GENETIC STUDIES ON *DROSOPHILA SIMULANS*. II. SEX-LINKED GROUP OF GENES[1]

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Received July 6, 1920

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INTRODUCTION

It has been shown in Part I of these studies (STURTEVANT 1920 c) that *Drosophila simulans* may be hybridized with *D. melanogaster*, and that the hybrids are sterile. It had been hoped, had the hybrids been fertile, that the genetic make-up of *simulans* could be studied through the hybrids. This hope disappeared when the hybrids were found to be sterile, so the problem had to be attacked in another way,—namely, by studying the genetics of pure *simulans*. A number of mutations have been obtained, and it has been possible to show that certain of these are allelomorphs of known mutations of *melanogaster*. The genetic behavior of *simulans* is now fairly well worked out, and can be compared in some detail with that of *melanogaster*. The data concerning the sex chromosomes will be presented in this paper, and the autosomes will be discussed in Part III of these studies.

[1] Contribution from the CARNEGIE INSTITUTION OF WASHINGTON.

SEX-LINKED MUTATIONS OF *Drosophila simulans*

Table 1 shows the sex-linked mutations that have been found in *D. simulans*. A brief description of each and an account of its origin follows.

Yellow. The original specimen was collected on a pile of decaying tomatoes at Lakeland, Florida, by Dr. C. W. METZ. He obtained a stock from it and sent it to me before *simulans* had been recognized as a distinct species. This was one of the first stocks of *simulans* used in the experiments here reported.

The mutant character looks exactly like the yellow *melanogaster* that is already known, described and figured (MORGAN and BRIDGES 1916). We shall see below that it is in fact the same character.

TABLE 1

Sex-linked mutations of Drosophila simulans.

NAME	CHARACTER AFFECTED	SYMBOL	LOCUS	DATE	DISCOVERY BY WHOM	STOCK
Yellow	Body color	y	0.0	May, 1919	C. W. METZ	Wild, Fla.
Yellow	Body color	y	0.0	Oct. 15, 1919	A. H. S.	Wild, N. H.
Prune	Eye color	p_n	3.0	Aug. 29, 1919	A. H. S.	y t_b linkage
Dwarf	Size	d_w	3.0	Oct. 1, 1919	A. H. S.	y t_b linkage
Rubyoid	Eye color	r_a[2]	11.3	Oct. 31, 1919	A. H. S.	y p_n linkage
Carmine	Eye color	c_a[2]	44.8	Sept. 17, 1919	A. H. S.	y, scarlet
Forked	Bristles	f	57.2	Sept., 1919	C. B. BRIDGES	y stock
Tiny-bristle	Bristles	t_b[2]	57.8	July 8, 1919	A. H. S.	Wild, Fla.
Lethals	Life				A. H. S.	

[2] If these mutants were treated as though they were mutants of *D. melanogaster*, rubyoid would have the symbol rb^d, carmine would be g^c, and tiny-bristle would have to be renamed.

On October 15, 1919, I found a single yellow male in a wild stock from Randolph, New Hampshire. This male was bred to wild-type females, and in F_2 there appeared many yellow males. One of these was crossed to a female known to be heterozygous for the original Florida yellow, and produced many yellow daughters. Since the two yellows were indistinguishable, and were shown by this experiment to be allelomorphic, the New Hampshire yellow was discarded. It was used in none of the linkage experiments recorded in this paper. It is possible that this race arose by contamination with the Florida yellow, rather than by mutation, as no conclusive check against such an accident was available.

Prune. A single male with a dark purplish translucent eye was found on August 29, 1919, in a culture of pure Florida ancestry (two females were used in making up this culture), that produced 81 other males, all with the usual red eye-color. A stock was obtained from this male, and

has been used extensively in the experiments here recorded. The eye-color looks almost exactly like the prune eye-color of *melanogaster*, and is in fact due to a mutation in the same locus, as we shall see later.

Dwarf. Culture 6883, from a single female heterozygous for yellow, counted in October 1919, produced 74 ♀♀, 3 not-yellow ♂♂, 27 yellow ♂♂. The family was continued as a lethal strain, and gave results consistent with the view that there was a sex-linked lethal present, which was very close to prune. Later it was noticed that the apparent cross-overs between prune and the lethal were all dwarfs. These dwarfs proved fertile, and it has been shown by breeding them that they actually carry the supposed lethal. The lethal (really semi-lethal) effect and the dwarf character are evidently due to the same gene, which is conveniently referred to as "dwarf," rather than "lethal," the original name.

