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COMPRESSED DEFICIENCY AND THE LOCATION OF THE SPINDLE ATTACHMENT IN THE X-CHROMOSOME OF DROSOPHILA PSEUDOÖBSCURA

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The two arms of the V-shaped *X*-chromosome of *Drosophila pseudoobscura* are equal in length in the spermatogonial metaphase plates (Metz,[1] Dobzhansky and Boche[2]). But in the salivary gland nuclei, one of them is about two-thirds of the length of the other (Tan,[3] Dobzhansky and Tan[4]). This difference is presumably due to the relative amount of heterochromatic material contained in the two arms (Bauer[5]). Genetically, according to the recently revised map of the *X*-chromosome (Sturtevant and Tan[6]), it has at least 180 crossover units. The correspondence of the genetically left and right limbs to the short and long arms of the salivary gland *X*-chromosome has been previously established (Tan[3]). But to date, the knowledge as to where the spindle fibre lies in the *X*-chromosome is lacking. Such information is desirable, especially for the investigation of the homology of chromosomes between *pseudoöbscura* and the related species of *Drosophila* such as *melanogaster*. This paper reports the cytological and genetic data of a deficiency for the gene compressed with a view to locating the spindle attachment in the *X*-chromosome of *Drosophila pseudoobscura*.

A strain of flies apparently containing a deficiency for the sex-linked gene compressed has been obtained among several chromosomal aberrations recently induced in *D. pseudoöbscura* by the use of x-rays. ♀ ♀ homozygous for the sex-linked genes yellow (*y*), singed (*sn*), vermilion (*v*), compressed (*co*) and short (*s*) were mated to wild-type ♂ ♂ which had been treated with x-rays. Most of the ♀ ♀ in the resulting offspring were, as was to be expected, wild-type; but one ♀ manifested the effects of the gene compressed in an exaggerated form, and in addition had divergent wings. This ♀ was backcrossed to *y sn v co s* ♂ ♂, and in the progeny were a number of daughters resembling their mother. The viability of this type of

♀ ♀ is good; no ♂ ♂ like them have ever appeared, however, indicating that the new type is lethal in the ♂. The exaggeration of the effects of compressed suggests that a deficiency involving the locus of that gene has arisen. The type has accordingly been named "compressed deficiency."

Table 1 gives the results of crosses between compressed deficiency ♀ ♀ heterozygous for the genes *y v co* and *y v co* ♂ ♂. It is clear that the ex-

TABLE 1

$\frac{co\text{-def.}}{y\ v\ co}$ ♀ ♀ × *y v co* ♂ ♂

	NON-CROSSOVERS			CROSSOVERS REGION 1			REGION 2			
CULTURE NO.	*co*-DEF.	*y-v-co*		*y-co*-DEF.	*v-co*		*v-y-co*	DEF. *co*		TOTAL
	♀	♀	♂	♀	♀	♂	♀	♀	♂	
1218	78	32	32	5	7	5	1	4	2	166
1219	64	39	19	14	4	3	3	4	3	153
	142	71	51	19	11	8	4	8	5	319

treme compressed individuals do not exist in ♂ ♂. The calculated crossover values from the data are 11.9% in the region between *y* and *v*, and 5.3% between *v* and *co*. The control crossover value between *y* and *v* (from table 2)

TABLE 2

$\frac{y\ v}{+\ +}$ ♀ ♀ × *y v* ♂ ♂ (Only ♂ offspring classed)

	NON-CROSSOVERS		CROSSOVERS		
CULTURE NO.	++	*y-v*	*v*	*y*	TOTAL
1068	96	61	15	14	186
1069	109	40	6	11	166
1070	95	71	8	11	185
1071	92	64	9	6	171
	392	236	38	42	708

is 11.3%. This shows that the crossing-over in this region between *y* and *v* is not at all affected by the presence of the compressed deficiency. In the region between *v* and *co*, the situation is quite different. Table 3 gives the

TABLE 3

$\frac{v\quad co}{mg}$ ♀ ♀ × *v co* ♂ ♂ (Only ♂ offspring were classed)

	NON-CROSSOVERS		SINGLE CROSSOVERS REG. 1		REG. 2		DOUBLE CROSSOVERS REGION 1, 2		
CULTURE NO.	*mg*	*v-co*	*co*	*v-mg*	*mg-co*	*v*	+++	*v-mg-co*	TOTAL
1072	43	52	19	11	4	3	2	..	134
1073	49	19	11	5	2	..	2	..	88
1074	78	43	20	17	3	5	3	2	171
1075	30	14	7	7	..	2	..	..	60
	200	128	57	40	9	10	7	2	453

data of the cross between *v co/mg* ♀ ♀ and *v co* ♂ ♂. It gives the crossover values between *v* and *mg* of 23.4% and between *mg* and *co* of 6.2%. Adding the above two values together, *v* and *co* should be 29.6 units apart. Even not counting the double crossovers, there are still 25.6 units. On comparing this with the value obtained in the presence of compressed deficiency, which is only 5.3%, it is clear that there is a considerable reduction of crossing-over in the latter.

