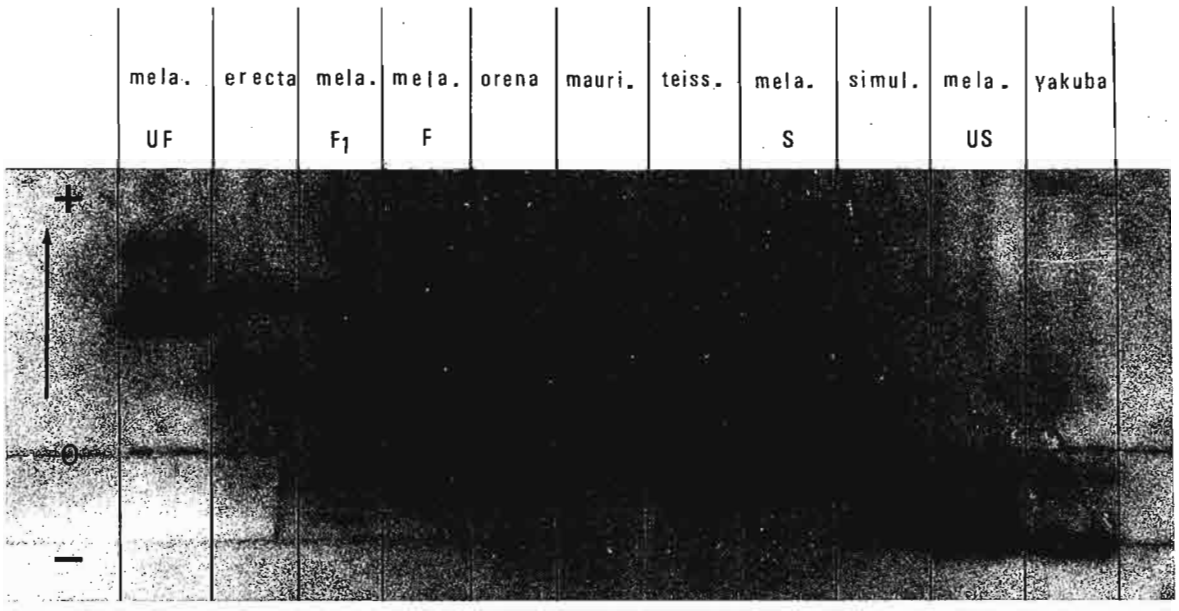

Fig. 1. Electrophoregram of Adh stained with isopropanol after starch gel electrophoresis (discontinuous buffer system of Poulik, 1957). From left to right: D. yakuba; D. melanogaster allele Ultra Slow; D. simulans; D. melanogaster Slow; D. teissieri; D. mauritiana; D. orena; D. melanogaster Fast; D. melanogaster Fl; D. erecta; D. melanogaster Ultra Fast.

Phylogenetic relationships between the various species were recently worked out using polytene chromosome structures (Lemeunier and Ashburner, 1975). Results here presented suggest that the genetic distance between the various species could be high. Of course, analysis of a single gene provides little information and studies of other loci are in progress.

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Mutants which cause abnormal rotation of the abdomen or genitalia.

A surprising number of loci can mutate to affect the development of the abdomen or genitalia in D. melanogaster such that the adult structures are out of alignment with the rest of the body. A study of the twisted locus (Davis 1975; Davis, DIS this issue) led to a search through the "Genetic Variations of D. melanogaster" (Lindsley and Grell 1968), aided by "The Mutants of D. melanogaster Classified According to Body Parts Affected" (Braver 1956). Although this search was not exhaustive for the main source (Lindsley and Grell 1968) and did not include current literature, it revealed 15 loci with one or more alleles reported to cause rotation of the genitalia or the abdomen (Table 1).

Table 1. Mutants of D. melanogaster causing genital or abdominal rotation.

Mutant	Chromosome	Sex Affected* Male	Female	Fertility Male	Female
Abruptex	X	G	-	+	+
curlex-twisted genitalia	X	G	-	-	+
shifted genitals	X	G	-	-	+
twisted	X	A	A	+	+
twisted genitals	X	G	G	±	+
abrupt^2	2	G	-	-	+
chaetelle	2	G	-	+	-
engrailed	2	G	-	±	+
fringed	2	A	A	+	-
rubroad	2	G	-	+	+
thickoid	2	G	-	+	+
rotated abdomen	3	A	A	-	-
rotated penis	3	G	-	-	+
Roughened	3	G	-	±	+
abdomen rotatum	4	A	A	-	±

*A indicates abdominal rotation; G indicates genital rotation; and - indicates no rotation.

These loci are scattered throughout the genome with each of the four chromosomes represented. All four of the mutants which cause abdominal rotation affect both sexes, but of the 11 which cause genital rotation, all but one are male specific. Although the single exception is named "twisted genitals", the original phenotypic description merely refers to an abnormal positioning of deformed external genitalia (Fahmy 1959). It is therefore possible that the mutant did not cause rotation. Unfortunately, it cannot be examined because it has been lost.

The degree of rotation is quite variable from locus to locus and from fly to fly for some loci. For example, males homozygous for rotated penis have genital rotation varying from normal to 270°. The direction of rotation in different mutants may be clockwise or counterclockwise. As used throughout this paper, "clockwise" and "counterclockwise" refer to flies as viewed from the posterior end. The abdomen rotatum locus has one allele (ar) which causes clockwise rotation and two alleles (ar^{57d} and ar^{57g}) which cause counterclockwise rotation.

