tation of the genetic data given above. On the assumption that the presence of an inversion in one limb of a chromosome does not reduce the crossing-over in the other limb, it follows that the region involving y, v and bb is located in the left limb of the X-chromosome. Consequently, the spindle fibre is certain to lie between the genes bb and co. As to the locus of magenta (mg), direct genetic evidence is not yet available. But the facts that the distance between co and the chromocenter in the right limb of the salivary gland X-chromosome is about one-fifth of the total length and that the crossover units between mg and co are only 6.2, suggest strongly that mg is located in the right limb of the X-chromosome. Since the distance between v and mg is rather large (23.4 units), and crossing-over between v and co (5.3) in the presence of the inversion is appreciably reduced, the argument for placing the spindle fibre between genes bobbed and magenta is quite convincing.

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OVARY TRANSPLANTS IN DROSOPHILA MELANOGASTER: MEIOSIS AND CROSSING-OVER IN SUPERFEMALES

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Individuals of *Drosophila melanogaster* with three X-chromosomes and two sets of autosomes were called "superfemales" by Bridges.[1] They occur among the progeny of triploid females mated to diploid males,[1] among the offspring of attached-X diploid females mated to diploid males,[2] and under certain other conditions. Superfemales are low in viability as compared with normal diploid individuals and are always sterile. With the development of a simple method of transplantation for use in studies of Drosophila[3] and with the demonstration that offspring can be obtained from transplanted ovaries,[4,5] the authors were led to investigate the possibility of obtaining progeny from superfemales by transplanting their ovaries to normal females. Aside from its bearing on the problem of the nature of sterility in the superfemale, such a study might, if it provided

a method of obtaining progeny from superfemales, furnish a useful means of studying chromosome pairing and crossing-over among three homologous chromosomes under conditions less complicated than those in the triploid where the manner of disjunction of the autosomes is known to be related to crossing-over in the X-chromosomes.[6] Actually, although offspring can be obtained from superfemales by transplantation, the results are such that the use of the method as a means of studying such problems as crossing-over is strictly limited.

Methods.—Donor superfemale larvae were selected from the progeny of matings of attached-X y (yellow body color) w (white eye color) females by lz (lozenge eye shape) males on the basis of sex and Malpighian tube color. From such a mating two types of female larvae are expected, y $\overset{\frown}{w/y\ w}$ (XX) which have white Malpighian tubes, and y w/y w/lz (XXX) which have yellow Malpighian tubes (Beadle[7]). Incidentally, examinations of the larvae produced by such crosses provide a direct demonstration of the correctness of the conclusion arrived at indirectly by Dobzhansky[6] that normal diploid female and superfemale zygotes are produced in approximately equal numbers in such a mating. As recipients of the ovary transplants *fes* (female-sterile, characterized by rudimentary ovaries) *lt* (light eye color) female larvae were used (from mating; *fes lt* / *Cy* × *fes lt*—*Cy* designates the dominant character Curly wing, associated with inversions). Since the female-sterile character has been shown by Clancy and Beadle[9] to show autonomous development in transplantation experiments, the use of *fes* females as hosts is convenient for it is then known that any eggs produced originate in the implanted ovary.

Development of Superfemale Ovary-Transplants.—In one series of transplants, determinations of the frequencies of attachment of the implanted ovaries to the oviducts of the host were made by dissection. The results are summarized in table 1. There are two types of host females,

TABLE 1

FREQUENCIES OF ATTACHMENT OF SUPERFEMALE OVARY-IMPLANTS

HOST	IMPLANT		PER CENT ATTACHED	THREE OVARIES ATTACHED
	ATTACHED	FREE		
Cy/fes lt	11	5	68.8	4
fes lt	17	19	47.2	1

Cy/fes lt in which the normal ovaries are fully developed, and *fes lt* in which the normal ovaries are rudimentary. In the case of the *Cy/fes lt* hosts the normal ovaries were larger than the implanted ones, while in the *fes lt* hosts the size relations were reversed. It is evident that superfemale ovaries can compete successfully with either normal or *fes* ovaries in becoming attached to the oviducts. The number of individuals is so small

that little significance can be attached to the observed percentages of attachment; they are roughly of the same order as frequencies of attachment found by Ephrussi and Beadle[4] and by Clancy and Beadle[9] in other types of experiments.

Females of the constitution *fes lt*, into which superfemale ovaries had been implanted, laid eggs on the second day after eclosion. In *Cy/fes lt* female hosts of this age, the superfemale implants were found to contain only immature eggs (10 individuals examined). Dissections of *Cy/fes lt* on the fourth and fifth day after eclosion, showed mature eggs in the superfemale implants (9 individuals). In all instances, however, the superfemale ovaries were markedly smaller than the normal ovaries of the host. It is apparent that superfemale ovaries mature more rapidly in the absence of competing normal ovaries than in their presence.

