

MUTABLE CHARACTERS OF *DROSOPHILA VIRILIS*

I. REDDISH-ALPHA BODY CHARACTER *

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INTRODUCTION

In a preliminary report on the behavior of the "reddish" body-color character (DEMEREK 1926a) it was suggested that the unusual results obtained in different experiments could readily be explained by the assumption that reddish mutates frequently to the wild-type. This assumption has been made still more probable by the results obtained in recent studies on reddish. It is also supported by the work on the behavior of the miniature- α wing character (DEMEREK 1926b) and the magenta- α eye-color character (DEMEREK 1927a), both of which revert

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in the same way as reddish does. In this paper an endeavor will be made to give a detailed account of the results obtained only in experiments with reddish. The details of the experiments with miniature- α and magenta- α will be presented in subsequent papers of the same series.

NOMENCLATURE

To designate a character showing frequent heritable changes, the terms "mutable", or "frequently mutating" will be used. The process of change will be called "mutation", and also "reversion"; since in the case of reddish it was observed that the change occurs only in one direction, namely from reddish to wild-type. Thus the term "mutation" and its derivatives are applied both to the reversion of a mutant character to the wild-type, as well as to the origin of the mutant character from the wild-type.

The Greek alphabet is used to distinguish mutable from constant allelomorphs.

The symbol $re-\alpha$ will be applied to the mutable reddish. Since reddish is an allelomorph to yellow, and yellow has been known longer (METZ 1916) than reddish the strictly correct symbol for the mutable reddish would be $y^{re-\alpha}$. As a matter of convenience, however, the shortened symbol $re-\alpha$ will be used in this paper.

THE ORIGIN OF REDDISH

The character called reddish was found twice in matings involving in both cases the stock line, concave, approximated, telescoped. The period of seventeen months elapsed between the first and the second origin. The first reddish is mutable; and will be called reddish- α while the second reddish is constant, and will be called reddish-1. The second reddish was found by Miss MILDRED S. MOSES, to whom the writer is indebted for permission to use the data relating to the origin of reddish-1 and also for the use of flies bearing that character in experiments.

The origin of reddish-alpha

In experiments planned to test the effect of centrifugal force on the behavior of sex chromosomes, a cross was made in which a centrifuged yellow vermilion female was crossed with a sepia scute short rough male; and among a total of 104 offspring, a female was found which had several extra veins on both wings. To determine the inheritance of this character, the offspring of the female were tested for two generations. When it was found to be a dominant autosomal character, a cross was made to

determine the chromosome in which it was located. For that purpose, a concave approximated telescoped female was crossed with a sepia vermilion branched-veins male; and five of the F_1 females were backcrossed with concave approximated telescoped males. In one of the backcrosses, half of the males had a reddish body; and in another backcross, among a total of 217 flies, one reddish male was found. The remaining three backcrosses gave no reddish flies.

Subsequent tests showed that the extra-veins character was a recurrence of branched, the latter having been already described (METZ, MOSES and MASON 1923). Reddish flies, therefore, originated from the cross between a newly found branched and concave approximated telescoped flies. They were found on January 8, 1924, in two separate matings. In one case, half of the males were reddish; indicating that the female parent (P_1) was heterozygous for the character. It is possible that in this case the mutation occurred late in the P_2 female, affecting only a few germ cells, one of which was transmitted to the P_1 female; or that the mutation occurred early in the development of the P_1 female, making it heterozygous for reddish; or that the mutation affected a few P_2 males. In the second mating noted above, where only one reddish male was found among 217 flies, the possibility is not excluded that it came as a contamination from the other mating, where many such males were found. It is, however, at least as probable that it originated as an independent mutation, affecting only a few germ cells of the P_1 female, as that it came as a contamination.

All reddish flies used in the experiments were progenies of the mating which gave half of the males reddish. The single reddish male found in the other mating was not used in breeding.

The origin of reddish-1

To locate a certain newly found character, which turned out to be another allelomorph of branched, Miss M. MOSES made a cross between the character in question and concave approximated telescoped flies from the stock culture. On June 16, 1925, in one of two backcrosses, one reddish male was found among a total of 145 flies. Reddish-1, therefore, originated, similarly to reddish- α , in a backcross involving the newly found character branched and concave approximated telescoped.

Breeding experiments with the original reddish-1 male showed that it was heterozygous for the characters concave approximated and telescoped. Since there were no reddish- α flies which could have had a

similar genetic constitution, at that time in the laboratory, it is unlikely that the first reddish-1 male was a contamination from reddish- α . The results of crosses between reddish- α and reddish-1, which will be discussed later, made the possibility of contamination having occurred still more improbable.

Attempts to obtain other reddish mutants

Both reddish- α and reddish-1, as already stated, originated in matings involving branched and concave approximated telescoped characters. The character, branched, used in these different crosses, came from unrelated sources; but the concave approximated telescoped flies were in both cases taken from the same stock line. It is probable that it was due to chance that both of the reddish mutations occurred in the progenies of crosses where flies from a particular line were used; but there is a possibility that the line concave, approximated telescoped, used in both cases, was potentially mutable to reddish. To test that possibility, the cross between concave approximated telescoped and branched flies was repeated seven times; and 217 F₁ females from these crosses were backcrossed with concave approximated telescoped males. Among 16,890 offspring of these backcrosses no reddish flies were found. These results indicate that if the concave approximated telescoped line mutates to reddish at all, the frequency of such mutations is very low.

DESCRIPTION

The body, wings, legs, bristles and hairs of the reddish flies are reddish-yellow; and contrast with the dark gray color of these parts of the body in wild-type flies, and the yellowish gray color in yellow flies. The color of the flies varies with the age and condition of the cultures. Extreme variations of reddish and yellow might overlap in color of the body; but no case has been observed where reddish and yellow could not be distinguished by the color of the hairs and bristles, which is yellowish gray in reddish and gray in the yellow flies.

Reddish- α and reddish-1 can not be distinguished.

PARTIAL MAP OF THE SEX CHROMOSOME

Several sex-linked characters were extensively used in the experiments which will be discussed in this paper. For a better understanding of the data the partial map of the X-chromosome given in figure 1 may be useful. The majority of the characters mentioned in the map have already been described (METZ, MOSES AND MASON 1923). The descriptions

of some of them, however, are not yet published, since the characters were only recently found by either Dr. C. W. METZ or Miss MILDRED S. MOSES, to whom the writer is indebted for the use of the material.

INHERITANCE OF REDDISH-ALPHA

Reddish- α was found to be a sex-linked recessive character. The crosses between reddish females and not-reddish males always gave not-reddish females and reddish males; and from the matings where not-reddish females and reddish males were used, all the F_1 generation was not-reddish.

