± 6	33 ± 3	29 ± 5	32 ± 3	
5	35 ± 4	40 ± 3	24 ± 3	28 ± 10	33 ± 3	
12	39 ± 3	26 ± 3	33 ± 6	—	33 ± 3	
53	40 ± 5	36 ± 5	19 ± 3	36 ± 7	33 ± 2	
8	41 ± 6	30 ± 3	35 ± 7	23 ± 5	34 ± 3	
66	41 ± 5	28 ± 7	33 ± 11	—	34 ± 5	
11	38 ± 3	29 ± 6	37 ± 5	42 ± 6	35 ± 2	
41	41 ± 9	36 ± 2	31 ± 4	35 ± 6	35 ± 2	
31	46 ± 7	40 ± 4	15 ± 5	46 ± 8	36 ± 3	
45	45 ± 4	23 ± 6	23 ± 5	43 ± 6	37 ± 3	
63	55 ± 5	43 ± 6	35 ± 6	32 ± 5	43 ± 3	
49	52 ± 7	36 ± 12	25 ± 6	53 ± 6	45 ± 4	
Control	83 ± 2	70 ± 4	80 ± 2	81 ± 2	80 ± 1	

p and $\bar{p}$ are the over-all hatching frequencies of sets of respectively 5–10 and 20–40 individual G2 females. Their standard errors (S.E.) were calculated from formula 9.8.4, p. 241, in Snedecor & Cochran (1967).

3. RESULTS AND DISCUSSION

(i) *Inducer efficiency of the* i⁺X *chromosomes extracted from the* Otanu *strain*

Variations of inducer efficiency among inducer strains have already been reported (Bucheton *et al.* 1976). It must be noted that, in this case, the whole paternal genome of the *SF* females was of inducer origin. In the present paper the inducer efficiency of single *Otanu X* chromosomes was compared by means of *SF* females whose paternal genome did not contain any other major chromosome of inducer origin except this *X* chromosome (Fig. 1, experiments *A*).

The results, given in Table 1, provide evidence for the two following points:

(1) A significant reduction in the average female fertility is observed which, in each of the 4 successive tests, depends on the choice of the clone. Obviously, the differences observed between the various generations of the same clone are in some cases statistically significant. However, these variations appear to be random

and do not reflect any tendency of the clones to undergo systematic changes. They must be due to random variations in the average reactivity of the mothers of the G2 females. It appears therefore legitimate to pool for each clone all the measurements of the 4 experiments. The pooled results clearly show the existence of two well-distinguishable groups of clones (I and II). With the available data it does not seem possible to discuss further the continuous variation observed within both groups. Let us, however, note that in the next experiments (expt. *B*), as a precaution, group I will be divided into two subgroups (Ia and Ib); group Ib will be shown to give results similar to those of group Ia but clearly different from group II.

(2) The higher average fertility in group II could be the result of heterogeneous individual hatchabilities, some of the females being fertile whereas the others exhibit the same sterility as those of group I. That this is not the case is indicated by the rather small standard errors observed. This homogeneity suggests that *Otanu* fourth chromosomes are not responsible for the observed difference: statistically they are present in only half of the G2 females and, if active, would therefore introduce a bimodality within the corresponding distributions.

These genetical variations in the ability of *X* chromosomes to reduce the female fertility do not appear to be due to dominant sterility genes but are more probably explained by variations in inducer efficiency. This hypothesis is supported by the tendency for the fertility differences between the two groups to disappear at the same time as the *SF* sterility when the G2 females age (results not shown). However, these differences of inducer efficiency might be due to modifier genes of the *SF* sterility rather than to the *I* factor itself. The results of experiments *B* help to clarify this point.

(ii) *Inducer efficiency of the chromosomes contaminated by* Otanu X *chromosomes of different inducer efficiencies*

Eleven experiments *B* were carried out with the mating scheme of Fig. 1. In this sample of 11 *Otanu X* clones, the different groups Ia, Ib and II were respectively represented by clones 18–29–20, 30–40 and 74–53–8–66–31–49. The purpose was to compare the inducer efficiencies of third chromosomes which had been contaminated in G2 females by different *X* chromosomes. Among the potentially contaminated third chromosomes only those carrying the *Sb* marker were tested for their inducer efficiency.

