

A GENE IN DROSOPHILA MELANOGASTER THAT TRANSFORMS FEMALES INTO MALES

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A CULTURE, counted in April, 1944, gave 20 males of an unexpected phenotype (wild type for a series of sex-linked alleles) that could not be accounted for by any of the usual interpretations current in *Drosophila* genetics. These males were sterile, but studies of descendants of their sibs have shown their nature.

It is now clear that these were XX diploids—that is, had the usual composition of normal females, but were homozygous for a third chromosome recessive gene that may be called “transformer” (symbol *tra*). Heterozygotes (*tra*⁺/*tra*) do not differ from wild type in any way yet detected, nor do XY *tra/tra*—that is, the gene is recessive and also has no effect on males. XX *tra/tra* individuals appear like normal males. They have fully developed sex-combs, male-colored abdomen, normal male abdominal tergites, anal plates, external genitalia, genital ducts, sperm pump, and paragonia, and show the usual rotation of the genital and anal segments through 360°. They mate with females readily and normally. The testes, however, while normal in color, elongate, curved, and attached to the ducts, are much reduced in size. The testis size is variable, but in no case does it approach that found in the normal brothers. In two respects these specimens resemble females: they are often larger than their XY brothers, and they more often appear in first counts from cultures, suggesting that their development rate approaches that of females.

These XX *tra/tra* individuals are all wholly sterile. It seemed possible that this was due to their not carrying a Y chromosome. Since the gene is an autosomal recessive, it was easy to transfer it to an attached-X line, and to obtain XX Y *tra/tra* specimens. These differ in no way from those without a Y, and are equally sterile. These same cultures should give XX X *tra/tra*—that is, superfemales homozygous for the new gene. In a large series of cultures only one such specimen has been obtained, indicating that the gene does not increase the usual very low viability of superfemales. This one specimen had the beaded wings characteristic of superfemales, but had the male genitalia of XX *tra/tra*; it did, however, have sex-combs with only about half the normal number of teeth, and accordingly may be taken as indicating that superfemales are not as strongly modified toward maleness as are ordinary females—perhaps the best support yet produced for the view that superfemales are more “female” than are females.

The gene has also been introduced into a triploid line. 3X₃A *tra/tra/tra* triploids resemble the corresponding diploids—that is, they are males with large wing-cells and ommatidia, with small testes, and they are sterile. Unfortunately, as the experiment was carried out, the 2X₃A (triploid intersex) classes could not all be identified with certainty; however, large numbers of

possible $2X_3A$ *tra/tra/tra* were tested, and no fertile males were encountered. It seems certain that such specimens are sterile, and it is probable that they still have the abnormal wings and eyes usual among triploid intersexes. It is not known whether one or two doses of *tra* have any influence on the sex grade of triploid intersexes.

A few preliminary tests having indicated that *tra* lies in chromosome III, it was balanced against "*Dcx*", a third chromosome carrying the dominant Dichaete (lethal when homozygous) and a complex rearrangement that usually prevents effective crossing over except near the ends of the chromosome. A few sample results follow:

$\varnothing w^a/w^a Dcx/tra \times \sigma^+ w^+ Dcx/tra \rightarrow 108 \varnothing D, 78 \sigma^+ , 120 \sigma^+ D w^a, 63 \sigma^+ w^a$ (plus $1 \sigma^+ D$, due either to non-disjunction of the X's of the mother, or to crossing over between *D* and *tra*).

$\varnothing w^a/w^a Dcx/tra \times \sigma^+ w^+ tra/tra \rightarrow 64 \varnothing D, 50 \sigma^+ , 47 \sigma^+ D w^a, 60 \sigma^+ w^a$.

$\varnothing \overline{y}^v Dcx/tra \times \sigma^+ w^a tra/tra \rightarrow 137 \varnothing y v D, 1$ super- $\varnothing +$ (described in text), $126 \sigma^+ y v, 194 \sigma^+ w^a D, 190 \sigma^+ w^a$ (plus $1 \sigma^+ y v D$ evidently due either to detachment of the X's of the mother or to crossing over between *D* and *tra*).

Using this strain it is easy to get males known to be homozygous for *tra*, and accordingly tests for its locus in chromosome III can readily be made. The methods used are not new in principle, so it need only be stated that they show the gene to lie between *st* (locus 44.0) and *cp* (locus 45.3). This places it in the left limb of III (= element D).

The effects of *tra* on the phenotypes of mutant characters showing sexual dimorphism have been studied in a few cases. Scute-3 is lethal in females but fully viable in males (DUBININ 1933). It appears that this lethal effect is not overcome by homozygous *tra*—that is, $sc^3/sc^3 tra/tra$ did not survive.

Eosin (w^e) is paler and more yellowish in males than in females (BRIDGES and BREHME 1944), and facet (*fa*) is more extreme in males than in females (BRIDGES and BREHME 1944). In both these cases it is known that the normal sexual dimorphism is not due to the presence of a Y in the males and its absence in the females. In both these mutant types, the XX *tra/tra* individuals resembled their XX *tra⁺/tra* sisters, and differed distinctly from their XY brothers.

In all three tested instances, therefore, the XX *tra/tra* individuals were like the females rather than the males with respect to sexual dimorphism dependent on mutant genotypes—though they were like males rather than females in the sexual characters (other than size and development rate) in which normal males and females differ.

One other similar test was carried out, with the semi-dominant sex-linked gene Bar (*B*). *B/B* and *B/+* in XX *tra/tra* closely resemble the same two types in their sisters.

It may be argued that the transformed individuals are better described as intersexes, rather than as males. I have preferred to call them males simply because they are indistinguishable from males in ordinary experiments—unless one dissects out their testes, and even the testes show no female characteristics. Perhaps the best reason for considering them intersexes is the short

sex-combs found on the single transformed superfemale that was seen. In any case, the gene is more extreme in its shifting of the sex of the individual than is any other yet described in any *Drosophila*. Only that recorded by LEBEDEF (1934) for *D. virilis* was shown to be due to a gene in element D. The specimens here described resemble the most extreme types recorded by LEBEDEF, but the extreme variability that he observed is here absent. It remains doubtful whether or not the genes in the two species represent corresponding loci. The present gene is certainly different from the one previously described intersex gene in *D. melanogaster*, since that lies in the second chromosome (L. V. MORGAN, in MORGAN, REDFIELD, and MORGAN 1943).

A mutant type of this sort, if the gene is autosomal, may easily be overlooked. It will give a sex ratio of 3 ♀ : 5 ♂ if both parents are heterozygous, but this will be difficult to distinguish from 1 : 1. The mating of heterozygous female × homozygous male gives 1 ♀ : 3 ♂, but this mating will be less likely to occur. The most likely situation for its detection will be that which actually led to the discovery of this one—namely, the presence of males of classes, with respect to sex-linked genes, that appear impossible from the known parentage. In those species where element D is part of X, detection through the distortion of the sex ratio should be easier.

SUMMARY

A recessive gene, *tra*, lying between 44.0 and 45.3 in the third chromosome of *Drosophila melanogaster*, transforms diploid females into sterile males.

The gene is without effect on males (that is, on XY diploids).

A single specimen indicates that *tra/tra* superfemales are intersexual but strongly male-like.

No fertile triploids homozygous for *tra* were obtained.

The gene is without effect on the sexual dimorphism of the mutant types scute-3, eosin, and facet—in all three of these cases the XX *tra/tra* specimens resemble normal females, rather than normal males, in the manifestation of the mutant phenotypes.

LITERATURE CITED

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