

The genetics of the Xasta mutant of *Drosophila melanogaster*

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1. INTRODUCTION

The Xasta (*Xa*) variant of *Drosophila melanogaster* was the first X-ray induced mutation to be isolated in the U.S.S.R. (Serebrovsky & Dubinin, 1930). Phenotypically it is a dominant wing mutation. The heterozygote has a wing with a deeply notched edge. The extent to which the edge is cut varies between individuals and from one genetic background to another, but is always discernible from the wild type. The homozygote, which rarely if ever survives, is stated by Bridges & Brehme (1944) to have wings resembling the vestigial mutant.

Genetic and salivary gland analysis by Sturtevant (1934) and Morgan, Bridges & Schultz (1936) showed that the *Xa* condition could be attributed to a translocation between the right arms of chromosomes II and III superimposed upon two inversions. The details of these chromosome changes as given by Bridges & Brehme (1944) are as follows: In(IIR)*Cy*; left break after weak 42A2 and before very weak 42A3, right break after very strong capsule 58A and before very strong doublet 58B1. In(IIIR)*P*; left break after the heavy doublet of 89C1-2, right break between the two medium doublets near right end of 96A. Translocation; break in IIR just basal to In(IIR)*Cy* just to the left of the big capsule A1-2, break in IIIR within In(IIIR)*P* following 89D4.

Because the break point for the translocation in IIIR is within the inversion it moves an inversion from the proximal to the distal end. Thus, when the appropriate portions are exchanged, one of the two abnormal chromosomes has a very long right arm with two inverted segments, while the other has a short right arm with a very small inverted portion (Figs. 1, 2). One of the second and one of the third chromosomes in the *Xa* heterozygote are therefore structurally abnormal and this condition will be written as *Xa*, or IIX*a* or IIIX*a* if the two abnormal chromosomes have to be referred to separately. Structurally normal second and third chromosomes will be indicated as N, IIN, or IIIN or merely by symbols of the mutant markers present on them in certain of the experiments.

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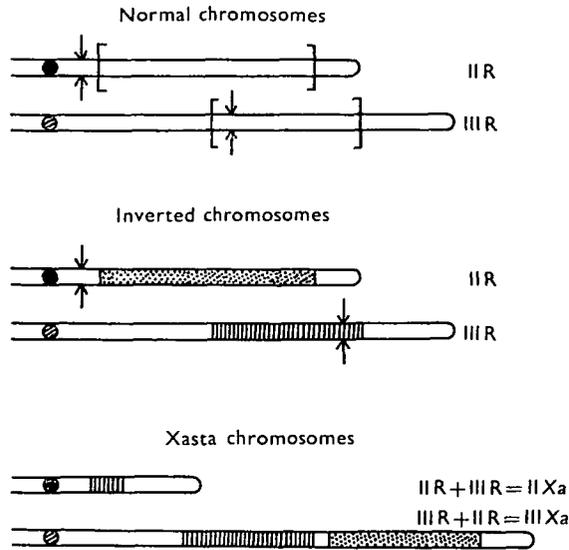


Fig. 1. Derivation of the chromosomes of the Xasta complex. Brackets indicate inverted regions and arrows the points of chromosomal breakage prior to translocation.

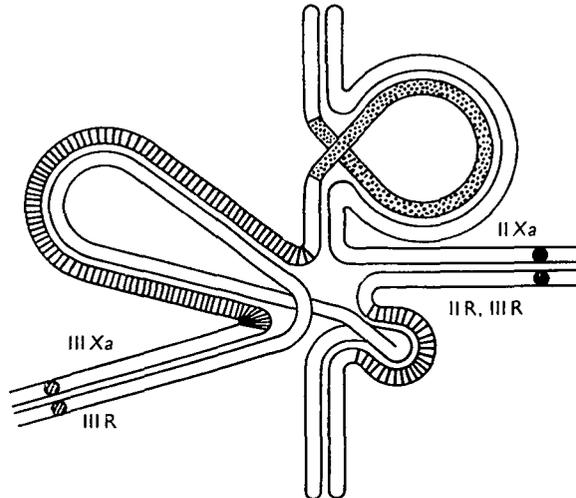


Fig. 2. Supposed pairing relationships within the right arms of chromosomes 2 and 3 in a Xasta heterozygote.

