

SEGREGATION AND RECOMBINATION OF THE GENES FOR TINGED,  
BLOOD, BUFF, AND CORAL IN *DROSOPHILA MELANOGASTER*.

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In a previous paper I reported the origin of blood and tinged, two sex-linked eye mutants in *Drosophila*. Both mutants gave complete linkage with white, eosin and cherry and consequently formed with the red of the wild type a sextuple system of multiple allelomorphs. Safir and Lancefield later reported buff and coral, two other members of this system, as shown by their linkage to white. T. H. Morgan has kindly supplied me with stocks of buff and coral and this paper records the combinations made with these two stocks to my stocks of blood and tinged. The results of these crosses bear out the expectation that, since blood and tinged are allelomorphic to white and buff and coral are allelomorphic to white, the mutants buff, coral, tinged and blood should show allelomorphism to each other.

The evidence from such a system is significant as it bears on the nature of the change that takes place in the chromosomes of mutant stocks. If the different mutants are a result of losses of materials that lie at different levels on the sex-chromosome, then the wild type eye should result in the daughters on crossing any two of these mutants, since the daughter receives two sex-chromosomes and each would restore the missing allelomorph of the other. As a matter of fact the daughters from all combinations are com-

pounds, with eyes intermediate in color between the parent types. If the genes for these different eye colors are allocated at different levels on the sex chromosome there should appear among the grandsons eyes of the wild type as a result of the phenomenon of crossing over. The evidence presented from these combinations is consistent with that obtained from other tests in showing that this does not occur.

The nomenclature employed is that used in other publications for the members of this system.—white *w*, tinged *w<sup>t</sup>*, buff *w<sup>b</sup>*, eosin *w<sup>e</sup>*, cherry *w<sup>c</sup>*, coral *w<sup>co</sup>*, blood *w<sup>b</sup>*, red *W*.

The female is expressed by the formula *XX*, the male *XO*, consequently the formula for a tinged eyed female is *w<sup>t</sup>w<sup>t</sup>XX*, a tinged eye male *w<sup>t</sup>XO*.

The following tables give the results of the combinations made between the different members of this allelomorphous series. The genetic composition of the parents (*P*), the children (*F*<sub>1</sub>), and grandchildren (*F*<sub>2</sub>) are expressed in terms of the nomenclature stated above. The numbers indicate the number of flies realized from the different combinations.

1. *Linkage of Buff and Tinged*

(a) Buff ♀ by Tinged ♂.

*P.* *w<sup>b</sup>w<sup>b</sup>XX* . *w<sup>t</sup>XO*

*F*<sub>1</sub>. *w<sup>b</sup>w<sup>t</sup>XX* *w<sup>b</sup>XO*

(1). 52 58

(2). 200 185

(3). 406 301

<i>F</i> <sub>2</sub>	<i>w<sup>b</sup>w<sup>b</sup>XX</i>	<i>w<sup>b</sup>w<sup>t</sup>XX</i>	<i>w<sup>b</sup>XO</i>	<i>w<sup>t</sup>XO</i> .
1 .....	135			112
1a .....	155			110
2 .....	84			56
2a .....	58			28
3 .....	129			136
3a .....	83			65
4 .....	136			118
4a .....	45			53
5 .....	91			70
5a .....	130			93
6 .....	75			115
6a .....	85			96
7 .....	23			30
7a .....	95			108
Total .....	1324			1190

The buff females and the tinged-buff compounds are practically inseparable. The two classes of males can be separated into buff and tinged males but are here classified together. The wild red eyed form did not appear in the F<sub>1</sub> or F<sub>2</sub> generation. The F<sub>2</sub> males and females show a slight variation in color although we were unable to separate the two on a color basis.

(b) Buff ♂ by Tinged ♀

P.	wbuXO	. wtwtXX
F <sub>1</sub>	w <sup>t</sup> wbuXX	w <sup>t</sup> XO.
	(1) 30	31
	(2) 256	200
	(3) 94	85

The tinged males and the tinged-buff compound females of the F<sub>1</sub> are inseparable on a color basis as one might expect since the two colors are separated by such a small margin.

F <sub>2</sub>	w <sup>t</sup> w <sup>t</sup> XX	w <sup>t</sup> wbuXX	w <sup>t</sup> XO	wbuXO.
1.....	72		48	
2.....	127		103	
3.....	113		65	
4.....	242		186	
5.....	68		47	
6.....	112		82	
Total.....	734		531	

The F<sub>2</sub> males can be separated with difficulty.