Between the genes vermilion and magenta there lie the mutant genes miniature (*m*), dusky (*dy*), forked (*f*) and bobbed (*bb*). They are located very close to each other.[6] As a matter of fact, their exact sequence has not been clear until recently it was found by Prof. Sturtevant that bobbed lies in the rightmost position in the series of these four genes. The data shown in table 4 give the crossover values between *y* and *bb* of 8.3% and

TABLE 4

$\frac{mg}{y\ bb}$ ♀ ♀ × *mg* ♂ ♂ (Only ♂ offspring were classed)

	NON-CROSSOVERS		SINGLE CROSSOVERS REG. 1		SINGLE CROSSOVERS REG. 2		DOUBLE CROSSOVERS REGIONS 1,2		
CULTURE NO.	*mg*	*y-bb*	*bb*	*y mg*	*+++*	*y-bb-mg*	*bb-mg*	*y*	TOTAL
1154	64	42	3	4	6	3	2	2	126
1155	100	88	6	5	17	12	2	6	236
	164	130	9	9	23	15	4	8	362

between *bb* and *mg* of 13.8%. When compressed deficiency ♀ ♀ heterozygous for *y bb* were mated to *y bb* ♂ ♂ (table 5), there was 12.9% of crossing-over between *y* and *bb*, showing that there is even an increase in the frequency of crossing-over in this region over the controls. Among three

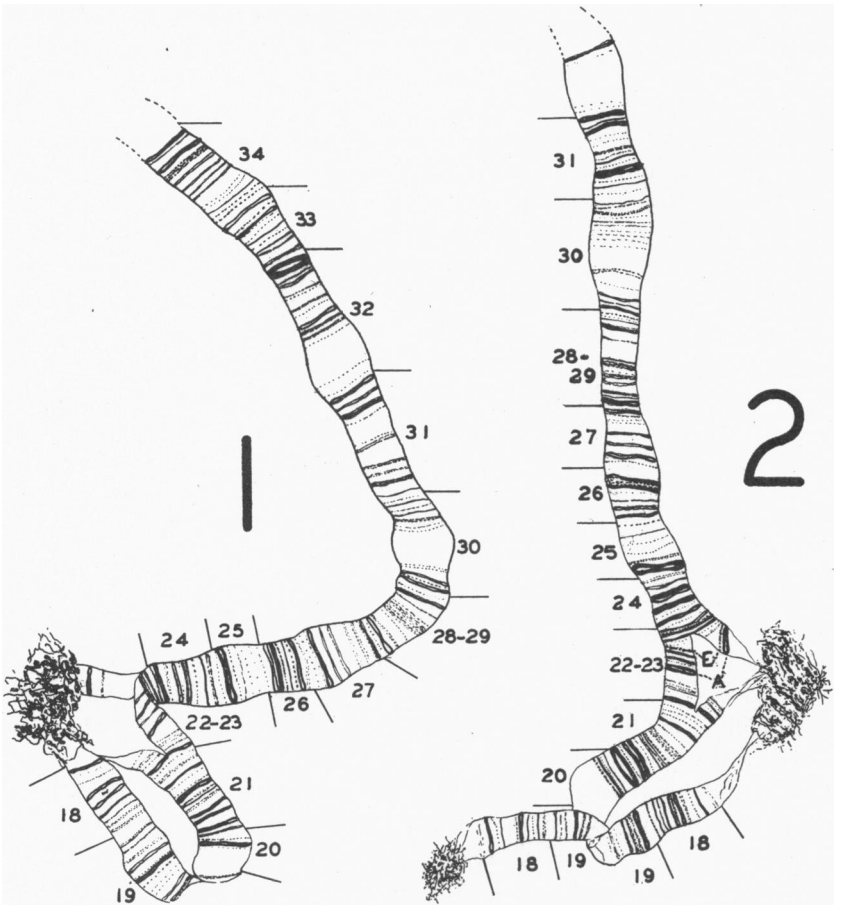
TABLE 5

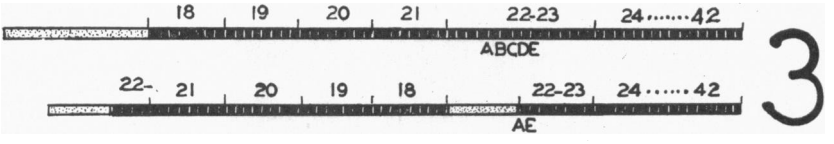
$\frac{co\text{-def.}}{y\ bb}$ ♀ ♀ × *y bb* ♂ ♂ (Only ♂ offspring classed)

		SINGLE CROSSOVERS		
	NON-CROSSOVERS	REG. 1	REG. 2	
CULTURE NO.	*y = bb*	*bb*	*++*	TOTAL
1152	65	9	..	74
1156	64	10	..	74
1157	57	9	2	68
	186	28	2	216

cultures, only one gave two flies representing the recombination of *bb* and *co*. The crossover value thus obtained is 0.93%, which when compared to the region between *bb* and *mg*, 13.8%, shows an almost complete suppression of crossing-over in this region in the presence of the compressed deficiency.

