

irrespective of crossing-over in the other? No, there occurs "interference" in the rabbit chromosome as well as in chromosomes of *Drosophila*. Chance coincidence of crossing-over in the two regions should occur as the product of their respective frequencies or $14.4 \times 26.8 = 3.8$ per cent. This would call for the occurrence of 18 double crossovers in a population of 477 individuals, whereas only 13 have been recorded.

Summary.—Linkage studies on rabbits involving simultaneously the three genes *C*, *Y* and *B*, show (1) that all three genes are borne in the same chromosome; (2) that the order of the genes is *CYB*; (3) that the cross-over percentage between *C* and *Y* is 14.4 ± 1.0 per cent; (4) that the crossover percentage between *Y* and *B* is 26.8 ± 1.4 per cent; and (5) that the crossover percentage between *C* and *B* is (in complete agreement with earlier observations) 35.8 ± 0.8 per cent. Double crossing-over occurs in less than the frequency expected on the theory of probability, hence "interference" is demonstrated for a mammalian chromosome.

¹ Pease, M. S., *Zeit. ind. Abst.-Vererb.*, Bd. 46, also *Supplementband*, 2.

² Publ. No. 337, Carnegie Inst. Wash., 1926.

³ *Zeit. ind. Abst.-Vererb.*, 52, 1929.

RÔLE OF THE AUTOSOMES IN THE *DROSOPHILA PSEUDO-OBSCURA* HYBRIDS

BY TH. DOBZHANSKY

W. G. KERCKHOFF LABORATORIES, CALIFORNIA INSTITUTE OF TECHNOLOGY, PASADENA

Communicated October 9, 1933

Lancefield¹ discovered that the species *Drosophila pseudoobscura* consists of two races, called race *A* and race *B*, respectively. Completely sterile males and partially fertile females appear in the offspring if the races are intercrossed. Males coming from the cross, $B \text{♀} \times A \text{♂}$, have rudimentary testes that are smaller in size than the testes of normal males. Testes of the $A \text{♀} \times B \text{♂}$ hybrid males are normal in size but incapable of producing functional sperm. Lancefield¹ and Koller² have studied the localization of the factors responsible for the sterility of the hybrids; they backcrossed hybrid females to males of the parental races, and observed the testis size and the sterility (vs. fertility) of the male offspring. The results are summarized by Lancefield in the following statement: "a son, who received from his mother an *X*-chromosome derived from the same race as his father, usually had testes of normal or nearly normal size, while a son who received the other *X*-chromosome from his mother usually had small testes." Males possessing an *X*-chromosome of one race and a majority of the autosomes and the *Y*-chromosome of the other race are, thus,

sterile, and usually have small testes. Whether the *Y*-chromosome, or the autosomes, or both, are concerned in the production of sterility cannot be determined from the data of Lancefield and Koller, since any back-cross male necessarily possesses the *Y*-chromosome and a majority of the autosomes of the same race. More critical data may be obtained by studying hybrid males possessing no *Y*-chromosome at all (*XO* males).

Such males were observed in pure race *A* by Schultz.³ They had testes of normal size and structure, but proved to be sterile. The sterility of these non-hybrid *XO* males has, however, nothing to do with that of the hybrid males. According to Shen,⁴ the sterility of the *XO* males in *Drosophila melanogaster* is due to an abnormal function of the vas efferens rather than to that of the testis itself. Schultz³ observed also F_1 hybrid *XO* males, and found them to have small testes.

