heterozygous for certain other white lines (called B whites), abnormal ratios are thrown by *Rl* and by *Pn* if the latter appears to have the constitution Pp_2. The mutant *Wy* has occurred in the offspring of parents heterozygous for Line 1 and B whites; but never in the offspring of Line 1, of A whites, nor of parents heterozygous for Line 1 and A whites. Crosses between Line 1 and three different B whites have given F_1 plants with normal pollen and ovules.

[1] Blakeslee, A. F., 1924. "Distinction between Primary and Secondary Mutants," these PROCEEDINGS, **10**, 109–116.

[2] Belling, J. and A. F. Blakeslee, 1924. "The Configurations and Sizes of the Chromosomes in the Trivalents of 25-Chromosome Daturas," these PROCEEDINGS, **10**, 116–120.

[3] Blakeslee, A. F., 1924. Quoted in *Yearbook of Carnegie Institution of Washington*, No. **23**, 1924, pp. 24–27.

[4] Belling, J., 1924. Quoted in *Yearbook of Carnegie Institution of Washington*, No. **23**, 1924, pp. 28–30.

[5] Belling, J., 1914. "On the Inheritance of Semi-sterility in Certain Hybrid Plants." *Zeitsch. ind. Abst. Vererbungslehre*, **9**, Heft 5, 303–342.

[6] Belling, J., 1915. *Rept. Fla. Agr. Exp. Sta.* for 1914. Pp. 81–105.

[7] Belling, J., 1925. "A Unique Result in Certain Species Crosses." *Zeitsch. ind. Abst. Vererbungslehre*. (In press.)

[8] Belling, J., 1925. "On the Origin of Species in Flowering Plants." *Nature*, **116**, 279. (Aug. 22).

REDDISH—A FREQUENTLY "MUTATING" CHARACTER IN DROSOPHILA VIRILIS

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The body-color character "reddish" used in the experiments described below was first found in one of five identical pair matings which were back crosses involving several autosomal characters. Half of the males and none of the females from this pair mating were reddish, indicating that reddish is a sex-linked recessive character and that the parent female was heterozygous for it. Later experiments confirmed this interpretation.

Behavior of Reddish in Crosses with Yellow.—In appearance, reddish is very similar to the sex-linked character yellow body-color which has been known for a long time in Drosophila virilis.[1] Reddish, however, can be easily distinguished from yellow by its brighter color and still better by the color of hairs and bristles which is gray on yellow flies and yellowish on reddish flies.

Because of its similarity to yellow the first cross made with reddish was the cross between reddish and yellow, for the purpose of testing the possibility of reddish being an allelomorph of yellow. When it was found that F_1 females from such a cross were phenotypically yellow, it was assumed that reddish was a new allelomorph of yellow. Fortunately, however, an F_2 generation was bred from that cross. In this F_2 generation of 271 flies, 112 were reddish, 129 yellow and 30 were wild-type. These results made the assumption of allelomorphism very questionable. From a cross between two allelomorphs, which behave regularly, wild-type flies should not be obtained. Since there is no precedent in Drosophila, or as far as I am aware, in any other organism, for such behavior of two recessive non-allelomorphic characters, the case of reddish indicated either a novel complementary behavior of two recessive factors in heterozygous condition or an exceptional behavior of an allelomorph of yellow.

A Map of the "Left" End of the X-Chromosome.—Since the factors located in the "left" end of the X-chromosome were extensively used in the crosses considered here, the following map of that region of the chromosome will be an aid in interpreting the data.

PILOSE	SEPIA	YELLOW	SCUTE	VERMILION
0	0.18	2.18	2.88	21.88

The map of the "left" end of the X-chromosome.

Cross between Reddish and Sepia Yellow Scute Vermilion.—Since the crosses described above indicated that reddish is an allelomorph of yellow or is located in the region close to yellow, a cross was made between reddish and sepia yellow scute vermilion—involving a majority of known factors located in that region of the X-chromosome. In the course of the experiments this same cross has been repeated over and over for other purposes, thus giving a large amount of comparable data. Table 1 gives the summary of these data obtained from 31 independent experiments involving 168 F_1 females.

