

A CASE OF CONDITIONED DOMINANCE IN *DROSOPHILA OBSCURA*

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(With Plate XXXI.)

DESCRIPTION.

THE only case of conditioned dominance recorded as such in the literature of *Drosophila* is that described by Lebedeff (1932) in which the recessive character, ruffled, assumed a dominant effect in the heterozygous condition when in the presence of the gene, Rounded. Nevertheless, Morgan and Bridges (1913) have earlier found that several genes for recessive light eye colours show a diluting effect in the heterozygous form in flies that are at the same time homozygous for other light eye colour genes. These also must be recognised as cases of conditioned dominance, a genetic situation which offers especially useful material in any attempt to study the nature of genic action and of intergenic relations. An instance of this sort has recently been observed in *Drosophila obscura*, a preliminary account of which is given in this paper.

The mutation to be described was first noted in a single female among the progeny of a mating between a female heterozygous for Pointed, yellow, vermilion, snapt, and a male carrying the same sex-linked genes, both being heterozygous for a newly arisen mutant character similar to scute in *D. melanogaster*. The eyes of this female were lighter and more yellowish than those of the vermilion sibs, and the presence of a new mutant allelomorph of vermilion was suspected. The colour was much paler than that produced by the interaction of heterozygous white on vermilion, and moreover the difference remained clearly perceptible as the female grew older.

This light-eyed female was mated to a wild type brother; and her sons were of two distinct classes, ordinary vermilion and light vermilion, a fact which strongly confirmed the idea that the new character was sex-linked and allelomorphic to vermilion. But when the light-eyed males were bred in pairs to their wild type sisters, the offspring produced by some of these matings contained, in addition to wild type, vermilion and light vermilion, two entirely new and unexpected types of eye colour. One of these was a dark brownish purple colour, clearly dis-

tinguishable from wild type both by its translucency and by a deficiency for red pigment. Though superficially it bears a resemblance to the well-known second chromosome gene, purple, in *D. melanogaster*, the resemblance is restricted to flies of middle age, and in the purple of *D. obscura* there has been observed no gradual deepening through yellowish pink, ruby and red as described by Morgan and Bridges (1919) in the case of *D. melanogaster*. Indeed, though in newly hatched flies the colour is sometimes extremely light it is always characterised by a lack of red pigment; at its lightest it may be described as yellowish brown. The males of this class showed a completely white abdomen, and when they were dissected it was seen that in place of the bright orange tint which distinguishes males of this species only a faint trace of creamish colour was present in the testicular sheath. It will be remembered that this colourless condition of the testicular sheath is also associated with white eye in both *D. melanogaster* and *D. obscura*.

The other unexpected class of flies which appeared in these F_2 cultures was at first indistinguishable from the familiar white eye, but in later cultures it was observed that there was a considerable degree of variation, ranging from the greyish white typical of this mutation in this species to pinkish cream, though the general effect among the large majority of flies was nearer to pure white, the more deeply pigmented ones being rare. Further work with purple shows that this variation in the double recessive is due to the action of different allelomorphs of purple, two of which have been isolated. Table I gives the numbers obtained in two of these cultures.

TABLE I.

Progeny of two light vermilion ♂♂ by wild type sisters.

Constitution of parents	Type of progeny	♀♀	♂♂	Totals	Expected
$\overset{v}{\text{pr}}$ ♂♂: Y +	Wild type	53	45	98	93
	Vermilion	26	33	59	31
	Light vermilion	14	8	22	62
$\overset{v}{\text{pr}}$ ♀♀: + +	Purple	21	19	40	31
	White	15	13	28	31
	Totals	129	118	247	

The hypothesis regarding the nature of light vermilion had therefore to be abandoned, and an explanation sought which would account for the presence of three new characters instead of one.

Various matings were arranged in order to test the constitution of each class of flies, and it was found that, when light vermilion males and

two classes in most of the counts is probably explained. Thus, on the hypothesis that white females were homozygous for both purple and vermilion, and that purple in the heterozygous condition had a modifying effect on vermilion, *all* the sons of white females should have appeared light vermilion.