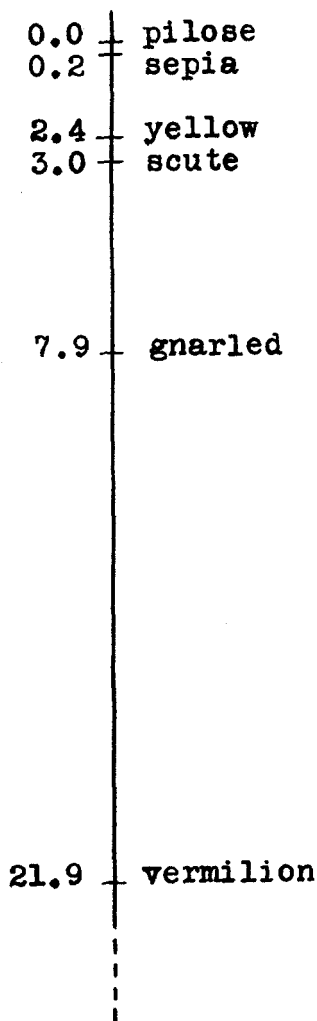
Allelomorphism to yellow

FIGURE 1.—Map of left end of sex-chromosome.

If two allelomorphs are recessive to wild-type, the F_1 generation when they are crossed is usually intermediate. It could not be of the wild-type, since it is assumed that allelomorphs are located in homologous loci, and only two of them can be present in the usual type of inheritance. Two non-allelomorphic recessive characters on the other hand, always give a wild-type F_1 generation. In the F_2 generation of the crosses between two allelomorphs, only parental and F_1 types are expected. Bar in *Drosophila melanogaster* (STURTEVANT 1925) is the only case where two allelomorphs combine in one chromosome, and that rarely. It has often been pointed out that, in all cases where several allelomorphs are known, they affect the same character. The difference between them is rather quantitative than qualitative; therefore the test for allelomorphs should show (a) that the F_1 generation from a cross between two of them is not of the wild-type; (b) that they do not recombine in the F_2 generation (c) that their position in respect to other genes is the same (except in case of such chromosomal abnor-

malities as duplication or inversion), and (d) also that they affect the same character.

Reddish and yellow fulfill these requirements. When intercrossed,

TABLE 1
Data from the crosses with "constant" reddish- α , showing linkage relations.

CONSTITUTION OF F ₁ ♀'s		r_e $s_e y \delta_c v$	r_e $pl \delta_c$				$s_e r_e$ $pl \delta_c$	$pl r_e$ $s_e y \delta_c v$	$r_e \theta_n$ $s_e y \delta_c v$			
			1st experiment	2nd experiment	3rd experiment	Total			1st experiment	2nd experiment	Total	
F ₁ pedigree number		969	505	710	711	..	966	967	968	970	..	
No. of F ₂ matings		23	6	10	7	23	15	16	22	14	36	
Total ♀		1972	500	434	301	1235	1222	1349	1812	978	2790	
♂ ²	0*	a†	849	268	173	137	578	533	530	610	274	884
		b	664	207	134	86	427	593	471	537	347	884
	1	a	26	4	1	1	6	2	1	17	7	24
		b	22	1	4	3	8	1	..	13	12	25
	2	a	6	6	1	..	7	18	6	2	1	3
		b	7	3	2	..	5	10	4	3	1	4
	3	a	193	1	21	43	19	62
		b	151	6	33	36	13	49
	4	a	103	48	151
		b	113	49	162
	1-3	a
		b	1	1
	1-4	a	1	..	1
		b	1	1	2
	Total		1919	489	315	227	1031	1164	1066	1479	772	2251

* In this and the following tables "0" signifies non-crossover classes; "1" classes resulting from crossing over in the first region, etc.

† The class having r_e is always placed in column a.

F₁ females were always yellow or nearly so. Since the color of the body of the flies varies with age and environmental conditions, it is difficult to detect slight differences due to the genetic constitution; and it is not

TABLE 2
Data from the crosses $r_e/s_e \ y \ s_c \ v \ \text{♀} \times \ s_e \ y \ s_c \ v \ \text{♂}$.

Number of experiments		32	
Number of matings		184	
♀'s	r_e and y	11053	
	Reversions	+ v $v \ s_c$	138 22 18
	Total	11231	
	0	r_e $s_e \ y \ s_c \ v$	4067 3648
♂'s	1	$s_e \ r_e$ $y \ s_c \ v$	92 75
	2	$r_e \ s_c \ v$ $s_e \ y$	25 37
	3	$r_e \ v$ $s_e \ y \ s_c$	984 885
	1-3	$s_e \ r_e \ v$ $y \ s_c$.. 3
	2-3	$r_e \ s_c$ $s_e \ y \ v$	1 ..
	Reversions	+ v s_c	118 30 23
	Total		9988
	Total	y and r_e	20870
		Reversions	349

possible to determine with certainty if reddish yellow females are not lighter than homozygous yellow females. If there is any difference between these two types of females it is very slight.

Soon after its discovery, two lines of reddish- α were isolated: one which mutated frequently to wild-type; and one in which reddish- α behaved like a constant character. In the F_2 generations from the crosses between yellow and "constant" reddish- α , only reddish and yellow offspring were obtained; as was to be expected, if these two characters were allelomorphs. In table 1. 11,347 progeny from such crosses are listed. Table 1 gives

TABLE 3
Data from the crosses $pl\ re/s_e\ y\ s_e\ \text{♀} \times s_e\ y\ s_e\ \text{♂}$.

Number of experiments			12
Number of matings			98
♀'s	r_e and y		5462
	Reversions	\dagger s_e s_e	68 5 1
	Total		5536
♂'s	0	$r_e\ pl$ $s_e\ y\ s_e$	2119 2299
	1	r_e $pl\ s_e\ y\ s_e$.. 2
	2	$s_e\ r_e$ $pl\ y\ s_e$	57 37
	3	$pl\ r_e\ s_e$ $s_e\ y$	12 29
	Reversions	pl $pl\ s_e$	51 5
	Total		4611
	Total	r_e and y Reversions	

the data from crosses involving constant reddish- α and pilose, sepia, yellow, scute, gnarled and vermilion, which indicate that reddish- α is located in approximately the same region of the chromosome as yellow.

Finally both yellow and reddish- α are similar in effect, as is the case, as already stated, with all known allelomorphs belonging to one group.

This evidence supports the assumption that reddish- α is an allelomorph of yellow.

Mutability of reddish-alpha

There is, however, a line of reddish- α which does not behave like the line described in the previous section. When reddish from that line is crossed with yellow, F_1 females are yellow, as usual; but in the F_2 generation, in addition to reddish and yellow flies, wild-type flies appear in a variable number. If reddish is an allelomorph of yellow, as the analysis of the data from table 1 indicates, then these wild-type flies are exceptions from the usual behavior of allelomorphs. Or the wild-type flies obtained in crosses between reddish- α and yellow might be crossovers between these two factors; which would indicate that reddish and yellow are not allelomorphs, and that the composition of the F_1 generation in crosses between them was exceptional.

TABLE 4
Data from the crosses $r_e/p_l s_c \text{ } \text{♀} \times p_l s_c \text{ } \text{♂}$.