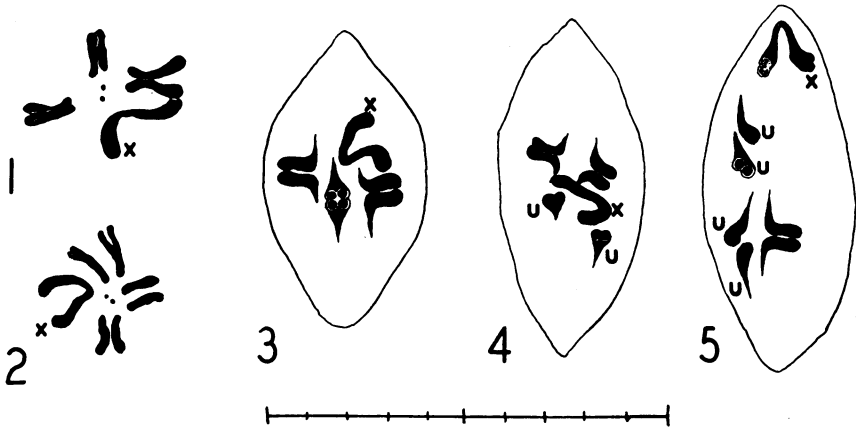
Through non-disjunction of the *X*-chromosomes at the reduction division in hybrid females, males having no *Y*-chromosome may be obtained in the backcrosses of the hybrid females to normal males. Various *B* race strains (Seattle-4 and Seattle-6) were crossed to race *A* strains (La Grande-2 and Texas). The F_1 hybrid females were backcrossed to race *A* males carrying in their *X*-chromosome the dominant gene Pointed (*P*). Regular offspring expected to appear in the next generation are Pointed (*XX*) females and wild-type (*XY*) males. Exceptional offspring (due to non-disjunction of the *X*-chromosomes in the mother) are wild-type (*XXY*) females and Pointed (*XO*) males. These four classes were, indeed, observed (table 1).

TABLE 1
OFFSPRING OF THE CROSS HYBRID ♀ × POINTED ♂

PARENTAGE OF THE MOTHER	P ♀	WILD ♂	WILD ♀	P ♂
Seattle-6 ♀ × La Grande-2 ♂	2306	1204	3	10
Seattle-4 ♀ × La Grande-2 ♂	1387	781	2	7
Seattle-4 ♀ × Texas ♂	1760	1095	5	8
Texas ♀ × Seattle-4 ♂	89	54	..	3
Total	5542	3134	10	28

Some of the wild-type (*XY*) males shown in table 1 had very small testes, others had testes of normal or intermediate size. This is the normal result observed in the backcrosses of hybrid females to normal males. More important for our purposes is that the Pointed (*XO*) males manifested the same degree of variability of the testis size as their wild-type sibs. Some of these *XO* males were studied cytologically. Numerous spermatogonial division figures were observed; in every figure a large *V*-shaped *X*-chromosome, and no *Y*-chromosome, was found (Figs. 1 and 2), proving that these males were actually *XO*. The histological structure of the testes was, however, as variable as their size. Some of the *XO* males possessing testes of normal size have apparently normal spermatogonia and first sper-

matocytes. At meiosis all the autosomes pair regularly, but the *X*-chromosome, having no partner, is left as a univalent (Fig. 3). The first meiotic division is normal. The *X*-chromosome, undivided though showing the equational split, sometimes passes precociously to one of the poles; sometimes on the contrary, it lags on the spindle after the autosomes have disjoined. Two kinds of second spermatocytes are observed: some carry the *X*-chromosome, and others carry no heterochromosomes. The second meiotic division is normal, and normal spermatids are produced. The mature spermatozoa are, however, distinctly irregular, having short worm-shaped heads instead of the very long and slender ones. Sometimes the



Figures 1 and 2, spermatogonial metaphase plates of the hybrid *XO* males. Figures 3 to 5, metaphase or early anaphase of the first meiotic division in the hybrid *XO* males. *X*, the *X*-chromosome; *U*, the univalent autosomes. The scale represents 10 micra.

head is even egg-shaped, the chromatic substance composing it being filled with large vacuoles.

