LINKAGE GROUP-KARYOTYPE CORRELATION IN THE HOUSE FLY, *MUSCA DOMESTICA* L., CONFIRMED BY CYTOLOGICAL ANALYSIS OF X-RAY INDUCED Y-AUTOSOMAL TRANSLOCATIONS

DALE E. WAGONER

Metabolism and Radiation Research Laboratory, Entomology Research Division, Agr. Res. Serv., USDA, Fargo, North Dakota 58102

Received June 17, 1968

THE relationship between the linkage groups and specific chromosomes of the house fly, *Musca domestica* L., karyotype was recently established (WAGONER 1967) by cytological analysis of X-ray induced heterozygous translocations between various combinations of autosomes. The five linkage groups previously reported (HIROYOSHI 1960; MILANI 1961; TSUKAMOTO, BABA, and HIRAGA 1961) were found to correspond to the five pairs of autosomes also previously reported (STEVENS 1908; PERJE 1948; BOYES and NAYLOR 1962). The results met expectation because 1) no cases of sex-linked inheritance have been reported in the house fly, and 2) the sex chromosomes appear to be entirely heterochromatic. Further cytological analyses of X-ray induced *Y*-autosomal translocations verified the relationships previously established.

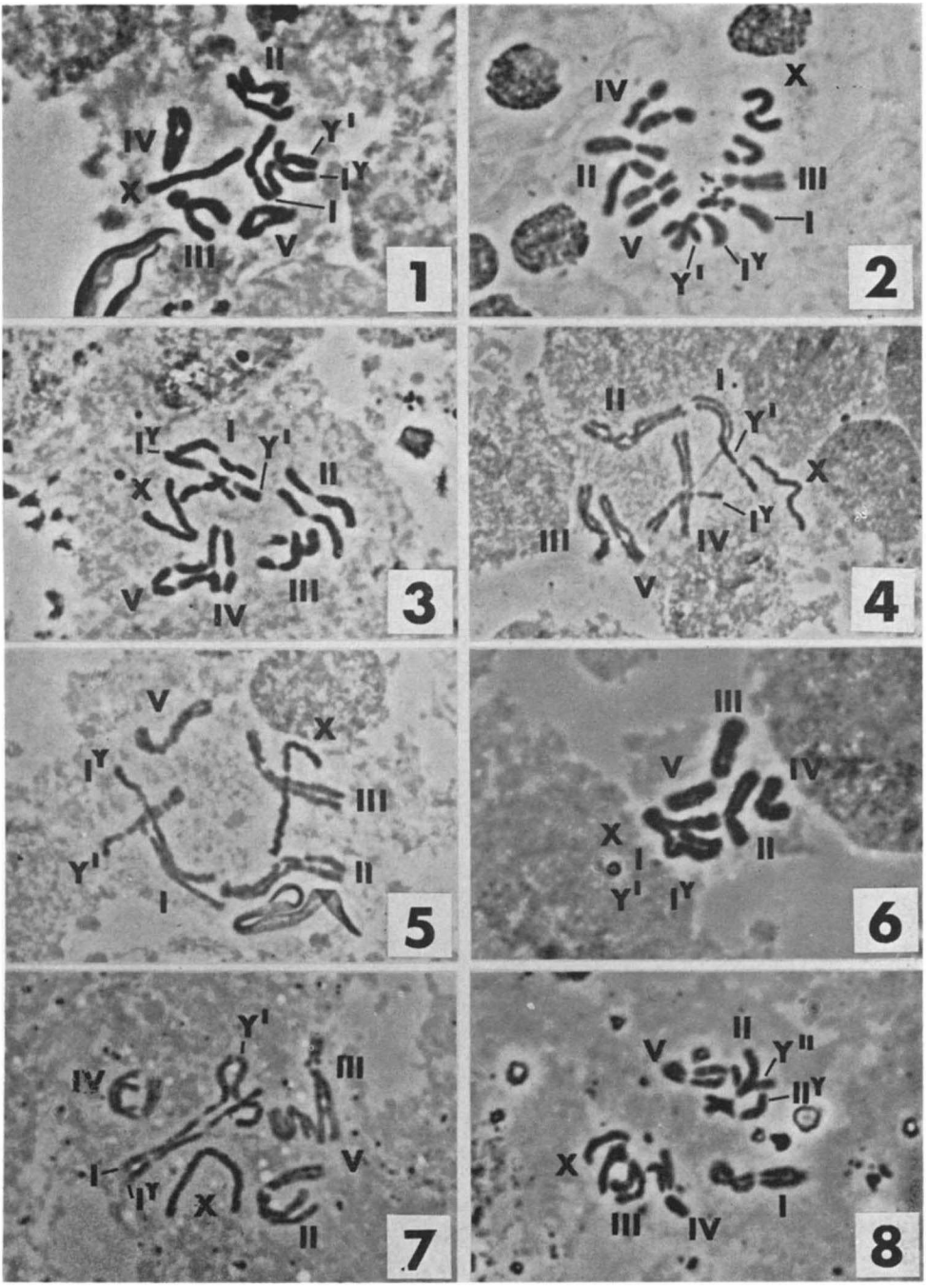
MATERIALS AND METHODS

The crosses, mutant markers used to derive the translocation stocks, rearing methods, cytological techniques, and method of X-ray administration were the same as those described earlier (WAGONER 1967). PERJE's (1948) numbering of the house fly karyotype was used where *X* and *Y* represent the sex chromosomes and the Roman numerals I-V represent the autosomes starting with the longest and ending with the shortest pair. Males are heterogametic (*XY*).

All *Y*-autosomal translocations were either induced in adult males of the normal phenotype (Fargo wild type) or in males marked with the dominant mutant *Rl* (Rolled wings). Females carrying recessive mutant markers on appropriate autosomes were crossed with treated males and individual F_1 males were backcrossed to the marked females so that when *Y*-autosomal translocations were induced, the progeny would show a pattern of holandric inheritance, that is, males that were normal in phenotype (or *Rl*) and mutant females (or *Rl*+). Continual selection to perpetuate these stocks was unnecessary because all male progeny carried the *Y*-autosome, autosome-*Y* translocated chromosomes, and all female progeny carried the *X* chromosome and the marked autosome from the male parent. The female parent contributed only *X* chromosomes and marked autosomes.

