Germinal Changes in the Bar-Eyed Race of Drosophila During the Course of Selection for Facet Number.*

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In recent discussions two explanations of the effect of selection have been offered. According to the first of these the results obtained are due merely to a sorting out of differences existing in the stock at the beginning of selection. According to the second, new germinal differences arise during the course of selection.

Among those who admit the continued production of new germinal differences there is a disagreement as to the manner in which the germinal changes occur. Some hold the view that the changes consist wholly of the production of new unit factors or genes. Others on the contrary believe that gradual change in the original genes is the principal mode of action and even that selection itself is an efficient determiner of the direction of such variation.

It is my intention to mention briefly some of the results bearing on this problem which have been obtained in the course of selection for facet number in the bar-eyed race of Drosophila ampelophila.

Bar-eye appeared in 1913 as a single mutant male in a full-eyed stock. This male gave rise to the bar-eyed stock in which the faceted region of the eye is bar shaped and the facet number is reduced from one thousand or more to about one hundred. An analysis of the hereditary behavior of bar-eye shows that it differs from full-eye in a single sex-linked genetic factor which acts as an incomplete dominant, the heterozygous condition being intermediate between bar and full-eye. My stock was obtained from Professor T. H. Morgan in January, 1914, and since that time experiments on selection for high-facet and for low-facet number have been in progress, but not in a continuous series because of loss of the lines on several occasions. In these experiments it has been shown that selection for low-facet and for high-facet number is effective, and low-bar, high-bar, emarginate eye and full eye have been produced

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from bar-eye. The analysis of the factors involved has yielded the following results:

1. Germinal diversity was present in the stock at the beginning of selection.

2. This germinal diversity was due to accessory unit factors or genes and not to differences in the bar-gene.

3. New accessory genes producing somatic differences of small degree have appeared during the course of selection. Some of these are located in the autosomes.

4. New accessory genes producing somatic differences of marked degree have also appeared during the course of selection. These also are autosomal.

5. Reverse mutation in the bar gene causing a return to the original full-eye both somatically and genetically was observed several times.

Original Germinal Diversity.

That germinal diversity was present at the beginning of the experiments is indicated by the pronounced effect of the early selections. Crosses between the high selected lines and the low selected lines show that the factors causing the difference are not sex-linked as is the main bar factor. This absence of sex-linkage shows that the difference between high and low lines can not be due to original diversity in the bar gene nor to accessory factors originally present in the sex chromosomes. The factors involved must be in the autosomes. Such differences in autosomal factors might have been present in the parental full-eyed stock from which the bar was derived. They would then have been transferred to the bar-eyed stock at the time of its formation, which involved not only change in the bar gene in a single male but also the crossing back with a full-eyed female to produce the bar-eyed stock.

Germinal Changes of Small Degree.

That the original diversity is not a sufficient explanation of the effectiveness of selection and that germinal changes continued to occur during the progress of selection in some of the lines is indicated by the continued effect of selection in these lines for many generations. It is highly improbable that a sustained effectiveness of this kind could have lasted for twelve generations, as in line V, merely as a result of the continued sorting out of an original diversity without additions to the diversity due to the formation of new genes or change in old ones. After such long continued and still effective selection reciprocal crosses between high and low lines still give no indication of sex-linkage. The germinal changes of small degree which must be assumed to explain such a long continued effect of selection therefore are not changes in the bar gene nor are they due to new accessory genes occurring in the sex chromosome. New genes must have arisen in the autosomes. Experiments are under way to determine their chromosomal loci more definitely.

Germinal Changes of Marked Degree.

In the high facet selection line marked mutations have occurred which have yielded full-eyed individuals indistinguishable from the wild ones which originally mutated to form the bar stock. These new full-eyed flies are genetically of two distinct types. One type is the result of a reverse mutation involving the return of the bar gene to the original full-eye-producing condition. Its hereditary behavior is similar to that of the wild Drosophila in all the tests that have been made.

The other type retains the bar gene unchanged, the somatic appearance of full eye being due to the formation of a modifying gene outside of the sex chromosome. This new gene is effective in producing full eye when present in double dose in females heterozygous for the bar gene. Such full-eyed females when crossed with wild full-eyed males produce males half of whom are bar and females half of whom are heterozygous bar.

In males with the bar gene and in females homozygous for bar the double dose of the new gene produces an eye which is nearly full but which differs from full in the presence of a defect at the anterior margin. Such an eye may be designated by the term "emarginate." Emarginate females when crossed with full wild males give males all of whom are bar and females all of whom are heterozygous bar. The reciprocal cross gives males all of whom are full and females all of whom are heterozygous bar. Numerous tests bear out in detail the hypothesis as stated above indicating that the chromosomal formula for this type of female with a full eye is $\frac{B}{\quad}\ \frac{m}{m}$, for the emarginate-eyed female $\frac{B}{B}\ \frac{m}{m}$, and for the emarginate-eyed male $\frac{B}{\quad}\ \frac{m}{m}$. Experiments are under way to determine the exact locus of the new gene.

CONCLUSIONS.

The data obtained are of interest in a number of ways:

1. Bar-eye may return to the full-eyed somatic condition by two distinct routes. (a) Reverse mutation in the bar gene may bring the individual back to the condition of the full-eyed stock not only in somatic appearance but also in genetic behavior. (b) A similar somatic appearance of full-eye may be produced by a mutation in one of the autosomes which leaves the original bar gene unchanged, as proven by the fact that the crosses between new full-eyed females and full-eyed wild males yield low bar individuals. Change in a gene and production of new genes without change in the principal gene may produce the same result somatically. Breeding tests alone can show the difference. The change in the principal gene brings the individual truly to its original condition.

2. Both of these mutations occurring as they did in the course of upward selection furnished material of immediate value in aiding the progress of upward selection so that it is proper to say that with the aid of mutations occurring during the course of the experiment the bar-eyed mutant was returned to its original full condition. It is not intended, however, to emphasize the fact that these mutations have so far appeared only in the high line and not in the low line. Whether this is merely a matter of chance or has a fundamental significance can be determined only by further observation.

3. The genetic behavior of the type of full eye due to the addition of an accessory factor is similar to that of the individuals of the high selected line before the appearance of the mutants of large degree. The difference between high bar and low bar is due to accessory factors in the same way. In other words the accessory factors with pronounced somatic effect are different in no respect but degree from the the accessory factors with small effect which form the ordinary materials for the action of selection.

4. It is evident that with respect to this one character, facet number, three separate conditions contributed to the effectiveness of selection; first, the differences in accessory autosomal genes present at the beginning of selection; second, the new autosomal genes arising during the course of selection, and, third the mutations in the bar gene. The

original differences are comparatively of low degree, and the new autosomal genes represent in some cases small differences in somatic appearance and in one case a large difference. The mutations in the bar gene so far have been of large degree in all cases, bringing the bar stock back to its original condition.

5. The demonstration of all three of these modes of producing an effective selection in the case of a single character indicates clearly that the selection problem and with it the problem of stability of the unit factor or gene is not capable of solution by any single formula.