2. MATERIALS AND METHODS

The following *Drosophila* stocks were used: Xasta: several stocks were maintained $Xa:N$; $Xa:III N, III H^2$ and $Xa:IIN, III, bx^3, Cbx, Ubx, bxd, pbx$. The latter symbols refer to the closely linked mutants of the bithorax region (Lewis, 1963). Wild-type mass-mated stocks of Oregon, Crimea, Samarkand, Ealing. Curly/Moiré: Curly (*Cy*) contains the inversions $In(IIL)Cy$ and $In(IIR)Cy$; Moiré (*Mé*)

contains two breaks similar to those in In(III L)*P* and In(III R)*P*. Plum/Stubble: Plum (*Pm*) carries In(III R)*Pm*; Stubble is symbolized as (*Sb*). 'All' multiple-marker stock for chromosome II carries aristaless (*al*), dumpy (*dp*), black (*b*), purple (*pr*), curved (*c*), plexus (*px*), and speck (*sp*); 'rucuca' multiple marker stock for chromosome III carries roughoid (*ru*), hairy (*h*), thread (*th*), scarlet (*st*), curled (*cu*), stripe (*sr*), ebony (*e*), claret (*ca*).

The flies were cultured on standard oatmeal *Drosophila* medium in 3 × 1 in. glass tubes, 1 lb jam jars or small population cages carrying replaceable 2 × $\frac{3}{4}$ in. tubes (Whittington, 1963). Egg hatchability studies were carried out either by direct observation of eggs laid in tubes or alternatively by allowing flies to lay eggs for 16 h on a disk of food medium inserted on a slide within a vial. The eggs were transferred to a disk of agar and 24 h later the unhatched eggs were counted.

3. RESULTS

The segregation of Xasta in crosses

Where necessary the *Xasta* stocks were first out-crossed to a wild-type stock to free the *Xa* complex from the associated markers which had been used to maintain the stocks in a balanced lethal condition. Reciprocal crosses were then made on a number of occasions between *Xa* heterozygotes (*Xa*:N) and wild type and between *Xa* heterozygotes. *Xa* heterozygotes would be expected to produce four types of gametes, the orthoploid gametes IIN,IIIN and IIX*a*,IIIX*a* and the aneuploid gametes IIN,IIIX*a* and IIX*a*,IIIN. Crosses between *Xa* heterozygotes and wild-type flies would be expected to produce offspring in the ratio of 1 *Xa*:1 wild type since genotypes involving the aneuploid gametes would be lethal. Furthermore, irrespective of the sex of *Xasta* or wild parents, only 50% of the eggs laid by the parents should hatch. In intercrosses of heterozygous *Xa* flies the following four classes of offspring would be expected, wild type, *Xa* flies from the union of IIN,IIIN and IIX*a*,IIIX*a* gametes, *Xa* flies from the union of IIN,IIIX*a* with IIX*a*,IIIN gametes, and finally homozygous IIX*a*,IIIX*a* flies, although this latter class from previous evidence would not be expected to emerge as adults. Thus a ratio of 4*Xa*:1 wild type should occur within the progeny while, depending on the hatchability of *Xa* homozygote eggs, 37.5 or 31.25% of eggs would hatch.

The results showed excellent agreement with the expectation for the backcross but gave highly significant deviation from the 4:1 ratio expected from the *Xa* intercross (Table 1). The egg hatchability figures were in close agreement with those expected, namely 51.5 and 32.9% in backcrosses and intercrosses respectively (Table 1).

The majority (47%) of larvae which hatched from the backcrosses survived to adulthood but the number of surviving progeny from intercrosses was reduced from 32.9 to 26.4%. This latter value agrees well with an earlier estimate of 26.8% survival from this cross (Peat, 1960).

Further experiments were designed to test whether *Xa* heterozygotes produced equal frequencies of the four expected types of gametes. The first reciprocal

crosses were made between *Xa* heterozygotes carrying either *Cy,Mé* or *Pm,Sb* as markers for the non-translocated second and third chromosomes. The crosses (*Xa:Pm,Sb* × *Xa:Cy,Mé*) were expected to yield *Xa* flies with *Cy,Mé*, *Pm,Sb*, *Pm,Mé* and *Cy,Sb* characters in equal numbers. The results, however, showed that the number of *Xa* flies arising from aneuploid gametes (IIP*m*,IIIX*a*, with

Table 1. Numbers of *Xasta* and normal-winged progeny from intercrosses and backcrosses between *Xasta* *Xa:N* and wild-type (+ +) flies on several different occasions, and the hatchability of eggs from further matings expressed as a percentage of the number of eggs hatched from crosses between wild-type flies