RESULTS AND DISCUSSION

Reciprocal translocations were induced between the *Y*-chromosome and the chromosome containing the *Rl* (Rolled-wing) mutant or the *ac*+ (ali-curve) marker. Both markers represent the same linkage group and were previously


II
IV
X
Y'
I^Y
I
V
III
1
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X
II
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Y'
X
II
V
IV
III
3
I
II
Y'
X
III
I^Y
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X
I^Y
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Y'
II
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5
III
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IV
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II
Y'
I^Y
6
Y'
IV
III
I
V
I^Y
X
II
7
II
V
Y^II
II^Y
X
III
IV
I
8

assigned to chromosome I. The subsequent cytological studies of spermatogonial and spermatocyte I cells in the process of mitotic or meiotic divisions, respectively, confirmed their location on chromosome I (Figures 1–7). A loose mitotic pairing of homologous chromosomes occurs in somatic cells in the house fly as it does in other Diptera.

Translocations were induced between the *Y* chromosome and the chromosome containing the *car*$^+$ (carnation eye color) or the *ar*$^+$ (aristapedia) marker. Both markers represent the same linkage group and were previously reported to be located on chromosome II. The subsequent cytological examination showed the *Y*-chromosome pairing with chromosome II, thus confirming the location of this linkage group (Figures 8–10 and 9′–10′).

Male flies from genetic tests that showed the *Y* chromosome reciprocally translocated to the *bwb*$^+$ (brown-body color) marker were studied cytologically. In previous studies *bwb* was assigned to chromosome III. The cytological examination of the *Y-bwb*$^+$ translocations confirmed the location of *bwb*$^+$ on chromosome III (Figures 11–13 and 11′–13′).

