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Maternal Effect as a Cause of the Difference between the Reciprocal Crosses in *Drosophila pseudoobscura*

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Notes:

intuition that in cases of quadratic friction the theory shows an increase of damping effect when the elevation of the wave increases. This is a new feature in the theory of wave propagation; it is introduced by the non-linear character of our wave equation.

The Determination of k (Volume Factor).—The coefficient c_f is supposed to be given by the physical conditions of the channel. The value of k will then depend entirely on the average elevation of the wave.

An infinite number of waves other than the ones here investigated may exist in a channel, depending on the initial elevations and speeds. It is, however, probable that if we start with a local swelling initially at rest it will propagate and deform as the wave of same average height investigated above. The origin of time to be chosen depends on the height of the wave front as shown by equation (9). The average height or volume determines the coefficient k to be used for the corresponding theoretical curve. The type of initial condition here mentioned may be roughly identified with conditions arising from a sudden input of water at a given point of a river or a channel and propagating as a flood wave.

4. *Conclusion.*—An exact solution of the equation of propagation of waves with quadratic damping has been found. It shows that high amplitude waves are more quickly damped and how this damping effect depends on both the volume of the wave and the friction coefficient of the channel. The solution may be interpreted physically as representing certain types of flood waves.

*MATERNAL EFFECT AS A CAUSE OF THE DIFFERENCE
BETWEEN THE RECIPROCAL CROSSES IN DROSOPHILA
PSEUDOÖBSCURA*

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Reciprocal crosses not infrequently produce different results; this fact is sometimes quoted as an evidence for cytoplasmic inheritance, although the fallacy of the argument has been repeatedly pointed out. It is to be granted, however, that the cause of the difference between reciprocal crosses has not been adequately analyzed in most cases. An approximation toward such an analysis is now possible in the hybrids between race *A* and race *B* of *Drosophila pseudoöbscura* Frolowa.

The cross $B \text{ ♀} \times A \text{ ♂}$ produces in F_1 generation sterile males having

small testes; the male offspring obtained in the F_1 of the $A \text{ } \varnothing \times B \text{ } \sigma$ cross is likewise sterile, but the testes are normal in size.¹ The data bearing on the problem of the mechanism responsible for this difference may be summarized under the following headings.

(1). *The Difference between the Reciprocal Crosses Does Not Extend Beyond the F_1 Generation.*—Lancefield¹ found that the F_1 females are fertile, and can be back-crossed to males of either parental race. Irrespective of whether the female is an $A \text{ } \varnothing \times B \text{ } \sigma$ or a $B \text{ } \varnothing \times A \text{ } \sigma$ hybrid, the males resulting from the backcrosses have testes varying from normal to a very small size. The variations are due to the different combinations of the chromosomes of the parental races: a male carrying an X -chromosome of race A and a majority of the autosomes of the same race has large testes, while a male having a race A X -chromosome and race B autosomes has small testes, irrespective of whether it has race A or race B cytoplasm. The same holds true for males carrying race B X -chromosome: such males have large testes if the autosomes come also from race B , and small testes with race A autosomes. Every one of the three large autosomes present in the karyotype of the species is thus concerned with the testis size in the hybrids.² Experiments are now in progress to establish whether males having identical chromosomes and different cytoplasm have testes of precisely the same size, but it is already clear enough that the effect of the cytoplasm in the backcrosses, if any, is negligible as compared with the F_1 generation.

(2). *Testis Size Is Not Affected by Lack or Excess of Y -Chromosomes in Males of Pure Races.*—Schultz³ has observed race A males having no Y -chromosome (XO). He obtained a number of such males in the offspring of normal females crossed to males carrying a translocation between the Y -chromosome and one of the autosomes. About 3% of the males in the offspring of this cross are XO (75 out of the total of 2080 males in the combined data of Drs. J. Schultz and A. H. Sturtevant). Schultz obtained also XYY males (in the progeny of XXY females). The XO and XYY conditions were checked cytologically in some cases. The XYY males have testes of normal size and are fertile. XO males are sterile, but their testes are normal in size and in histological structure. The writer obtained a single XO male in race B (in the progeny of females treated with x-ray and crossed to normal male). This male had testes of normal size; lack of the Y -chromosome was established genetically and checked cytologically.

(3). *Lack of Y -Chromosome Does Not Affect Testis Size in the Hybrids.*—Schultz³ obtained XO hybrid males by crossing race B females to males carrying the translocation mentioned above. They had small testes, just as their XY sibs. The present writer⁴ observed XO males in the backcrosses of $B \text{ } \varnothing \times A \text{ } \sigma$ hybrid females to race A males. Their appearance is due to primary non-disjunction of the X 's in the mother. These males

had testes variable in size and structure, in a manner similar to their XY sibs.