Progeny.—From eight egg-laying *fes lt* females with superfemale ovary-implants, mated to Bar (*B*) males, 256 eggs were collected over a period of five days. Of these 256 eggs, only 13 (5.1 per cent) hatched, and all of the resulting larvae died within 24 hours. From a total of 21 similar females, similarly mated, all eggs were collected over a period of four weeks. From an estimated several thousand eggs, 30 gave rise to adults. These are listed in table 2. From the constitutions of the hosts and of the implanted

TABLE 2

PROGENY OF FEMALE-STERILE FEMALES WITH IMPLANTED SUPERFEMALE OVARIES

$(y\ w,\ \overset{\frown}{XX}/lz)$, MATED TO BAR MALES

FEMALES	NUMBER OF INDIVIDUALS	MALES	NUMBER OF INDIVIDUALS
wild type	1	*lz*	13
y w	8	*lz* (haplo-4 (?)	1
B/lz (tested for genotype)	4	*B*	2
B	1		

ovaries, it is clear that the yellow-white females and the lozenge males constitute evidence that the superfemale ovaries gave rise to the eggs from which these offspring developed. As an additional check, two yellow-white females were tested; both gave offspring of types indicating that, as expected, they carried attached-*X* chromosomes. Two lozenge males were tested and found to be fertile. Four of the five Bar females were found by progeny tests to be *B/lz* in constitution.

At the end of the period of egg collection, five *fes lt* females were dissected; each was found to have one well-developed ovary (superfemale) attached to an oviduct and two rudimentary ovaries (*fes*), one attached and one free.

Crossing-Over.—Twenty-six apparent non-crossovers and only one crossover are listed in table 2. Unfortunately the one wild type female died before a progeny test could be made. It is evident that crossing-over

among the X-chromosomes in the superfemale is infrequent. It is a simple matter to compare this frequency with that observed in triploid females with two X-chromosomes attached. From the data of Beadle[10] it is known that apparent single crossovers between the spindle attachment (locus $66\pm$) and yellow (locus 0.0) occur with a frequency of about 7 in 16 (combined data from $\overparen{XX}$ and X gametes). Statistically considered, it is practically certain that the frequency observed in the progeny of transplanted superfemale ovary is less than this ($p = \;<0.0001$ that they could be samples of identical populations—Warwick's tables[11]).

Discussion.—From the above results it is clear that superfemale ovaries, transplanted to *fes* diploid females, are able to develop and to give rise to eggs of normal appearance in spite of the fact that in their normal positions such ovaries never give rise to fully developed eggs (Dobzhansky[8]). There is a definite effect of the host, but since superfemales are normally very weak, this host-implant influence may very well be primarily one of nutrition.

The high mortality observed among the eggs from superfemales was quite unexpected. With normal meiosis in $\overparen{XXX}, 2A$ individuals (A designating one complete set of autosomes), only two types of eggs are expected, $\overparen{XX}, A$ and X, A. Fertilized by X, A and Y, A sperm, there should be four classes of zygotes: $\overparen{XXX}, 2A$; $\overparen{XX}Y, 2A$; $\overparen{XX}, 2A$; and $XY, 2A$. The first of these is of course superfemale in constitution, but should show normal larval development. The remaining three types of zygotes represent normal sexual types and should, so far as genetic constitutions of the zygotes themselves go, show normal development. Among the 30 adults observed, three of the four expected types are represented. It is known that individuals of the fourth type, superfemales, usually die during pupal stages of development. Two patroclinous males (B) were observed. These individuals must have originated by fertilization of a no-X egg (non-disjunction) by an X sperm. In addition to the exceptional Bar males, one lozenge male had the appearance of a haplo-4 individual; it presumably resulted from non-disjunction of the fourth chromosomes.

The results given above, a very low frequency of crossing-over, a relatively high frequency of non-disjunctional types and the high egg and larval mortality, are all indicative of irregular meiosis. It is known from various types of evidence that, in general, crossing-over is a normal and essential part of the meiotic mechanism (Darlington[12]). There are several known instances of failure of crossing-over associated with irregular chromosome distribution at meiosis (e.g., Gowen[13] in Drosophila). The case described here is of particular interest in that failure of normal crossing-over and the presumably subsequent irregular distribution of meiotic

chromosomes apparently result from chromosome unbalance. Two types of control experiments indicate that the female-sterile host is not responsible for this behavior: Wild type diploid ovaries grown in *fes* hosts give rise to fully viable eggs, and from many normal diploid females into which superfemale ovaries had been implanted the offspring obtained were entirely from the normal ovaries of the host, suggesting that, under these conditions, superfemale ovaries are functionally similar to those·grown in *fes* hosts. Since there are no marked irregularities in somatic development of a superfemale individual that would indicate disturbances in mitotic cell division, we can conclude that the particular chromosome unbalance characteristic of such individuals has a specific effect on the meiotic mechanism. A simple interpretation follows the assumption that the difficulty lies in the mechanism normally responsible for crossing-over.

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AN EFFECT OF THE Y-CHROMOSOME ON THE SEX-RATIO OF INTERRACIAL HYBRIDS OF DROSOPHILA PSEUDOÖBSCURA

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It was shown by Lancefield (1929) that *D. pseudoöbscura A-B* hybrid females, when back-crossed either to *A* or to *B* males, give sex-ratios among their offspring that may deviate widely (in either direction) from 1:1. My own experience confirms this result; I have, however, never found a significant excess of male offspring unless the father was descended from certain of the older mutant stocks. Back-crossing to males from wild stocks or to males whose ancestry could be traced wholly to recently collected wild stocks has never resulted in significantly more than 50 per cent male offspring.