

# LINKAGE GROUPS IN *DROSOPHILA PSEUDO-OBSCURA*.

WITH NOTES ON HOMOLOGY AND THE NATURE OF GENIC ACTION.

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(With Plates II and III and Two Text-figures.)

IN a recent paper (1934) we described the second linkage group of characters (orange, Scute, purple) in *Drosophila pseudo-obscura*. In this we deal with certain members of the 1st, the 3rd, the 4th and the 5th groups.

## CHROMOSOME I.

Snapt (*sp*), tilt (*tl*) and sepia (*se*) are three genes which appear to reside in the left arm of the X-chromosome. They are separated so widely from each other, however, that until suitable mutations become available for the marking of intermediate loci, their precise location remains impossible.

*Snapt (sp)* (Plate III, figs. 1 and 2).

In October 1930, in a Pointed yellow vermilion stock, there were found two males in which the second longitudinal vein came to an abrupt end in the middle of the wing. The same culture produced seven more males with this new character in the next generation. To this character we gave the name snapt, only to learn later that, in every respect save that of sex dimorphism, it would appear to be identical with the autosomal character *radius incompletus* of the 3rd group of *melanogaster* as described by Borissenko (1930). Matings of the first two males with virgin sisters produced non-snapt offspring, the females of which were then mated to the seven snapt males of the later generation. We assumed that snapt was a sex-linked recessive, and therefore expected equal numbers of snapt and of non-snapt males and females among the progeny. But all the snapt individuals were males, although there was no deficiency in the number of the females. Small mass cultures of this generation gave large numbers of snapt males, whilst among the females there were two that were snapt, and from these cultures were raised which gave all snapt males and an occasional snapt female.

16 *Linkage Groups in Drosophila pseudo-obscura*

A Pointed yellow vermilion snapt male was then mated to a wild-type female and gave a progeny of 99 wild-type males and 121 Pointed females. Nine of these daughters were back-crossed to Pointed yellow vermilion snapt males, whilst others were used in a mass back-cross culture. Table I shows the total offspring of the nine pair matings. It became clear that snapt separated freely from Pointed yellow and vermilion in the male, and that in all of the eight classes in which snapt was included, very few females appeared: instead of the 877 snapt females expected, only 33 presented themselves. On the other hand, the whole of the 753 snapt males expected actually appeared. But though this character is always manifest in the male its range of expression is very wide (Plate III, figs. 1 and 2, show two varieties of snapt). The vein may be entirely absent, only slightly shortened, or there may be small gaps along its length. It remains to be shown whether

TABLE I.

*Total offspring of nine pair test-cross matings showing deficiency of snapt females.*

Nature of matings:		Pointed yellow vermilion snapt								♀♀ × Pointed							
		+	+	+	+	+	+	+	+								
		yellow vermilion snapt ♂♂.															
Region ...	0	1		2		3		1, 2		1, 3		2, 3		1, 2, 3		Total	
Class ...	+	<i>Pyvsp</i>	<i>P</i>	<i>yvsp</i>	<i>Py</i>	<i>vsp</i>	<i>Pyv</i>	<i>sp</i>	<i>y</i>	<i>Pvsp</i>	<i>yv</i>	<i>Psp</i>	<i>Pyvsp</i>	<i>v</i>	<i>yvsp</i>		<i>Pv</i>
Males	197	202	156	150	36	17	145	172	11	18	155	151	31	38	12	14	1505
Females	386	16	326	2	67	1	447	7	28	2	346	23	4	65	1	34	1755

this variation is due to environmental factors, to genetic modifiers, or to the action of both, but it would seem that selection can and does affect both the degree of expression in the male and also the percentage of penetration in the female. The figures given in Table I show that snapt is to be found at some point on the left arm of the X-chromosome not less than 50 units from vermilion. The fact that it gave almost the maximum of recombination with both Pointed and yellow shows that it is not situated between these two loci, for the distance between them is not more than 62 units.

*Tilt (tt)* (Plate III, fig. 3).

For the purposes of the discussion which is to follow, it is necessary to refer to this character which conforms fairly exactly to the autosomal tilt of *melanogaster* described by Bridges and Morgan (1923). It is sex-linked, recessive, and is probably on the left arm of the X. It takes the form of a gap in, or shortening of, the 3rd longitudinal vein, associated with a distinct upward tilting of the distal portion of the wing. The tilting

appears to be the direct result of the defect in the 3rd vein, for a slight shortening of the vein is not accompanied by a tilting of the wing, whereas a gap in the middle portion of the vein, even though quite small, is associated with a pronounced tilt. Moreover, it is to be noted that shortening of the 2nd, 4th and 5th veins does not produce the tilt effect. The investigation of this character is still embarrassed by the existence of yet another and so far unrecognised factor producing shortening of the other wing veins. Furthermore, tilt, like snapt, is largely sex-limited.

*Sepia* (*sc*) (Plate II, figs. 1 and 2).