NUMBER OF EXPERIMENTS	NUMBER OF MATINGS	TOTAL ♀	♂						TOTAL	
			0		1		2			Reversions
			r_e	$p_l s_c$	$r_e p_l$	s_c	$r_e s_c$	p_l		+
6	75	5207	2196	1978	31	50	17	27	150	4449

In tables 2, 3 and 4 a summary is given of the data from crosses involving reddish- α and pilose, sepia, yellow, scute and vermilion. From table 2, which summarizes crosses between reddish- α and sepia yellow scute vermilion, it can be seen that the not-reddish and not-yellow classes (listed under the heading of reversions) offer an obstacle to the usual analysis of the data. As already pointed out in an earlier paper (DEMEREK 1926); if all classes are considered together, it is not possible to locate reddish in the region of the chromosome where it belongs. When an analysis is made in that way, reddish does not fit into the linear arrangement of the genes. It is not probable that crossing over is responsible for the occurrence of these not-reddish and not-yellow classes; since double crossovers between the sepia and scute regions would be required to obtain the observed combinations. The distance between sepia and scute is about 3 units, which is much too short to allow any double crossovers, especially as many as there would be if the not-reddish and not-yellow flies were assumed to be double crossovers. The same holds true when the data given in tables 3 and 4 are analysed.

The problem looks much simpler if the analysis is made without the

not-reddish and not-yellow classes. Then reddish behaves in the same way as in the crosses discussed in the previous chapters; that is, as an allelomorph of yellow. In that case, however, it is necessary to account for the origin of the not-reddish and not-yellow classes. An examination of the data given in the columns headed "reversions" in tables 2, 3 and 4, reveals that all these classes have the reddish chromosome, in which the wild-type allelomorph has been substituted for reddish. As already indicated, crossingover can not account for that substitution. The only other probable assumption is that in these cases reddish mutated back to the wild-type allelomorph. That assumption would easily account for the origin of all the observed classes. If it is assumed that reddish is an allelomorph of yellow and frequently reverts to wild-type, then all

TABLE 5

Comparison between reddish and not-reddish classes in crosses with constant and mutable reddish- α .

CROSS	MUTABLE REDDISH						CONSTANT REDDISH			
	r_e		Not r_e		Reversions		r_e		Not r_e	
	Total	Percent	Total	Percent	Total	Percent	Total	Percent	Total	Percent
$r_e \times y v$	223	40.2	251	45.2	81	14.6	479	53.0	424	47.0
$r_e \times p_l s_c$	2062	50.0	1911	46.4	149	3.6	769	56.6	589	43.4
$r_e \times s_e y s_e v$	5024	51.5	4551	46.6	186	1.9	3214	52.8	2877	47.2
$r_e p_l \times s_e y s_e v$	2019	47.2	2203	51.6	51	1.2	551	48.6	583	51.4

wild-type classes from crosses between reddish and sepia yellow scute vermilion could be interpreted as reversions. That would separate them from the remaining classes, and eliminate all the difficulties otherwise encountered in the explanation of the results.

If reddish- α reverts frequently to the wild-type allelomorph, it ought to be expected that, in the experiments involving mutable reddish- α the reddish classes would be in deficiency when compared with the not-reddish classes. Moreover, it is to be expected that the deficiency would correspond to the number of reversions. Unfortunately there is a differential viability between reddish and yellow flies, which is still more pronounced if pilose or sepia and scute are present. That prevents a direct comparison between the reddish and not-reddish classes. When, however, the reddish classes from the experiments with mutable reddish are compared with the reddish classes from experiments with constant reddish (table 5), and both of them are compared with the not-reddish classes of the same experiments, it is noticeable that the mutable reddish shows a deficit approximately equal to the number of reversions.

Constancy of reverted-reddish-alpha

To test the behavior of the wild-type flies which originated as reversions from the mutable reddish- α , 42 wild-type males were mated to sepia yellow scute vermilion females. All F₁ females were wild-type, and of 18,811 F₂ offspring, none was reddish. These results indicate that the mutations in the reddish locus occur in one direction only, namely, from reddish to wild-type, and not from wild-type to reddish.

TABLE 6

Distribution of reversions among the progenies of single females which females came from a pair mating.

PEDIGREE NUMBER	TOTAL NUMBER OF FLIES	NUMBER OF REVERSIONS	PERCENTAGE OF REVERSIONS
2881	101	3	2.97
2882	153	0	..
2883	95	1	1.05
2884	118	1	.85
2885	156	3	1.92
2886	118	1	.85
2887	136	12	8.82
2888	136	0	..
2889	33	3	9.09
2890	199	5	2.51
2891	115	4	3.48
2892	115	1	.87
2893	125	1	.80
2894	135	0	..
2987	103	2	1.94
2988	112	3	2.68
2989	55	5	9.09
2990	123	3	2.44
Total	2,128	48	2.26

INHERITANCE OF REDDISH-1

Experiments with reddish-1 indicated that it is an allelomorph of yellow and reddish- α ; and also that, unlike reddish- α , it does not revert to the wild-type. In crosses between reddish-1 and yellow, all F₁ females were yellow; and, among 15,103 F₂ progenies, nothing but yellow and reddish flies was observed.

TIME OF OCCURRENCE OF MUTATIONS

Reversions of reddish- α to the wild-type were observed only among the progenies of females heterozygous for reddish- α . Numerous homozygous females were tested, and also several homozygous reddish- α stocks

were kept for many generations; but in no case did any change in reddish appear. Males also always behaved as constant reddish. Numerous F_1 females from crosses of yellow females by reddish males were examined, but none of them were of the wild-type. Reversions to wild-type occurring in reddish- α males would also have been noticed in stocks homozygous for reddish.

Females heterozygous for mutable reddish- α gave numerous reversions. All of these reversions affected the whole fly, indicating that the mutations occurred at the formation of the ova. If mutations occurred in somatic cells, it would be expected that mosaics would develop frequently, which was not the case. Throughout the experiments a close watch was kept for reddish and wild-type mosaics, but none was observed. If they occur at all they must be very rare. This makes negligible the hypothesis that the reversions occurred early in the somatic development.

If reversions of reddish to wild-type occurred in the oogonial divisions, one mutation would affect a group of germ cells, and the result would be that the reverted flies would appear in groups. This was not the case (table 6). In the low mutating line, usually single wild-type flies were obtained from individual females. With increase in the frequency of mutations the number of wild-type flies from single females increased also. The occurrence of reversions in groups, however, was an exception rather than a rule; which makes it improbable that the mutations occurred in the oogonial divisions, and points to the maturation division as the possible seat of the change. A relation was observed between crossing over and the occurrence of mutations, which suggests that both processes occurred at the same time, and supports the assumption that the mutations occurred at the maturation divisions.

In table 4, the data are given from the crosses between mutable reddish- α and pilose scute. From these data it can be seen that reddish mutated in the females which had in one chromosome reddish- α , and in the other chromosome the wild-type allelomorph. From the data given in tables 2 and 3, it is evident that reddish- α mutated in the females which were heterozygous for its allelomorph yellow. The data from table 8 show that reddish- α mutated in reddish- α over reddish-1 females. Reddish- α therefore mutates at the maturation divisions of females having in one chromosome mutable reddish- α , and in the other chromosome one of its allelomorphs; that is, wild-type, yellow or reddish-1. No mutation has been observed in the females homozygous for mutable reddish- α .

Wild-type which originated by a mutation from reddish- α behaves like any other wild-type; that is, it keeps the reddish- α mutating when heterozygous with it. This can be seen from the data in table 7; which

TABLE 7

The F_2 data from a cross between a reddish- α sepia female and a pilose scute vermilion male.