Cross		Progeny		Ratio type	Expectation	χ ²
Female	Male	<i>Xa</i>	Wild type			
<i>Xa:N</i>	+ +	637	619	1.03:1	1:1	{ 0.26 0.47 0.21 —
		81	90	0.90:1		
+ +	<i>Xa:N</i>	683	666	1.02:1		
		129	129	1.00:1		
Total		1530	1504	—	—	0.22
<i>Xa:N</i>	<i>Xa:N</i>	650	193	3.37:1	4:1	{ 4.41* 6.95** 0.002 2.04
		364	120	3.03:1		
		290	74	3.91:1		
		481	142	3.39:1		
Total		1785	529	—	—	11.84**

Cross		Eggs laid	Eggs hatched	Corrected hatchability
Female	Male			
<i>Xa:N</i>	+ +	333	157	48.4
		297	146	51.1
+ +	<i>Xa:N</i>	346	172	50.9
		224	113	52.2
<i>Xa:N</i>	<i>Xa:N</i>	287	92	32.9
		269	85	32.8
+ +	+ +	211	206	100
		272	262	100

II*Xa*,III*Mé* and II*Cy*,IIIX*a* with II*Xa*,IIIS*b*) were much lower than those formed by the union of the orthoploid gametes (Table 2). In this experiment the normal winged flies should have been *Cy,Mé,Pm,Sb* but none were observed. The lethality appears to be due to the interaction of the four markers since both *Xa* flies with *Cy,Pm* and *Xa* flies with *Mé,Sb* were viable. No flies were observed that could have arisen from unbalanced zygotes. The experiment was repeated by crossing *Xa:Cy,Mé* and *Xa:Pm,Sb* to *Xa:N* flies. The results were similar to those obtained previously except that the normal winged flies *Pm,Sb* and *Cy,Mé* survived and, as expected, were as frequent as *Xa* flies arising from each class of orthoploid gametes (Table 2). As in the previous cross, the difference in the numbers of *Xa* flies arising from aneuploid and orthoploid gametes was greater where *Xa:Cy,Mé*

Table 2. Numbers of offspring in each class derived from the union of orthoploid (O) or aneuploid (A) gametes in a series of crosses between *Xasta* flies heterozygous for marker genes

Parents	<i>Xa:Cy,Mé</i>	<i>Xa:Pm,Sb</i>	<i>Xa:N</i>	<i>Xa:Pm,Sb</i>	<i>Xa:N</i>	<i>Xa:Cy,Mé</i>	<i>Xa:N</i>	<i>Xa:Cy,Mé</i>	<i>Xa:N</i>	<i>Xa:Cy,Mé</i>	<i>Xa:Ca,St</i>
Female	—	<i>Xa:Pm,Sb</i>	<i>Xa:N</i>	—	<i>Xa:Pm,Sb</i>	<i>Xa:N</i>	—	<i>Xa:Cy,Mé</i>	<i>Xa:N</i>	—	<i>Xa:Ca,St</i>
Male	—	<i>Xa:Cy,Mé</i>	<i>Xa:Pm,Sb</i>	—	<i>Xa:Cy,Mé</i>	<i>Xa:N</i>	—	<i>Xa:Pm,Sb</i>	<i>Xa:N</i>	—	<i>Xa:Ca,St</i>
Progeny O	121	82	<i>Xa:Pm,Sb</i>	134	40	<i>Xa:Cy,Mé</i>	147	49	<i>Xa:Ca</i>	90	90
O	120	90	<i>Xa:N</i>	107	26	<i>Xa:N</i>	148	60	<i>Xa:St</i>	92	92
O	—	—	<i>Pm,Sb</i>	107	30	<i>Cy,Mé</i>	157	40	<i>Ca,St</i>	69	69
A	17	58	<i>Xa:IIIN,IIISb</i>	75	23	<i>Xa:IIICy,IIIN</i>	99	3	<i>Xa:Ca,St</i>	51	51
A	20	39	<i>Xa:IIIPm,IIIN</i>	83	22	<i>Xa:IIIMé</i>	84	2	<i>Xa:N</i>	66	66
Hatchability (%)	28.4	30.8	—	36.4	—	—	24.0	—	—	—	—
$\chi^2_{(3)}$ for equality of all classes	149.9	25.5	—	21.5	8.1*	—	24.4	93.2	—	—	—
$\chi^2_{(1)}$ for equality within orthoploid classes	0.1	0.4	—	4.2	0.1	—	0.4	4.0	—	—	—
$\chi^2_{(1)}$ for equality within aneuploid classes	0.2	3.7	—	0.4	3.3	—	1.2	0.2	—	—	—

(* , ** , *** indicate significance at $P = 0.05, 0.01$ and 0.001 respectively.)

was the female parent. The hatchability of eggs from matings of the above type was lower than in crosses between *Xa*:N flies.