For each experiment, G2 females were aged until the hatchability of their eggs reached 20–40 %, and four successive samples of ten G3 males carrying *Cy* and *Sb* chromosomes were then taken from their surviving progeny. Because of the differences of fertility, all experiments, at this generation, could not be carried out simultaneously: in group II experiments the mothers of G3 males were 4–9 days old; they were respectively 9–14 and 12–17 days old in group Ib and group Ia experiments. The matings of G3 and G4 were designed to produce females carrying the possibly contaminated *Sb* (*rc*) chromosomes in an entirely reactive genetic background, such that none of the other chromosomes had been in the same

nucleus as an *i* chromosome. These G5 females were then allowed to mate with their brothers to measure their fertility.

The results presented in Fig. 2 need discussion on the four following points:

(1) In the three groups of experiments there are many females with a hatchability lower than 75 %. It was found that the average fertility of any sample of such females increases with age. Therefore it may be inferred that most of them are actually *SF* females, whose sterility was induced by a *Sb* chromosome that had been contaminated in G2 females.

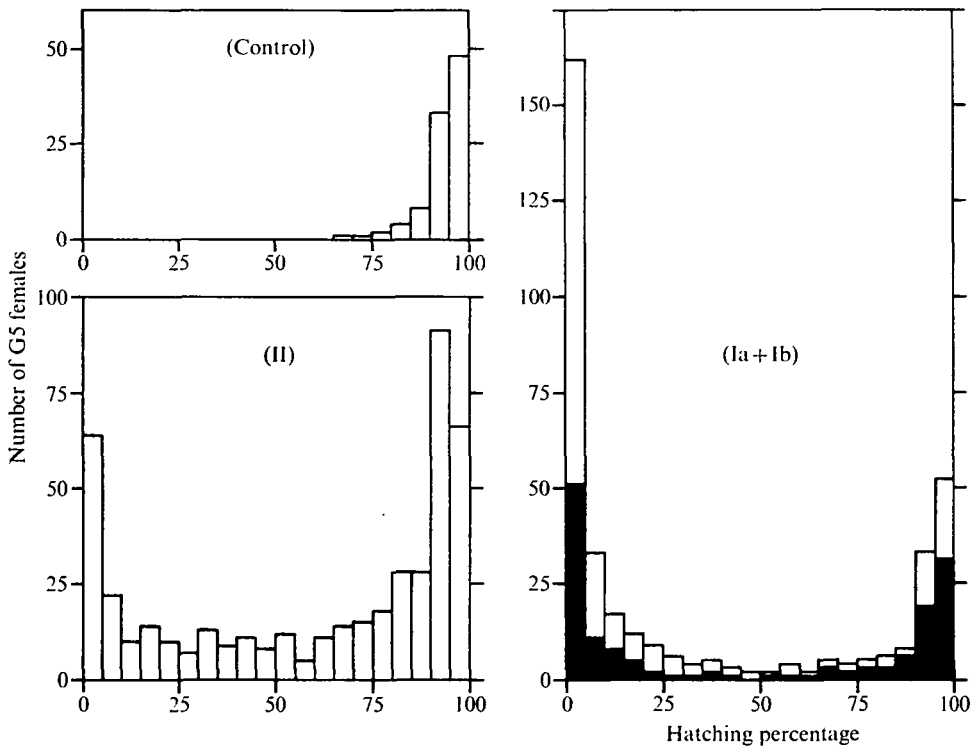

Fig. 2. Histograms showing the fertility distribution of the individual G5 females bred in the 11 experiments *B* and the control experiment (see text and Fig. 1). In histogram II are pooled the females bred in the six group II experiments. The three group Ia experiments (figured in white) and the two group Ib experiments (figured in black) are gathered in the same histogram (Ia+Ib). The hatching percentages were determined on the sum of two successive layings of about 40 eggs each.

(2) Considering the females with a hatchability higher than 75 % two cases are observed. In groups Ia and Ib experiments the great majority of them are clearly as fertile as the control females. On the contrary, in addition to normally fertile females, histogram II contains a noticeable proportion of females with a somewhat reduced fertility. The results do not allow determination of whether this slight sterility was actually induced by *Sb* chromosomes with a very *weak* inducer efficiency. In any case, although being noteworthy, the possibility that genetic

heterogeneity, including at least two classes, exists among the contaminated chromosomes of group II experiments is of secondary importance for the purpose of the present paper.

