Intersexes Dependent on a Maternal Effect in Hybrids Between Drosophila repleta and D. neorepleta

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correlated with seed viability but rather with the inherent genetic constitution of a plant since by use of the potentiometer and equilibrium potential determinations, one is enabled to segregate from a given population those seeds with superior growth characteristics. Further, these potential differences between seeds have been highly correlated with the growth of progeny which were one generation removed. For these reasons, the potentiometer may prove to be a useful tool for plant breeders.

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Burr, H. S., *Yale Jour. Biol. & Med.*, 9 (1) 65–76 (1936).
Burr, H. S., these PROCEEDINGS, 29 (6) 276–281 (1943).
Jones, D. F., *Genetics*, 30, 527–542 (1945).
Singleton, W. R., and Nelson, O. E., Jr., *Bull. Conn. Exper. Sta.*, No. 490 (1945).

INTERSEXES DEPENDENT ON A MATERNAL EFFECT IN HYBRIDS BETWEEN DROSOPHILA REPLETA AND D. NEOREPLETA

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Drosophila repleta Wollaston and *D. neorepleta* Patterson and Wheeler are closely similar species, the former widely distributed and the latter known from Guatemala. It was found by Dr. E. Novitski that these species occasionally cross, and that the F_1 females sometimes give a few offspring when mated to repleta males (see Wharton 1942 and Sturtevant 1946).

I have found a sex-linked recessive white-eyed mutant type in *D. repleta* (actually not quite white, but retaining only a slight tinge of color). At least 5000 neorepleta females have been crossed to white repleta males (in a few cases the repleta males carried singed, another sex-linked recessive, rather than white). These matings included at least 500 mass cultures, of which 74 produced hybrid offspring—a total of 532 females and 635 males, all wild type for the sex-linked mutant characters used. The males had very narrow testes, and were wholly sterile. The females were variable; most of them had bristles somewhat reduced in size ("minute"), and many of them had three anal plates instead of the usual two—this last character suggesting intersexuality.

About 400 of these F_1 females were mated to white repleta males, and offspring were obtained from 34 of them—the total output being 70 wild-type females, 9 white females, 42 wild-type males and 58 white males. The expectation is for these classes to be equal; there is evidently a great

deficiency of white females. Of the 9 recorded in this class, notes made on two make it possible to be certain (in the light of later results, to be described below) that they were intersexes, and it is possible that some of the other 7 were also of this nature, as were probably a few of the white males.

The wild-type males from this first backcross resembled the F_1 males in having long narrow testes and in being sterile. The wild-type females, however, included some moderately fertile individuals, which were again crossed to white repleta males. Such successive backcrosses of wild-type females to white repleta males have now been continued through many generations, and have resulted in strains presumably pure repleta in composition except for a section of the X-chromosome near the locus of white. In some of these strains the double recessive, white singed, has been used instead of white; and in these strains all the wild-type males are sterile and have narrow testes, while all the white-singed males have normal testes and are as often fertile as are white-singed males with no neorepléta chromosomes in their immediate ancestry. Tests of the few crossovers between white and singed indicate that the locus of the narrow-testis gene (or genes) lies between white and singed, and very near white.

The wild-type females from the backcrosses, when mated to white repleta males, appeared to fall into two classes; some of them gave the four types of offspring in approximately equal numbers, whereas others continued to give a marked deficiency of white daughters. The daughters of the first type of female always repeated the first type of result; but the females of the second type commonly yielded few offspring, and their very existence as a distinct type was at first uncertain because of the confusing effects of sampling errors in the small families obtained from them. Finally, however, after four successive backcrosses, a single female of this type was obtained which was more fertile, and her descendants have retained this fertility. Presumably the neorepleta gene responsible for the unusual ratios was at first linked to another gene that decreases fertility in females largely repleta in constitution, and in this case the infertility gene was lost by crossing over. The later studies have all been carried out with descendants of this more fertile female. There are, however, enough fragmentary data to make it clear that the behavior is essentially the same in lines derived from other F_1 hybrids—i.e., the results are really due to genes derived from neorepleta, rather than to a mutation that occurred in this line.