Finally, an experiment similar to those above was carried out using recessive markers to avoid the complicating effect of the inversions. *Xa* flies carrying *st* within the translocation complex and rucuca markers (specifically *ca*, *st*) on the accompanying normal chromosomes were mated with *Xa* flies carrying *ca* in the complex and, again, the rucuca markers on the normal chromosomes. Although *ca* is normally a third chromosome locus it becomes, because of translocation, a marker for the second chromosome when combined with the *Xa* complex (Fig. 1). The results showed that *Xa* progeny again arose more frequently from orthoploid than aneuploid gametes, but the number of normal winged flies was lower than expected (Table 2). The ratio of *Xa* flies from aneuploid and orthoploid gametes in this experiment was 0.64:1.

Table 3. *The frequency of recombination between a series of marker genes in the second and third chromosomes in Drosophila melanogaster as affected by the Xasta complex*

Genes	Chromosome 2			Genes	Chromosome 3		
	Standard map distance	Xasta	% change relative to control		Control map distance	Xasta	% change relative to control
<i>al-dp</i>	13.0	14.6	+ 12.3	<i>ru-h</i>	21.8	25.2	+ 15.2
<i>dp-b</i>	35.5	38.0	+ 7.0	<i>h-th</i>	20.6	24.8	+ 20.2
<i>b-pr</i>	6.0	8.3	+ 38.3	<i>th-st</i>	0.9	1.3	+ 44.5
<i>pr-c</i>	21.0	0.9	- 95.7	<i>st-cu</i>	7.1	5.1	- 28.2
<i>c-px</i>	25.0	0.002	- 100.0	<i>cu-sr</i>	16.4	1.3	- 92.1
<i>px-sp</i>	6.5	0	- 100.0	<i>sr-e</i>	8.4	0	- 100.0
				<i>e-ca</i>	29.9	1.2	- 96.0
Flies scored		1675	—	—	1351	1737	—

The effect of Xasta on recombination within the second and third chromosomes

The effect of the *Xa* complex on recombination within the second and third chromosomes was studied in backcrosses of two multiple marked stocks 'all' and 'rucuca'. A backcross of rucuca/+ to rucuca was used to obtain comparative figures for the recombination values of genes on the third chromosome, but a similar experiment with the second chromosome markers was affected by the low viability of the 'all' stock and the published map distance of Bridges & Brehme (1944) was used instead. The results showed that in *Xa* flies recombination was increased in the left arms of both chromosomes II and III (Table 3). Recombination was found to occur within the IIR(*Cy*) inversion. Three flies in 1675 were observed to undergo double recombination for the curved locus and this would suggest that single recombination leading to bridge and fragment formation might be even more frequent. This would be expected to lead to the production of unbalanced gametes and thus lower egg viability. However, backcrosses involving *Xa*

showed no reduction in egg viability except that forecast by the production of aneuploid gametes IIXa,IIIN and IIN,III Xa . It seems, therefore, that abnormal chromosomes must enter the polar bodies (Sturtevant & Beadle, 1936).

The observed increase in recombination in the presence of inversions and translocations on chromosomes other than those tested for recombination has also been reported by other workers (Cooper, Zimmering & Krivshenko, 1966; Redfield, 1957; Williamson, 1966) but the cause of this effect is not understood.

The behaviour of Xasta in populations

Initially Xa flies taken from a stock segregating normal winged flies were used to start five small population cages maintained at 20 °C, 27 °C, and a temperature fluctuating daily from 19 to 26 °C. The entire population (varying from 50 to 150) was classified at approximately fortnightly intervals from January 1959 until January 1960. Xa flies were present in all cages throughout the experiment at ratios of between 4 and 8 Xa :1 wild type.