PEDIGREE NUMBER	♀	0		2		3		4		REVERSIONS	
		$se\ r_e$	$pl\ sc\ v$	$pl\ r_e$	$se\ sc\ v$	$se\ r_e\ sc\ v$	pl	$se\ r_e\ v$	$pl\ sc$	se	$sc\ v$
2516	47	9	13		1			5	3		
7	102	15	27			1		3	10	1	1
8	47	11	13		1			3	5	1	1
Total	196	36	53		2	1		11	18	2	2

give the F_2 results of a cross between a reddish- α sepia female and a pilose scute vermilion male. This male was a reversion obtained from a reddish- α pilose scute over sepia yellow scute vermilion female.

TABLE 8

Comparison of frequency of mutability in reddish- α /reddish-1 and reddish- α /yellow females.

PEDIGREE NUMBER	NUMBER OF MATINGS	NUMBER OF MATINGS GIVING REVERSIONS	TOTAL		PERCENTAGE OF REVERSIONS
			y and r_e	Reversions	
Offspring of $re-\alpha/re-1$ females					
2816	10	3	1160	7	0.6
2817	20	13	2506	24	0.9
2818	1	1	122	1	0.8
2819	5	2	655	5	0.8
Total	36	19	4443	37	0.8
Offspring of $re-\alpha/y$ females					
2816	3	..	338
2817	29	17	3022	30	0.10
2818	1	1	93	7	7.0
2819	3	1	324	6	1.8
Total	36	19	3777	43	1.1

To determine if there was any difference in the frequency of mutations between the reddish- α over yellow and reddish- α over reddish-1 females, the same reddish- α male was mated to yellow and reddish-1 females, and the F_2 results of these crosses compared. A summary of the experiments, which were repeated four times, is given in table 8.

They indicate that reddish- α mutates with equal frequency when heterozygous with yellow or with reddish-1.

FREQUENCY OF REVERSIONS

About half of the progenies of females in which reddish- α mutates to wild-type, carry the reddish- α gene; since, as already mentioned, reddish- α can mutate in heterozygous females only. The ratio between

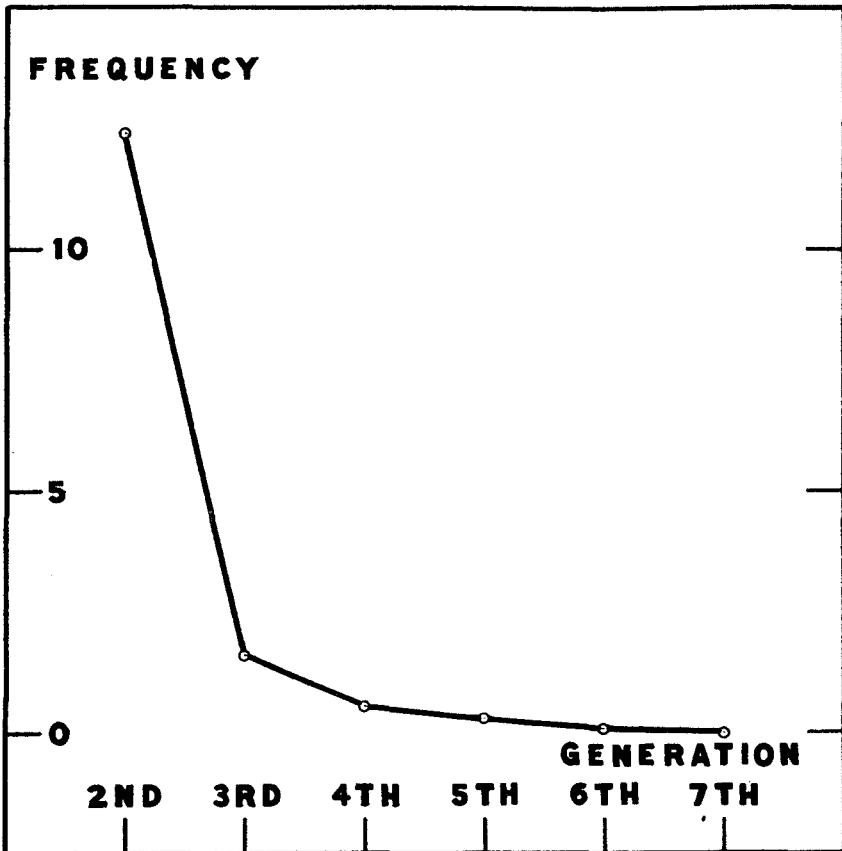


FIGURE 2.—Frequency of reversions of reddish- α to wild-type, immediately after the origin of reddish- α .

the number of reversions and the number of progenies carrying the reddish- α gene would give a measure of the frequency with which reddish- α mutated to the wild-type. Since in many experiments the reddish- α and not-reddish- α progeny had not been counted separately (and in some experiments it was not possible to separate them), the frequency

of reversions throughout this paper is expressed not by the proportion between the number of reversions and the number of progeny carrying the reddish- α gene, but by the proportion between the number of reversions and the total number of the progeny. Since approximately only half of the total number of progeny of heterozygous females was expected to carry the reddish- α gene, the "frequency" of reversions as the term is used in this paper will amount to about half of the actual frequency.

Mutability of reddish-alpha at the time of origin

The progenies of yellow reddish- α females offer the best material for the determination of the frequency with which reddish- α reverts to wild-type; since among these progenies all classes, namely, yellow,

TABLE 9

Frequency of reversions of reddish- α to wild-type, immediately after the origin of reddish- α .

GENERATION	TOTAL NUMBER OF FLIES	NUMBER OF REVERSIONS	FREQUENCY OF REVERSIONS PERCENTAGES*
2nd	241	30	12.4
3rd	9633	152	1.6
4th	8022	48	0.6
5th	2147	7	0.32
6th	11532	5	0.043
7th	4041	0	0.0

* Since the reddish gene was present in half of the gametes only and in calculations total number of flies was used, the frequency of reversions was about twice as large as given in this column.

reddish- α and reversions, can easily be distinguished. When reddish- α was found, one of the first crosses made with it was with yellow. The same cross was repeated for different purposes through many generations. This made it possible to determine the frequency with which reddish- α reverted in different stages of the experiments.

Fig. 2 represents the curve and table 9 gives the actual data on the frequency with which reddish- α mutated to the wild-type during the second to seventh generation after it was found. At that time the matings were made at random, without any selection to increase the frequency of of reversions. As can be seen from both fig. 2 and table 9 the frequency reversions decreased rapidly in succeeding generations; until in the seventh generation no reversion was found among 4041 individuals. In the second generation after the origin of reddish- α , the females heterozygous for reddish- α gave 12.4 percent of reversions; two "gener-

ations later, similar females gave 0.6 percent of reversions; and in the sixth generation, among 11,532 offspring, only 5 reversions were observed.

Effect of selection on the mutability of reddish- α

The mutable reddish- α stock was kept up for a long time by back-crossing reddish- α over sepia yellow scute females with sepia yellow scute males. Since there is no double crossing over between sepia, yellow and scute, all yellow females from that cross had the genetic constitution of their mother. It was therefore possible to perpetuate the cross by mating yellow females with sepia yellow scute males from the same culture.

