

similar fashion with tertiaries to give the effect of pure-breeding types if crossing over did not take place.

<sup>4</sup> Buchholz, J. T., and Blakeslee, A. F., these PROCEEDINGS, 16, 190-195 (1930).

<sup>5</sup> Blakeslee, Albert F. In press, Proceedings of the Sixth International Congress of Genetics.

<sup>6</sup> *Datura tatula* differs from *D. stramonium* only by the dominant gene for purple in contrast to white flowers and *D. inermis* differs from *D. stramonium* by the recessive gene for spineless capsules. These forms seem no more worthy of specific rank than a number of gene mutations which have occurred spontaneously in our standard line of *D. stramonium* and seem better included in the latter species.

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### EVERSPORTING AS A FUNCTION OF THE Y-CHROMOSOME IN *DROSOPHILA MELANOGASTER*<sup>1</sup>

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Many eversporting characters have been encountered in plants and animals. Some cases seem best explained as unstable genes which mutate frequently (Emerson,<sup>2</sup> Demerec<sup>3,4,5,6</sup>). This paper describes cases of eversporting eye color in *Drosophila melanogaster* in which the incidence of sports is apparently dependent upon the distribution of an extra Y-chromosome.

Wild type males were treated with x-ray and mated to untreated females. Their first and second generation descendants were examined for sex-linked and dominant autosomal mutations. Three sex-linked mutations causing mottled eye color appeared, called mottled-1, mottled-2 and mottled-3.

Each of these mottled stocks produces, under certain conditions, red-eyed flies which are apparent reversions to wild type. Eversporting in mottled stock is not new. Muller<sup>7</sup> describes a mottled stock which segregates into dark and light mottled classes. He finds it possible to select darks which produce mostly dark progeny, and lights which produce mostly lights. Patterson<sup>8</sup> describes a different situation. He finds that red eyed flies from his mottled line produce the same proportion of mottled progeny as do their mottled sisters.

Our mottled stocks differ from each other in their amount of mottling. We have some evidence that an environmental agent, probably temperature, plays a large part in determining how much color is to be present in the eyes of mottled flies. Mottled-3, and to a less extent mottled-1, approach and actually overlap normal red eye color in their range of

variation. Breeding red eyed flies reveals that they fall into two classes: one comparable with Patterson's red eyed flies—merely normal overlaps which breed exactly like mottled flies; the other comparable with Muller's dark mottled class—a different genotype. This latter type of ever-sporting we have attributed to the *Y*-chromosome—a phenomenon hitherto undescribed.

The analysis of ever-sporting in mottled-2 will be presented first. Mottled-2 is linked with the *X* and fourth chromosomes. The *X*-chromosome is broken into two segments. The smaller segment contains the normal allelomorphs of yellow, white (?), facet and echinus, and is free. The larger *X* segment contains the rest of the *X*-chromosome including the normal allelomorph of ruby, and is attached to the fourth chromosome at its left or ruby end. Mottled-2 is semi-lethal to males, but when males do survive they are fertile. Homozygous females rarely survive and have not been found fertile as yet. By mottled-2 females, we mean females which are heterozygous for both *X* segments and for a normal *X* carrying white. The chromosome constitutions of mottled-2 males and females are represented by the following formula:

$$\text{mottled-2 } \sigma \text{ } \overline{\text{---}} \text{---} \cdot \text{---} \quad \text{mottled-2 } \varnothing \text{ } \overline{\text{---}} \text{---} \cdot \text{---}$$

in which — means the small free *X* segment,  $\overline{\text{---}}$  means the larger *X* segment attached to a fourth chromosome,  $\overline{\text{w}}$  means a normal *X* carrying white,  $\text{---}$  means a *Y* and  $\bullet$  means a normal fourth chromosome. The second and third chromosomes are normal and are not represented. All flies of the constitutions shown have mottled eyes. Our stock is kept by mating normal yellow, white, echinus, crossveinless, (*y*, *w*, *ec*, *cv*) males to mottled females whose normal *X*'s carry *y*, *w*, *ec*, *cv*. The progeny from such matings are white females, mottled females, and white males in about equal numbers, and a few mottled males. No hyperploid individuals are produced, and no red eyed nor haplo-IV progeny. Crossing over between mottled and *y*, *w* or *ec* has never occurred; *cv* crosses over less than 1 per cent. Thus it is evident that the broken *X*-chromosome in mottled-2 females behaves as an unbroken unit, its only abnormality being reduced crossing over. The case of mottled-2 males is very different. Separation of the two *X* segments, non-disjunction of the broken *X* and the *Y*, and non-disjunction of the fourth chromosomes, all occur very frequently, resulting in many hyperploid and non-disjunctional exceptions in addition to regular offspring. The exceptions of interest here are those which occur when non-disjunction of the broken *X* and the *Y* takes place. If such non-disjunction occurs in a mottled-2 male mated to a normal homozygous white female, the result is a red-eyed daughter of the constitution  $\overline{\text{---}} \text{---} \cdot \text{---}$ . (or a white-eyed *XO* son); if it occurs in a mottled-2 male