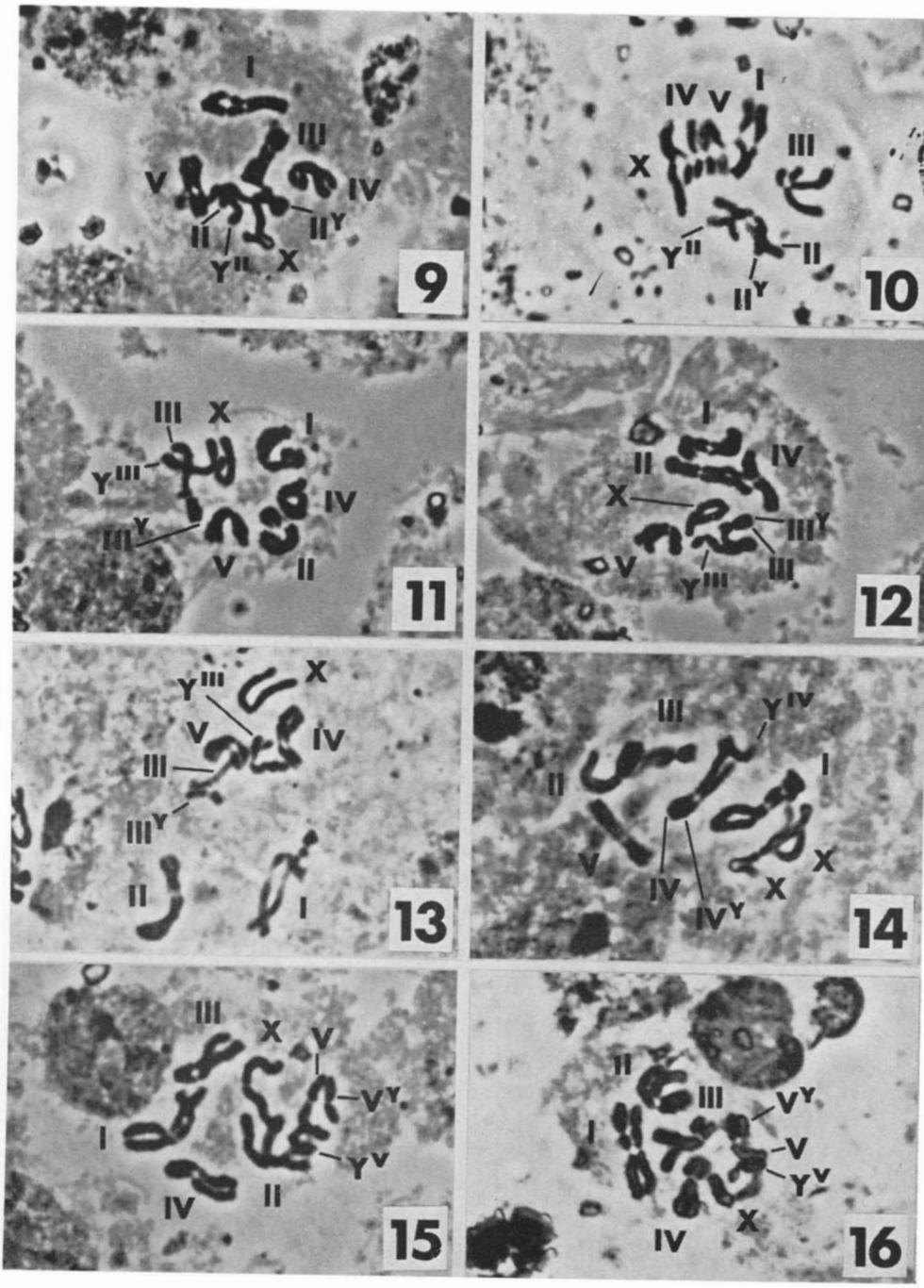
Translocations were induced between the *Y* chromosome and the chromosome containing the *ct*$^+$ (cut-wing tip) or *ye*$^+$ (yellow eye color) marker. Both markers were previously assigned to chromosome IV. The subsequent cytological analysis confirmed the earlier assignment (Figure 14 and 14′).

Translocations were induced between the *Y* chromosome and the chromosome containing the *ocra*$^+$ (ocra-eye color) marker. This mutant was previously assigned to chromosome V. The subsequent cytological analysis of the *Y-ocra*$^+$ translocations confirmed the earlier assignment of this linkage group to chromosome V (Figures 15–16 and 15′–16′).

The chromosomes from a *Y*-IV translocation in which the males contained two *X*'s, the Y^{IV}, IV^{Y} reciprocally translocated chromosomes, and a normal chromosome IV are shown in Figure 14. (Normally the male contains only one *X* chromosome; see other figures.) The situation was discovered in the F_{16} generation of the stock, but earlier generations had not been studied cytologically. All males examined contained the same *XX* complement. It is postulated that sex-chromosome disjunction was impaired in the males of this stock and that a case or cases of nondisjunction that had occurred in a male or males of an earlier generation(s) gave rise to the *X*, *X*,Y^{IV}, IV^{Y}, *IV* male(s). Subsequently, the *XX* male(s) replaced the males with a single *X*.

An alternative explanation is that the *Y*-autosome translocation was induced in a sperm that already contained an *X* and a *Y* chromosome (by nondisjunc-

FIGURE 1.—*Y*-I translocation, spermatogonial metaphase × 1,500.
FIGURE 2.—*Y*-I translocation, spermatogonial metaphase × 1,400.
FIGURE 3.—*Y*-I translocation, spermatogonial prophase (late) × 1,200.
FIGURE 4.—*Y*-I translocation, spermatogonial prophase × 1,000.
FIGURE 5.—*Y*-I translocation, spermatogonial prophase × 1,250.
FIGURE 6.—*Y*-I translocation, meiosis I prophase (late) × 1,550.
FIGURE 7.—*Y*-I translocation, spermatogonial prophase × 1,400.
FIGURE 8.—*Y*-II translocation, spermatogonial metaphase × 1,400.