In these crosses again, in addition to reddish and yellow classes non-reddish and non-yellow flies were obtained. In an ordinary case they would represent cross-overs between the reddish and yellow loci. Closer analysis of the data, however, shows that in the present case they cannot be accounted for in that way. If an assumption were made that they are crossovers it would mean that reddish is located about 3.65 units from yellow, because in a total of 9259 flies 169 cross-overs were obtained.[2] The reddish locus, therefore, should be either to the left of pilose or between scute and vermilion. The first difficulty in the analysis was met in trying to determine which of these positions was held by the locus of reddish. By taking into account all classes obtained from the crosses between sepia yellow scute vermilion and reddish it can be seen that there is no place in that region of the chromosome where the reddish locus could be placed. An analysis of the data in table 1 shows this clearly. Here,

TABLE 1

GROUPING OF MALE CLASSES FROM THE CROSS $\frac{\text{se y sc v}}{\text{re}}$ ♀ × re OR se y sc v ♂, IN REGARD TO CROSSING-OVER IN DIFFERENT REGIONS, ASSUMING DIFFERENT POSITIONS FOR THE LOCUS OF REDDISH

ASSUMED ORDER OF LOCI	re AND y CLASSES										NON-re AND NON-y CLASSES		
	se y sc v	re	y sc v	se re	se y	re sc v	se y sc	re v	y sc	re sc	+	v	sc v
FREQUENCY	3363	3767	71	80	36	24	827	918	3	1	116	30	23
se y sc v / re	0[3]	0	1–2	1–2	3	3	4	4	1–2–4	3–4	1	1–4	1–3
se|y sc v / re	0	0	1	1	3	3	4	4	1–4	3–4	1–2	1–2–4	1–2–3
se y|sc v / re	0	0	1	1	3	3	4	4	1–4	3–4	2–3	2–3–4	2
se y sc|v / re	0	0	1	1	2–3–4	2–3–4	4	4	1–4	2–3	3–4	3	2

assuming different positions for reddish, it is shown in what region the crossing over should have occurred to give the observed classes. From that table it can be seen that reddish does not fit at all in any of the four possible positions. In which ever position reddish is assumed to be, some of the double cross-over classes are disproportionally high. In this cross, the occurrence of any of the double cross-over classes, except those involving the fourth region, would be an exception in itself. According to the published data[4,5] and those of Dr. C. W. Metz and Miss M. S. Moses not yet published, the smallest distance in which double cross-overs have been observed is more than fifteen units in length. In this case, the distance is less than five units long. The occurrence of any double cross-over in so small a distance would be very abnormal and the occurrence of so many double cross-overs as were observed is highly improbable.

Analysis as given in table 1 does not exhaust all possible recombinations because those which would bring yellow and reddish in the same chromosome are left out. There were two reasons for doing this. The first was that those cross-over classes probably do not occur at all, as will be shown later in the discussion of the cross between pilose scute and reddish, and the second is that nothing more than a guess could be made as to the phenotype of reddish yellow flies.

Cross between Reddish and Pilose Scute.—This cross brings out more clearly the points which were obscured in the cross between reddish and sepia yellow scute vermilion because in this case all characters involved are easily distinguishable whether alone or combined. In this cross, as in the previous one, no place for reddish could be found in the part of the chromosome where reddish should be located. As may be seen from table 2 all of the three possible positions for reddish are eliminated after a comparison is made between different cross-over classes. In this cross,

TABLE 2

GROUPING OF MALE CLASSES FROM THE CROSS $\frac{\text{pl sc}}{\text{re}}$ ♀ × re OR pl sc ♂, IN REGARD TO CROSSING OVER IN THE DIFFERENT REGIONS, ASSUMING DIFFERENT POSITIONS FOR THE REDDISH LOCUS

ASSUMED ORDER OF LOCI / FREQUENCY	re 1280	pl sc 1119	re sc 5	pl 9	re pl 13	sc 22	+ 62
$\frac{\text{pl sc}}{\text{re}}$	0	0	2	2	1–2	1–2	1
$\frac{\text{pl sc}}{\text{re}}$	0	0	2	2	1	1	1–2
$\frac{\text{pl sc}}{\text{re}}$	0	0	1–2	1–2	1	1	2

again, the assumed double cross-over classes are large notwithstanding the fact that the distance between the farthest loci is less than five units. They are so large in comparison with the single cross-over classes as to make it highly improbable that reddish can be located in any of these three positions.