From females of this more fertile line, backcrossed to white repleta males, a total of 33 wild-type daughters (of females giving a deficiency of white daughters) have been tested by white males. Of these, 16 gave approximately $1 + ♀ :1$ w ♀ $:1 + ♂:1$ w ♂; the remaining 17 all gave a deficiency of white females. The total counts from these 17 were: $472 + ♀$, 5 w ♀, 63 w intersexes, $482 + ♂$, 339 w ♂. The 5 white females pre-

sumably represent crossing over between the loci of white and of the critical gene in the X derived from neorepleta. Their nature can be more accurately determined when other sex-linked genes are introduced in the crosses; it is, however, already clear that the gene concerned is not the same as that responsible for the narrow testes of the hybrid males.

The intersexes are of an extreme type, with gonads very small (rudimentary ovaries in those cases where they were found at all); external genitalia missing or of abnormal male type; wings usually not expanded, and, when they are, usually with thickened veins; one or more (sometimes all four) scutellar bristles often absent. They are weak individuals—and evidently usually die before emergence. It is to be supposed that such preimaginal mortality is responsible for the difference in number of wild-type females (472) and white intersexes (63). While no systematic study has been made, white-eyed flies have been found dead in their puparia in such cultures.

These results suggest that there is an autosomal dominant gene, derived from neorepleta, that so conditions the eggs (before meiosis) that two repleta X-chromosomes result in the development of intersexes rather than females. Evidently the action comes before meiosis, and the autosomal gene in question may be absent in the intersexes themselves. This interpretation has been confirmed by tests of the white brothers of intersexes. Such males, when crossed to pure repleta females, gave normal offspring of both sexes; but some of their daughters (presumably half of the daughters from half of these males, though the data are not extensive enough to establish this), when mated to repleta males, gave only intersexes and males.

It will be seen that this last experiment shows that the intersexes are not dependent on the presence of neorepleta cytoplasm, since their mothers were offspring of pure repleta females. The experiment also shows that the autosomal gene from neorepleta has no phenotypic effect on females that have received it from their father. The result likewise agrees with the earlier ones in indicating that an individual with two repleta X's is intersexual whether or not it carries this gene, provided the gene was present in its mother.

Conclusions.—D. neorepleta carries an autosomal gene which, when present in single dose in a hybrid female, makes her eggs male in potentiality. This predisposition to maleness is only partially overcome by two repleta X's, and male-like intersexes result. One repleta X and one neorepleta X are sufficient to produce normal females. This autosomal gene is present in two doses in pure neorepleta eggs. Two neorepleta X's are sufficient to cause such eggs to develop into normal females; but in the F_1 hybrids, having one neorepleta X and one from repleta, some of these eggs develop into females with male-like anal plates.

Presumably the essential sex-determining mechanism is the same in the two species, but both the male-determining action of the autosomal gene and the female-determining action of the X are stronger in neorepleta.

Sturtevant, A. H., "On the Dot-Chromosomes of *Drosophila repleta* and *D. hydei*," *Genetics*, 31 (1946) (in press).

Wharton, L. T., "Analysis of the Repleta Group of *Drosophila*," *Univ. Texas Publication* 4228, pp. 23–52 (1942).

THE MECHANISM OF POSITION EFFECT—EXPERIMENTS ON THE PHENOTYPIC EXPRESSION OF POSITION EFFECTS IN RELATION TO CHANGES IN PAIRING OF NEIGHBORING CHROMOSOME REGIONS

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In a previous paper[1] we discussed two alternative types of interpretation of the phenomenon of position effect, and expressed a predilection for one of these alternatives, partly on the grounds that it seemed to lend itself more readily than the other to experimental tests. The hypothesis as to the mechanism of position effect that we thereupon elaborated was closely related to some early suggestions of Muller.[2,3] Briefly stated, it postulated the following chain of events. In an organism such as Drosophila, where somatic pairing occurs, chromosomal aberrations change the pairing relationships of the chromosome regions adjacent to the breaks, or facing the breaks. The forces which bring about pairing may thus achieve a new distribution on either side of a gene located near to or facing a break. Such a change in pairing forces might subject this gene to a changed condition of stress. Now, if we visualize the gene as a complex folded protein molecule, or part of such a molecule, the specific activity of which is determined by the spatial configuration of specific groups on its surface, then a change of stress might be expected to lead to a change in the degree of extension of the folded protein, hence to a change in the spatial relationship of the active group, and so finally to a change in the specific activity of the gene, which change may be manifested phenotypically as a position effect.

We concluded that if this hypothesis were valid it should be possible, given an already existing position effect, to modify its phenotypic expression by further changing the pairing relationships of the chromosome regions in the immediate neighborhood of the affected gene. Moreover, it seemed clear that it would not be necessary for this purpose to alter the