(4). *Males Coming from the $B \text{ } \varnothing \times A \text{ } \sigma$ Cross Have Small Testes Even if They Carry the X -Chromosome of Race A .*—Orange Curly race B females were crossed to beaded yellow short Bare purple race A males. Orange and purple are autosomal recessives; Bare and Curly autosomal dominants, lethal when homozygous; beaded, yellow and short sex-linked recessives. Regular male offspring from this cross are wild-type, Bare, Curly and Bare Curly; they have small testes. Among several thousands of such males, one beaded yellow short Bare, one beaded yellow short Bare Curly and one beaded yellow short males were found. These three exceptional males are due to non-disjunction of the X -chromosomes in the mother, and must be XO in constitution (the XO condition was established cytologically in one of them). The testes in these males were as small as in their sibs.

(5). *Males Coming from $A \text{ } \varnothing \times B \text{ } \sigma$ Cross Have Small Testes if They Carry the X -Chromosome of Race B .*—Race A females homozygous for the sex-linked recessives eosin, magenta and short were treated with x-rays, and crossed to wild-type race B males. Regular males in the offspring are eosin magenta short. Among about two thousand such males; one wild-type male was found. Cytologically it was found to be XO ; it had distinctly small testes.

Conclusions.—The F_1 hybrid males from the $A \text{ } \varnothing \times B \text{ } \sigma$ cross normally have the X -chromosome of race A , the Y -chromosome of race B and the cytoplasm of race A . The F_1 males from the cross $B \text{ } \varnothing \times A \text{ } \sigma$ have the X and the cytoplasm from race B , and the Y from race A . In either case, half of the autosomes come from race A and half from race B . Which of these elements determine the differences between the reciprocal crosses?

Presence of a Y -chromosome is not necessary for the development of large testes, since large testes may be present in XO males (see paragraphs 2 and 3). An interaction between the Y -chromosome of race A and the hybrid autosomes, or race B cytoplasm is not necessary for formation of small testes, since small testes can be produced in other circumstances (paragraphs 1, 3, 4, 5). Small testes may be present in XO males having an X -chromosome of race A (paragraph 4) or of race B (paragraphs 3 and 5). The conclusion is justified that the Y -chromosome is not concerned with the determination of the testis size in F_1 hybrids.

Small testes are produced in F_1 hybrid males under two conditions: (a) if they carry hybrid autosomes in race B cytoplasm (paragraphs 3 and 4), it being in this case immaterial whether they carry race A or race B X -chromosome, and (b) if race B X -chromosome is present together with the race A cytoplasm (paragraph 5). F_1 hybrid males have large testes if race A X -chromosome is present in race A cytoplasm.

In short, testis size in F_1 hybrids is determined by an interaction between the chromosome complement and the cytoplasm. We are dealing either with a real cytoplasmic effect (determination by the intrinsic properties of the cytoplasm, independent of the chromosomes it carries or carried), or with a maternal effect (determination of the properties of the cytoplasm by those of the chromosomes it carried before fertilization). The data available permit a discrimination between these two possibilities. A back-cross male having one half of its autosomes from race *A* and the other half from race *B* has small testes irrespective of the source of its cytoplasm. Furthermore, back-cross males having either kind of *X*-chromosomes and either kind of cytoplasm may have large or small testes depending upon the combination of the autosomes they carry. Hence, in *Drosophila pseudoöbscura*, the difference between the F_1 generations of the reciprocal crosses is due to a maternal effect and not to a plasmatic inheritance.

¹ Lancefield, D. E., "A Genetic Study of Crosses of Two Races or Physiological Species of *Drosophila Obscura*," *Zeits. ind. Abst. Vererbungsl.*, 52 (1929).

² Unpublished data of the writer.

³ Morgan, T. H., Bridges, C. B., and Schultz, J., "The Constitution of the Germinal Material in Relation to Heredity," *Carnegie Inst. Year Book*, 29 (1930).

⁴ Dobzhansky, Th., "Rôle of the Autosomes in the *Drosophila pseudoöbscura* Hybrids," *Proc. Nat. Acad. Sci.*, 19, 950-953 (1933).

THE DETERMINATION OF SEX IN *HABROBRACON*

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In the parasitic wasp, *Habrobracon juglandis* (Ashmead), as in other hymenoptera, males are normally haploid, arising from unfertilized eggs. It has been shown by Anna R. Whiting (1925), however, that following inbreeding, males may arise from fertilized eggs. These males are diploid, inheriting a chromosome set from each parent, and are referred to, therefore, as biparental (Torvik 1931). They are commonly sterile. Why some diploid zygotes should give rise to males and others to females has proved a very puzzling problem, and a problem of double interest because of its probable bearing on the normal mechanism of sex determination in the hymenoptera. In other groups of plants and animals a doubling of the whole chromosome complement does not produce changes comparable to the change of sex that it produces in the hymenoptera. Since fertilized and unfertilized eggs have the same chromosomal balance, and, in most respects at least, the same complement of genes, there is no obvious reason why the one should give rise to females and the other to males.