I
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V
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II
IIIY
IIY
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YII
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IIY
10
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I
YIII
IV
IIIY
V
II
11
I
II
IV
X
IIIY
V
YIII
III
12
YIII
X
V
IV
III
IIIY
II
I
13
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YIV
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I
V
IV
X
IVY
14
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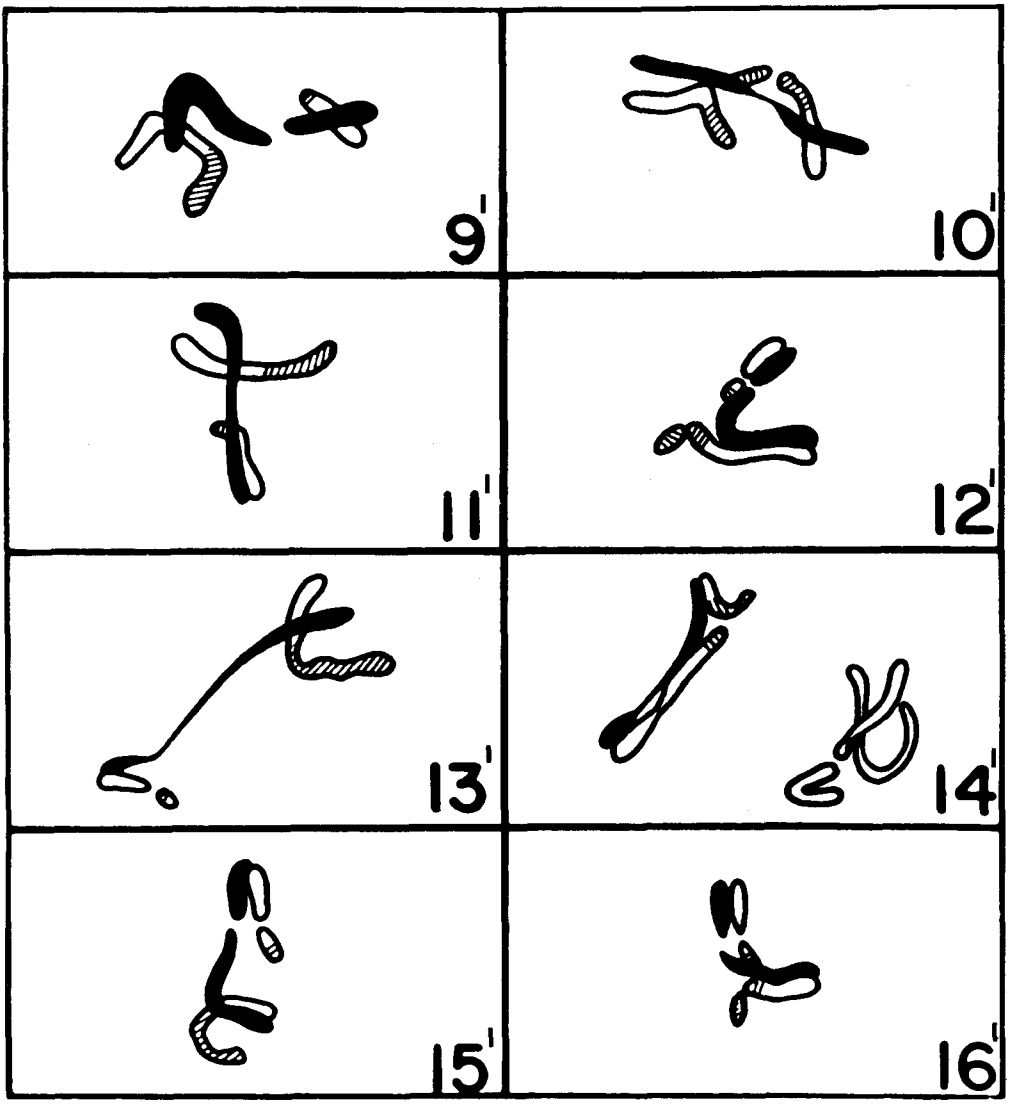

*FIGURES 9'–16'.—Diagrammatic representations of the corresponding translocations pictured in Figs. 9–16. The nontranslocated autosome is solid black, the translocated autosome is not filled in, and the translocated *Y* chromosome is crosshatched.