Cytologically, the salivary gland chromosome configurations of deficiency ♀ ♀ heterozygous for the gene *v* were studied. Since homozygous *v* larvae





EXPLANATION OF FIGURES

Figures 1 and 2—Salivary gland chromosome configurations in the right limb of the *X*-chromosome of *Drosophila pseudoöbscura* from larvae heterozygous for compressed deficiency.

Figure 3—Diagrammatic representation of the sequence of genes. Above is the sequence of the normal chromosome and below the sequence of the compressed deficiency. The dotted region represents the heterochromatic area, and the solid black, the euchromatic region.

can be distinguished from the heterozygotes by the color of the Malpighian tubules, there was no difficulty in selecting desired ♀ larvae for dissection, especially since crossing-over between *v* and *co* has been considerably reduced in the presence of the deficiency.

Figures 1 and 2 are camera lucida drawings of the salivary gland chromosomes of heterozygous compressed deficiency individuals. The numbering of the sections is the same as adopted by Dobzhansky and Tan.[4] The right limb of the *X*-chromosome runs from sections 18 to 42. Only the proximal part of it is shown in each of the figures. In both of them there is formed a typical inversion loop involving a part of the heterochromatic area. One end of the inversion lies in the sections 22–23 and the other end in the heterochromatic region, which is embedded in the chromocenter. The inversion figure is especially clear in figure 1, in which the inverted regions of the two strands are almost completely paired. In figure 2, the two strands in sections 18 to 19 and the heterochromatic area are unpaired. The inverted strand is apparently attached to the chromocenter in three places. Figure 2 is especially clear in showing that several bands are missing in the inverted strand. Apparently there are five bands in the normal strand which can be homologized to only two bands in the inverted strand. Assuming that the five bands in the normal strand are *A*, *B*, *C*, *D* and *E*, the break of the inversion in the euchromatic area is just below band *A*. Judged from the intensity and characteristic band pattern, the two bands in the inverted strand are the homologs of *A* and *E*. The three missing bands are therefore *B*, *C* and *D*; *B* being very light and *C* and *D* relatively heavy.

For the sake of clearness in comparison, the sequences of the normal strand and the inverted strand are diagrammatically represented in figure 3. The dotted region indicates the heterochromatic area and the solid black the euchromatic region. That the deficient region does not lie next to the break of the inversion but a band away from it is very interesting, since it follows that four breakages occurred in this chromosome. How this aberration originated is not clear. It is possible that the deficiency arose as a position effect of the inversion.

Correlation of the genetic with the cytological data from the study of this deficiency justifies the conclusion that the gene compressed is located in the region between bands *A* and *E* in sections 22–23. It is possible but improbable that the recessive compressed effect may be the result of a position effect of these breakages. Such cases have been reported in the locus cubitus interruptus of *D. melanogaster*.[7] Even if this were true here, the locus compressed could not be located much farther away from the region which shows the deficiency of bands.

The association of an inversion with compressed deficiency as demonstrated by the cytological picture is especially significant for the interpre-

tation of the genetic data given above. On the assumption that the presence of an inversion in one limb of a chromosome does not reduce the crossing-over in the other limb, it follows that the region involving *y*, *v* and *bb* is located in the left limb of the *X*-chromosome. Consequently, the spindle fibre is certain to lie between the genes *bb* and *co*. As to the locus of magenta (*mg*), direct genetic evidence is not yet available. But the facts that the distance between *co* and the chromocenter in the right limb of the salivary gland *X*-chromosome is about one-fifth of the total length and that the crossover units between *mg* and *co* are only 6.2, suggest strongly that *mg* is located in the right limb of the *X*-chromosome. Since the distance between *v* and *mg* is rather large (23.4 units), and crossing-over between *v* and *co* (5.3) in the presence of the inversion is appreciably reduced, the argument for placing the spindle fibre between genes bobbed and magenta is quite convincing.

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OVARY TRANSPLANTS IN DROSOPHILA MELANOGASTER: MEIOSIS AND CROSSING-OVER IN SUPERFEMALES

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Individuals of *Drosophila melanogaster* with three *X*-chromosomes and two sets of autosomes were called "superfemales" by Bridges.[1] They occur among the progeny of triploid females mated to diploid males,[1] among the offspring of attached-*X* diploid females mated to diploid males,[2] and under certain other conditions. Superfemales are low in viability as compared with normal diploid individuals and are always sterile. With the development of a simple method of transplantation for use in studies of Drosophila[3] and with the demonstration that offspring can be obtained from transplanted ovaries,[4,5] the authors were led to investigate the possibility of obtaining progeny from superfemales by transplanting their ovaries to normal females. Aside from its bearing on the problem of the nature of sterility in the superfemale, such a study might, if it provided