THE BEADEX LOCUS IN DROSOPHILA MELANOGASTER: THE GENOTYPIC CONSTITUTION OF Bx^r

BY M. M. GREEN

DEPARTMENT OF GENETICS, UNIVERSITY OF CALIFORNIA, DAVIS, CALIFORNIA

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It is known that the sex-linked Beadex (*Bx*) wing mutants in *Drosophila melanogaster* are of two types: dominant to and recessive to wild-type.[1] On the basis of experiments in which crossing over was demonstrated between Bx^1 (dominant) and Bx^r (recessive),[2] it was determined that Bx^1 represents a simple mutation of Bx^+, while Bx^r is a tandem duplication in which Bx^+ is duplicated. It was postulated that the wild-type alleles of the recessive mutants small eye (*sy*) and fused (*fu*) wing veins are also duplicated in Bx^r. It is the purpose of this report to confirm the postulate which includes fu^+ and sy^+ in duplicate as components of Bx^r.

The mutants *sy*, *Bx* and *fu* have been localized at positions 59.2, 59.4 and 59.5 on the X chromosome.[1] Assuming Bx^r to be a tandem duplication for all three loci, the precise Bx^r genotype would be represented by the notation: $sy^+\ Bx^+\ fu^+\ sy^+\ Bx^+\ fu^+$. To test whether the fu^+ locus is included in the Bx^r duplication the following experiments were performed using the mutants Bx^r, Bx^1, *fu* and *f* (recessive forked bristles-locus 56.7). From ♀ ♀ of the genotype $Bx^r/f\ Bx^1\ fu$ exceptional ♂ progeny are expected depending upon the pairing and crossing over between Bx^1 and Bx^+ of the duplication.

If Bx^1 pairs with Bx^+ in the left section of the Bx^r duplication as follows:

$$\begin{array}{l} \qquad sy^+ \ldots Bx^+ \ldots fu^+ \ldots sy^+ \ldots Bx^+ \ldots fu^+ \\ f \ldots\ldots sy^+ \ldots Bx^1 \ldots fu \end{array}$$

crossing over between Bx^1 and *fu* will produce exceptional ♂♂ of the genotypes $f\ sy^+\ Bx^1\ fu^+\ sy^+\ Bx^+\ fu^+$ and $sy^+\ Bx^+\ fu$. Crossovers between sy^+ and Bx^1 produce no individuals phenotypically separable from crossovers between *f* and sy^+.

Conversely if Bx^1 pairs with Bx^+ in the right section of the Bx^r duplication as follows:

$$\begin{array}{l} sy^+ \ldots Bx^+ \ldots fu^+ \ldots sy^+ \ldots Bx^+ \ldots fu^+ \ldots \\ \qquad\qquad f \ldots\ldots\ldots sy^+ \ldots Bx^1 \ldots fu \ldots \end{array}$$

crossing over between sy^+ and Bx^1 will produce exceptional ♂♂ of the genotypes $sy^+\ Bx^+\ fu^+\ sy^+\ Bx^1\ fu$ and $f\ sy^+\ Bx^+\ fu^+$. Crossovers between Bx^1 and *fu* produce no individuals phenotypically separable from crossovers occurring to the right of *fu*.

It is to be noted that if Bx^r is a duplication for fu^+ then the exceptional

♂♂ *f Bx*^{1} *Bx*$^+$ and *Bx*$^+$ *Bx*^{1} should be *fu*$^+$ in phenotype. If *fu*$^+$ is not in the duplication, the *Bx*$^+$ *Bx*^{1} ♂♂ would be *fu*. Among ca. 5000 ♂ progeny of ♀ ♀ *Bx*^{r}/ *f Bx*^{1} *fu*, 7 ♂♂ *f Bx*^{1} *Bx*$^+$ and 2 ♂♂ *Bx*$^+$ *Bx*^{1} were recovered; all were *fu*$^+$ in phenotype thereby fulfilling expectation. Moreover, if the genotypes of the *f Bx*^{1} *Bx*$^+$ and *Bx*$^+$ *Bx*^{1} ♂♂ are as noted, then it should be possible to recover the *fu* mutant from *Bx*$^+$ *Bx*^{1} but not from *f Bx*^{1} *Bx*$^+$.