Table 2. *Average fertility of the G5 females which have a lower hatchability than 75 %*

Clone	Successive series a		b		c		d	
no.	*N*	%	*N*	%	*N*	%	*N*	%
18 (Ia)	18	6·3	15	2·6	19	9·3	7	23·2
29 (Ia)	20	16·8	12	4·8	16	15·9	13	9·1
20 (Ia)	20	1·1	16	5·1	6	24·2	18	6·6
30 (Ib)	20	6·8	0	—	19	11·6	14	37·9
40 (Ib)	8	0·6	0	—	19	6·8	11	2·3
Total	86	7·7	43	4·2	79	11·3	63	16·3
53 (II)	8	45·2	0	—	9	32·5	2	0
8 (II)	20	23·3	10	29·1	10	59·1	15	43·4
74 (II)	0	—	0	—	19	2·7	4	53·6
31 (II)	19	19·3	12	43·3	20	13·1	6	37·9
66 (II)	2	52·9	11	11·5	8	67·1	10	18·2
49 (II)	16	35·3	6	29·3	16	3·7	4	53·0
Total	65	27·8	39	29·2	82	20·9	41	36·2

a, b, c and d are four series of G5 females corresponding respectively to the four successive samples of G3 males (see text and Fig. 1). *N*: no. of females with a lower hatchability than 75 %. %: hatching percentage of the total no. of eggs laid by these females. A statistical comparison of groups I and II was performed after angular transformation of the 39 hatching percentages (Snedecor & Cochran, 1967).

(3) Concerning the sterile females, the histograms of groups Ia and Ib, divided into seven classes (0–5-10–15–25–40–60–75 %) do not show any significant difference ($\chi^2 = 4{\cdot}4$; $0{\cdot}5 < P < 0{\cdot}7$). On the other hand, the average fertility of these females is obviously higher in group II than in group I. This fertility is presented in Table 2 for all experimental series. In spite of rather large variations between the four series of each experiment, the mean of the 21 series of group II is significantly higher than that of the 18 series of group I ($t = 3{\cdot}93$; $P < 0{\cdot}001$). Moreover, it must be pointed out that the choice of the 75 % limit certainly underestimates the difference between the two groups.

(4) As a first hypothesis, it could be assumed that this difference is related to the age of the females in which contamination occurred. In group I the G2 females were older than in group II and there might perhaps be an increase with age of the efficiency of the contaminated chromosomes. This interpretation is ruled out by a comparison of the successive series of the same experiment. In particular, in the set of experiments II (see Table 2) there is no tendency for the mean hatching percentage to decrease from one series to the next. One may conclude, therefore, that the inducer efficiency differences observed between the contaminated chromosomes are directly related to those of the contaminating elements.

Finally, it must be pointed out that such a correlation between the inducer efficiencies of the contaminating and contaminated chromosomes clearly show that the observed difference between *X* chromosomes of groups I and II actually concerns the *I* factor; the *SF* sterility modifier gene(s) previously assumed are indeed not expected to be involved in the contamination process. Conversely, if it is a real variation of inducer efficiency, the difference between subgroups Ia and Ib can be explained by such modifier gene(s).

4. CONCLUSION

Bucheton *et al.* (1976) have reported quantitative variations in the efficiency of inducer strains to induce more or less intense *SF* sterility. Similar variations were assumed to exist between second chromosomes of recently caught wild strains (Pélisson, 1975; Picard & Pélisson, 1979), and also between third chromosomes of a laboratory population (Kearsey *et al.* 1977). The present results confirm these previous findings: with respect to their inducer efficiency, the *Otanu* laboratory strain contains at least two genetically different types of i^+ *X* chromosomes. This difference seems to be transmitted through the chromosomal contamination process: third chromosomes contaminated by the *weakest* type of *X* chromosomes show, on average, correspondingly *weaker* inducer efficiencies than those contaminated by the *stronger* type.

These results do not provide a clear understanding of the nature of the *I* factor; nevertheless, they may help to choose between the two following hypotheses which have been suggested to account for chromosomal contamination:

(1) In the first hypothesis it is assumed that '*i* genes' are present on all chromosomes; but these genes are active only on i^+ chromosomes. Chromosomal contamination would involve derepression of the corresponding genes on *r* chromosomes. The observed correlation between the characteristics of the contaminating and contaminated chromosomes seems to make rather unlikely such a hypothesis.

(2) On the contrary, the second hypothesis seems to account better for such results: it assumes the insertion in contaminated chromosomes of some DNA sequence(s) originating from the contaminating chromosomes. There is evidence for such transposable elements in *Zea mays* (for review, see Fincham & Sastry, 1974) and in *Drosophila melanogaster* (Green, 1969; Ising & Ramel, 1976). The similarities in genetic behaviour between these eucaryotic transposable elements and the procaryotic DNA insertion sequences (IS) were recently pointed out by Nevers & Saedler (1977). Other investigations are presently in progress in our laboratory to test this insertion hypothesis.

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