

Preferential Segregation of the Fourth Chromosomes in *Drosophila melanogaster*

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PNAS 1934;20;515-518
doi:10.1073/pnas.20.9.515

This information is current as of December 2006.

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Notes:

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*PREFERENTIAL SEGREGATION OF THE FOURTH
CHROMOSOMES IN DROSOPHILA MELANOGASTER*

BY A. H. STURTEVANT

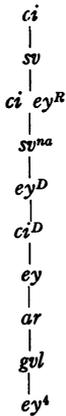
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Communicated August 4, 1934

The present study is concerned chiefly with the behavior of a duplicating chromosome derived from the undescribed scute allelomorph known as scute-10-2. This allelomorph, obtained by x-raying scute-10, is associated with a reciprocal 1-4 translocation. The X-chromosome is broken near its left end, between the loci of silver and broad, and the short terminal piece (loci from yellow to silver) is exchanged for a section of the fourth chromosome that includes all the known loci of that chromosome (with the possible exception of cubitus-interruptus, which is difficult to test, since this translocation shows the position effect recently described by Dubinin and Sidoroff¹). The small chromosome, made up of the left end of X attached to the spindle-fibre region of 4, may be obtained in individuals (of either sex) that are otherwise normal diploids.² If the normal X's of such hyperploids carry the recessive gene for yellow, the flies are wild-type in appearance because of the presence of +^y in the duplicating chromosome. This fact has been used, in the present experiments, to study the distribution of the fragment at meiosis.

If hyperploid females of the³ constitution $\frac{y}{y}$ dupl. $\frac{ey^D}{gvl}$ are mated to yellow males there results, not the expected ratio of 1 eyeless : 1 wild-type : 1 yellow eyeless : 1 yellow, but a ratio of 2:1:1:2 (actual numbers obtained, 604 : 307 : 334 : 701). That is to say, the duplicating chromo-

some goes to the same pole as dominant eyeless twice as often as it goes to the same pole as grooveless. This result has been obtained consistently in many different experiments; it is immaterial whether the duplication was received from the same parent as ey^D (observed numbers 347 : 193 : 202 : 397) or from the same parent as gvl (257 : 114 : 132 : 304), though in the latter case the appearance is such as to suggest 67 per cent of crossing-over. Similar results may be obtained for other combinations of fourth-chromosome genes, though the disproportion is not always so great (see table below).



There is in fact a definite seriation of the tested fourth chromosomes, such that ci is always "preferred" to any other type, while any other type is preferred to ey^4 . This seriation is shown in the diagram. It is useful in that it enables one to make accurate qualitative predictions, as has been demonstrated repeatedly.

Quantitatively the results have not yet been worked into a complete scheme, though regularities are obviously present. As the table shows, "preference" is in general strong in combinations of chromosomes that are far apart on the diagram (though never going beyond the 2:1 ratio), weaker in combinations of neighboring chromosomes.

TABLE 1
PERCENTAGE OF ASSOCIATION WITH SCUTE-10-2 DUPLICATION⁴

OPPOSED CHROMOSOME	PREFERRED CHROMOSOME								
	<i>ci</i>	<i>sv</i>	<i>ci ey^R</i>	<i>sv^{na}</i>	<i>ey^D</i>	<i>ci^D</i>	<i>ey</i>	<i>ar</i>	<i>gvl</i>
<i>sv</i>	52.2 ±2.5								
<i>ci ey^R</i>	51.0 ±1.1	51.3 ±1.3							
<i>sv^{na}</i>	53.1 ±1.1	..	56.0 ±0.7						
<i>ey^D</i>	56.2 ±2.2					
<i>ci^D</i>	..	56.1 ±2.4	..	58.1 ±1.8	59.6 ±2.3				
<i>ey</i>	..	62.3 ±2.6	60.3 ±2.7			
<i>ar</i>	56.2 ±3.3	62.6 ±2.2	61.0 ±2.4	..		
<i>gvl</i>	60.7 ±2.6	65.2 ±1.7	67.6 ±1.0	57.8 ±1.2	67.1 ±0.8	55.3 ±1.5	54.6 ±2.0	50.8 ±1.4	
<i>ey⁴</i>	..	66.7 ±1.9	..	61.3 ±3.5	59.4 ±4.1	51.8 ±2.0

The sequence appears to be a linear one; but at both ends of the diagram we are concerned with differences that are so slight that more data will be required before they can be considered certainly significant. The

three top chromosomes may be actually equivalent, and the seriation among the last four may require modification.

Other chromosomes are being studied, including two crossover ones. These should throw light on the mechanism concerned, but are not yet ready to report on.