Finally, a white male was out-crossed to a wild type female and the offspring mated *inter se*. Table II gives the numbers obtained from two successful pair matings. The daughters were wild type and purple in a 3 : 1 ratio, the sons being of the five types expected. The discrepancy which appears in the numbers of the three classes of which vermilion forms an element is due to the presence of a peculiar lethal which eliminates a quarter of the male offspring of this line, and which is now being studied.

DISCUSSION.

I. *Time interaction.* There are two points of interest connected with the phenotypic expression of the double recessive, vermilion purple, which seem to bear on the question of order of genic action in development. It has been noted that this class of fly is white eyed. A somewhat similar case is reported by Agol (1931) in *D. melanogaster* where flies carrying apricot and ruby were white eyed, and Wright (1932) reports that the double recessives vermilion brown and scarlet brown were white eyed. This type of interaction between genes seems to point strongly to a differential time action as being solely responsible for the effect produced. If it is assumed that the vermilion factor causes a premature cessation in the formation of pigment and that the purple factor causes a delay in the starting of this process, it is easy to see that when these genes, together, are operative, they can act in a complementary manner, with the result that no pigment at all is produced.

The other point of interest concerns the relation of the pigment present in the eye to that present in the testicular sheath. It may be assumed that because the testis sheath of white-eyed males is devoid of colour that the gene at the white locus controls the formation of colour both in the eye and the testis sheath. This view is supported by the fact that the other allelomorphs of white co-exist with a similar and graded effect of colour in the testis. But in the case now described the purple gene, though permitting a considerable development of colour in the eye, yet inhibits it almost completely in the testis. This may be explained on the hypothesis that different genes for colour control the production or suppression of different kinds of pigment, as well as the time of its

deposition. Thus, though the purple eye here described is often actually darker than the wild type eye, yet its darkness seems to be due not to the presence of more pigment but to a deficiency in respect of red pigment which gives the brighter effect to the wild type eye. Though darker it is thus always comparatively thin and translucent, while the wild type eye is opaque. Since the pigment normally contained in the testicular sheath is bright orange, it is easy to see that the specific action of one and the same gene in suppressing or greatly reducing the development of this red pigment could render the testis colourless, and at the same time leave the eye brownish purple instead of dark red. Combining these two effects we have a genetic demonstration of the order in which the process of pigmentation occurs in the developing embryo, red pigment being first deposited simultaneously in the eye and in the testicular sheath, and at a later stage (the stage at which the inhibiting action of vermilion begins and that of purple ceases) the deposition of brown pigment in the normal eye takes place.

The sort of effect described as dilution which is produced when one gene is present in the duplex and the other in the simplex state supports the view that the action of both these genes is definitely an inhibiting action. For, dilute vermilion is light vermilion, or vermilion in which the red pigment is only partly inhibited, and dilute purple is pale purple, or purple in which the brown pigment is partly inhibited. In neither case does the "dilution" appear as a mixture of both colours.

II. *Quasi-allelomorphism*. The rare occurrence of cases where a condition resembling dominance is established in the presence of a specific gene, and the normally dominant action of the wild type allelomorph is partly overcome, would appear to be of special interest as affording a useful indication of the specific co-ordination that exists between genes in their relation to each other and as regards their rôle in developmental physiology.

The phrase "conditioned dominance" which is applied to these cases may be misleading, inasmuch as it begs the question and complicates the already intriguing problem of the nature of dominance; at any rate the situation may be looked at from another point of view, and other genetic relations than those of dominance and recessivity should be considered.

It is possible, and strongly suggested by the large mass of data that has been collected on the genetics of *Drosophila*, that some sort of homogeneity akin to that which exists between allelomorphs may exist in different degrees between other genes also, by reason of the similarity of their functions even though they are widely separated in space on the

chromosomes. Of the many genes concerned with the development of eye colour in *Drosophila*, whether they influence the production of the different pigments directly, or regulate the rate and order of their deposition, or produce their effect in some other way, it is conceivable and highly probable that no single process is the function of any single gene.

The manifold effects of single genes are a matter of simple observation, but the converse of this fact is also worth considering, namely, that every character or part of a character is probably related to many genes.