One of the outstanding features of this cross is the failure to obtain the reciprocal class for the wild-type class which is the largest of the recombination classes. The reciprocal class would be pilose reddish scute. By crossing pilose reddish with scute flies it was possible to obtain pilose reddish scute flies which eliminated the possibility that that combination is not viable. The other possibility—i.e., that of low viability of pilose reddish scute flies—is also eliminated, because in the cross between pilose reddish scute and sepia yellow scute vermilion 116 flies of first parental class and 100 flies of second parental class were obtained, which shows that pilose reddish scute flies are at least as viable as sepia yellow scute vermilion flies, which are considered to have fairly good viability.

The Hypothesis.—When the results obtained from the cross between reddish and yellow were discussed, two possible interpretations were suggested, i.e., (1) that reddish is not an allelomorph of yellow, but only behaves uniquely in the crosses with yellow giving yellow F_1 generation or (2) that reddish is an allelomorph of yellow, which behaves exceptionally because in F_2 of the cross, reddish $\times$ yellow, wild type flies are found.

The first hypothesis appears to be untenable, because if reddish is not an allelomorph of yellow, but is an independent sex-linked character, it would be expected that it would behave in crosses as other mendelian characters do. The results from the crosses between reddish and sepia yellow scute vermilion, and between reddish and pilose scute, show clearly that that is not the case. The F_2 data from these crosses were so exceptional that it was not possible to "locate" reddish in the chromosome in the usual manner.

On the second hypothesis (i.e., that reddish is an allelomorph of yellow which behaves exceptionally) it is necessary to find an explanation for the occurrence of wild-type flies observed in the F_2 generation of crosses between reddish and yellow. Closer examination of the data from the cross between reddish and sepia yellow scute vermilion (table 1) shows that 116 out of 169 wild-type[6] males had the reddish chromosome from which reddish has been removed, and the rest of them had the same modified chromosome which had crossed-over in the yellow scute or scute vermilion region with the sepia yellow scute vermilion chromosome. Apparently all wild-type males obtained in this cross had the reddish chromosome in which the wild allelomorph was substituted for the reddish. Crossing over is the usual way by which one factor is substituted in a chromosome for the other one. In this case, however, as already indicated, crossing over cannot explain this substitution of wild for reddish. The mechanism by means of which this substitution is made is not known as yet and the word "mutation," used in its broadest sense, will be applied in describing it. It is assumed that reddish frequently "mutates" to wild-type.

Test of the Hypothesis.—The results of all experiments made so far, can be explained by the assumption that reddish is an allelomorph of yellow and that it mutates frequently to wild-type. When that assumption is made it is to be expected that the F_1 generation from a cross between reddish and yellow will be yellow or nearly so, and also some wild-type flies will be expected in the F_2 from the same cross. This hypothesis, also accounts for all irregularities observed in the results obtained from crosses between reddish and sepia yellow scute vermilion and between reddish and pilose scute. All wild-type classes obtained in the two crosses are results of mutation of reddish to wild-type. That separates them from the regular cross-over classes and eliminates all irregularities in behavior encountered otherwise in analysis of results.

[1] Metz, C. W., *Genetics*, **1**, 1916 (591–607).

[2] This would represent only half of the total cross-overs because no reciprocal cross-over class is represented. This feature is discussed in later paragraphs.

[3] In this and in the following table "0" signifies non-cross-over classes, "1" classes resulting from crossing over in the first region, etc.

[4] Metz, C. W., M. S. Moses and E. D. Mason, *Washington, Carnegie Institute Publ.*, **328**, 1923.

[5] Weinstein, A., these PROCEEDINGS, **6**, 1920 (623–639).

[6] Wild-type in this case refers to the body color only.

THE EXPLANATION OF HYBRID VIGOR

By W. E. Castle

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It is a fact well known to breeders of animals and plants that crossing two pure breeding but different strains or varieties of the same species, as a rule produces offspring more vigorous in growth than either parental variety. Many investigators ascribe this increase in vigor to the fact that the cross-breds are *heterozygous* for all genetic factors in which the parents differed. Accordingly they designate the phenomenon heterozygosis, or in the simplified terminology suggested by Shull, *heterosis*. Shull (1911) referring to some of his earlier observations on the effects of cross-breeding maize says "I assumed that the vigor in such cases is due to the presence of heterozygous elements in the hybrids, and that the degree of vigor is correlated with the number of characters in respect to which the hybrids are heterozygous."...."Mr. A. B. Bruce proposes a slightly different hypothesis in which the degree of vigor is assumed to depend upon