

BUFF, A NEW ALLELOMORPH OF WHITE EYE COLOR IN DROSOPHILA

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In the course of certain experiments to find out the frequency of the occurrence of primary non-disjunction in *Drosophila* (see BRIDGES 1916), I found a new eye color mutation, "buff" (July 28, 1915), which has proven to be a new allelomorph of white.

Eosin miniature females had been mated to wild males, giving, as expected in the F_1 generation, eosin miniature males and wild type females. But along with these two kinds of flies, there appeared also in one bottle two, and in another eight, females which were long-winged like their normal sisters, but whose eye color was lighter than that of standard eosin females and a little darker than that of eosin males.

These light-eyed females were put into a new bottle where they produced offspring, having evidently been fertilized by their eosin miniature brothers. Unfortunately little attention was paid to the nature of the offspring of the females. Apparently a majority of the sons were eosin with some lighter in eye color. Only one of these males was bred, a miniature male whose eye color was much lighter than eosin, being a pale cream or "buff."

The experiments which are to follow prove that the buff color of this male is a new allelomorph of white. One of the important theoretical questions with respect to a new member of a series of allelomorphs is its origin, whether directly from the wild by a single act of mutation, or indirectly from an already existing mutant member of the series (see MORGAN, STURTEVANT, MULLER and BRIDGES, 1915, Chap. 7). Because of the uncertainty with respect to the offspring of the original light females we cannot be entirely sure in this case whether buff arose from the wild type of the father or from the eosin of the mother. It seems more probable that the buff arose from the wild type of the father for on this view we may explain the light color of the mothers as eosin-buff compound, this light color being without explanation if the buff arose from the eosin.

The buff miniature male was mated to a wild female and gave in the F_1 generation only red daughters (195) and red sons (187) which shows buff to be recessive. About half the F_2 males but none of the F_2 females showed the "buff" color, which is thus shown to be due to a sex-linked gene (table 1). Not one of the sons was eosin in color;

TABLE 1
P₁ wild ♀♀ × buff miniature ♂♂. F₁ wild type ♀♀ × F₁ wild type ♂♂.

F_2 wild type ♀♀	Non-crossover ♂♂		Crossover ♂♂		Total males	Crossovers	Crossover value
	Buff min.	wild type	Buff	min.			
612	172	194	104	94	564	198	35.2

therefore if buff is eosin plus a modifier which reduces the color to a pale cream then this modifier must be very closely linked to eosin. There remained besides this possibility still two other possibilities: buff might be a simple allelomorph of white or might be in another locus altogether.

The amount of crossing over between buff and miniature (35.2 per cent) is in agreement with the amount of crossing over between white and miniature, therefore the view that buff occupies the white locus seemed the more probable one. In subsequent generations (table 2) back-cross experiments were run which furnished in both males and females additional linkage data similar to that of the males of table 1.

TABLE 2
Wild type ♀♀ heterozygous for buff and miniature back-crossed to buff miniature ♂♂.

Non-crossovers		Crossovers		Total	Crossovers	Crossover values
Buff min.	Wild type	Buff	Min.			
512	524	284	302	1622	586	36.1

The buff females which appeared in these back-crosses were of identically the same color as the buff males. This is strong evidence against the modifier-view that buff is eosin plus a linked diluter; for of the great number of tested combinations of eosin with other eye colors (including specific diluters of eosin) there has not yet been found a single one in which eosin does not retain its bicolorism, that is, in which the females are not *darker* than the corresponding males.

Between the two remaining possibilities, namely that buff is a simple allelomorph of white, and that buff occupies a locus distinct from white, we are able to decide by finding more accurately the locus of buff. This was done by finding the amount of crossing over between buff and yel-

low (yellow is at the zero point of the X chromosomes). Yellow, buff and miniature were used in the same experiment so that the occurrence of the very small double crossover class might give conclusive evidence as to the location of the genes.

A buff miniature female was mated to a yellow male and yielded in the F_1 generation wild type females and buff miniature males. A few of these were inbred and gave (table 3) in the males the desired linkage information. The yellow buff miniature males were used to run two three-point back-crosses (tables 4 and 5).