The result clearly showed that $Xasta$ could be maintained in populations despite its lethality in the homozygous condition. It is possible that in this experiment the selective advantage of heterozygous Xa flies over wild type was determined by the presence of undetected semi-lethal genes on the normal chromosomes of the Xa flies used in this experiment. But in three similar replicated population-cage experiments Xa maintained itself against chromosomes from each of Ealing, Oregon and a Crimea mass-mated stock for periods of over 6 months in each experiment at average ratios of 6.5, 6.1 and 6.7 Xa :1 wild type respectively. In the experiment with Crimea the Xa flies were backcrossed twice to the wild-type stock before flies from Xa intercrosses were released into the cages to begin the experiment.

Xa , however, maintained itself less well when more medium was supplied. When cultured in 1 lb jam jars against Oregon chromosomes the ratio of Xa to wild-type flies declined from 5:1 to fixation of the wild-type phenotype in 4 months. Evidently the selective advantage of $Xasta$ depends to a great extent on the intensity of the larval competition. In this latter experiment another group of flies was maintained in similar jars, but on a medium containing a steadily increasing concentration (1–6.6%) of sodium chloride (Hossain, 1964). The number of flies emerging from the saline medium was less than that which emerged from the normal medium, but the ratio of Xa to wild-type flies remained high. A series of experiments were also carried out by allowing the Xa and normal flies which emerged from the high saline medium to lay eggs first on a normal and then on saline medium. On each occasion the ratio of Xa :+ in the offspring was higher from the saline than the normal medium. The ratios were 1.7 and 13.01, 3.4 and 25.0:1, and 1.0 and all Xa from the normal and saline medium respectively. Evidently the Xa genotype is better adapted than normal-winged flies to abnormal environments.

The earlier conclusion that the survival of Xa in populations depends largely on the intensity of competition amongst the larvae was supported by further results.

An increasing number of *Xa* females mated to *Xa* males were allowed to lay eggs on normal medium in 3×1 in. specimen tubes and the mean results over three replicates showed that the ratio of *Xa*:+ in the progeny rose from 3.4:1 where only one female was present per tube to 10.9 *Xa*:1+ when 12 flies were present. An experiment was also conducted to examine the possibility that overcrowded conditions could also disturb the 1*Xa*:1 wild-type ratio expected for crosses between *Xa* and normal-winged flies. Twenty-seven female *Xa* flies mated to wild-type males laid eggs in a single 3×1 in. specimen tube containing normal medium until the first progeny were about to emerge. The newly hatched flies were removed every 12 h and at the end of the first week 47 *Xa* and 25 normal-winged flies had emerged. This represents a significant departure from the 1:1 ratio expected ($\chi^2_1 = 7.3$, $P < 0.05$). During the second week a further 28 *Xa* and 52 normal flies emerged to yield a final result (75 *Xa*:74 wild type) that did not differ from the 1:1 ratio expected. It is clear that competition delayed the development of a proportion of the normal-winged offspring but these did eventually emerge.

4. DISCUSSION

It was initially proposed that *Xa* heterozygotes should yield four types of gametes in equal proportions and produce eggs with hatchabilities of 50% and 37.5 or 31.25% in backcrosses and intercrosses. The results, however, showed that fewer *Xa* flies arose from the union of aneuploid than from orthoploid gametes. The ratio between the two gametic types was approximately 0.64:1. The excess progeny from orthoploid gametes may be due either to a greater tendency for alternate rather than adjacent chromosome segregation from the ring formation at meiosis or, alternatively, to a lower viability of the actual aneuploid gametes. The former alternative seems more likely. However, if only four types of gametes are produced, then the relatively higher frequency of orthoploid gametes should raise the hatchability of eggs in backcrosses to 61% and in intercrosses to 46.1% and these values are clearly in excess of the 50 and 32.9% observed. It is therefore proposed that, at least in one sex, more than four types of gamete are produced.

First, the extra class of unbalanced gametes may arise as the result of recombination within the inversions. This would be expected in *Drosophila melanogaster* to occur only in the female and the effect was illustrated in these experiments by the fact that the hatchability of eggs from females with inversions (*Cy, Mé* or *Pm, Sb*) mated to wild-type males were reduced (57.4 and 77.4%) relative to that of eggs from the reciprocal crosses, 95.5 and 97.0% respectively. Similarly, the hatchability of eggs from *Xa* females carrying *Cy, Mé* and *Pm, Sb* in crosses to wild type was also reduced (41.4 and 46.5%) below the expected 50%.