In April 1933, among the progeny of a female carrying miniature in one *X*, and vermilion in the other, and heterozygous for several other mutant characters not yet described, a miniature male with very dark brown eyes and a yellowish testis sheath was encountered. He was at once mated to a beaded female, and in the  $F_2$  the new character reappeared. It was then noted that the darkening of the eye was a process which took place almost entirely after emergence, for the eye colour of the newly-hatched flies (Plate II, fig. 1) was no darker though somewhat browner than that of their wild type brothers. After emergence the eye colour darkened rapidly to become, in the old fly, almost black with a real purplish hue (Plate II, fig. 2). Since it resembled the 3rd chromosome mutant of *melanogaster*, *sepia*, described by Bridges and Morgan (1923), to it we gave this name.

A miniature *sepia* male was crossed to a yellow female.

Table II shows that the percentage of recombination of *sepia* with yellow was 40, and with miniature 38. These figures did not indicate on

TABLE II.

		Nature of $P_1$ cross: $\frac{\text{miniature sepia}}{\text{yellow}}$ .								
		Total males in nine $F_1$ pair matings.								
Region ...		0		1		2		1, 2		
Class ...		<i>m</i> <i>sc</i>	<i>y</i>	<i>ym</i> <i>sc</i>	+ + +	<i>m</i>	<i>y</i> <i>sc</i>	<i>ym</i>	<i>sc</i>	Total
		177	138	19	21	103	86	8	18	570

which arm of the *X* *sepia* was to be placed, since there are some 60 units above yellow and nearly 100 below miniature unmarked. If *sepia* were on the right arm, it should then be fairly close to beaded which is some 40 units away from yellow. So a beaded miniature *sepia* snapt male was mated with a wild type female, and pair matings of the  $F_1$  made. Table III gives the results obtained from seven such pair matings. The

18 *Linkage Groups in Drosophila pseudo-obscura*

high percentage of recombination with beaded (46) showed that sepia could not be above yellow.

Table IV gives the results of a three point experiment involving miniature, sepia and snapt. The order indicated by these figures is miniature, sepia, snapt, but recombination of all three genes with one another is so high as to suggest either that there are more than 100 units involved, or else that the frequency of crossing-over along the left arm of the *X* is abnormally high.

TABLE III.

		Nature of $P_1$ cross: $\frac{\text{beaded miniature sepia snapt}}{+ \quad + \quad + \quad +}$ .										
		Total males obtained.										
Region ...	0	1	2	3	1, 2	1, 3	2, 3	1, 2, 3				
Class ...	+ <i>bmsesp</i>	<i>b msesp</i>	<i>bm scsp</i>	<i>bmsc sp</i>	<i>m bscsp</i>	<i>bsp msc</i>	<i>sc bmsp</i>	<i>bse msp</i>	<i>bse msp</i>	<i>bse msp</i>	Total	
	43 14	12 21	27 12	21 10	19 9	6 10	14 9	6 6	6 6	6 6	239	

TABLE IV.

		Nature of $P_1$ cross: $\frac{\text{miniature sepia snapt}}{+ \quad + \quad +}$ .				
		Total males obtained in eight $F_1$ pair matings.				
Region ...	0	1	2	1, 2		
Class ...	+ <i>mseps</i>	<i>m seps</i>	<i>mse sp</i>	<i>mep se</i>	<i>mep se</i>	Total
	138 86	88 83	108 44	46 84	84	677

TABLE V.

		Nature of $P_1$ cross: $\frac{\text{sepia snapt}}{+ \quad +}$ .				
		Total males in 14 pair matings.				
		Non-cross-overs		Cross-overs		
Class ...	+ <i>sesp</i>	<i>sc sp</i>	<i>sc sp</i>	<i>sc sp</i>	Total	
	478 367	257 216	257 216	216	1318	

Table V gives the figures of another sepia snapt cross. The percentage of recombination between the two genes is slightly lower. But for the present nothing more definite can be said than that snapt and sepia are both to be found on the left arm of the *X*.

On the other (right) arm of the *X* two mutations have occurred in already known loci, one an allelomorph of white, and the other allelomorph with yellow.

*Eosin*<sup>2</sup> (*w*<sup>e2</sup>) (Plate II, figs. 5 and 6).

In February 1934 there appeared among the progeny of a Stubble eyeless mating two males with an eye colour which we now regard as

probably identical with that described by Lancefield (1922) and named eosin by him. The colour is a clear yellowish brown resembling in the mature eosin fly that of the young purple eye (Plate II, fig. 5). It suggests a deficiency for red and a partial deficiency for brown as well, and so for this reason the eye is paler than is that of purple<sup>1</sup> flies of the same age. The testis sheath is yellowish whilst that of purple<sup>1</sup> is almost white. From this it is inferred that in the eosin eye there is a larger proportion of yellow than in the purple<sup>1</sup>. These males were mated to white<sup>5</sup> females, in order to ascertain if the new eye colour belonged to the white series of alleles; to wild type females, in order to obtain a pure stock; and to vermilion females, in order to determine the combined effect of vermilion and eosin.

The daughters of the white females had an eye colour which was only slightly paler than that of the eosin male. When pure eosin females were obtained it was noted that their eye colour was somewhat darker than that of the eosin males. The vermilion eosin combination proved to be pale lemon (Plate II, fig. 6).

