

Evidence for Multiple Sex Factors in the X-Chromosome of *Drosophila melanogaster*

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PNAS 1931;17;513-518
doi:10.1073/pnas.17.9.513

This information is current as of December 2006.

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Notes:

tuberosus is definitely seven. There is some indication of a deep constriction near one end of one of the longer chromosomes (Fig. 5).

Prophase, metaphase, and telophase division figures of the microspore nucleus of *L. latifolius* have also been observed. The microspores of this species (Fig. 7) are slightly smaller, and the chromosomes during division occupy a greater proportion of the cell than do those of *L. tuberosus* (Fig. 5). On the basis of these figures, the writer is able to confirm Winge's² count of seven for *L. latifolius* as the haploid number of chromosomes for this species.

¹ Corti, R., *N. Giorn. Bot. Ital.*, **37**, 278-279 (1930).

² Winge, Ö., *J. Geneti.*, **8**, 133-138 (1919).

³ Kawakami, J., *Bot. Mag. Tokyo*, **44**, 319-329 (1930).

⁴ Latter, Joan, *Annals. Bot.*, **40**, 277-313 (1926).

⁵ Punnett, R. C., *Proc. Roy. Soc. London*, **B102**, 236-238 (1927).

⁶ Maeda, T., *Bot. Mag. Tokyo*, **42**, 191-195 (1928).

⁷ Maeda, T., *Mem. Coll. Sci. Kyoto Imp. Univ.*, **B5**, 89-123 (1930).

⁸ Sakamura, T., *J. Coll. Sci. Tokyo*, **39**, 1-221 (1920).

EVIDENCE FOR MULTIPLE SEX FACTORS IN THE X-CHROMOSOME OF *DROSOPHILA MELANOGASTER*

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Communicated July 21, 1931

The data presented here permit a decision between two alternative hypotheses regarding sex determination in *Drosophila melanogaster*. Bridges^{1,2,3} has shown that the sex of an individual in this form is determined by a relation between the number of the X-chromosomes and that of the autosomes. From his studies of a variety of sex types (table 1), he has concluded that the X-chromosome turns the course of development toward femaleness, the autosomes toward maleness.

Further material for the analysis of this problem comes from the study of the effects of fragments of the X-chromosome in diploids (L. V. Morgan,⁴ Painter and Muller,⁵ Dobzhansky, unpublished). Here it appears that the addition of certain of the duplications for parts of the X to the chromosome complement of a diploid male or female produces little or no effect on the sex type. Yet it should be noted that, while this is true for the shorter fragments, when longer fragments are involved, males become sterile and otherwise abnormal, and females become more like superfemales.

Two hypotheses have been proposed to account for the data. As a result of his work on triploid intersexes, Bridges advanced the idea that,

like any other group of characters, those concerned with sex are determined by the action of many genes. These are so distributed through the chromosomes that the X contains a preponderance of female-determining genes, the autosomes relatively more of those that are male-determining. From this point of view, the course of development depends on the ratio between the numbers of the genes of different types.

This theory of "genic balance" is sufficient to account for the data. It is not, however, necessary. An alternative hypothesis has been offered by Goldschmidt, on the basis of his work with *Lymantria*⁶—a system in which sex is determined by the relation between a single female factor (in the X in *Drosophila*) and a single male factor (in the autosomes). With the additional assumptions of modifying factors and of variations in the "strength" of the primary genes, such a system can be made to account for the previously published data on intersexes. A similar conclusion has been indicated by Painter and Muller⁵ and Muller,⁷ from the

TABLE I
RELATION OF SEX TO CHROMOSOMES IN *DROSOPHILA* (AFTER BRIDGES, LOC. CIT.)

SEX	X-CHROMOSOMES	SETS OF AUTOSOMES	SEX INDEX
Superfemale	3	2	1.5
Female	1	1	1.0
	2	2	1.0
	3	3	1.0
	4	4	1.0
Intersex	2	3	0.67
Male	1	2	0.50
Supermale	1	3	0.33

fertility of males carrying a duplicating fragment of the X-chromosome—specifically, that the "sex differentiators" were not present in such a fragment.