mated to a homozygous white attached- $X$  female, ( $\widehat{XX}Y$ ), the result is a red eyed son of the constitution  $\overline{\overline{w}}\overline{\overline{bb}}$ , (or a white-eyed daughter with no  $Y$ ). If bobbed is introduced into the mottled-2 and white stocks before making the former of the matings just described, the  $Y$ -chromosome can be followed by its inhibition of the expression of bobbed. That is,  $XO$  males and  $XX$  females look bobbed, but  $XY$  males and  $XXY$  females do not look bobbed. The red-eyed daughters from a mating of a mottled-2,  $bb$  male with a homozygous  $w$ ,  $bb$  female do not look bobbed, but all their mottled sisters do look bobbed. When a red-eyed female ( $\overline{\overline{w}}\overline{\overline{bb}}\overline{\overline{bb}}$ ), is mated to a  $w$ ,  $bb$  male ( $\overline{\overline{w}}\overline{\overline{bb}}$  : ) she has  $w$  ( $\overline{\overline{w}}\overline{\overline{bb}}$  : ) sons; mottled ( $\overline{\overline{w}}\overline{\overline{bb}}\overline{\overline{bb}}$  : ) sons;  $w$ ,  $bb$  ( $\overline{\overline{w}}\overline{\overline{bb}}$  : ) daughters;  $w$ , not- $bb$  ( $\overline{\overline{w}}\overline{\overline{bb}}$  : ) daughters; mottled,  $bb$  ( $\overline{\overline{w}}\overline{\overline{bb}}\overline{\overline{bb}}$  : ) daughters; and red eyed, not- $bb$  ( $\overline{\overline{w}}\overline{\overline{bb}}$  : ) daughters.

On cytological examination of oögonial divisions, mottled-2 females are found to have typical chromosome figures, but every figure from red-eyed females contains an extra chromosome, which looks like a  $Y$ .

Mottled-2 provides another example of the effect of the  $Y$ -chromosome on mottling of eye color. When mottled-2 males are mated to homozygous white  $\widehat{XX}Y$  females, many hyperploid daughters are produced of the constitution  $\overline{\overline{w}}\overline{\overline{bb}}\overline{\overline{bb}}$ . Their eyes are dark mottled—distinctly mottled

but very much darker than typical mottled-2. But occasionally a hyperploid daughter from such a mating has very light mottled eyes, even lighter than typical mottled-2. On the assumption that these represented  $\overline{\overline{w}}\overline{\overline{bb}}\overline{\overline{bb}}$  females which received no  $Y$ , due to non-disjunction of the  $X$  and  $Y$  in the father, one of these pale mottled hyperploid females was mated to a  $w$ ,  $B$ ,  $bb$  male. She had one  $w$ ,  $B$ ,  $bb$  son and he looked bobbed—proof that he received no  $Y$  from her.

The analysis of eversporting in mottled-3 is complicated by the fact that two distinct types of eversporting take place. Mottled-3 is linked with the  $X$ , second and third chromosomes. Males do not survive. Females are represented by the formula  $\overline{\overline{w}}\overline{\overline{bb}}\overline{\overline{bb}}$  in which  $\overline{\overline{w}}\overline{\overline{bb}}\overline{\overline{bb}}$  means the  $X$ , second and third chromosome complex responsible for mottling,  $\overline{\overline{w}}$  means a normal  $X$  carrying white and  $\wedge$  means a normal second or third chromosome. The fourth chromosomes are not involved. The symbol  $\overline{\overline{w}}\overline{\overline{bb}}\overline{\overline{bb}}$  is intended to represent only the fact of genetic linkage. No cytological evidence of attachment has been found.