TABLE 10
Effect of selection on the frequency of reversions.

GENERATION	TOTAL NUMBER OF FLIES	NUMBER OF REVERSIONS	PERCENT OF REVERSIONS
1	591	23	3.9
2	196	7	3.6
3	578	6	1.0
4	45	4	8.9
5	180	8	4.4
6	92	2	2.2
7	415	14	3.4
8	491	12	2.4
9	171	3	1.8
10	362	4	1.1
11	795	21	2.6
12	796	25	3.1
13	5731	145	2.5
14	7625	99	1.3
15	5727	276	4.8
16	4890	178	3.6
Total	28,685	827	Average 2.9

Pair matings were always used to propagate a line. Since reddish- α mutates in heterozygous females only, this was the simplest way to keep a reddish- α stock which was certain to be mutating.

If many pair matings were made from a culture which gave a high number of reversions, the number of reversions in the offspring varied from zero to as high as, or higher than, in the parent culture. It has been shown before that the frequency of reversions decreased rapidly if the matings were made at random. If, however, the matings were made from cultures which gave a high number of reversions, the frequency of reversions did not decrease, but remained more or less constant. That can be seen from table 10, which records the results of an experiment

where selection was carried on for sixteen generations with the purpose of increasing the frequency with which reddish- α mutated. During that time the line was propagated from the cultures which gave the highest number of reversions. By this selection increase in the mutability was not attained, but neither did a decrease occur. The mutability in the line remained approximately the same. In individual cultures, the number of reversions was as high as 25 percent; but in the totals of different experiments the mutability rarely exceeded 10 percent.

A relation was found to exist between the mutability of the parent culture and the mutability of the offspring. Offspring of a highly mutable culture are likely to give more highly mutable cultures than the offspring of a less mutable one (table 11). The increase in the mutability, however, does not go behind a certain limit which is between three and five percent.

TABLE 11
Comparison between the mutability of parents and offspring.

MUTABILITY OF PARENT CULTURE PERCENT	NUMBER OF CUL- TURES	DISTRIBUTION OF MUTABILITY IN OFFSPRING										TO- TAL No. of cul- tures
		0		1 Percent		1-5 Percent		5-10 Percent		10 Percent		
		Number of cultures	Percent	Number of cultures	Percent	Number of cultures	Percent	Number of cultures	Percent	No. of cul- tures	Percent	
0	17	88	77.9	5	4.4	13	11.5	5	4.4	2	1.8	113
less than 1	16	72	64.3	15	13.4	17	15.2	7	6.3	1	0.8	112
1-5	32	65	37.6	11	6.4	62	35.8	29	16.8	6	3.4	173
5-10	19	10	11.8	7	8.2	39	45.9	22	25.9	7	8.2	85
more than 10	7	5	25.0	1	5.0	9	45.0	3	15.0	2	10.0	20

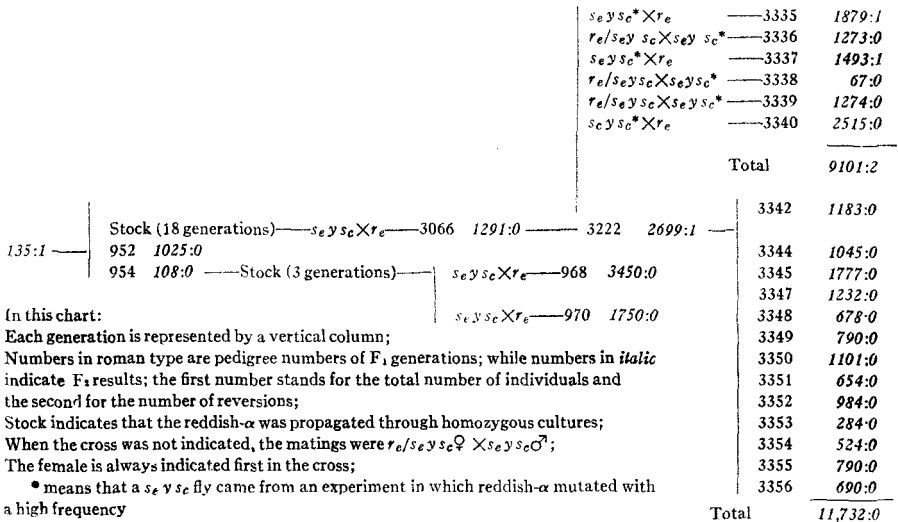
Constancy of reddish-alpha

As can be seen from table 11 constant cultures (with no reversions) were found among the offspring of highly as well as among the offspring of little mutable cultures. This was almost without exception. The lack of reversions was probably due in some of the cultures to the small numbers of individuals; in others, however, it was probably caused by the constancy of reddish- α .

Two males were taken from a very mutable culture which gave 16 reversions out of 97 individuals. They were mated to sepia yellow scute females from stock. In the F_2 generation from one of the matings, among 1307 flies, there was only one reversion; and in the F_2 from the other mating there were no reversions among 425 flies. Both of the males

came from a highly mutable culture; but offspring of one of them had very low mutability, and the offspring of the other was either of very low mutability or possibly constant. The number of individuals in this experiment was large enough to indicate a difference in mutability between the parents and the offspring.

It is evident from the chart that reddish- α can become constant or nearly so. Three lines originated from a culture which had very low mutability and which gave one reversion among 135 individuals. One of these lines was discontinued after one F_2 generation had been obtained in which no reversion was found among 1025 individuals. The other line



was continued for several generations, and 5308 offspring of females heterozygous for reddish- α were examined, none of them being a reversion. In these two lines reddish- α behaved as a constant gene in a total of 6333 individuals. The third line was kept as homozygous reddish- α for about eighteen generations. To test its mutability it was crossed to sepia yellow scute; and further propagated by backcrossing with sepia yellow scute males, and through crosses between reddish and sepia yellow scute flies. Among 24,823 flies of this line there were only three reversions. It might be questioned, however, whether these three reversions did not originate in a different way to the others, since all three were crossovers in the yellow-scute region. It is unlikely that they came into the experiment by contamination, since at that time no stock of the same genetic constitution was in existence in the laboratory. In any case, the frequency of

TABLE 12
 Comparison of the frequency of reversions among the offspring of young and old females.