#### *Cuprous (y<sup>e</sup>).*

Among the progeny of a purple<sup>2</sup> pair, flies of both sexes, with a distinct greenish dark yellow body colour were observed in March 1934, and from these a stock was quickly secured. To the new character the name "cuprous" was assigned. Cuprous males were mated with yellow females. The offspring consisted of yellow males and of females which were intermediate in body colour between yellow and cuprous. Cuprous is always separable from wild type, though it grows brownish with increasing age. As a working character it is not so good as is its allele yellow, which at all ages is much more sharply distinguished from wild type.

#### CHROMOSOME III.

Glass (*gl*) and Stubble (*Sb*) form the nucleus of a linkage group which we propose to assign to the 3rd chromosome. These mutant characters are not sex-linked, they are not linked with members of the 2nd group already described or with those of the 4th group (see below), and the high rate of crossing over between the two genes makes it highly improbable that the small 5th chromosome can claim them. They were both found in February 1932 within a week of each other among the progeny of a yellow vermilion pair, the male of which was singed and the female heterozygous for this character.

*Glass (gl)* (Plate II, fig. 7).

Six females and four males with abnormal eyes were observed and from them a true-breeding stock was secured without difficulty. The character was given the name "glass" for the reason that it seemed to conform closely to the description of the mutant of the same name in *melanogaster* as described by Bridges and Morgan (1923), although the expression of the character differs in the two species. In *pseudo-obscura* the eye is reduced in size but to a less degree than in *melanogaster*. There is a smooth, colourless rim around the eye, and in the central area the facets have lost both their sharpness and regularity, forming a surface apparently composed of irregular rounded projections, whilst the hairs are more numerous than in the wild type and point in all directions to give the eye an appearance of extreme roughness. The pigment appears to be greatly reduced (equally so in both sexes in *pseudo-obscura*, whereas in *melanogaster* the character is sex-dimorphic), only a thin pinkish or brownish hue usually remains. In combination with vermilion the glass eye is creamish. Glass is easily recognised by the naked eye; but although the viability and productivity of the stock are excellent, the usefulness of the character is limited—it cannot be usefully combined with any of the mutant eye colours.

*Stubble (Sb)* (Plate II, fig. 7; Plate III, fig. 4).

A few days after glass was first encountered a single female with noticeably short thick bristles was found in the same culture. The character was regarded as a variant of singed, though unlike any singed observed previously. This female, presumed not to be a virgin, was isolated together with a singed brother. The short thick bristle character reappeared in half of her offspring, and since she herself was heterozygous for singed, half of the flies with this new character were also singed. To the new character the name "Stubble" was given for the reason that (in the heterozygous form) (Plate II, fig. 7) it is exactly similar to the 3rd chromosome mutant of the same name in *melanogaster* (Morgan, Bridges and Sturtevant, 1925). Stubble, it was noted, exaggerated the twisting of singed bristles. By outcrossing to wild type Stubble was freed from other mutant characters, and flies homozygous for Stubble were obtained: they were small and weak and did not live to breed. In the homozygous form (Plate III, fig. 4) the bristles are mere stumps and the wings, legs and general conformation of the fly, completely normal in the heterozygous form, are markedly abnormal. The wings are broader than normal and are often spread and curved or warped either in an upward or downward

direction; commonly they show great irregularities of size and shape, and the body as a whole presents a cramped or hunched appearance. The legs, especially the third pair, are commonly curved, swollen, twisted or bent. At this time it seemed that the physical disabilities of the homozygous Stubble must make it impossible to obtain a pure stock, for repeated attempts to maintain small mass cultures failed. Yet it did not seem to be that the flies were infecund, or the matings necessarily infertile, for occasionally a homozygous female mated with a heterozygous brother or to a wild type male produced offspring. For many generations Stubble was maintained in the heterozygous form until about a year after its discovery one homozygous culture proved to be successful, and from this time no difficulty in maintaining a pure stock has been encountered. It is of interest to record that Stubble, as now exhibited, differs from the character when first observed in that the peculiar deformities are somewhat less pronounced. Stubble thus provides an excellent example of a character which, when first observed, was on the borderland of lethality, and which, a year or so later, has become one of the best among genetically useful mutants. We are unable to decide whether this change in the nature of the character has been the effect of selection on gene environment or whether, since its first appearance, the Stubble gene has mutated slightly to yield a less unbalanced condition of the organism.

Stubble in the homozygous form is easily recognisable by the naked eye, and in the heterozygous form by low magnification. The double dominant Scute Stubble is viable in homozygous condition and forms a combination equivalent in usefulness to the Star Dichæte of *melanogaster*.

Glass, having given recombination in  $F_2$  with both purple and short (see below), was tested against Stubble. Females heterozygous for both glass and Stubble were backcrossed to glass males.

Table VI shows the results given by six pair matings. About 47 per cent. recombination between glass and Stubble was observed. To provide

TABLE VI.