TABLE 3
 P_1 buff miniature ♀♀ × yellow ♂♂. F_1 wild type ♀ × F_1 buff miniature ♂.

No.	F_2 females				F_2 males								Total males
	Non-cross-overs		Crossovers		$y \frac{w^{br}}{m}$		$y \frac{w^{br}}{m}$		$y \frac{w^{br}}{m}$		$y \frac{w^{br}}{m}$		
	Buff min.	Wild type	Buff	Min.	Yellow buff min.	Buff Wild type	Yellow buff min.	Buff	Yellow buff	Min.	Yellow buff	Min.	
1	71	58	36	35	57	60	2	3	31	43	—	—	196
2	41	39	26	37	43	29	—	1	20	19	—	—	112
3	39	50	24	22	33	34	1	1	22	17	—	—	108
4	62	64	28	40	43	65	3	1	20	28	—	—	160
5	43	52	19	19	39	46	—	1	25	24	—	—	135
6	34	39	31	22	35	31	1	—	28	22	—	—	117
7	28	48	21	19	33	39	1	1	24	23	—	—	121
8	27	27	14	13	27	24	—	2	13	8	—	—	74
9	44	38	23	30	33	40	1	3	18	24	—	1	120
10	49	62	27	20	39	45	2	—	27	28	—	—	141
Totals	438	477	249	257	382	413	11	13	228	236	0	1	1284
	915		506		795		24		464		1		

TABLE 4
Wild type ♀♀ heterozygous for yellow, buff and miniature [$y \frac{w^{br}}{m}$] back-crossed to yellow buff miniature males.

No.	$y \frac{w^{br}}{m}$		$y \frac{w^{br}}{m}$		$y \frac{w^{br}}{m}$		$y \frac{w^{br}}{m}$		Total
	Yellow	Buff min.	Yellow buff min.	Wild type	Yellow min.	Buff	Yellow buff	Min.	
1	79	96	3	5	58	59	—	—	300
2	66	88	—	1	41	57	—	—	253
3	56	50	—	1	30	29	—	—	166
4	74	75	2	6	45	54	1	—	257
5	53	48	1	2	29	25	—	—	158
	328	357	6	15	203	224	1	0	
Total	685		21		427		1		1134

TABLE 5

*P*₁ yellow buff miniature ♀ × wild ♂. *F*₁ wild type [*y w^{br} m*] × *F*₁ yellow buff min. ♂.

No.	<i>y w^{br} m</i>		<i>y</i> <i>w^{br} m</i>		<i>y w^{br}</i> <i>m</i>		<i>y</i> <i>w^{br} m</i>		Total
	Yellow buff min.	Wild type	Yellow	Buff min.	Yellow buff	Min.	Yellow min.	Buff	
1	32	37	3	3	27	24	—	—	
	42	29	1	1	16	19	—	—	
2	39	38	1	—	17	17	—	—	
	32	38	—	—	24	40	—	—	
3	55	56	3	—	19	16	1	—	
	48	45	1	—	29	26	—	1	
4	31	43	—	1	24	17	—	—	
	33	24	1	—	11	22	—	—	
5	45	47	1	2	29	25	—	—	
	60	51	2	—	16	28	—	—	
6	45	53	1	3	18	24	—	—	
	36	35	—	—	22	21	—	—	
7	35	27	1	—	14	16	—	—	
	28	27	—	2	13	17	—	—	
8	22	31	3	1	13	23	—	—	
	30	33	—	1	11	11	—	—	
9	25	44	—	—	18	18	—	—	
	25	29	—	1	9	14	—	—	
10	29	36	1	—	19	15	—	—	
	31	32	—	2	15	19	—	1	
11	38	36	—	3	22	20	—	—	
	52	31	1	1	24	17	—	—	
12	41	53	2	3	25	23	—	—	
	50	46	2	1	24	33	—	—	
13	53	66	2	2	26	26	—	—	
	40	42	1	2	21	21	—	—	
14	71	82	2	1	43	59	—	—	
	71	53	2	1	33	37	—	1	
15	34	33	1	—	16	21	1	—	
	36	37	2	1	15	15	—	—	
16	53	54	1	3	29	40	—	—	
	55	51	1	2	27	33	—	—	
17	38	51	1	2	24	21	—	1	
	34	40	1	1	21	26	—	—	
18	38	30	1	—	31	19	—	—	
	38	43	2	2	19	20	—	—	
19	33	31	1	—	15	22	1	—	
	43	37	2	1	15	15	—	—	
20	31	34	1	1	19	30	—	1	
	38	45	1	—	13	25	—	—	
Totals	1610	1650	46	44	826	935	3	5	5119

TABLE 6

*P*₁ eosin ♀♀ × buff miniature ♂♂. *F*₁ eosin-buff ♀ × *F*₁ eosin ♂.