A gene becomes known only when it mutates, and the aberrant nature of the effects produced by the mutated gene gives an indication of part of the function, or at least of the general nature of the function, of the normal gene at that particular locus. But the study of allelomorphic series also shows that no single mutation is likely to indicate the whole field of action of any gene. Similarly, a survey of effects produced by many mutated genes shows that very similar and even indistinguishable effects may be produced by genes in entirely different loci. All the known facts, in short, go to show that in the gene complex causes and effects are very closely interwoven. Hence, while we are sure that the members of a pair of genes which are produced by the division of one gene are identical in every respect, there seems no reason to doubt that between other genes some degree of homogeneity may exist, that is, that genes at different loci may be identical in part—if not all—of their function. Consequently, a degree of interference with each other's effects would be possible under suitable conditions and the result might be regarded not as a case of assumed dominance, but rather as one of quasi-allelomorphism.

If the two genes in question occupied identical loci on the chromosomes they would, when present together, produce a dilution effect, but, since they occupy different loci their action is complicated by the fact that two pairs of genes instead of one are involved, and the end-result is conditioned by the proportion of (in this case dominant) wild type to (recessive) mutant allelomorphs present. When the latter are both present only in the simplex state their effect is inhibited by the two wild-type allelomorphs. But when either of the mutant forms is present in the duplex state, one dose of the other may suffice to enable it to express itself partially, for the proportion is now three not-wild to one wild-type gene. The result of this proportion in the case described here is a dilution of vermilion or of purple as the case may be. But it is postulated that this

effect is only achieved because of some fundamental similarity in the nature of the two genes concerned. Such forms of genic interaction as are found in specific modifiers, disproportionate modifiers and multiple factors may find a common interpretation here. But it is possible that most instances of genic parity escape recognition from the circumstance that the changes produced by mutation in similar genes may fall short of one another in their effects, for we know that this may happen even in the case of simple allelomorphous forms, as Serebrovsky (1930) has shown in the case of scute.

SUMMARY.

An autosomal recessive eye colour purple in *D. obscura* is described. The mutant is similar to purple in *D. melanogaster* but is peculiar in that it acts as a dominant diluter of vermilion. The double recessive vermilion purple is white. The time interaction of the two genes is discussed with reference to the process of pigmentation.

It is suggested that the modes of interaction of these two genes, vermilion and purple, may be explained on the assumption that they are similar in nature and in function, and hence behave as allelomorphs.

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EXPLANATION OF PLATE XXXI.

Fig. 1. Homozygous purple.

Fig. 2. Wild type.

Fig. 3. Homozygous vermilion.

Fig. 4. Homozygous vermilion with heterozygous purple.

Figs. 5 and 6. Homozygous vermilion with homozygous purple.

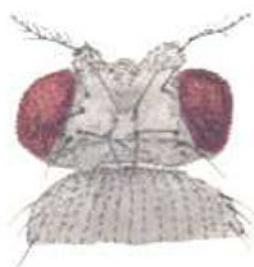


Fig. 1.

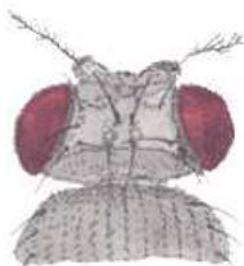


Fig. 2.

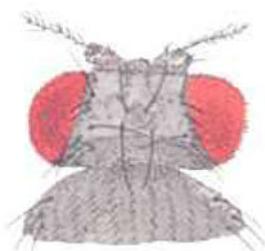


Fig. 3.

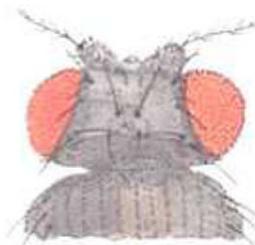


Fig. 4.

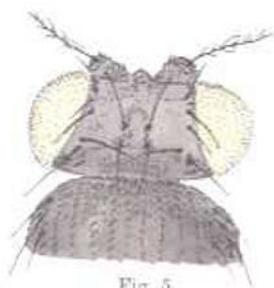


Fig. 5.

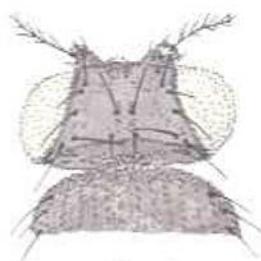


Fig. 6.