Nature of cross:	$\frac{\text{Stubble} +}{+ \text{glass}} \text{♀♀} \times \text{glass} \text{♂♂}$			
	Non-cross-overs		Cross-overs	
Pair	<i>Sb</i>	<i>gl</i>	+	<i>Sbgl</i>
1	45	30	36	35
2	34	31	29	36
4 and 5	25	28	38	20
7	33	22	28	18
9	36	30	22	21
Totals	173	141	153	130

a check some heterozygous males were backcrossed to glass females: the offspring showed no recombination.

## CHROMOSOME IV.

Two autosomal recessive genes, short 4 ( $s_4$ ) and jaunty ( $j$ ) have been shown to give independent assortment with both the Scute and Stubble groups and have therefore been assigned to the remaining rod-shaped autosome.

*Jaunty (j).*

Jaunty was found in a miniature stock, the combination miniature jaunty yielding an effect very much like the dominant Curly character in *melanogaster*. But, freed from miniature, the new mutant gene gave an effect much more like the 2nd chromosome recessive jaunty of *melanogaster* (Bridges and Morgan, 1919), and so to it this name was given. The wings are upturned at the tips, usually only the posterior half of the wing being involved as is the case in *melanogaster* jaunty and simplex ski.

*Short<sub>4</sub> (s<sub>4</sub>) (Plate III, fig. 5).*

Whilst a stock of jaunty was being built up, several flies with shortened veins were noticed in the cultures. This new character seemed to be identical with, and a reappearance of, the sex-linked short of Lancefield (1922). The fourth and fifth longitudinal veins only were involved, the

TABLE VII.

Pair	Nature of cross: $\frac{\text{short}_4 \text{ jaunty}}{+ \quad +} \text{♀} \times \text{short}_4 \text{ jaunty} \text{♂}$ .			
	Non-cross-overs		Cross-overs	
	+	$s_4 j$	$s_4$	$j$
1	100	83	9	13
4	106	93	11	11
5	109	89	16	9
6	80	65	8	7
7	60	66	5	5
9	77	75	11	11
Total	532	471	60	56

fifth being shortened up to the level of the posterior cross vein, occasionally slightly above or below this, whilst the fourth extended to a point about midway between this level and the marginal vein. The posterior cross vein itself is often incomplete and may be entirely absent if the culture is raised in low temperatures. Though we called this gene short<sub>4</sub> solely for the reason that the character seems to correspond closely to the sex-

linked short of Lancefield, in our opinion it is a homologue, and probably an allelomorph of the 2nd chromosome recessive abrupt of *melanogaster*.

When one of the short<sub>4</sub> jaunty females was outcrossed to a wild type male the offspring, both males and females, were wild type. In the  $F_2$  short<sub>4</sub> and jaunty reappeared together, giving a low percentage of recombination, this suggesting that they were on the same chromosome and fairly close together. The figures given in Table VII obtained from the mating of females heterozygous for short<sub>4</sub> jaunty with short<sub>4</sub> jaunty males from stock, gave a recombination value of 9.8 per cent., the closest linkage figure yet obtained in our stocks for autosomal genes.

#### CHROMOSOME V.

##### *Tangled (tg).*

While none of the mutants now being studied can with certainty be assigned to the dot-like 5th autosome, it is highly probable that one known to us as tangled, and affecting wing venation is really a representative of the 5th linkage group. The longitudinal veins in the distal part of the wing approach each other in pairs to give the appearance of being entangled with each other. It is not sex-linked and gives independent assortment with the Scute and Stubble groups, but so far the tests with short<sub>4</sub> and jaunty, though suggestive of independence, are not altogether conclusive, for the tangled wing is often tilted and so blistered that the observation of the veins is made most difficult.

#### NOTES.

- (i) *On the homology of the chromosomes of pseudo-obscura and melanogaster.*

Metz (1916), Lancefield (1922), Lancefield and Metz (1922) have all suggested that one arm of the V-shaped X-chromosome of *Drosophila pseudo-obscura* and *Drosophila willistoni* corresponds to part of, if not all of, the rod-shaped X's of such species as *Drosophila melanogaster*. Koller (1932) further suggested that the other arm of the V-shaped X corresponds to a portion of one of the autosomes in those species (such as *melanogaster*) with a rod-shaped X-chromosome; the rearrangement being the result of a series of translocations. Certain of the facts presented in this paper bear upon this matter for they would appear to show that:

- (a) A considerable portion of the left arm of the V-shaped 3rd chromosome of *melanogaster* is homologous in part or in whole with the

rod-shaped autosome of *pseudo-obscura* which we have designated the 3rd.

(b) The constitution of the right arm of the *melanogaster* 3rd possesses a considerable degree of homology with the left arm of the *pseudo-obscura* X.