Experiments in which this proposition was tested were carried out in the following manner. Females of the genotypes (1) *f Bx*^{1} *Bx*$^+$/*Bx*$^+$ *car* (recessive carnation eye color—locus 62.5) and (2) *Bx*$^+$ *Bx*^{1}/*f Bx*$^+$ *car* were obtained. Assuming the constitution of *Bx*$^+$ *Bx*^{1} and *f Bx*^{1} *Bx*$^+$ chromosomes to be as noted above, the following exceptional ♂ progeny are expected. In (1), if pairing occurs between *Bx*^{1} and *Bx*$^+$ as follows:

$$\begin{array}{l} f \ldots sy^+ \ldots Bx^1 \ldots fu^+ \ldots sy^+ \ldots Bx^+ \ldots fu^+ \\ \qquad sy^+ \ldots Bx^+ \ldots fu^+ \ldots car \end{array}$$

crossing over between *Bx*^{1} and *fu*$^+$ will produce exceptional ♂ progeny *f sy*$^+$ *Bx*^{1} *fu*$^+$ *car* and *sy*$^+$ *Bx*$^+$ *fu*$^+$ *sy*$^+$ *Bx*$^+$ *fu*$^+$ (phenotypically *Bx*^{r}), with no *fu* ♂♂ being recovered. Crossovers between *sy*$^+$ and *Bx*^{1} produce no exceptional progeny. Similarly, pairing of *Bx*$^+$ with *Bx*$^+$ accompanied by crossing over within the paired section produces no exceptional progeny.

In (2) if pairing occurs between *Bx*^{1} and *Bx*$^+$ as follows:

$$\begin{array}{l} sy^+ \ldots Bx^+ \ldots fu^+ \ldots sy^+ \ldots Bx^1 \ldots fu \\ \qquad\qquad f \ldots\ldots\ldots sy^+ \ldots Bx^+ \ldots fu^+ \ldots car \end{array}$$

crossing over between *sy*$^+$ and *Bx*^{1} will produce exceptional ♂ progeny *f sy*$^+$ *Bx*^{1} *fu* and *sy*$^+$ *Bx*$^+$ *fu*$^+$ *sy*$^+$ *Bx*$^+$ *car* (phenotypically *Bx*^{r} *car*). In this cross the mutant *fu* would be recovered. Crossing over between *Bx*^{1} and *fu* will produce ♂♂ *f sy*$^+$ *Bx*$^+$ *fu* and *sy*$^+$ *Bx*$^+$ *fu*$^+$ *sy*$^+$ *Bx*^{1} *fu*$^+$ *car*. (The latter is inseparable phenotypically from crossovers between *fu*$^+$ and *car* and therefore not detectable.) Pairing of *Bx*$^+$ with *Bx*$^+$ accompanied by crossing over within the paired section produces no exceptional progeny.

The results obtained from crosses (1) and (2) only partly bear out expectation. In cross (1) among 6210 F_1 ♂♂, exceptional ♂♂ as follows were obtained: 4 *Bx*^{r}, 4 *f Bx*^{1} *fu car*, 1 *f Bx*^{1} *car*. In cross (2) among 6422 F_1 ♂♂, exceptional ♂♂ as follows were obtained: 2 *Bx*^{r} *car;* 3 *f Bx*^{1} *fu;* 2 *f fu*. These results substantiate the hypothesis that *fu*$^+$ is duplicated in *Bx*^{r}. However, the recovery of *fu* ♂♂ in cross (1) does not agree with expectation and merits further consideration here. These results suggest that not only is *fu*$^+$ duplicated in *Bx*^{r}, but at least one additional gene locus to the right of *fu*$^+$ is similarly duplicated. Since no mutants between *fu* and *car* have been reported,[1] this gene locus will be

designated as x. It is now possible to reconstruct the $Bx^r/f\ Bx^1\ fu$ cross by describing Bx^r as a tandem duplication with the notation $sy^+\ Bx^+\ fu^+\ x\ sy^+\ Bx^+\ fu^+\ x$. In the cross of ♀ ♀ $Bx^r/f\ Bx^1\ fu$ only the following pairing scheme need be reconsidered. (Pairing of Bx^1 with Bx^+ in the right section of Bx^r will produce results identical to those considered previously.)

$$\begin{array}{l} \qquad sy^+ \ldots Bx^+ \ldots fu^+ \ldots x \ldots sy^+ \ldots Bx^+ \ldots fu^+ \ldots x \\ f \ldots\ldots sy^+ \ldots Bx^1 \ldots fu \ldots\ldots x \end{array}$$

