

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 twisted³ males and its effect on internal and external structures.

Developmental rotation ¹	Ejaculatory duct loop ²	Relationship of genitalia to the abdomen	
		Degree out of phase	Direction out of phase
180° to 360°	1/2 - 1	180° to 0°	counterclockwise
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.

spect 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 twisted³ 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.

References: Beatty, R.A. 1949, Proc. Roy. Soc. Edinburgh B 63:249-270; Braver, N.B. 1956, The Mutants of *D. melanogaster* Classified According to Body Parts Affected; Davis, B.K. 1975, Genetics 80:s25; Davis, B.K. 1979, DIS this issue; Fahmy 1959, DIS 33:93-94; Gleichauf, R. 1936, Z. wiss. Zool. 148:1-66; Lindsley, D.L. and D.H. Grell 1968, Genetic Variations of *D. melanogaster*, Carnegie Inst. Wash. Publ. 627; Miller, A. 1950, in: Biology of *Drosophila*, ed. M. Demerec.

Davis, B.K. Virginia Polytechnic Institute and State University, Blacksburg, Virginia. 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

Table 1. Recombinant progeny in selected regions among 1157 total progeny sons from a cross of $w^m f/y$ $td\ su(w^a)$ w^a females and Canton S wild type males.

Region	Recombinants	Percent Recombinants
y - td	0	0.0
td - w	15	1.3
y - w	15	1.3
w - m	344	29.7
m - f	229	19.8

(1/26 X 1.5). The $su(w^a)$ locus is also at 0.1 map units and td has arbitrarily been placed proximal to $su(w^a)$ in this discussion.

The map position and phenotype of tricky dicky are quite similar to those of twisted, a mutant which was discovered by Demerec in 1928 (Lindsley and Grell 1968). It is located at 0.4 map units and causes clockwise rotation of the abdomen in both males and females. A second allele, tw^2 , was discovered by Mohr in 1932 (Lindsley and Grell 1968), but has been lost. It caused male genitalia to be out of line in a counterclockwise direction from the twisted abdomens. A complementation test showed that females heterozygous for td and tw (obtained from the California Institute of Technology stock center) all have the abdomens out of line with the rest of their bodies. Therefore, td is in fact an allele of tw and it is necessary to drop the name tricky dicky. It will henceforth be referred to as tw^3 .

Both alleles cause late hatching. Following outcrossing, the tw allele showed several new phenotypic features, all with incomplete penetrance. These were etched or absent tergites, leg deformities, pointed wings and small rough eyes.

The new allele tw^3 causes frequent sterility among both males and females. Indeed, as noted above, it was isolated as a male sterile mutant. However, those flies which are not sterile produce as many progeny as do their nonmutant siblings. Both the sterility and the abdominal twist are recessive in females.

The internal anatomy was examined first for 11 tw^3 males who failed to produce any progeny with wild type females. They all showed normal reproductive systems including motile sperm. Other tw^3 males, selected on the basis of having the genitalia and anal plate out of line with the abdomen, also had normal reproductive systems in almost all cases. Most of the reproductive systems of a sample of tw males with etched or absent tergites were also normal. Apparently, the sterility in some individuals results primarily from mechanical difficulties with copulation. Of course, in those males in which the genitalia are out of line with the abdomen, the internal structures are correspondingly displaced. This point is discussed further in a second note (Davis, DIS this issue).

Preliminary tests of chromosome behavior in males showed that both alleles cause a low but significant frequency of nondisjunction. Males hemizygous for tw but with unmarked fourth chromosomes were crossed to $C(4)RM, ci\ ey^R/0$ females. The males produced 1.5% nullo-4 sperm (3/204) which is about 37 times the control frequency (0.04% - see Table 3 in Davis 1971). Males hemizygous for tw^3 were mated to bb attached-X females. These males produced 1.0% (8/798) sperm with neither an X nor Y chromosome, which is about seven times the control frequency (0.14% - see Table 3 in Davis 1971).

Females were tested for meiotic nondisjunction by crossing them to $Y^S X.Y^L, In(1)En, v\ f\ B/0; C(4)RM, ci\ ey^R/0$ tester males (Table 2). Since the fourth chromosomes in the females

regions. This suggests that there are no chromosome rearrangements involving the X chromosome, which was confirmed by polytene chromosome analysis. The tricky dicky locus lies between 0.0 (based on no recombinants with y) and 0.2 (based on 1.3 percent recombinants with w).

A second cross was $y\ su(w^a)\ td\ w^a/+ +$ females mated to $y\ su(w^a)\ td\ w^a/Y$ males. Among 3746 male and female progeny were 14 w^a , 11 $y\ td$, and one y , representing 25 recombinants between the tricky dicky and white loci and one recombinant between the tricky dicky and yellow loci. This would place the tricky dicky locus 1/26 of the distance between the yellow and white loci or at approximately 0.1 map units

Table 2. Disjunction data for chromosomes 1 and 4 from females with unmarked fourth chromosomes mated to $Y^S X \cdot Y^L$, $In(1)En$, $v f B/O$; $C(4)RM$, $ci ey^R/O$ males.