Rubyoid. Culture 7108, of pure Florida ancestry, contained a single female, that carried one yellow prune X while the other X was supposed to be wild-type. At least 38 sons (33 of them not yellow) had a new eye-color, much paler than prune. The female in 7108 evidently had in her "wild-type" (maternal) X a new mutation. The mother of this female produced no rubyoid sons, nor did 9 tested sisters of 7108, though at least five of these probably carried the same maternal X (so far as the left-hand end was concerned) as did 7108. The situation is, however, somewhat obscured by the fact that the mother of 7108 and some of her sisters were heterozygous for dwarf, which acted practically as a lethal; and also by the possible presence of a second lethal in the same general region.

The color of the rubyoid eye is somewhat darker than that of ruby *melanogaster*, with which it is allelomorphic, but is of the same general nature.

Carmine. This eye-color appeared first in a single male, from a culture made up with two females, both heterozygous both for yellow and for the autosomal recessive scarlet. The original mutant male was also yellow. The culture from which he came was of pure Florida stock, and was a daughter culture of 6701, in which prune first appeared.

Carmine closely resembles the *melanogaster* mutant of the same name. As we shall see, both are allelomorphic to the more familiar garnet of *melanogaster*. The eye-color is paler than that of rubyoid.

Forked. This mutant was discovered by Dr. C. B. BRIDGES in September 1919, in a stock of the Florida yellow. BRIDGES found that it was sex-linked, and that it gave free crossing over with yellow. The data on its linkage presented here, however, are all from my own experiments, made with a stock obtained from BRIDGES.

The character is exactly like the forked of *melanogaster*, which has been described and figured by MORGAN and BRIDGES 1916). The two characters are due to mutations in the same locus, as will appear below.

Tiny-bristle. A single female, of the Florida stock, was found to have an extra dorsocentral bristle. This character reappeared in only one of her descendants; but 38 of her 66 sons had small bristles. The small-bristle character is a sex-linked recessive in inheritance. There are several other effects associated with it. The flies hatch somewhat later than their normal brothers and sisters, and are more easily killed, as larvae or pupae, by unfavorable conditions. All the females so far tested have been completely sterile. In addition the eyes are often slightly roughened, and may have a slight nick in the anterior margin, and the abdominal bands are less pigmented than in wild-type flies and may be somewhat irregular.

Lethals. At least two lethals, besides the semi-lethal dwarf, have been found. Both were near the yellow locus, and were therefore not favorable for studying crossing-over relations, since this region is sufficiently well workable through yellow, prune and rubyoid. These lethals were therefore discarded, and it seems not worth while to present here what few data were obtained concerning them.

PARALLELISM OF SEX-LINKED MUTATIONS IN *simulans* AND *melanogaster*

The seven sex-linked characters described above all resemble sex-linked characters already known in *D. melanogaster*. Since the two species can be crossed, with the production of wild-type females, it is possible to find out if the mutant genes in the two species are allelomorphic. If a wild-type individual of either species is crossed to an individual of the other species that carries a recessive mutant gene, the daughters (except the one non-disjunctional exception referred to in Part I) are always wild-type in appearance, just as they are when a similar cross is made within either species. That is, each species carries the dominant normal allelomorphs of all the recessive mutant genes of the other species that have been tested. If, then, we cross a mutant race, say yellow, of *simulans* to a yellow race of *melanogaster*, we can determine whether or not the mutations have affected the same wild-type allelomorph, i.e., whether or not they are themselves allelomorphic. For clearly, if the hybrid females are not yellow, each parent has introduced the normal allelomorph of the mutant gene present in the other race, and the mutant genes are not allelomorphic. But if the hybrid females are yellow, then neither parent carried the normal

allelomorph of the yellow gene present in the other parent; and, since the wild-type flies do carry such allelomorphs wherever the test has been made, it follows that the two mutant yellows must be allelomorphs. We may now consider the data that have been obtained in experiments designed to test the allelomorphism of the seven sex-linked mutants of *D. simulans*.

Yellow

Eleven females from a stock of *melanogaster* pure for yellow and for white were mated to 19 yellow *simulans* males. Ninety-three yellow white females (*melanogaster*, and due to non-virginity of the mothers), 117 yellow white males (also *melanogaster* and due to non-virginity), and 41 yellow females (hybrid, and not white) were produced. The 41 yellow females that were not white prove that the two yellows are allelomorphic.