This does not, however, seem evident to us, since it is clear that the development of the sex characters may involve threshold reactions (Goldschmidt, Dobzhansky, loc. cit.). Therefore, we expected that, although in the diploid duplications produced no change, the study of their effects upon intersexes might provide more conclusive data. The intersexes are quite sensitive to both genetic and environmental influences, presenting a series from extreme male to extreme female type. These changes may be brought about by genes which show no appreciable effect on the normal males and females (Dobzhansky^{8,9}). Likewise, temperature is effective in changing the grade of intersexual development, whereas in the normal sexes, no effect is obvious. On this basis, we should expect the intersexes to provide a more sensitive measure of the presence of sex factors in a given section of chromosome than the males or females.

The results of our experiments have justified this point of view. We find that in every case, the intersexes containing an additional frag-

ment of the X-chromosome are more female type than those without the fragment. This affords a definite confirmation of the multiple factor hypothesis suggested by Bridges.

Our studies concern six duplications of different lengths, whose characteristics are shown in table 2.

TABLE 2
THE LOCI IN THE X-CHROMOSOME INCLUDED (+) AND DELETED (-) IN THE
DUPLICATIONS

DUPLICATION	Loci															
	y	sc	svr	kz	br	pn	w	cv	v	g	r	f	B	fu	cr	bb
112	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-
107	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+
118	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+
134	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-
126	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-
L. V. M.	+	+	+	+	+	+	-	-	-	-	-	-	-	+	+	+

Individuals carrying the duplications (except in the case of Dup. L. V. M.) are very nearly normal in appearance, and both sexes are fertile. There are minor differences from the wild type—occipital bristles are present, other bristles are occasionally duplicated and there are slight abnormalities in the wing shape. Duplication L. V. M. flies are more strikingly different from normal, and the males are sterile. The duplications 112, 107, 118 and L. V. M. belong to the class of “deletions” (Painter and Muller).⁴ Cytologically, 112 is the shortest, 107 next longer, then 118, and L. V. M. is the longest of all. Duplication 126 is a very short section of the middle of the X, attached to chromosome III. Finally, Duplication 134, which has not yet been studied cytologically, belongs to the peculiar “eversporting” type, like that of Patterson and Painter.¹⁰

For those duplications which produce fertile males, the technique of procuring the intersexes is simple. Stocks of triploids were obtained homozygous for a gene included in and suppressed by the duplication (e.g., yellow for 112, 107, 118 and 134, forked for 126). To these triploids were mated males carrying the duplication and containing in the normal X the mutant gene in question. This procedure allowed the comparison, in the progeny, of two types of intersexes out of the same culture—the intersexes carrying the duplication which have the mutant-gene suppressed, and the intersexes free from the duplication which manifest the characters of the mutant gene.

Males carrying the L. V. M. Duplication are sterile. For this type, another technique was attempted, the production of the duplication-carrying triploids by means of the third-chromosome recessive gene discovered by Gowen. This attempt proved unsuccessful, due to the high

sterility of the stocks; but in an unrelated experiment involving the duplication, a number of triploids appeared spontaneously. A stock of such triploids could unfortunately not be established, due to the mode of disjunction of the X's and the duplication. Nevertheless, enough intersexes carrying the duplication were produced to make the effect of this, the longest duplication involved in the experiment, fully apparent.

Intersexes which appeared in the cultures were classified according to their sexual type. Six classes of intersexes were distinguished—class I is the extreme male-type, classes V and VI are the extreme female type (class VI has no sex-combs). These classes are based on the characters of the external genitalia, which are, however, correlated with the internal structures as well as with the secondary sexual characters (Dobzhansky, loc. cit.). These classes are, of course, arbitrary, and we are unable at present to ascribe to the differences between them a functional significance expressed in quantitative terms.

The results obtained are shown in tables 3 and 4.