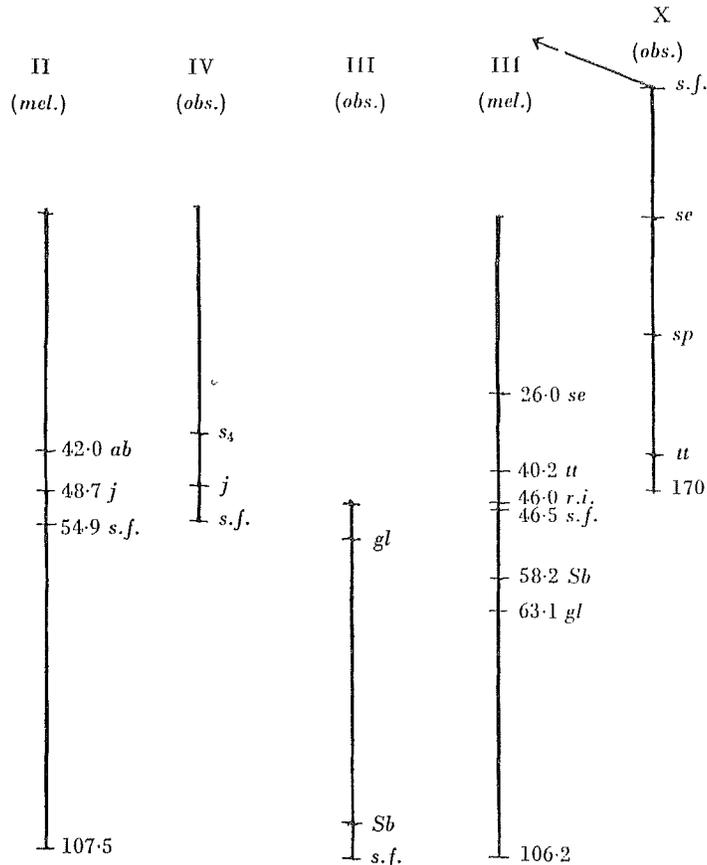
(c) Possibly the right arm of the V-shaped 2nd of *melanogaster* is in part homologous with the small rod-shaped autosome of *pseudo-obscura* which we have called the 4th.

The left arm of the *melanogaster* 3rd is about 60 units in length with Stubble about 12 units from the spindle fibre attachment and with glass 5 units away from Stubble. Cytological observation makes it likely that this is approximately the length of the two larger rod-shaped autosomes of *pseudo-obscura*, one of which, we suggest, includes Stubble and glass, but separated not by 5 units as in *melanogaster* but by the greater part of the length of the chromosome. This marked change in linkage value could be accounted for by postulating that two inversions within the arm of the chromosome had occurred in such a way as to separate the genes but not to alter the total chromosome length. One inversion occurring in the portion between the point of the spindle attachment and a point just below Stubble would bring this gene nearer the spindle and widen the distance between it and glass. A second inversion including the whole region below Stubble would extend the separation of the two genes to almost the whole length of the chromosome. The validity of this assumption will of course be tested as and when other mutant genes between these points and identical in the two species present themselves. The physiological differences which make the homozygous form of Stubble lethal in one species and not in the other may possibly be referred to the readjustment of genic environmental influences that would follow from these inversions, or to some actual modification of the gene if the break occurred very close to it; or the difference may be one of ordinary allelism.

The constitution of the right arm of the *melanogaster* 3rd shows, by the same method of comparison, a considerable degree of homology with the left arm of the *pseudo-obscura* X. Certainly the three sex-linked genes *snap*, *tilt* and *sepia* of *pseudo-obscura* are exceedingly like the *radius incompletus*, *tilt* and *sepia* respectively of *melanogaster*. But it is a matter of greater difficulty to visualise the process by which the required rearrangement could have occurred, for the whole of the right arm of the *melanogaster* 3rd is less than half the length of the left arm of the X of *pseudo-obscura*, and moreover these three genes are further separated each from the other than they are in *melanogaster*. A single inversion could perhaps

explain the increase in the distance between sepia and snapt, but there would still remain an equal length of chromosome separating these genes from tilt.

The identity of the jaunty genes in the two species seems fairly



Text-fig. 1.

certain. Furthermore, it is not unlikely that the gene we have called short<sub>4</sub>, because of its close correspondence with Lancefield's sex-linked short, is actually allelomorphic to the abrupt of *melanogaster* which is separated from jaunty by about 7 units; our calculations, based on little over 1000 flies, give 10 per cent. recombination between the jaunty and short<sub>4</sub> of *pseudo-obscura*.

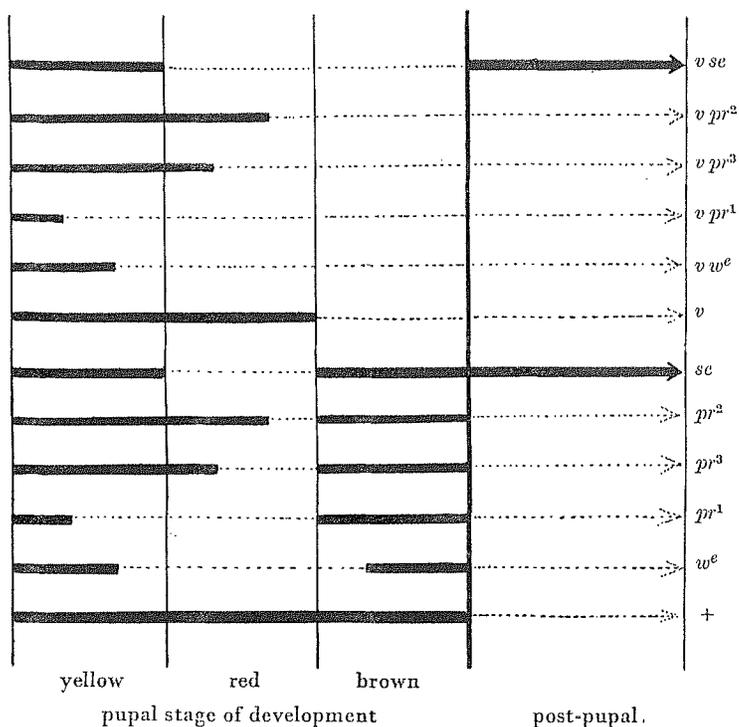
(ii) *On the nature of the action of genes for eye colour.*