2. *Linkage of Buff and Blood.*

(a) Buff ♀ by Blood ♂.

P.	wb <sup>u</sup> w <sup>b</sup> XX	. w <sup>b</sup> XO
F <sub>1</sub>	wbuwbXX	wbuXO
	202	198

F<sub>1</sub> Females compounds uniform deep red—males like buff.

F <sub>2</sub>	wbuwbXX	wbuwbXX	wbuXO	wbXO
1.....	51	72	50	69
2.....	45	46	49	37
3.....	130	148	117	119
4.....	158	152	168	139
Total.....	384	418	384	364

Males and females in the F<sub>2</sub> are easily separated into the different classes.

(b) Buff ♂ by Blood ♀.

P.  $w^{bu}XO$  .  $w^bwbXX$ F<sup>1</sup>  $w^bw^bXX$        $w^bXO$ 

117                  104

F<sub>1</sub> Males typical of blood eyes—light when young—turn very dark with age. Females lighter than blood and do not turn so dark with age.

F <sub>2</sub>	$w^bw^bXX$	$w^bwbXX$	$w^{bu}XO$	$w^bXO$
1.....	79	83	60	58
2.....	66	79	45	54
3.....	139	182	147	112
4.....	79	67	74	77
Total.....	363	411	326	301

## 3. Linkage of Coral and Tinged.

(a) Coral ♀ by Tinged ♂.

P.  $w^{co}w^{co}XX$  .  $w^tXO$ 

F <sub>1</sub>	$w^{co}wtXX$ 27		$w^{co}XO$ 22	
F <sub>1</sub> Flies	Lighter than coral stock		Same color as coral stock	
F <sub>2</sub>	$w^{co}w^{co}XX$	$w^{co}wtXX$	$w^{co}XO$	$w^tXO$
1.....	79	94	79	84
1a.....	78	70	75	56
1b.....	46	40	33	29
2.....	74	78	65	47
2a.....	57	62	62	58
3.....	40	43	51	54
Total.....	374	387	365	328

(b) Coral ♂ by Tinged ♀.

P.  $w^{co}XO$  .  $w^t w^t XX$

$F_1$	$w^t w^{co} XX$ 44		$w^t XO$ 36	
$F_2$	$w^t w^t XX$	$w^t w^{co} XX$	$w^t XO$	$w^{co} XO$
1 .....	31	48	33	35
1a.....	63	60	61	60
1b.....	5	7	4	8
2 .....	68	54	74	52
2a.....	68	68	53	61
2b.....	24	18	9	14
Total .....	259	255	234	230

4. *Linkage of Coral and Blood.*

(a) Coral ♀ by Blood ♂.

P.  $w^{co} w^{co} XX$  .  $w^b XO$

$F_1$	$w^{co} w^b XX$ 18		$w^{co} XO$ 18	
$F_1$ Flies	Female just a hint lighter than male.		As these flies become older the sexes are indistinguishable.	
$F_2$	$w^{co} w^{co} XX$	$w^{co} w^b XX$	$w^{co} XO$	$w^b XO$
1 .....	116		103	
1a.....	159		135	
2 .....	49		81	
2a.....	180		178	
Total .....	945		497	

The two classes of males can be separated when young. Females cannot be separated with certainty. They show a variable range as is true of blood which overlaps the coral.

## (b) Coral ♂ by Blood ♀.

P.       $w^{co}XO$                        $w^{bw}bXX$ 

$F_1$	$w^{bw}w^{cu}XX$ 18	$w^{b}XO$ 17		
$F_1$ Flies	Females and males same color; dark as males. A mere hint that females are lighter.			
$F_2$	$w^{bw}bXX$	$w^{bw}w^{cu}XX$	$w^{b}XO$	$w^{cu}XO$
1 .....	103		116	
1a .....	143		107	
1b .....	21		27	
2 .....	162		146	
2a .....	126		122	
2b .....	82		70	
Total .....	637		588	

## 5. Linkage of Coral and Buff.

## (a) Coral ♀ by Buff ♂.

P.       $w^{co}w^{co}XX$                        $w^{bu}XO$ 

$F_1$	$w^{cu}w^{bu}XX$ 31	$w^{cu}XO$ 29		
$F_1$ Flies	Much lighter than coral	Same color as stock coral.		
$F_2$	$w^{cu}w^{cu}XX$	$w^{cu}w^{bu}XX$	$w^{cu}XO$	$w^{bu}XO$
1 .....	57	40	49	44
1a .....	50	56	45	40
Total .....	107	96	94	84

(b) Coral ♂ by Buff ♀.