PEDIGREE NUMBER	NUMBER OF MATINGS	♀'s				♂'s						TOTAL ♀ AND ♂		Percentage of reversions	
		Total		Reversions		0		1		2		Total			Reversions
		r_e and y	δ_c	r_e	δ_c	r_e	δ_c	$r_e \delta_c$	$\delta_e y$	r_e and y	Reversions				
Offspring of young females															
1283	10	453	21	4	205	182	2	6	2	2	399	25	852	50	5.9
1232	5	131	5	1	65	59	2	127	1	258	7	2.7
1285	1	9	1	..	13	1	14	1	23	2	8.7
1296	2	222	1	2	86	86	1	1	1	2	176	5	398	8	2.0
1299	2	84	5	2	47	48	95	4	179	11	6.1
1300	1	86	1	..	41	42	1	1	1	1	86	..	172	1	.6
1301	1	55	3	1	27	41	69	3	124	7	5.6
1547	2	138	5	..	43	62	1	1	1	1	112	7	250	12	4.8
1684	2	92	53	33	87	1	179	1	.6
1664	1	64	18	17	1	1	1	..	37	2	101	2	2.0
1727	1	19	1	1	12	9	21	3	40	5	12.5
1728	4	212	4	..	96	107	1	..	1	1	209	2	421	6	1.4
1730	1	82	2	..	37	38	..	1	76	1	158	3	1.9
1731	2	63	2	1	51	45	96	4	159	7	4.4
1732	5	268	7	1	97	139	3	2	3	..	236	4	504	12	2.4
1738	1	69	..	1	27	22	50	1	119	2	1.7
1607	1	75	1	..	39	43	1	1	84	1	159	2	1.3
1646	7	420	11	..	152	156	6	2	..	2	318	9	738	21	2.8
Total	49	2542	70	15	1109	1125	8	17	8	11	2292	74	4834	159	3.3

TABLE 12 (Continued)
 Comparison of the frequency of reversions among the offspring of young and old females.

PEDIGREE NUMBER	NUMBER OF MATINGS	♀'s				♂'s						TOTAL ♀ AND ♂						
		Total		Reversions		0		1		2		Reversions		Total		r _c and y	Reversions	Percentage of reversions
		r _c and y	+	S _c	r _c	s _c /y _c	s _c /r _c	y _c	r _c /y _c	s _c /y _c	s _c /r _c	+	x _c	r _c and y	Reversions			
Offspring of old females																		
1283	10	468	2	..	198	212	8	4	1	1	3	424	3	892	5	.6
1232	5	268	109	79	3	2	193	..	461
1285	1	63	25	12	1	38	2	101	2	2.0
1296	2	113	1	..	45	50	..	1	1	1	..	96	2	209	3	1.4
1299	2	156	3	..	71	67	..	2	2	140	..	296	3	1.0
1300	1	62	25	21	1	1	48	..	110
1301	1	51	3	1	21	24	1	1	1	..	46	2	97	6	6.2
1547	2	114	3	..	53	50	1	1	2	2	4	107	4	221	7	3.2
1684	2	136	44	41	2	2	89	..	225
1664	1	50	14	19	1	1	34	1	84	1	1.2
1727	1	50	1	..	20	26	46	..	96	1	1.0
1728	4	166	1	..	89	65	1	1	2	1	1	159	1	325	1	.3
1730	1	48	1	..	24	24	48	..	96	1	1.0
1731	2	75	2	..	30	25	3	56	3	131	5	3.8
1732	5	256	3	..	123	125	..	1	4	1	1	1	..	253	2	509	5	.98
1738	1	17	10	8	18	..	35
1607	1	50	20	16	1	..	1	38	..	88
1646	7	322	2	1	145	159	2	2	2	4	9	1	..	314	10	636	13	2.0
Total	49	2465	21	2	1066	1023	22	17	10	9	26	4	..	2147	30	4612	53	1.1

reversions was so low as to be almost negligible; and reddish- α of that line behaved more like a constant than like a mutable character.

The evidence accumulated from the experiments with mutable miniature- α character of *Drosophila virilis* indicated that the mutability of the miniature- α gene was affected by several other genes. It has been found that, in the presence of a certain dominant autosomal gene, an almost constant miniature- α becomes highly mutable. To determine if the absence of the proper modifying factor was responsible for the constancy of reddish- α , six crosses were made between reddish- α from the constant line and sepia yellow scute flies from the experiments in which reddish- α mutated with a high frequency. These crosses are marked with an asterisk on the chart. From the results it can be seen that the mutability of reddish- α was not influenced to any appreciable extent. Among a total of 9101 flies, only two reversions were obtained (both of which were crossovers in the yellow-scutel region). This makes it probable that the constancy of reddish- α was due to the gene itself rather than to the absence of factors which would increase the mutability.

EFFECT OF THE AGE OF THE FEMALE ON THE FREQUENCY OF MUTATIONS

In the course of experiments with mutable reddish- α , it has been noticed that the proportion of reversions was higher among the first hatched flies than among the flies which hatched later. This difference in the proportion of reversions among the early and late hatched offspring could be accounted for in two ways. Either the reversions hatched sooner than the other classes, or the proportion of reversions was larger in the first laid eggs. To determine which of these two possibilities was more probable, a comparison was made between the offspring which came from the eggs laid by young females, and the offspring from the eggs laid by the same females when old. In several experiments, pairs were kept in one set of culture bottles until the first offspring began to hatch, and then they were transferred to new culture bottles. Offspring in the first bottles came from the eggs laid by the females younger than four weeks, and the offspring in the second bottles came from females older than four weeks. The summary of the data of eighteen experiments involving 49 females is given in table 12, from which it can be seen that, in all except one experiment, the percentage of reversion was larger among the offspring of young females. When the data of all the experiments are added, the percentage of reversions in the offspring of young females is three times the percentage of reversion in the offspring of old females.

The result of this experiment indicates that the age of the flies influences the frequency of mutations of reddish- α to wild-type. In old females, that frequency is appreciably lower than in the young females.

CROSSING OVER AND REVERSIONS

As has been already pointed out in one of the previous chapters, crossing over can not be responsible for the appearance of reversions in crosses with reddish- α . The behavior of reddish can not be compared with the behavior of bar in *Drosophila melanogaster*; where, as has been shown by STURTEVANT (1925), the appearance of unexpected wild-type flies was always connected with crossing over in the bar region. In the case of reddish- α (tables 2, 3, 12 and 13) about 87 percent of reversions are non-crossovers in the regions adjoining reddish.

There is, however, a connection between crossing over and reversions of reddish- α . An examination of the data given in table 13 reveals a marked increase of yellow-scute crossovers in reversion classes as com-

TABLE 13

Male offspring of $s_e y s_c v/r_e$ females showing the amount of crossing over in different regions.

0	r_e $s_e y s_c v$	7589 7230
1	$r_e s_c$ $y s_c v$	195 146
2	$r_e s_c v$ $s_e y$	50 88
3	$r_e v$ $s_e y s_c$	1790 1785
1-3	$s_e r_e v$ $y s_c$.. 5
2-3	$r_e s_c$ $s_e y v$	2 3
Reversions	+	255
	v	48
	$s_c v$	46
Total		19,232

pared with the same crossovers of normal classes. The values given in table 13 are directly comparable, since all the data were obtained from

the same females. Unequal distribution of crossovers is still more evident from the analysis given in table 14, where the data for reddish and reversion classes of table 13 are brought together. From table 14 it can be seen

TABLE 14
Comparison between crossovers occurring in reddish and reversion classes.

CROSSOVER REGIONS	CLASSES		PERCENT OF REVERSIONS
	Reddish	Reversions	
0	7589	255	3.3
s_e-r_e	195	0	0.0
r_e-s_c	52	46	46.9
r_e-v	1790	48	2.6
Totals	9626	349	3.5

that among the crossovers in reddish-scutel region in 46.9 percent of possible cases reddish- α reverted to the wild type. On the other hand, in non-crossover class reddish- α reverted in 3.3 percent of possible cases, in the sepia-yellow crossover class there were no reversions and in the scute-vermilion crossover class the reddish- α reverted in 2.6 percent of possible cases.