TABLE 3
THE INFLUENCE OF THE DUPLICATIONS ON THE TYPE OF THE INTERSEXES

CLASSES OF THE INTERSEXES	DUPLICATION-CARRYING							CONTROL						
	I	II	III	IV	V	VI	N	I	II	III	IV	V	VI	N
Duplication														
126	8	26	17	21	1	—	73	5	9	7	2	1	—	24
112	—	6	10	100	44	1	161	40	50	42	53	1	—	186
107	—	—	5	129	85	9	228	58	116	74	58	—	—	306
118	—	—	10	91	87	15	203	66	59	28	16	—	—	169
134	—	—	2	36	47	11	96	61	188	91	91	2	—	433
L. V. M.	—	—	—	—	—	11	11	—	4	7	—	—	—	11

TABLE 4
THE MEAN TYPE OF THE INTERSEXES CARRYING THE DUPLICATION AND FREE FROM IT

DUPLICATION	CARRYING THE DUPLICATION	CONTROL	DIFFERENCE
126	2.74 ± 0.12	2.38 ± 0.21	0.36 ± 0.24
112	4.15 ± 0.055	2.59 ± 0.08	1.56 ± 0.10
107	4.43 ± 0.04	2.43 ± 0.06	2.00 ± 0.07
118	4.53 ± 0.05	1.97 ± 0.075	2.56 ± 0.09
134	4.70 ± 0.07	2.50 ± 0.06	2.20 ± 0.09
L. V. M.	6.00	2.6	3.4

It is obvious from tables 3 and 4 that the presence of the duplications results in a shift in the type of the intersexes toward the female. Furthermore, it is apparent that approximately the longer the duplication, the greater the shift in the type of intersex, from a very slight shift in the shortest, Dup. 126, until in the longest duplication (L. V. M.) all the intersexes are of the extreme female type. This can only be interpreted to

mean that in all portions of the X thus far studied, female-determining factors are present, and the degree of femaleness is proportional to the number of these factors.

This demonstration is completed by the fertility of one of the extreme female type intersexes carrying duplication L. V. M. Out of five such intersexes tested, this one proved fertile. She produced thirteen diploid offspring, tests of which showed that she contained two normal X's and the duplication; and one ordinary male-type intersex, proving her triploid for the autosomes. In order to strengthen this, measurements were made of the cell size in her wings, following the technique of Dobzhansky.¹¹ The results were undoubtedly triploid or intersex, removing the possibility that she might be a diploid duplication female in which there had been another occurrence of triploidy. This gives an almost diagrammatic form to the evidence: in the diploid, this duplication is sufficient only to give a sterile male; but added to the chromosome complement of an intersex, it produces a fertile female.

As we have already pointed out, these data fully uphold Bridges' hypothesis of genic balance. They are of especial value in this connection, since they cannot be construed as "mere" modifying factors—an arbitrary distinction at best. They show the same quantitative relations that have been defined as characteristic of the sex factors proper.

This method of analysis may be used further to map out the distribution of the sex factors in the X and in the autosomes, and even to evaluate their relative effectiveness. That there should be such differences in effectiveness is quite probable, and it is possible that some portions of the X should be male-determining and of the autosomes female-determining. It is now obvious, however, that sex in *Drosophila* is determined by the interaction of a number of genes, rather than by the relation between a single male and female factor.

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BODY PATTERN AS RELATED TO MAMMARY GLAND SECRETION

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Communicated August 13, 1931

The effects on body form of the testis as observed in castration—or of the pituitary as noted when it is pathological or experimentally removed as in the experiments of Cushing, Smith, and others, or altered by the animal's heredity as observed in the experiments of MacDowell and Smith—or of the ovary as seen in the work of Goodale on the plumage and structure of birds have made it good form to think of body form as a function of gland secretion rather than gland secretion as a function of body form. The case is reversed, however, when the dairy cattle breeder thinks of his cattle. LeCouteur's paper called attention to this relation of body pattern to milk secretion about 1834. Since that time the relations between body form and milk secretion have grown to include many more points of the growth pattern until more than twenty separate items of the body structure are included in those supposed to affect the amount of milk the cow is able to secrete.¹ Examination of the literature on the subject, however, reveals the fact that in a scientific sense the proof for these supposed relations is largely lacking.

In 1914 the writer commenced a study which has grown to include numerous aspects of this problem. The latest research has about 6000 Jersey cows measured in eight different particulars for its basic data, the measurements being collected by the American Jersey Cattle Club. These measurements include weight, height at withers, depth at withers, heart girth, paunch girth, width at hips, body length, and rump length. Besides these data, the age and parentage of all cows were known from their registration papers. The milk productions and butter-fat yields, etc., were