We have been fortunate in that in our stocks of *pseudo-obscura* no less than six useful mutant genes affecting eye colour have already become available for examination. Of these the purple alleles, sepia and vermilion, are perhaps the most interesting, and a study of them has permitted us to speculate concerning the possible nature of the action of such genes. It seemed to us that sepia, like the purples, acted by suppressing the red pigmentation, and that the vermilion gene was a suppressor of the brown. It was therefore predicted that the sepia vermilion combination would give a very pale eye colour. A miniature sepia male was mated to a *yvsn* female, and pair matings of the  $F_1$  individuals made. In the  $F_2$  a large number of sepia vermilion males were obtained. At the time of emergence the eye colour of these flies was an opaque greenish lemon (Plate II, fig. 3), whilst the colour of the testis sheath was similar to that of pure sepia flies. But further observation threw a flood of light on the action both of sepia and of vermilion, for, after emergence, the lemon colour darkened gradually to a brown, and in old flies, almost to the dark colour of pure sepias (Plate II, fig. 4). It became clear that the vermilion gene operates entirely during the pupal stages of development, whereas sepia evokes its greatest effect during post-pupal life. In the case of sepia and vermilion, as also in that of the purples, there is no effect to which the term "disproportionate modification," suggested by Bridges and Morgan (1923), can be applied, nor anything that can be properly ascribed to "interaction," for though the two genes affect the same developmental process—that of pigment formation—they do so at different times, at different stages of development, and neither in time nor in space do they combine or conflict with each other. Text-fig. 2 is an attempt to interpret graphically the nature of the action of such genes. In development there is a pupal and a post-pupal stage. Observations of the development of eye colour in the wild type flies permit us to describe this process as one in which first yellow pigment is formed, then red, and lastly brown, all within the pupal stage of development. The process then stops, there is no further pigment formation during post-pupal life, although there is a darkening of the eye with increasing age, not the result of a formation of fresh pigment but of changes in the pigment already deposited.

The action of the vermilion gene is to interfere with the normal processes of pigmentation in such a way as to prevent the formation of the brown, and it acts entirely within the pupal stage. The vermilion eye darkens with age, but remains vermilion to the end; in *pseudo-obscura* the

old vermilion fly is always clearly distinguishable from wild type, its eye colour never becomes brownish red.

The sepia gene interrupts the formation of the red during the pupal stage, and in addition so acts as to prevent the cessation of pigment formation which normally occurs at the beginning of the post-pupal stage of development. That this is so is clearly seen from the remarkable changes which take place in the vermilion sepia eye, for here the vermilion has



Text-fig. 2.

exercised its usual effect by inhibiting the normal formation of brown pigment before emergence, but in the post-pupal stage there is an abnormal accumulation of brown pigment due to the presence of the sepia gene, and the pale lemon colour with which the fly starts its life does not merely become a deeper lemon but is gradually transformed into an intense brown.

In the wild type eye, yellow, red and brown, and in this order during development, are laid down entirely during pupal life. Eosin, the purples and sepia constitute a series which suppress, in part or in whole, the red.