An unexpected result is that these preferences are very much reduced in the male, though apparently still present. In the two best-studied cases, $ci\ ey^R$ was preferred to gvl , the value being 52.9 ± 0.8 ; ey^D to gvl with a value of 51.9 ± 1.3 . This is not an effect of the Y -chromosome, since females with attached X 's and a Y give the same results as those with separate X 's and no Y .

A few similar duplicating chromosomes have been tested, in which the spindle-fibre attachment was derived from an X ; these, though they contained approximately the same "active" region as the scute-10-2 duplication, showed random segregation with respect to the fourth chromosomes tested.

Preliminary experiments with triplo-4 females (not carrying any duplicating fragment) indicate that here also certain combinations give non-random segregation. The diagram given above seems to apply, in that chromosomes near the top tend to go to the diplo-4 pole, those near the bottom to the haplo-4 pole. One example may be given. Several different chromosomes were tested against ey^D and ci^D at the same time. From such females the percentage of the haplo-4 eggs that contained only the third member of the set was determined, as follows: sv , 43.5 ± 2.3 ; $ci\ ey^R$, 33.8 ± 2.0 ; sv^{na} , 36.4 ± 1.5 ; gvl , 50.7 ± 1.8 ; ey^4 , 64.2 ± 1.9 (random segregation would, of course, give a value of 33.3).

It does not seem probable that the mutant genes concerned are themselves responsible for the relations described. Tests of crossovers should settle this question; but present indications are rather that the genes merely serve as convenient markers for chromosomes that differ in other respects (perhaps themselves genic). One reason for suspecting this is that two wild-type chromosomes, not yet fully analyzed, lie at different levels (one above sv^{na} , the other below ey^D).

The first hypothesis was that the fourth chromosomes concerned differed in having inversions or other structural differences. Cytological studies by Bridges (in press) show that the ey^D chromosome does in fact have a gross structural aberration; but nothing unusual has been detected in the other chromosomes, and it seems altogether improbable that structural differences are sufficiently widespread to account for the results.

The "preference" ratio for the duplication appears to have 2:1 as a definite limiting value. Such a simple ratio suggests a simple mechanism for the relation. If the result is referred back to what happens at the conjugation of the chromosomes it becomes possible to picture such

mechanisms; but their elaboration and discussion may be deferred until more information is available.

¹ *Amer. Nat.*, 68, 381 (1934).

² This duplication is regularly eliminated somatically in certain areas. It has been discussed in this connection by Ephrussi (these PROCEEDINGS, 20, 420 (1934)).

³ The fourth chromosome genes referred to in this paper by symbols are: *ar*, abdomen-rotatum; *ci*, cubitus-interruptus; *ci^D*, dominant cubitus-interruptus; *ey*, *ey^A*, *ey^R*, recessive eyeless allelomorphs; *ey^D*, dominant eyeless; *gvl*, grooveless; *sv*, shaven; *sv^{na}*, naked.

⁴ The values listed here as "probable errors" represent the probable percentage deviations from a 1:1 ratio $\left(67.45 \sqrt{\frac{1}{4n}} \right)$.

ON THE OCCURRENCE OF AN OREODONT SKELETON IN THE SESPE OF SOUTH MOUNTAIN, CALIFORNIA

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Communicated August 6, 1934

In a previous paper¹ I have noted the occurrence of two distinct types of oreodonts, namely, a leptauchenid and a species tentatively referred to the genus *Promerycochærus*, in the Sespe deposits as exposed on the flank of South Mountain, Ventura County, California. A third type of oreodont, the genus *Eporeodon*, is now recorded from this upper division of these continental beds.

Location of the Sespe deposits of South Mountain, with reference to the important horizons of the Sespe of the Simi Valley and Las Posas Hills regions, discussed in previous papers published in the PROCEEDINGS, is shown in figure 1. I am privileged to reproduce, through courtesy of the geological staff, Shell Company of California, the columnar section, figure 2, giving the Tertiary stratigraphic sequence at South Mountain. As will be noted in this section, the thick series of Sespe deposits grades upward without stratigraphic break into the marine Vaqueros (Lower Miocene).

The leptauchenids occur lower in the section than the level where *Promerycochærus? hesperus* was found, and range through a stratigraphic thickness of approximately 1000 feet. The position of *Eporeodon* is shown at Locality 157 Calif. Inst. Tech. Vert. Pale., and lies within the vertical range of the leptauchenids. The occurrence is approximately 1500 feet lower stratigraphically than that of *P.? hesperus*. The skeleton was found in a dominantly maroon-colored shale and siltstone which