Second, they may arise from the formation of a rod configuration rather than a ring at meiosis (Lewis & John, 1957). This configuration, which may occur in both sexes, could lead to the formation of monosomic and/or trisomic gametes. The rod configuration is made more likely by the relatively restricted length of chromosome available for chiasma formation at the ends of the second and third translocated chromosomes. If, however, trisomic gametes are produced, then their

production must be either very infrequent or restricted to one sex, as an experiment to test for non-disjunction of the centromeres showed that this phenomenon, if it occurred, failed to produce viable individuals.

If the unbalanced gametes are produced only by one sex, then *Xasta* females might produce gametes with the following frequencies 0.25 IIXa,IIIXa; 0.16 IIXa,IIIN; 0.16 IIN,IIIXa; 0.25 IIN,IIIN and 0.18 other unbalanced gametes, while *Xa* males might yield only the first four types of gametes at equal frequency (0.25). These values for the females are suggested because they satisfy the observed orthoploid-to-aneuploid frequency of 1:0.64 and also calculations adopting them result in egg hatchability values of 50% from backcrosses and 33 or 26.75% from intercroses depending on the hatchability from *Xa* homozygotes. These values are in close agreement with those observed in the experiments. Since the observed hatchability from intercroses was 32.9% and the final emergence of adults only 26.4%, it would seem that *Xa* homozygotes hatch, but do not mature into adults. Furthermore, the suggested gametic values yield ratios of 1*Xa*:1 wild in backcrosses and 3.28 *Xa*:1 wild in intercroses of *Xa* flies. The total numbers of flies obtained from intercroses in Table 1 do not differ significantly from those expected on the basis of this ratio ($\chi^2_1 = 0.33$).

If both sexes produce a proportion of unbalanced gametes, then the frequency of the gametic classes must be such as to yield 6.25 and 5.0% of offspring in the progeny from orthoploid and aneuploid gametes respectively. Thus where the frequencies are equal in the two sexes the gametic values are 0.25 IIXa,IIIXa; 0.20 IIXa,IIIN; 0.20 IIN,IIIXa; 0.25 IIN,IIIN and 0.10 other unbalanced gametes.

It is not clear from the above results whether one or both sexes do produce gametes of the types suggested, and confirmation involving direct study of male and female meiosis would be difficult.

The ratio of *Xa* to normal flies of 3.38:1 was found to be increased in favour of *Xa* under crowded conditions and *Xa* was maintained as a balanced polymorphic population in small cages in spite of the fact that only a small proportion of its progeny is viable. A selection coefficient 0.75 against the wild-type flies would be necessary to account for the observed 6 *Xa*:1 wild-type ratio in cages. *Xa*, however, was less able to maintain itself under conditions of greater food supply unless salt was added to the medium. It is possible that the ability to exist in a balanced polymorphic condition is due to the fact that *Xa* contains two inversions In(IIR)*Cy* and In(IIIR)*P* known to occur in natural populations. It seems likely that these inversions were probably present in the original irradiated flies (Serebrovsky & Dubinin, 1930) because the chances that irradiation produced two known inversions as well as the translocation are very low. It is, however, more likely that the wild-type larvae are affected by the presence of *Xa* larvae, perhaps through the effect of toxic secretions. This effect would be expected to be greatest when intercroses between *Xasta* flies are made because the ratio of *Xa*: wild-type flies is greater than from crosses between *Xa* and normal flies. The fact that the ratio of 1*Xa*:1 wild amongst the offspring from backcrosses may be disturbed by overcrowding shows that the effect depends upon the presence of *Xa* heterozygotes since

these do not occur in this cross. Evidence for the excretion of toxic substance from mutant *Drosophila* is increasing (Weisbrot, 1966) and this hypothesis would agree with the evidence that once the frequency of Xasta flies declines in a population, perhaps due to a liberal supply of food, the complete elimination of Xasta may follow. Similarly, rapid replacement of small quantities of food may favour the maintenance of the polymorphic condition. Finally, the Xasta mutant is clearly suitable for simple class demonstrations of the principles of balanced polymorphism.

SUMMARY

Xasta flies appear to segregate five types of gametes in unequal numbers, namely two which contain both or neither of the chromosomes affected by the translocation and inversions, two further classes which contain one affected and one unaffected chromosome, and finally the remainder which have an unbalanced chromosomal content. These conditions are necessary to fit the results observed in crosses involving the Xasta stock. Xasta exhibits balanced polymorphism under crowded conditions and this may be due to the production of toxic substances by *Xa* larvae which delay the development of wild type-larvae.

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