FIGURE 9 and 9'.—*Y*-II translocation, spermatogonial metaphase × 1,400.
FIGURE 10 and 10'—*Y*-II translocation, spermatogonial metaphase × 1,400.
FIGURE 11 and 11'.—*Y*-III translocation, spermatogonial metaphase × 1,300.
FIGURE 12 and 12'.—*Y*-III translocation, spermatogonial metaphase × 1,300.
FIGURE 13 and 13'—*Y*-III translocation, spermatogonial prophase (late) × 1,400.
FIGURE 14 and 14'.—*Y*-IV translocation, spermatogonial prophase (late) × 1,450.
FIGURE 15 and 15'.—*Y*-V translocation, spermatogonial metaphase × 1,400.
FIGURE 16 and 16'.—*Y*-V translocation, spermatogonial metaphase × 1,550.

tion). This alternative is a less attractive hypothesis because of the low probability that these two rare events would occur at the same time. However, the possibility cannot be ruled out. Also, nondisjunction of the *X* chromosomes in one of the stock females cannot be ruled out, though it is more likely to occur in an *X*, Y^{IV}, IV^{Y}, IV male than in an *X*,*X*, IV, IV female. DOBZHANSKY (1932) showed that *Drosophila melanogaster* males containing II-*Y* translocations showed increased primary nondisjunction.

HIROYOSHI (1964) made cytological examinations of house flies from strains collected in nature that showed holandric inheritance of one member of chromosome III. This type of strain segregated in the same way that a *Y*-III reciprocal translocation stock segregates, but no *Y*-chromosome was visible (thus no reciprocal translocation can be observed). Most males from these strains had two sex chromosomes, both of which appeared to be *X*'s. HIROYOSHI, therefore, postulated that a male-determining and a viability factor from the *Y* chromosome became attached to chromosome III and that the rest of the *Y* chromosome (the bulk of it) was subsequently lost. The male would appear *XO* at first but two types of males would arise in the progeny: (1) those that get no sex chromosome from their male parent and get an *X* from the female and (2) those that get an *X* from both parents (but are male because they received the now male-determining chromosome III). He further postulated that the males containing *XX* were superior to the *XO* males and replaced them in subsequent generations, because most strains showing this type of spontaneously occurring holandric inheritance of one member of the third pair of autosomes contained only *XX* males. Some populations were found in which *XO* and *XX* males were both present. HIROYOSHI explained these as more recent occurrences of the *Y* to autosome transfer (with subsequent loss of the rest of the *Y*). The *Y*-IV translocation stock obtained in the present test seems to support HIROYOSHI's theory with respect to the *XX* males being favored and replacing the males containing only one *X* chromosome.

I would like to acknowledge DR. R. MILANI of the Istituto di Zoologia, Università di Pavia, Pavia, Italy, and DR. T. HIROYOSHI of the Department of Genetics, Osaka University Medical School, Osaka, Japan, for originally supplying some of the mutant stocks used in this research. I would like to thank MR. CURTIS NICKEL and MR. ODELL JOHNSON of this Division for excellent technical assistance during the progress of this research, and DR. L. E. LACHANCE and DR. A. C. BARTLETT, of this Division, and DR. T. HIROYOSHI for their critical review of this manuscript. I would also like to thank MISS LEOLA KENNICKE, MISS CAROL SWISHER, MISS BARBARA ANDERSON, MISS GWENDOLYN CARTER, MISS JEAN KAUPPILA, MR. DARYL NELSON, and MR. DONALD SCHAAN, student assistants from N. Dak. State University, for laboratory assistance, MISS JENNIFER SWEENEY for cytological preparations, and MR. RENE FUGLESTAD of this Division for photographic assistance and plate preparation.

SUMMARY

Cytological analysis of X-ray induced *Y*-autosomal translocations in the house fly, *Musca domestica* L., confirmed the linkage group-karyotype correlation reported by WAGONER (1967). PERJE's (1948) method of numbering the chromosomes was used (where *X* and *Y* represent the sex chromosomes and Roman numerals I-V represent the autosomes starting with the longest pair and ending

with the shortest). The following relationships were confirmed: The *Rl* and *ac* mutants are located on chromosome I; the *ar* and *car* mutants are located on chromosome II; the *bwb* mutant is on chromosome III; the *ct* and *ye* mutants are on chromosome IV; and the *ocra* mutant is on chromosome V. A case (or cases) of nondisjunction in a *Y*-IV translocation stock is hypothesized to have produced males with two X's (an X,X,Y^{IV}, IV^{Y}, IV chromosome complement) instead of the normal X chromosome. The males containing XX replaced the males containing one X in subsequent generations.

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