From table 14 it could be seen also, that among 9626 reddish- α flies there were only 52 (0.54 percent) crossovers in reddish-scutel region, while among 349 reversions there were 46 (13.2 percent) crossovers in the same region. The percentage of yellow-scutel crossovers in reddish classes is lower than it would be normally expected. That deficiency, however, was probably caused by a poor viability of scute flies. An examination of the data given in table 13 shows that the scute class was in all except one case lower than its reciprocal class. A comparison of crossover percentages reveals that the crossing over in reddish-scutel region was 24.4 times as frequent among reversions as among the normal classes.

The data presented above indicate that almost one half of the crossovers in reddish-scutel region were reversions, or, when examined from a different angle, they show that the crossing over in reddish-scutel region was 24.4 times as high among the reversions as among the normal classes. The observed facts may be accounted for in two ways: (a) by the assumption that the total amount of crossing over in reddish-scutel region was not influenced by the occurrence of reversions but that the reversions occur about twelve times as frequently when the crossing over in reddish-scutel region occurs than when there is no crossing over, or (b) by the assumption that whenever the reversion occurs in one out of about thirteen cases

crossing over in reddish-scute region will occur also, irrespective of whether this crossing over would have occurred otherwise. According to the first assumption, it would be expected that the increase in the frequency of reversions would not change the total amount of crossovers in the reddish-scute region, but would only affect their distribution between the reversions and the normal classes. According to the second assumption, an increase in the amount of reversions would also result in the increase in the total of reddish-scute crossovers. According to either of the assumptions, however, the occurrence of reversions is stimulated with the close association of homologous chromosomes in reddish-scute region at the time when crossing over occurs.

In table 15 the data are summarized according to the amount of rever-

TABLE 15

Comparison between the frequency of reversions and the percentage of crossing over in the r_e-s_c region.

FREQUENCY OF REVERSIONS IN DIFFERENT EXPERIMENTS. PERCENT	AVERAGE FREQUENCY PERCENT	TOTAL NUMBER OF FLIES	PERCENT OF CROSSOVERS IN r_e-s_c REGION		
			Reversions	r_e and y classes	r_e and y and reversions
less than 0.5	0.3	4594	13.3	0.6	0.7
.5-1.0	0.8	3109	15.4	0.7	0.9
1-2	1.6	1348	9.5	0.5	0.6
2-3	2.3	2436	10.7	1.1	1.3
3-4	3.2	1455	6.5	1.1	1.2
more than 4	5.2	1625	16.5	1.1	1.8

sions obtained in different experiments. The results indicate that the amount of crossing over among reversions was approximately the same in the experiments which had a low frequency of reversions as in those in which the frequency was high. On the other hand, there is an indication that in the experiments which had a high frequency of reversions there was an increase in the total crossing over as well as in the percentage of crossing over in the reddish and yellow classes. These findings favor the second assumption.

It is unfortunate that it has not been possible to increase the amount of reversions much above five percent. The low frequency of reversions makes the reversion classes small and so prevents a more detailed analysis of the relation between the occurrence of reversions and crossing over in the reddish-scute region.

DISCUSSION

From the evidence obtained in different experiments with reddish- α the most fitting explanation for the unusual behavior of that character

seems to be the hypothesis that the gene for reddish- α reverts frequently to the gene for the wild-type. Several other hypotheses, which could explain the origin of wild-type flies in crosses with reddish- α , fail entirely to stand the crucial tests.

Any hypothesis explaining the behavior of reddish- α would have to assume that reddish- α is a sex-linked character and also an allelomorph of yellow. There can not be any question as to the validity of the first assumption. In the numerous matings in which reddish was used it never failed to show the characteristic behavior of a sex-linked character of *Drosophila*. The assumption of allelomorphism to yellow is well supported by: (a) linkage tests, which indicate that reddish- α is located in approximately the same region as yellow; (b) F₁ female progenies from crosses between reddish- α and yellow, which are always yellow; (c) F₂ results from these crosses, where only reddish- α and yellow males were obtained if the reddish- α parent used in the cross was from a constant line; and (d) by the fact that the reddish- α and yellow affect the same character, as it is the case with all known allelomorphs.

When reddish- α of a "mutable" line is crossed with yellow, all F₁ females are yellow, as expected; but among F₂ progenies, in addition to yellow and reddish- α flies, a few wild-type individuals appear. The number of wild-type flies varies in different cultures from zero to 20 percent. It is usually low, and rarely reaches above 10 percent. What is the origin of these unexpected wild-type flies? In addition to the hypothesis that they are due to the change of the gene for reddish- α to the gene for wild-type, is possible that they might be a product of: (a) the variability of reddish- α ; (b) recombination between reddish- α and yellow; (c) the complex nature of the reddish- α character; or (d) the abnormal behavior of chromosomes. Let us consider these possibilities in detail.

(a) If the exceptional wild-type flies were due to the variability of reddish- α , it would be expected that they would be genetically reddish- α . That, however, was not the case. A number of these flies was tested for two generations and they gave only wild-type progenies, without any reddish- α flies.

(b) It has been shown by STURTEVANT (1925) that in exceptional cases unequal crossing over occurs in the bar-region of sex chromosome of *Drosophila melanogaster*, and results in the recombination of allelomorphs. Similar process occurring in the reddish- α region could produce the wild-type flies. In that case, however, it would be expected that all wild-type flies would be crossovers. Quite the opposite was found, since only about

13 percent of the exceptions were yellow-scute crossovers, and almost none were crossovers in the sepia-yellow region. These results eliminate the possibility of the wild-type flies originating by unequal crossing over.

(c) By assuming that the reddish- α character is determined by duplicate genes a scheme could be devised which would explain the appearance of wild-type flies. The abnormally small and variable numbers of the wild-type flies could probably be explained by the assumption of differential viability. There are, however, other and more serious obstacles to that hypothesis. If the reddish- α character were determined by duplicate genes, one of them would be undoubtedly sex-linked and an allelomorph of yellow, and the other or others might be either autosomal or sex-linked. If any of the genes needed for the expression of the reddish- α character were an autosomal recessive, reddish- α would not behave as a sex-linked character. If it is assumed, however, that the autosomal gene is a dominant one, it would be expected to segregate freely with the gene in the sex chromosome. The expected result would be that the wild-type flies would appear among the progeny of heterozygous males as well as among the progeny of heterozygous females. That was not the case. Males from the cross reddish- α by yellow produced no wild-type flies, while the females from the same cross gave wild-type flies.

There are several reasons which eliminate the possibility of reddish- α being determined by duplicate genes located in the sex chromosome. It might be enough to consider one of them. If it is assumed that reddish- α is determined by two sex-linked genes, one of which is an allelomorph of yellow, then the wild-type flies observed in crosses between reddish- α and yellow, would constitute half of the crossovers between the duplicate genes determining reddish- α . It has been shown in table 14 that, in an experiment carried through sixteen generations, the average frequency of wild-type flies was about three percent. That would indicate that the other duplicate gene of reddish- α would have to be located about six units from yellow. If the wild-type flies were crossovers between the two duplicate genes it would be expected that all of them would be crossovers in the region six units on either side of yellow. The data given in table 10 show that they are not crossovers in the yellow-vermilion region, and also indicate that it is very unlikely that they are crossovers in the region on the other side of yellow.