Female X Chromosomes	Constitution of Ova Producing Recovered Progeny						Total Progeny	Percent Exceptions	
	X,4+	XX,4+	0,4+	X,0	XX,0	0,0		X	4
$y tw^3 su(w^a) wa / y tw^3 su(w^a) wa$	8094	2	2	2	1	0	8101	0.06	0.04
tw/tw	2425	4	13	3	1	0	2446	0.74	0.16
$tw/y tw^3 su(w^a) wa$	112	0	0	0	0	0	112	0.0	0.0

0.05% nullo-4 exceptions - see Table 1 in Davis 1971). However, homozygous tw females produced exceptions at rates which were 12 times ($18/2446 = 0.74\%$) and 3 times ($4/2446 = 0.16\%$) the control rates for the X and fourth chromosomes respectively. Although these rates of nondisjunction are modest compared to those of meiotic mutants which have been studied, they are significantly higher than control rates.

Females heterozygous for tw and tw^3 were also mated to the tester males. No exceptional progeny were recovered, although only 112 total progeny were scored. Heterozygous females mated to Canton S wild type males produced 231 progeny with no X exceptions. Fourth chromosome exceptions would not have been recognized. The low number of progeny scored prevents firm conclusions, but the data suggest that meiosis in heterozygotes is more like homozygous tw^3 than like homozygous tw .

A total of 335 tw/tw females mated to $C(3L)RM$, $se h rs^2$; $C(3R)RM$, $sbd gl e^s$ males produced 7 progeny while 207 tw/tw females mated to $C(2L)RM$, dp ; $C(2R)RM$, px males produced 3 progeny. Since viable euploid zygotes can only result from aneuploid ova, these females are also showing some low frequency of nondisjunction for the large autosomes. Crosses of 57 tw^3/tw^3 females to $C(3L)RM$, $se h rs^2$; $C(3R)RM$, $sbd gl e^s$ males produced no progeny.

Since tw/tw females show chromosome nondisjunction while tw^3/tw^3 females do not, an attempt was made to separate the morphological and nondisjunctional phenotypes. One generation of free recombination between the chromosome bearing tw and a Canton S wild type X was allowed. Twenty-three recombinant chromosomes with tw and 21 recombinant chromosomes with tw^+ were isolated in male progeny. Stocks were made of all 44 recombinant chromosomes, from which homozygous females were selected and tested for nondisjunction by mating to the same tester males used previously. Overall, the tw lines produced 21 X chromosome exceptions (0.31%) and 3 fourth chromosome exceptions (0.04%) among 6763 progeny while the tw^+ lines produced 29 X chromosome exceptions (0.23%) and 8 fourth chromosome exceptions (0.06%) among 12,824 progeny. Individual lines varied from no exceptions to about 1% exceptions in both groups. Thus the meiotic nondisjunction in females appears to be caused by genes which are independent of the twisted locus.

References: Davis, B.K. 1971, *Molec. Gen. Genetics* 113:251-272; Davis, B.K. 1975, *Genetics* 80:s25; Davis, B.K. 1979, DIS this issue; Lindsley, D.L. and E.H. Grell 1968, *Genetic Variations of D. melanogaster*, Carnegie Inst. Wash. Publ. No. 627.

De Salle, R., J.S. Yoon and L.H. Throckmorton, University of Chicago, Chicago, Illinois, and *Bowling Green State University, Bowling Green, Ohio. Karyotypes of two new species of the virilis group of *Drosophila*.

Recently, two new species have been discovered in the virilis group, one from Japan and one from western Canada. Their descriptions will be published shortly (Watabe and Higuchi, in publication; Throckmorton and Yoon, in preparation). A cytological study of them is underway. With respect to karyotypes, it shows the following. The species from Japan has a rod-shaped X, a submetacentric Y, one pair of small metacentrics, three pairs of rods, and a pair of dots. Preliminary analysis of the salivary gland chromosomes identifies the small metacentric as chromosome 2 of earlier workers, and the karyotype of this species may be the hypothetical primitive III of Hsu (1952) or very near to it. Approximately half of the male lar-

were not marked, diplo-4 and mono-4 ova were indistinguishable. Homozygous tw^3 females produced 0.06% X exceptions and 0.04% nullo-4 exceptions, rates which are remarkably close to control rates (0.06% X exceptions and

0.05% nullo-4 exceptions - see Table 1 in Davis 1971). However, homozygous tw females produced exceptions at rates which were 12 times ($18/2446 = 0.74\%$) and 3 times ($4/2446 = 0.16\%$) the control rates for the X and fourth chromosomes respectively. Although these rates of nondisjunction are modest compared to those of meiotic mutants which have been studied, they are significantly higher than control rates.