Crossovers between Bx^1 and fu will produce exceptional ♂♂ of the genotypes $sy^+\ Bx^+\ fu\ x$ and $f\ sy^+\ Bx^1\ fu^+\ x\ sy^+\ Bx^+\ fu^+\ x$ while crossovers between fu and x will produce ♂♂ $sy^+\ Bx^+\ fu^+\ x$ and $f\ sy^+\ Bx^1\ fu\ x\ sy^+\ Bx^+\ fu^+\ x$. Thus the assumption of x duplicated in Bx^r permits the extraction of two types of $f\ Bx^1\ Bx^+$ ♂♂; those carrying fu and fu^+ and those with two fu^+ loci. Phenotypically the two types are inseparable. It is obvious that the ♀ ♀ of cross (1) were derived from a ♂ of the former type. If the pairing scheme of cross (1) is considered in this light as follows:

$$\begin{array}{l} f \ldots\ldots sy^+ \ldots Bx^1 \ldots fu \ldots\ldots x \ldots sy^+ \ldots Bx^+ \ldots fu^+ \ldots x \\ \qquad sy^+ \ldots Bx^+ \ldots fu^+ \ldots x \ldots\ldots car \end{array}$$

crossovers between Bx^1 and fu will result in ♂♂ $f\ sy^+\ Bx^1\ fu^+\ x\ car$ (phenotypically $f\ Bx^1\ car$) and $sy^+\ Bx^+\ fu\ x\ sy^+\ Bx^+\ fu^+\ x$ (phenotypically Bx^r) while crossovers between fu and x will result in ♂♂ $f\ sy^+\ Bx^1\ fu\ x\ car$ (phenotypically $f\ Bx^1\ fu\ car$) and $sy^+\ Bx^+\ fu^+\ x\ sy^+\ Bx^+\ fu^+\ x$ (phenotypically Bx^r). This formulation fully accounts for the results obtained in cross (1), as well as those of cross (2) and it can be concluded that Bx^r is duplicated for Bx^+, fu^+ and x.

That the sy^+ locus is duplicated in Bx^r was demonstrated in much the same fashion. From ♀ ♀ of the genotype $Bx^r/sy\ Bx^1\ car$ exceptional ♂ progeny are again expected depending upon pairing and crossing over between Bx^1 and Bx^+ of the duplication.

If Bx^1 pairs with Bx^+ in the left section of the duplication as follows:

$$\begin{array}{l} sy^+ \ldots Bx^+ \ldots fu^+ \ldots x \ldots sy^+ \ldots Bx^+ \ldots fu^+ \ldots x \\ sy \ \ldots Bx^1 \ \ldots fu^+ \ldots x \ldots\ldots car \end{array}$$

crossing over in the interval Bx^1-x will produce exceptional ♂♂ of the genotypes $sy^+\ Bx^+\ fu^+\ x\ car$ and $sy\ Bx^1\ fu^+\ x\ sy^+\ Bx^+\ fu^+\ x$. Crossovers between sy and Bx^1 produce no individuals phenotypically separable from crossovers occurring to the left of sy.

Conversely if Bx^1 pairs with Bx^+ in the right section of the duplication as follows:

$$sy^+ \ldots Bx^+ \ldots fu^+ \ldots x \ldots \quad sy^+ \ldots Bx^+ \ldots fu^+ \ldots x$$
$$sy \ldots Bx^1 \ldots fu^+ \ldots car$$

crossing over between *sy* and Bx^1 will produce exceptional ♂♂ of the genotypes *sy* Bx^1 fu^+ *x* and sy^+ Bx^+ fu^+ *x* sy^+ Bx^1 fu^+ *x car*. Crossovers in the interval Bx^1-*x* produce no individuals phenotypically separable from crossovers between *x* and *car*.

It is to be noted that if Bx^r is duplicated for sy^+ then the exceptional ♂♂ Bx^+ Bx^1 *car* and Bx^1 Bx^+ should be sy^+ in phenotype. If sy^+ is not in the duplication, Bx^1 Bx^+ ♂♂ would be *sy*. Among ca. 3000 ♂ progeny of ♀♀ Bx^r/*sy* Bx^1 *car*, 3 ♂♂ Bx^1 Bx^+ *car* and 2 ♂♂ Bx^+ Bx^1 were recovered; all were sy^+. It follows that if the genotypes of the Bx^+ Bx^1 *car* and Bx^1 Bx^+ ♂♂ are as noted, then it should be possible to recover the *sy* mutant from Bx^1 Bx^+ but not from Bx^+ Bx^1 *car*.