(d) In all experiments, reddish- α showed a strictly sex-linked inheritance that eliminates the possibility of the unexpected behavior of reddish- α being due to an abnormal action of the autosomes. In numerous experiments made with reddish- α there was nothing to support the as-

sumption that the abnormal behavior of a whole sex-chromosome was responsible for the origin of the wild-type flies obtained in crosses with reddish- α . In table 16, the data are given which show that the wild-type

TABLE 16

Summary of experiments in which different regions of the original reddish- α chromosome were represented. (Solid line indicates the left-end of the original reddish- α chromosome and the broken line the replaced regions.)

TYPE OF THE X-CHROMOSOME	NUMBER OF EXPERIMENTS	NUMBER OF FLIES	
		Total	Reversions
—————	66	37,462	684
————— v + - - - -	12	4,549	84
— s_e + - - - - - - - - - -	2	1,459	19
- - - + —————	33	15,686	223
- - - + ————— v + - - - -	11	5,580	51
- - - + — s_e — s_e + - - - - -	9	4,214	35

flies occurred in the experiments in which the whole original chromosome carrying reddish- α was present as well as in the crosses in which different parts of that chromosome were replaced by the parts from the other sex chromosome. From table 16 it could be seen that the small part of reddish- α chromosome located between sepia and scute (about 3 units in length) was sufficient to produce the abnormality; and the data discussed on page 384 indicate that a gene, rather than a region of the chromosome, is responsible for the origin of the wild-type flies.

Reddish- α was found to mutate in one direction only, namely, from reddish- α to wild-type. Tests involving a large number of progenies of reverted reddish- α failed to detect any mutation in the opposite direction. Moreover, the mutability of reddish- α was found to be limited to a very short period of development, which has been located at the maturation divisions of heterozygous females. No mutation was observed in somatic cells, in homozygous females, or in males. What could be the reason for that narrowly restricted mutability of the reddish- α gene? Experimental evidence does not give as yet any answer to this question. It may be possible that the restriction is due to the quality of the gene itself, or it may be also possible that the reddish- α gene is potentially mutable in other periods of development, but that the stimulus which produces the

immediate change is lacking except at the maturation divisions of heterozygous females. It has been found that the potentially mutable gene of miniature- α behaves almost as a constant one until it is stimulated to mutate by some other gene. Two such genes were isolated; both autosomal dominants. One of them induces miniature- α to mutate with high frequency in somatic cells, but does not affect the mutability of germ-cells. The other one induces a high mutability of the germ-cells, not changing appreciably the mutability of somatic cells. Some condition similar to that found in the case of miniature- α would account for the restricted mutability of reddish- α . The attempt, however, to induce somatic mutability in reddish- α by the gene which stimulates miniature- α to mutate somatically, was not successful.

Restriction of the mutability of a mutable gene to limited periods in the development of the organism is not an unusual condition. IKENO (1923) described two recessive characters in *Plantago*, which when selfed, gave regularly a small number of the wild-type individuals. These wild-type plants were interpreted as due to reversions occurring at the formation of gametes, or in the somatic cells closely preceding the reduction division. Mosaic plants, which would be due to mutations during the late somatic development, were observed very rarely, if at all. Similarly IMAI (1925a) found that the cream-colored flower character of *Pharbitis* when selfed gave regularly about 6 percent dark colored plants. Variegated flowers were rarely observed. In a line of *Antirrhinum*, BAUR (1926) obtained regularly about 2 percent *crispa* plants. *Crispa* is a dominant character and lethal when homozygous. The origin of *crispa* plants could be interpreted as being due to the mutability of the gene for the wild-type to the gene for *crispa*. Since no mosaic plants were observed the mutability in this case was probably limited to maturation divisions. IMAI (1925b) described a mutable character in *Pharbitis* which had the gametic frequency of mutations of 0.40 percent, and the somatic frequency of 0.17 percent. In *Delphinium* (DEMEREC 1927b) a character is known which mutates with high frequency in the early stages of the development of plants, and with very high frequency in the late stages of development, but does not mutate at all or mutates with a very low frequency in the intermediate stages. The difference between the mutability of reddish- α and the mutability of the genes just mentioned appears to be only in the fact that the period of the mutability of reddish- α is still more limited than the period of mutability of these genes. Consequently the difference between the mutability of reddish- α and such genes producing variegation in plants would be that these genes mutate at all stages of the develop-

ment, while reddish- α mutates at the maturation divisions of heterozygous females only.

An attempt has been made (CHITTENDEN 1927) to explain the behavior of variegated pericarp of maize and other similar variegations found in plants as due to the plastid inheritance. The reddish- α case, however, is distinctly chromosomal in inheritance and any hypothesis to explain the observed behavior as being determined by cytoplasm seems to be inconceivable.

SUMMARY

Reddish- α was found in two sister matings in the backcross involving the character branched as well as concave approximated and telescoped. In one of the matings, about one half of the males were reddish; and in the other only one reddish male was found. The possibility is not excluded, but the probability is low, that the single male came as a contamination from the culture which had many reddish males.

Reddish-1 was found (by Miss M. MOSES) seventeen months later in a mating involving the same characters as the one in which reddish- α was found. The branched used in the second case had a different origin from the branched used in the first case, but the concave approximated telescoped flies came from the same line.

To test the possibility that in the concave approximated telescoped line mutations to reddish occur frequently; 16,980 offspring of the backcrosses involving branched, approximated and telescoped characters were examined. No reddish flies were found.

Both reddish- α and reddish-1 are sex-linked and allelomorphs of yellow.

In F_2 generations from crosses between reddish- α and yellow, in addition to reddish- α and yellow flies, few wild-type ones appear. Experiments indicate that these wild-type flies are not due to crossing over between reddish- α and yellow, that they are not due to the abnormal behavior of chromosomes, nor to the complex genetic nature of reddish- α . They are interpreted as being reversions of the gene for reddish- α to the gene for wild-type.

The wild-type flies which originated as reversions from reddish- α are genetically constant.

Reddish-1 does not revert to wild-type.

Reddish- α reverts to wild-type only in females which are heterozygous for reddish- α and one of its allelomorphs, namely, wild-type, yellow or reddish-1. No reversions were observed in somatic-cells, in homozygous females, or in the males.

The frequency of reversions was found to be very variable. It decreased from 12.4 percent in the second generation after the origin of the reddish- α , to zero in the seventh generation.

By using for matings flies from cultures which gave the highest number of reversions it has been possible to keep the frequency of reversions for sixteen generations at about three percent.

A positive relation was found to exist between the mutability of the parent culture and the mutability of the offspring.

A line was isolated in which reddish- α behaved as an almost constant character.

The age of the female reduces the frequency of reversions.

It was found that, in the classes which originated by reversions, the crossing over in the yellow-scutel region was increased 24 times over the normal amount. An analysis of the data indicates that the force which influences the reddish- α to revert to the wild-type at the same time causes the increase in the crossing over in the yellow-scutel region.

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