Prune

Seven *melanogaster* females from a stock pure for yellow and for prune were mated to six *simulans* males that were prune (not yellow). Thirty offspring were produced—all of them prune (not yellow) females, thus proving the mutant genes to be allelomorphic.

Dwarf

Hybrids have not been obtained in the case of the two dwarfs, and in *simulans* the mutant has been lost, so that we can get only indirect evidence here.

In both species the dwarf gene is a semi-lethal, and in both the dwarf males appear normal except for their small size and the pale color that is usually associated with small size arising from any cause (such as starvation of the larva) in Drosophila. The dwarf males are fertile in both species; in *simulans* the few females that have been tested have proved sterile. In *simulans* dwarf has not been found to cross over from prune (except in one doubtful instance) and accordingly has a locus of 3.0; in *melanogaster* I have reared many flies without getting a crossover between dwarf (known in this species as "lethal 10") and either yellow or scute, which are both located at 0.0. Dwarf prune crossovers in *melanogaster* have however been found on two occasions. Dwarf thus sticks closely to prune in *simulans*, and to yellow in *melanogaster*. The yellow prune crossover value is 1.1 in *melanogaster*, 3.0 in *simulans*. It seems probable that the two dwarfs are not identical, in spite of their similarity and the nearness of their loci, and that this case is similar to that of the two tiny-bristles discussed below. However, it

is possible that the dwarf locus is between the yellow and prune loci, and that the yellow prune crossing over in *melanogaster* is all or nearly all to the right of this locus, while in *simulans* it is all or nearly all to the left of it. This view is rendered improbable by a consideration of the crossover relations of rubyoid *simulans* and ruby *melanogaster*, to be discussed later. If the one doubtful prune dwarf crossover in *simulans* is really a crossover, he indicates that dwarf is to the right of prune, thus again negativing the above tentative interpretation; but as will appear below his nature is very doubtful.

Rubyoid

Nine *melanogaster* females from a stock pure for ruby were mated to 13 rubyoid *simulans* males. The offspring were 224 in number, all of them females with an eye-color intermediate between ruby and rubyoid. The two mutant genes are thus allelomorphs.

Carmine

Two *melanogaster* females from a stock pure for vermilion, garnet, small, and forked were mated to four carmine *simulans* males. The offspring consisted of 32 females, all with an eye-color intermediate between carmine and garnet. Since the mother had two eye-color mutations (vermilion and garnet), this case is not quite as certain as the others here described. But vermilion is a very different-looking color from the other two, which are quite similar; and carmine is almost exactly like the mutant of the same name known in *melanogaster*, which is an allelomorph of garnet. These facts, taken in connection with the observation that the eyes of the 32 hybrids did not look at all like vermilion, but were intermediate between carmine and garnet, leave no reasonable doubt that carmine *simulans* is an allelomorph of garnet *melanogaster*.

Forked

A *melanogaster* female from a stock pure for eosin, vermilion, and forked was mated to a forked *simulans* male. Forty-nine offspring were produced, all of them forked daughters. The two mutant genes are therefore allelomorphs.

Tiny-bristle

The tiny-bristle females are sterile in both species, so in this case it was necessary to use *melanogaster* females heterozygous for tiny-bristle. Two

tests were made. In the first case six females of the constitution[3] $\frac{v\,f}{t_b}$ were mated to 21 tiny-bristle *simulans* males. The following offspring resulted:

FEMALE			MALE			
Wild-type	v	vf	t_b	vf	v	t_b
99	78	26	10	14	11	19

The mothers were evidently not all virgin, since sons (and pure *melanogaster* sons) were produced. At least one of the females had mated with a vermilion forked *melanogaster* male, but the excess of females, especially in the wild-type class, indicates that some of the offspring were actually hybrids. Since the cross was not conclusive another test was made. Seven *melanogaster* females of the same constitution as before were mated to 12 tiny-bristle *simulans* males. The offspring are shown below:

FEMALE				MALE		
Wild-type	v	vf	f	t_b	vf	v
133	4	5	1	5	3	2

Though here again at least one of the mothers was not virgin, the very great excess of females leaves no doubt that most of the offspring were hybrids. And, as in the previous test, *no tiny-bristle daughters appeared.* The two mutant genes thus are not allelomorphic, though their effects correspond in detail, and are more numerous than those of most mutant genes.

MAP OF THE *simulans* X CHROMOSOME

All experiments designed to test the linkage between the sex-linked genes of *D. simulans* are summarized in tables 2, 3, and 4. The totals for each type of cross are given separately, but it has not seemed worth while to publish the counts for each individual culture.