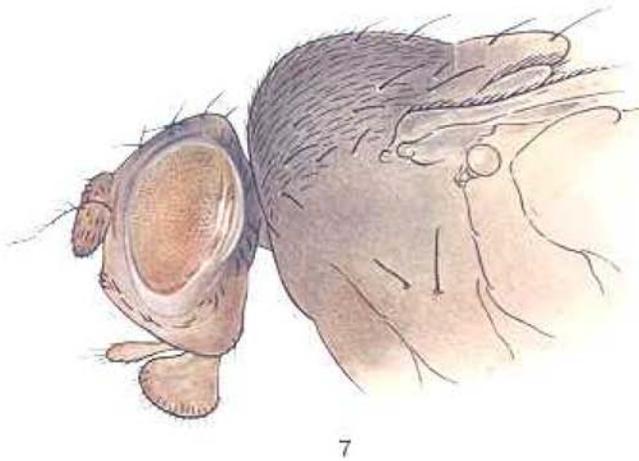
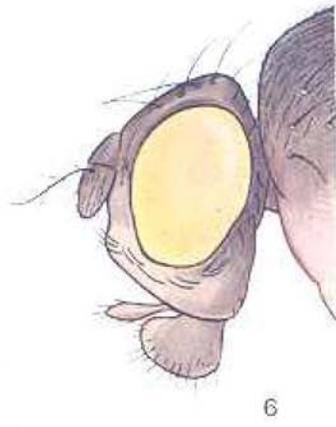
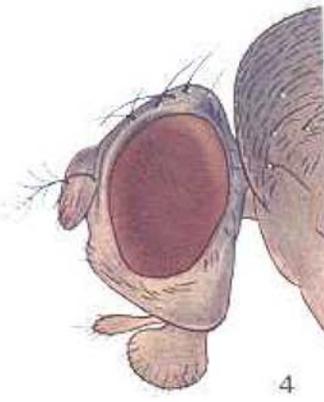
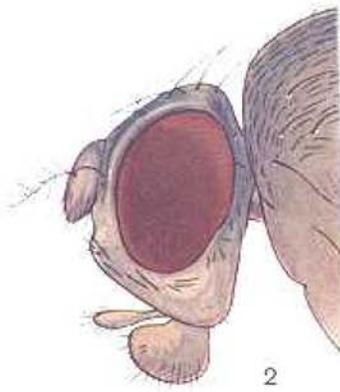
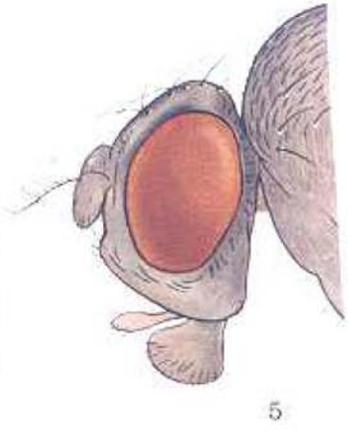
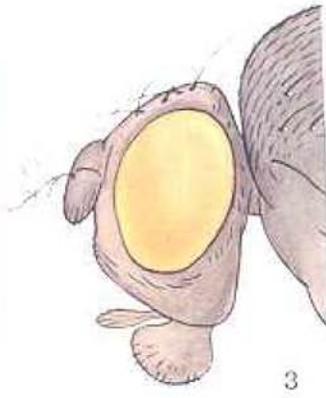
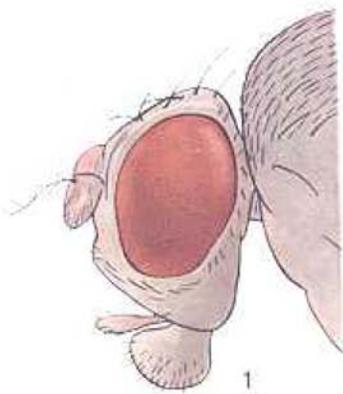
Eosin also suppresses in part both the yellow and the brown. Purple<sup>1</sup> suppresses also in part the yellow. Purple<sup>2</sup> and purple<sup>3</sup> suppress only a portion of the red. On the other hand, vermilion suppresses nothing but the brown. In combinations of the red suppressors with the brown suppressor, vermilion, therefore, the actual colour of the eye is determined by that portion of the yellow, red, brown of the wild type which remains unaffected by the action of either of the two mutant genes present. Thus, as could be predicted, the vermilion eosin eye is pale yellow, whilst the vermilion purple<sup>1</sup> eye is almost white.