Experiments to test this conclusion were carried out in the following fashion. Females of the genotypes (3) Bx^1 Bx^+/*f* Bx^+ *car* and (4) Bx^+ Bx^1 *car*/*f* Bx^+ were obtained. Assuming the constitution of the Bx^1 Bx^+ and Bx^+ Bx^1 *car* chromosomes to be as noted previously, the following exceptional ♂ progeny are expected. In (3) if pairing occurs between Bx^1 and Bx^+ as follows:

$$sy \ldots Bx^1 \ldots fu^+ \ldots x \ldots sy^+ \ldots Bx^+ \ldots fu^+ \ldots x \ldots$$
$$f \ldots sy^+ \ldots Bx^+ \ldots fu^+ \ldots x \ldots\ldots car$$

crossing over between *sy* and Bx^1 will produce ♂♂ *sy* Bx^+ fu^+ *x car* and *f* sy^+ Bx^1 fu^+ *x* sy^+ Bx^+ fu^+ *x* (the latter indistinguishable from crossovers between *f* and sy^+). Crossing over in the interval Bx^1-*x* will produce ♂♂ *sy* Bx^1 fu^+ *x car* and ♂♂ *f* sy^+ Bx^+ fu^+ *x* sy^+ Bx^+ fu^+ *x* (phenotypically Bx^r). As noted previously pairing between Bx^+ and Bx^+ accompanied by crossing over results in no exceptional progeny.

In (4) if pairing occurs between Bx^1 and Bx^+ as follows:

$$sy^+ \ldots Bx^+ \ldots fu^+ \ldots x \ldots sy^+ \ldots Bx^1 \ldots fu^+ \ldots x \ldots car$$
$$f \ldots\ldots sy^+ \ldots Bx^+ \ldots fu^+ \ldots x \ldots$$

crossing over between sy^+ and Bx^1 will result in exceptional ♂♂ of the genotypes *f* sy^+ Bx^1 fu^+ *x car* and sy^+ Bx^+ fu^+ *x* sy^+ Bx^+ fu^+ *x* (phenotypically Bx^r). Crossovers in the Bx^1-*x* interval will result in ♂♂ inseparable from crossovers between *x* and *car*. Again pairing between Bx^+ and Bx^+ accompanied by crossing over results in no exceptional progeny.

The results obtained from crosses (3) and (4) were those expected from the hypothesis. From cross (3) among 4419 F_1 ♂♂, 8 ♂♂ *sy car*, 7 ♂♂ *sy* Bx^1 *car* and 2 ♂♂ *f* Bx^r were recovered while from cross (4) among 5702 F_1 ♂♂, 3 ♂♂ *f* Bx^1 *car* were recovered. These results demonstrate that sy^+ is duplicated in Bx^r.

In summary it can be stated that in Bx^r the sy^+, Bx^+, fu^+ loci as well as x, a locus to the right of fu^+, are duplicated.

[1] Bridges, C. B., and Brehme, K. S., "The Mutants of *Drosophila melanogaster*," *Carnegie Inst. Wash. Publ.* **552**, (1944).

[2] Green, M. M., *Genetics* (in press) (1952).

*THE PSEUDOALLELISM OF WHITE AND APRICOT IN DROSOPHILA MELANOGASTER**

BY E. B. LEWIS

KERCKHOFF LABORATORIES OF BIOLOGY, CALIFORNIA INSTITUTE OF TECHNOLOGY, PASADENA

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The classical example of multiple allelism is the series of eye-color mutants at the white (*w*) locus in *Drosophila melanogaster*. The alternative interpretation of this series, namely, that it is made up of "pseudoalleles," or closely linked genes with similar effects, has usually been considered ruled out by two kinds of evidence. In the first place early attempts to resolve the series by crossing over failed in spite of numerous tests involving most of the mutants available at the time.[1-4] Secondly, a heterozygote for two different mutant genes of the series does not have the pheno type expected for non-allelic genes, namely, wild-type (or red) eye color, but instead has a mutant eye color which is usually intermediate between the colors of the two respective homozygotes. In recent years, however, several cases have been found in which non-allelic genes give a positive phenotypic test for allelism by virtue of a position effect.[5-7] In such cases, which have been termed "position pseudoalleles,"[7] mutant genes at the different loci (say, *a* and *b*) give a mutant phenotype in the $a\ +/+\ b$ heterozygote, but a wild-type, or more nearly wild-type, phenotype in the $a\ b/+\ +$ heterozygote.

With the above considerations in mind and with the aid of more adequate techniques for studying crossing over than were available in the early studies, the white gene and its so-called "allele," apricot, have been reinvestigated. This paper presents the evidence that these two genes occupy separate loci and that they constitute another example of position pseudoallelism. In what follows, the apricot gene, formerly symbolized as w^a will be designated by a new symbol, namely, *apr*.

In order to investigate the possibility of crossing over between *w* and *apr*, females with attached-X chromosomes were employed so that the two complementary products from any such crossing over would sometimes be recoverable simultaneously in a single individual. The first step was the