Rotation is often but not invariably associated with infertility or reduced fertility. Males homozygous for rotated penis are sterile even when the genitalia are not out of line. Males carrying twisted^3 may be sterile or fully fertile with no apparent differences in internal anatomy or in sperm motility (Davis, DIS this issue). The mutant chaetelle has the unusual property that many males have rotated genitalia, but the infertility occurs in females (Beatty 1949).

Why do so many loci cause rotation of the abdomen or genitalia? It is known that the normal development of the male reproductive system involves a complete clockwise 360° rotation of the terminal abdominal segments (Gleichauf 1936). This results in a complete clockwise loop of the ejaculatory duct around the rectum. Following the duct from its anterior connections with the paired vas deferens and accessory glands to its posterior connection with the penis, it originates ventrally, loops from the fly's left side over the dorsal rectum, and then down the right side to a ventral position (see Fig. 38 in Miller 1950). Either there are many genes which normally control this movement, or it is a process which can be readily interfered with by mutants. It might be argued that the four loci which cause abdominal rotation belong in a different category since they affect females as well as males. However, the fact that twisted^3 causes both genital and abdominal rotation (Davis, DIS this issue) strongly supports an association between the two types of mutants.

There are two general questions about the developmental mechanisms which account for the observed external roation of male genitalia in these mutants. The first is the direction of the rotation, either clockwise or counterclockwise. The second is the degree of rotation. For example, a specific male might have genitalia out of phase with the abdomen by 90° clockwise because (1) the normal clockwise rotation was incomplete, stopping at 90°; or (2) clockwise rotation continued beyond the normal 360°, to 450°; or (3) rotation was counterclockwise for 270°. Similarly, a male might have genitalia out of phase with the abdomen by 90° counter-

clockwise because (1) clockwise rotation stopped at 270°; or (2) rotation was counterclockwise for 90°; or (3) rotation was counterclockwise for 450°. Fortunately, the loop of the ejaculatory duct around the rectum serves as a record of the mechanism.

Table 2. Developmental rotation of the posterior abdominal segments in twisted[3] males and its effect on internal and external structures.

		Relationship of genitalia to the abdomen	
Developmental rotation[1]	Ejaculatory duct loop[2]	Degree out of phase	Direction out of phase
180° to 360°	1/2 - 1	180° to 0°	counter-clockwise
360° to 450°	1 - 1-1/4	0° to 90°	clockwise

1. The developmental rotation is always clockwise.
2. This shows the fraction of the rectum around which the ejaculatory duct is looped. The direction is always clockwise.

The mutant twisted[3] causes abdomens in both sexes to have a clockwise twist with respect to the rest of the body. Many males also have the genitalia and anal plate out of alignment with the abdomen, either in a clockwise or counterclockwise direction (Davis, DIS this issue). A number of twisted[3] males were dissected in saline solution to examine the ejaculatory duct. Some of the males were imbedded in paraffin and some were simply dissected on a glass slide. Those males in which the genitalia were in normal position with respect to the tip of the abdomen, although both features were twisted with respect to the rest of the body, showed the normal ejaculatory duct loop as described earlier. Apparently the twisting of the abdomen was superimposed upon the normal rotation. Those males in which the genitalia were out of phase with the tip of the abdomen showed that (1) the ejaculatory duct loop and therefore the developmental rotation is always clockwise, and (2) the loop varies from 1/2 to 1-1/4 times around the rectum and therefore the developmental rotation varies from 180° to 450° (Table 2). Thus, rotation between 180° and 360° gives the appearance of genitalia rotated counterclockwise, while rotation between 360° and 450° gives the appearance of genitalia rotated clockwise.

These results show that a mutant such as twisted[3] or a locus such as the abdomen rotatum locus for which rotation is apparently sometimes in one direction and sometimes in the other can be explained in terms of a single mechanism which alters the normal developmental process. Although the mutants which cause the abdomen or genitalia to be out of phase with the rest of the body are described in the literature as "rotated clockwise" or "rotated counterclockwise", this should be interpreted only in terms of morphological appearance and not as a suggested developmental mechanism.

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A new twist on an old mutant.

Among a number of male sterile mutants induced on the X chromosome of D. melanogaster by ethyl methane sulfonate, was one with a morphological phenotype. The abdomens of both sexes are rotated clockwise, varying from slight to 90°. In this report "clockwise" and "counterclockwise" refer to flies as viewed from the posterior end. Additionally, in males the genitalia and anal plate are often out of alignment with the abdomen, either in a clockwise or counterclockwise direction. This misalignment may be as much as 180°. At the suggestion of Jeffery C. Hall (pers. comm.), the mutant was named "tricky dicky" (td). Some features of the mutant have been reported previously (Davis 1975).

Females of the genotype w m f/y su(w^a) td w^a were mated to Canton S wild type males and the sons were examined to genetically map the tricky dicky locus. The number and percent of recombinants for various regions of the X chromosome are given in Table 1. The percents of recombinants for y-w, w-m, and m-f are in reasonable agreement with standard map distances (Lindsley and Grell 1968), with allowance for multiple crossing over within the two large