In a number of *XO* males having testes of normal size the spermatogenesis was found to be disturbed in a manner similar to that observed in *XY* males coming in the F_1 generation of the cross, $A \text{ } \varnothing \times B \text{ } \sigma$ (spermatogenesis in these latter males is described in a preliminary form by Dobzhansky⁵ and Dobzhansky and Boche⁶; a more detailed description is in progress). Some or all of the autosomes fail to pair at meiosis (in Fig. 4 two univalents are present, in Fig. 5 one can see four univalents). The first meiotic division is abnormal, the spindle elongates enormously at telophase, bends in a nearly complete ring, two or more daughter nuclei are formed, the cell body fails to divide. The second meiotic division is lacking, giant binucleated spermatids are produced, in which the nuclei lie in the part of the cell directed toward the center of the testis instead of toward the periphery, as is the case in normal spermatids. It is interesting to note that these ab-

normal spermatids are frequently formed in the hybrids from the spermatocytes in which all the chromosomes are paired completely. This fact suggests that the abnormal behavior of the spindle in the hybrids is not directly caused by a failure of chromosome pairing.

XO males having small testes show disturbances in the spermatogenesis similar to those observed in the *XY* males coming from the cross $B \varphi \times A \sigma$ (Dobzhansky and Boche⁶). The number of spermatogonia and of the first spermatocytes in such testes is much smaller than in normal testes. Chromosomes mostly fail to pair at meiosis. The first meiotic division is usually abortive, since the nucleus as well as the cell body frequently fail to divide (sometimes, however, the nucleus divides into several daughter nuclei of unequal size). The second division is absent, and the abnormal spherical or crescent-shaped spermatids that are formed finally disintegrate.

The *XO* males show, thus, all the degrees of the degeneration of the process of spermatogenesis, ranging from a practically normal course of this process, through the condition found in the $A \varphi \times B \sigma F_1$ hybrid males, and to the very profound disturbance observed in the $B \varphi \times A \sigma F_1$ hybrid males. The same great variability is shown by the *XY* hybrid males resulting from backcrosses. The genetic structure of all the *XO* males obtained in the progeny of any one cross (table 1) is similar in that they possess the same *X*-chromosome (derived from their father), and the same cytoplasm (derived from their mother and grandmother). They differ from each other only in that some of them possess more autosomal material of race *A* than others. It follows that the variability of the size and structure of the testes of *XO* hybrid males is due to the interactions between the *X*-chromosome of race *A* and the autosomes of race *B*. Whether or not the *Y*-chromosome has any effect on the hybrid testes remains an open question, though on the basis of the data presented above one may surmise that its effect, if any, is small as compared with that of the autosomes and the *X*-chromosomes.

¹ Lancefield, D. E., "A Genetic Study of Crosses of Two Races or Physiological Species of *Drosophila obscura*," *Zeits. ind. Abst. Verebungsl.*, **52**, 287-317 (1929).

² Koller, P. Ch., "The Relation of Fertility Factors to Crossing-Over in the *Drosophila obscura* Hybrids," *Ibid.*, **60**, 137-151 (1932).

³ Mentioned in T. H. Morgan, C. B. Bridges and J. Schultz, "The Constitution of the Germinal Material in Relation to Heredity," *Carnegie Institution Year Book*, **29**, 352-359 (1930).

⁴ Shen, T. H., "Zytologische Untersuchungen über Sterilität bei Männchen von *Drosophila melanogaster* und bei F_1 Männchen der Kreuzung zwischen *D. simulans* Weibchen und *D. melanogaster* Männchen," *Zeits. Zellforschung mikr. Anat.*, **15**, 547-580 (1932).

⁵ Dobzhansky, Th., "On the Sterility of the Interracial Hybrids in *Drosophila pseudo-obscura*," *Proc. Nat. Acad. Sci.*, **19**, 397-403 (1933).

⁶ Dobzhansky, Th., and Boche, R. D., "Intersterile Races of *Drosophila pseudo-obscura*," *Biol. Zentralblatt*, **53**, 314-330 (1933).