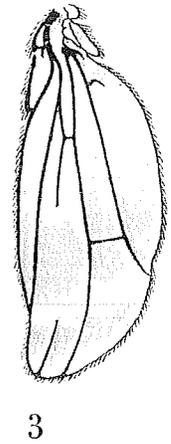
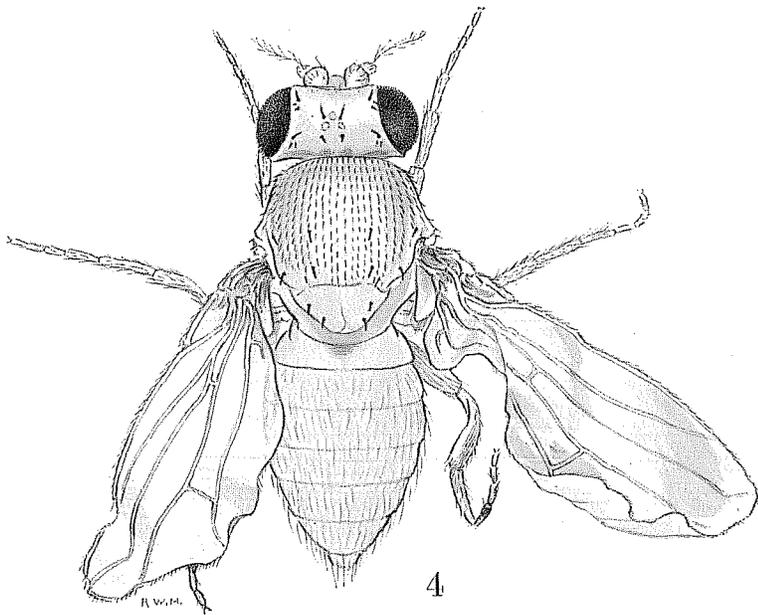
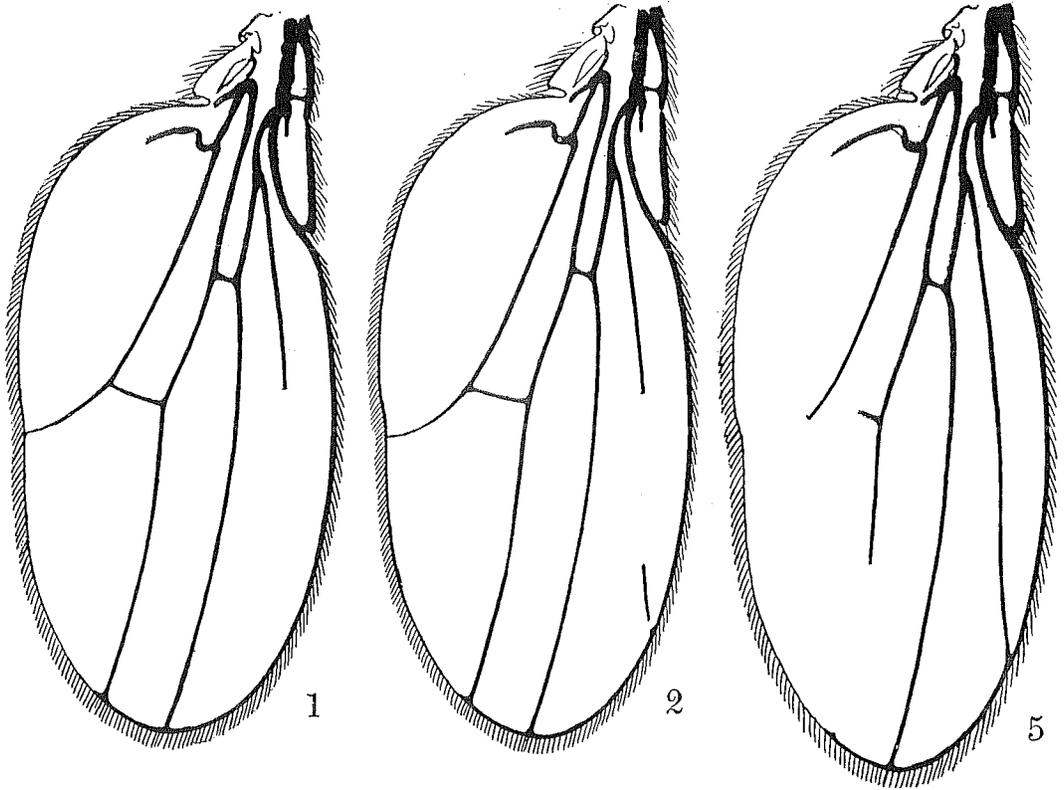
Support for the views suggested by this superficial analysis of the nature of the genes affecting eye colour can be found in a study of the colour of the testis sheath. In this there is no brown, and the development of the yellow and the red, which is always parallel to that in the eye, is easily observed and offers a convenient means of measuring the seriation of events and the proportion of these pigments in the eye, especially in those stocks in which, in the eye, slight differences in the proportion of the yellow and the red are masked by the presence of brown.

If the suggestions implied in this diagram are warrantable, it would follow that the so-called genes for eye colour are not themselves directly concerned with pigmentation at all, but exert their action upon the mechanism which is responsible for the formation and deposition of pigment. If it is assumed that the colour of the pigment is determined by the existing chemical possibilities of the particular stage of development at the time when the pigment is formed, then any factor which interrupts, defers or prolongs the process will necessarily alter its effect in terms of colour.

#### SUMMARY.

1. Snapt, tilt and sepia are three genes on the left arm of the X-chromosome. On the right are eosin, an allelomorph of white, and cuprous, an allele of yellow.
2. Stubble, a dominant, and glass form the nucleus of the 3rd linkage group, and short<sub>4</sub> and jaunty that of the 4th. Tangled, it is thought, belongs to the 5th.
3. It is suggested that: (i) a portion of the left arm of the 3rd chromosome of *D. melanogaster* is homologous in part or in whole with the 3rd autosome of *D. pseudo-obscura*; (ii) the right arm of *melanogaster* 3rd is in part homologous with the left arm of *pseudo-obscura* X, and (iii) the





right arm of *melanogaster* 2nd is in part homologous with *pseudo-obscura* 4th.

4. It is suggested that the apparently disproportionate effect of some genes affecting eye colour is in reality cumulative.

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## EXPLANATION OF PLATES II AND III.

## PLATE II.

- Fig. 1. Eye colour of pure sepia fly at emergence.
- Fig. 2. Eye colour of same fly when 3 weeks old.
- Fig. 3. Sepia vermillion at emergence.
- Fig. 4. Sepia vermillion at 3 weeks old.
- Fig. 5. Eosin.
- Fig. 6. Eosin vermillion.
- Fig. 7. Glass with heterozygous Stubble.

## PLATE III.

- Fig. 1. Snapt.
- Fig. 2. Snapt.
- Fig. 3. Tilt.
- Fig. 4. Homozygous Stubble.
- Fig. 5. Short<sub>4</sub>.