P.  $w^{co}XO$  .  $wbuwbuXX$

$F_1$	$wbuw^{co}XX$ 44		$wbuXO$ 37	
$F_1$ Flies	Lighter than buff Lighter than coral Lighter than blood?		Same color as buff stock.	
$F_2$	$wbuw^{bu}XX$	$wbuw^{co}XX$	$w^{bu}XO$	$w^{co}XO$
1 .....	57	41	46	45
1a.....	253	233	239	277
1b.....	45	25	33	29
2 .....	198	203	166	175
2a.....	20	19	29	20
Total.....	573	521	513	446

Compound ♀ much lighter than ♂.

6. *Linkage of Tinged and Blood.*

(a) Tinged ♀ by Blood ♂.

P.  $w^t w^t XX$  .  $w^b XO$

$F_1$	$w^t w^b XX$ 33		$w^t XO$ 2)	
$F_1$ Flies	All lighter than blood, but darker than tinged.		Males like tinged stock.	
$F_2$	$w^t w^t XX$	$w^t w^b XX$	$w^b XO$	$w^t XO$
1 .....	74	98	71	78
1a.....	109	105	104	97
2 .....	37	36	21	32
2a.....	57	52	46	63
2b.....	29	22	26	28
Total.....	306	313	268	298

(b) Tinged ♂ by Blood ♀.

P.                      wtXO                      .                      w<sup>b</sup>w<sup>b</sup>XX

F <sub>1</sub>	wtw <sup>b</sup> XX 18		w <sup>b</sup> XO 17	
F <sub>1</sub> Flies	Females much lighter than males.		Typical of blood stock Sexes easily separated on color basis.	
F <sub>2</sub>	w <sup>b</sup> w <sup>b</sup> XX	w <sup>b</sup> w <sup>t</sup> XX	w <sup>b</sup> XO	w <sup>t</sup> XO
1 .....	52	55	41	45
1a.....	68	68	47	61
1b.....	9	9	5	4
2 .....	35	31	42	47
2a.....	164	160	112	136
2b.....	45	45	26	33
Total .....	373	368	273	326



7. *Linkage of Coral to Eosin.*

(a) Eosin ♀ and Coral ♂.

P.  $w^e w^{e0} XX$  .  $w^{e0} XO$

F <sub>1</sub>	$w^e w^{e0} XX$ 108 200		$w^{e0} XO$ 94 200	
F <sub>1</sub> Flies	Indistinguishable from coral compound does not seem to modify.		Typical of eosin; slight color change with age.	
F <sub>2</sub>	$w^e w^{e0} XX$	$w^e w^{e0} XX$	$w^{e0} XO$	$w^{e0} XO$
9a.....	60	55	60	57
	40	54	71	47
11a.....	30	30	24	35
	60	68	65	70
11b.....	15	10	14	16
	62	60	59	48
F <sub>2</sub> Flies	Like Eosin ♀ ♀	Slightly darker than ♀ but not as dark as males.	Like eosin ♂	Much like blood when old but not as dark

(b) Eosin ♂ by Coral ♀.

P,                     $w^eXO$                     ,                     $w^{cu}w^{cu}XO$ 

F <sub>1</sub>	$w^e w^{cu} XX$ 125		$w^{cu} X O$ 115	
F <sub>1</sub> Flies	The eye colors are hard to distinguish. The females seem to be a little lighter than the males; darker when old.			
F <sub>2</sub>	$w^{cu} w^{cu} XX$	$w^{cu} w^e XX$	$w^e X$	$w^{cu} X$
1 .....	166		70	90
1a .....	59		36	40
1b .....	107		17	34
2 .....	196		98	97
3 .....	87		40	50
3a .....	80		31	41
Total .....	695		292	352

8. *Summary.*

The genes for buff and coral known to be allelomorphous to white have here been tested with tinged and blood, two other genes allelomorphous to white. The expectation is that since both are allelomorphous to white, they will be allelomorphous to each other. The results of the different combinations made verify the expectations. Sufficient evidence has accumulated to show that these are members of the same allelomorphous series. The fact that the red eyed fly does not appear in the F<sub>1</sub> or F<sub>2</sub> bears out the assumption that the different members of this multiple allelomorphous series are but different expressions of the same material particle and that they occupy identical loci on the sex-chromosome.

9. *Literature.*

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