Table 5 shows the total data for each pair of loci.

These data, more especially the three- and four-point data (tables 3 and 4), show clearly that the sequence of the genes is yellow, prune, ruby-oid, carmine, forked, tiny-bristle. Dwarf is close to prune, and its position has already been discussed.

[3] v = vermilion, t_b = tiny-bristle, f = forked.

TABLE 2

Two-point linkage experiments with the X chromosome of D. simulans.

LOCI	TYPE OF CROSS	NON-CROSSOVERS		CROSSOVERS		TOTAL
y p_n	*y* p_n × +	1504	1438	39	50	3031
	y × p_n	395	427	18	8	848
y r_d	*y* r_d × +	114	130	6	11	261
	y × r_d	98	103	15	15	231
y c_a	*y* c_a × +	1120	951	514	461	3046
	y × c_a	80	111	69	57	317
y f	*y f* × +	173	191	116	117	597
y t_b	*y* t_b × +	493	190	162	410	1255
	y × t_b	296	347	311	221	1175
p_n r_d	p_n × r_d		66	8		74
p_n c_a	p_n × c_a		181	78		259
p_n t_b	p_n × t_b	12	97	75	17	201
d_w r_d	d_w × r_d	359	45	48	0	452
r_d c_a	r_d × c_a			12		90
r_d *f*	r_d × *f*	47	51	19	28	145
r_d t_b	r_d × t_b	78	160	87	21	346
c_a *f*	c_a × *f*	71	82	5	5	163
c_a t_b	c_a × t_b	42	95	21	7	165

NOTE. In tables 2, 3 and 4, the column headed "Loci" shows not only the loci concerned, but also their sequence. In the third and following columns classes are entered under their headings indicating the type of crossing over they represent. In every case that class which includes the individuals bearing the dominant (wild-type) allelomorphs in the left-hand locus concerned is placed first, and is followed by the contrary class.

TABLE 3

Three-point linkage experiments with the X chromosome of D. simulans.

LOCI	NATURE OF CROSS	NON-CROSSOVERS		SINGLE CROSSOVERS				DOUBLE CROSSOVERS		TOTAL
				Region 1		Region 2				
y p_n d_w	*y* p_n × d_w	58	501	18	0	0	1[4]	0	0	578
y p_n *f*	*y* p_n × *f*	130	127	3	0	65	73	1	0	399
y p_n t_b	*y* p_n t_b × +	68	30	0	0	26	48	0	0	172
	y p_n × t_b	49	109	3	8	98	35	1	2	305
	y × p_n t_b	27	54	3	0	25	9	0	1	119
	y t_b × p_n	77	21	2	7	13	52	4	0	176
y r_d c_a	*y* c_a × r_d						25	5		284
y r_d *f*	*y* × r_d *f*	86	91	10	11	33	34	2	1	268
	y f × r_d	391	355	56	46	180	200	23	11	1262
y r_d t_b	*y* r_d t_b × +	14	10	4	2	4	8	1	1	44
	y r_d × t_b	3	33	3	0	15	5	1	1	61
	y t_b × r_d	126	36	9	30	25	102	16	4	348
y c_a *f*	*y* c_a × *f*	725	719	419	383	134	109	34	32	2555
y c_a t_b	*y* c_a t_b × +	167	29	54	110	16	45	19	8	488
	y c_a × t_b	38	61	49	27	10	9	1	13	208
	y t_b × c_a	56	35	24	46	14	6	6	7	194
r_d c_a *f*	r_d × c_a *f*			58				8		349
r_d *f* t_b	r_d t_b × *f*	84	20	23	23	0	0	0	1	151

[4] This individual was yellow prune dwarf in appearance; but frayed was later found to be in the stock, and may have been responsible for his small size. He was sterile.

In constructing the map, the yellow prune, yellow rubyoid, carmine forked, and forked tiny-bristle values of table 5 have been used directly. These are based on large enough numbers to be reasonably accurate, and the distances are all short enough so that possible double crossovers must be so rare as to be negligible.

TABLE 4

Four-point linkage experiments with the X chromosome of D. simulans.