No.	F ₂ Females		F ₂ males				Total males	Crossover values
			Non-cross-over ♂		Crossover ♂			
	Eosin	Eosin buff	Eosin	Buff min.	Eosin min.	Buff		
1	81	83	66	68	35	43	212	37
2	44	49	50	41	16	20	127	28
3	71	80	46	40	30	18	134	36
4	54	57	26	28	14	19	87	38
Total	261	260	188	177	95	100	560	35

TABLE 7

*P*₁ white ♀♀ × buff miniature ♂♂. *F*₁ white-buff ♀ × *F*₁ white ♂.

No.	F ₂ females		F ₂ males				Total males	Crossover values
			Non-cross-over ♂		Crossover ♂			
	White	White-buff	White	Buff min.	White min.	Buff		
1	53	47	29	25	14	14	82	34
2	65	64	50	35	22	35	142	40
3	45	43	24	32	11	15	82	32
4	52	49	25	31	13	13	82	32
Totals	215	203	128	123	60	77	388	35.3

TABLE 8

*P*₁ cherry ♀♀ × buff miniature ♂♂. *F*₁ cherry-buff ♀ × *F*₁ cherry ♂.

No.	F ₂ females		F ₂ males				Total males	Crossover values
			Non-cross-over ♂		Crossover ♂			
	Cherry	Cherry-buff	Cherry	Buff min.	Cherry min.	Buff		
1	66	65	38	31	20	20	109	34
2	66	76	34	31	10	18	93	30
3	74	75	51	51	35	28	165	38
4	69	65	44	63	30	29	166	38
Totals	275	281	167	176	95	95	533	35.6

By considering the smallest or double crossover classes of tables 3, 4 and 5, it is seen that all the data are consistent with the assumption that the gene for buff lies in the X chromosome between the genes for yellow and miniature, as does white. Furthermore the amount of cross-

TABLE 9
Summary of linkage data.

Genes	Total	Crossovers	Crossover values	Crossover values by MORGAN and BRIDGES
Yellow bu ♀	7537	145	1.9	1.1
Buff min.	14811	5258	35.5	33.2
Yellow min.	7537	2787	36.9	34.3

ing over between yellow and buff is approximately the same as that between yellow and white or any of the other allelomorphs of white.

These linkage experiments limit our possibilities still further; for if buff is due to a gene having no relation to white, then this gene must still be very close to the locus for white, since the linkage relations of buff are practically identical with those of white. The next series of tests effectually proved that the gene for buff must occupy the same locus as white.

The other allelomorphs of white when crossed to each other give intermediates ("compounds") and just such compounds were obtained when a buff miniature male was mated to white, eosin and cherry. In each case the F_1 generation yielded females whose eye color was intermediate between the two eye colors which entered the combination. The white-buff compound was the lightest of the three and the cherry-buff the darkest. No red-eyed flies appeared.

The F_2 from the compounds furnished more compounds in the females, while the male counts showed that the amount of crossing over with miniature is the same for buff as for white, eosin or cherry (tables 6, 7 and 8).

In conclusion, (1) The data have shown that buff is due to a sex-linked gene whose linkage relations are the same as the linkage relations of white (table 9). (2) The occurrence of compounds effectually disposes of the possibility that buff is due to a gene having no other relation to white than a neighboring locus in the chromosome. (3) Against the modifier-of-eosin view we have urged the strong argument of the lack of bicolorism in buff. (4) The linkage experiments have furnished evidence that no modifier could be separated from eosin by crossing over; for in 14251 flies in which such a crossover might have appeared none was found (table 9). (5) We are led then to the conclusion that buff is a simple allelomorph of white. (6) From the evidence upon the