A mottled-3 culture produces some females with mottled eyes and some with red eyes; we believe that all the mottled females are  $\frac{w}{w} \frac{\wedge \wedge}{\wedge \wedge}$ ; some red eyed females are  $\frac{w}{w} \frac{\wedge \wedge}{\wedge \wedge}$  and some are  $\frac{w}{w} \frac{\wedge \wedge}{\wedge \wedge}$ . The data upon which this conclusion is based were obtained by mating mottled and red eyed females singly to *w*, *B*, *bb* males. Primary non-disjunction of the *X*-chromosomes occurs at a high rate in mottled-3 females, so that all such matings will produce *w*, *B*, *bb* males and not-*B* females in addition to the regular offspring expected of such matings. The *w*, *B*, *bb* males will look bobbed if they are primary exceptions from a  $\frac{w}{w} \frac{\wedge \wedge}{\wedge \wedge}$  mother; they will look not-bobbed if they are secondary exceptions from a  $\frac{w}{w} \frac{\wedge \wedge}{\wedge \wedge}$  mother. All the *w*, *B*, *bb* sons of mottled mothers looked bobbed; some red-eyed mothers had *w*, *B*, *bb* sons which looked bobbed; other red eyed mothers had *w*, *B*, *bb* sons which looked not-bobbed. No not-*Bar* daughters from any type of mother had mottled eyes. All the mothers which produced *bobbed* sons also produced mottled daughters. The mothers which produced *not-bobbed* *w*, *B*, *bb* sons produced no mottled daughters. We interpret these data to mean that some of the ever-sporting in mottled-3 is a function of the *Y*-chromosome. The other type of ever-sporting in mottled-3 has a different explanation, possibly environmental as suggested earlier.

Eversporting in mottled-1 is also of two types, both rare. Mottled-1 is linked with the *X*, second and third chromosomes. Males of the constitution  $\frac{w}{w} \frac{\wedge \wedge}{\wedge \wedge}$  are fairly viable, sterile and have mottled eyes. Females of the constitution  $\frac{w}{w} \frac{\wedge \wedge}{\wedge \wedge}$  have mottled eyes. Occasionally mottled-1 varies in its phenotypic expression far enough to overlap normal eye color. Non-disjunction has never been observed. Triploidy arose twice in mottled-1 stock. Mottled triploids  $\left( \frac{w}{w} \frac{\wedge \wedge}{\wedge \wedge} \right)$ , mated to *w* males, quite consistently produced mottled triploid and white diploid offspring and a few red-eyed diploid daughters. These red-eyed females, mated to white males, had white, red and mottled offspring. At the time these flies were in existence the function of the *Y*-chromosome in this respect had not been discovered. It now seems very probable that that type of ever-sporting may be analogous to ever-sporting in mottled-2 and mottled-3, due to an extra *Y*-chromosome.

In conclusion, we have attributed ever-sporting eye color in our mottled stocks to the well-known mechanism of non-disjunction of the *X* and *Y* chromosomes—primary non-disjunction being responsible for the initial appearance of sports; and secondary non-disjunction for their continued appearance in later generations.

A more detailed presentation of this work will appear in the near future.

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<sup>2</sup> Emerson, R. A., "Genetical Studies of Variegated Pericarp in Maize," *Genetics*, 2, 1-35 (1917).

<sup>3</sup> Demerec, M., "Reddish—a Frequently 'Mutating' Character in *Drosophila virilis*," *Proc. Nat. Acad. Sci.*, 12, 11-16 (1926).

<sup>4</sup> Demerec, M., "Miniature- $\alpha$ —a Second Frequently Mutating Character in *Drosophila virilis*," *Ibid.*, 12, 687-690 (1926).

<sup>5</sup> Demerec, M., "Magenta- $\alpha$ —a Third Frequently Mutating Character in *Drosophila virilis*," *Ibid.*, 13, 249-253 (1927).

<sup>6</sup> Demerec, M., "Behavior of Two Mutable Genes of *Delphinium ajacis*," *J. Genetics*, 24, 179-193 (1931).

<sup>7</sup> Muller, H. J., "Types of Visible Variations Induced by X-Rays in *Drosophila*," *Ibid.*, 22, 299-334 (1920).

<sup>8</sup> Patterson, J. T., "A New Type of Mottled-Eyed *Drosophila* Due to an Unstable Translocation," *Genetics*, 17, 38-59 (1932).

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## THE HIGHER CRYSTALLINE PLATEAU OF SOUTHEASTERN BRAZIL

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There has been considerable discussion concerning the relationship between the German concept of the "primärrumpf," and the American concept of the penepplain.<sup>1</sup> The word "primärrumpf" cannot easily be translated. It was introduced by Walther Penck to describe a surface of relatively slight relief which is maintaining or actually decreasing its relief in spite of continuous uplift. Penck's thesis challenges the interpretation of all high-level uniform surfaces as having resulted from baseleveling followed by uplift. He maintains that under certain conditions of accelerated uplift the headwater areas of a drainage system will not feel the effects of rejuvenation. While the larger, lower courses of a stream may be able to overcome the rise of the land and maintain or quickly reestablish a graded condition, the upper parts of the stream system will not be able to do this. According to Penck a convex nick will be formed in the stream profile, bearing no relation to rock structure, and for a time the upper portion of the stream will be graded with reference to the top of this nick rather than to any general regional baselevel. In this way a high altitude surface is supposed to develop with actually decreasing local relief in spite of a constantly increasing altitude.

Such a high altitude surface of apparently decreasing relief exists in