LOCI	NATURE OF CROSS	NON-CROSSOVERS		SINGLE CROSSOVERS						DOUBLE CROSSOVERS						TRIPLE CROSSOVERS		TOTAL
				Region 1		Region 2		Region 3		1, 2		1, 3		2, 3				
y r_d *f* t_b	*y* r_d *f* t_b × +	54	23	2	10	21	57	1	0	5	3	0	0	0	0	0	0	176
y c_a *f* t_b	*y* c_a *f* × t_b	99	126	95	69	25	23	1	1	9	11	1	1	0	0	0	0	461
	y c_a t_b × *f*	398	193	169	311	51	65	0	3	34	15	4	0	0	0	0	0	1243
	y × c_a *f* t_b	39	107	69	28	12	10	1	0	2	8	0	0	0	0	0	0	276

TABLE 5

Total data for each pair of loci in the X chromosome of D. simulans.

LOCI	TOTAL	CROSSOVERS	PERCENTAGE OF CROSSING OVER
y p_n	5628	168	3.0
y d_w	578	19	3.3
y r_d	2651	299	11.3
y c_a	9064	3266	36.0
y f	7513	3131	41.6
y t_b	6977	3194	45.8
p_n d_w	578	1	0.2
p_n r_d	74	8	10.8
p_n c_a	259	78	30.1
p_n *f*	399	139	34.8
p_n t_b	973	406	41.7
d_w r_d	452	48	10.6
r_d c_a	723	108 × 2	29.9
r_d *f*	2002	664	33.1
r_d t_b	1126	424	37.6
c_a *f*	4974	616	12.4
c_a t_b	3311	492	14.9
f t_b	2583	15	0.6

The rubyoid carmine value, which is necessary in the construction of the map, is not so easily determined. The direct method, of crossing the two mutants and determining the amount of crossing over between them, is not entirely satisfactory, because rubyoid and carmine cannot be distinguished from each other or from the double recessive, rubyoid carmine, with any degree of certainty. All three are, however, easily distinguishable from the wild-type. Several counts from females with rubyoid in one X

and carmine in the other are recorded in table 5. Since the wild-type flies constitute one-half of the total number of crossovers, we may calculate the crossover percentage by doubling this number and dividing it by the whole number of offspring. This method indicates a crossover percentage of 29.9.

The value just obtained is open to some question, since it is based on rather small numbers and since it would be seriously affected by viability complications, owing to the fact that only one of the crossover classes was distinguishable. Accordingly two other methods of calculating the value have been carried out. The first of these consists in using the well-established yellow carmine value, 36.0, corrected for observed yellow rubyoid carmine double crossing over (3.5 percent, which must be doubled and added to 36.0 for our purpose). The resulting value, 43.0, minus the observed yellow rubyoid value of 11.3, gives a second rubyoid carmine value, 31.7.

TABLE 6

Coincidence in the X chromosome of D. simulans.

LOCI	TOTAL FLIES	NUMBER OF DOUBLE CROSSOVERS	PERCENTAGE OF CROSSOVERS, REGION 1 + REGION 2	COINCIDENCE
y p_n d_w	578	0	3.3	
y p_n *f*	399	1	35.8	50
y p_n t_b	772	8	45.2	72
y r_d *f*	1706	45	43.9	74
y r_d t_b	629	32	57.5	81
y c_a *f*	4535	145	50.1	68
y c_a t_b	2870	139	56.4	77
r_d *f* t_b	327	1	41.2	127

NOTE. The first three experiments and the last one showed such small numbers of double crossovers that the coincidence values are not significant. They have been included here only for the sake of completeness.

The third method of calculation is based on the well-established rubyoid forked value, 33.1. Corrected for observed rubyoid carmine forked double crossing over (4.6, which must be doubled), this value becomes 42.3. Subtracting the observed carmine forked value of 12.4 gives 29.9 as a third value for rubyoid carmine. The three values, 29.9, 31.7, and 29.9, show quite as close an agreement as was to have been expected. The average of the three, 30.5, has been used in constructing the map.

There is, however, another difficulty here. The value 30.5 corresponds to a distance long enough so that double crossing over must be supposed to occur within it. There is no method of ascertaining how much to allow for such double crossing over, until mutations in the region are discovered

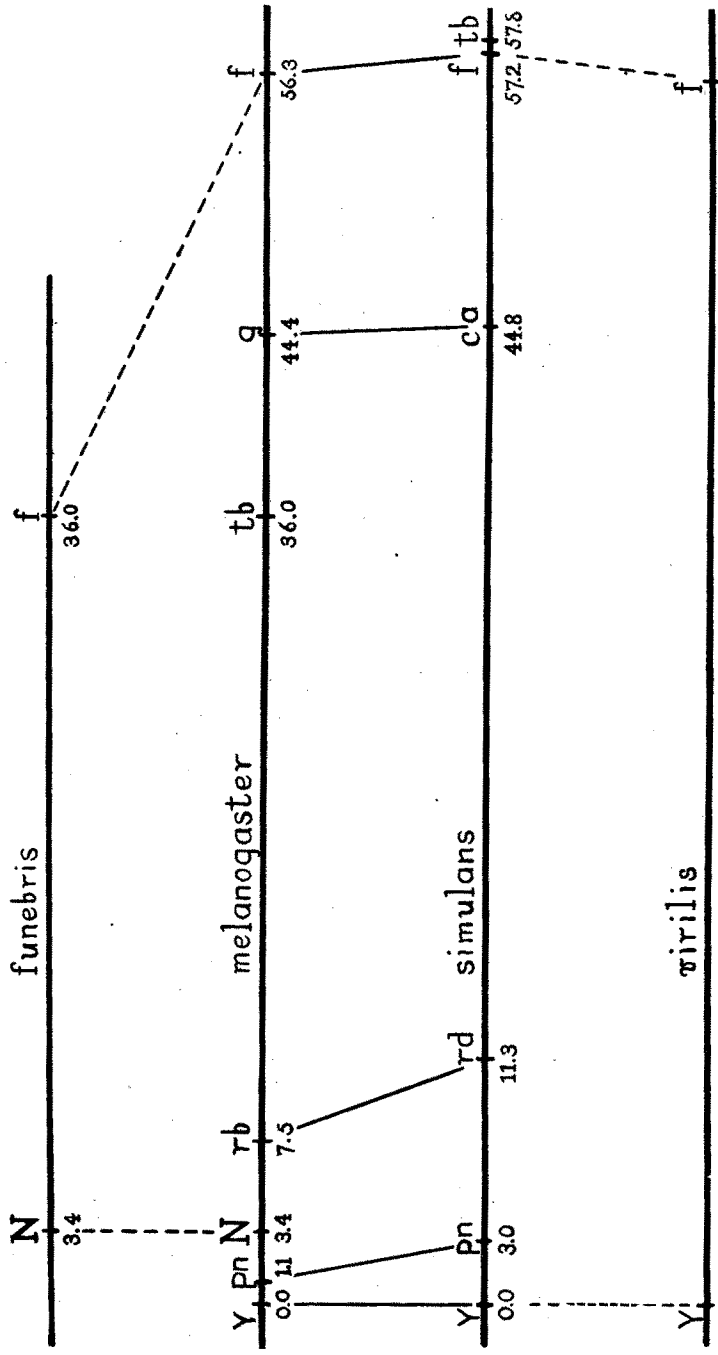

FIGURE 1.—Maps of the X chromosomes of four species of Drosophila. The dotted lines connect genes that are inferred to be allelomorphic because of the similarity of the characters concerned; the solid vertical lines connect genes that have been definitely shown to be allelomorphic.

and studied. However, we shall see in the following section that the double-crossing-over relations in the X of *simulans* that can be studied, are very similar to those of the X of *melanogaster*. Accordingly it seems legitimate to correct the rubyoid carmine value by the addition of three units, which is about the correction that would be necessary for a like value in the X of *melanogaster*. The value 33.5 has therefore been adopted as corresponding to the "distance" between the two loci. It must, however, be emphasized that later work may show that this value requires changing by a few units.

The resulting map, together with a map of the corresponding loci of *D. melanogaster* (chiefly from extensive data collected by Dr. C. B. BRIDGES and in part unpublished) (compare BRIDGES 1919 for some of the loci), is shown in figure 1.[5] This map shows that the sequence of the five corresponding loci in the two species is the same, but that the amount of crossing over is not the same. In the left-hand end of the chromosome there is more crossing over in *simulans*, in the middle there is probably somewhat less, while in the right-hand end there is about the same amount. This difference in amount of crossing over is not surprising, since it has been shown (BRIDGES 1915, PLOUGH 1917, STURTEVANT 1919, etc.) that the amount of crossing over is not constant even within the same species. I have shown in the paper referred to that genetic factors may cause changes, even greater than those here described, in the second chromosome of *D. melanogaster;* and also that such changes, as in the present case, do not always affect different parts of the same chromosome proportionately.

The previous studies on linkage variations within one species have all shown that the sequence of the loci is not altered by such variations as occur. That the present example shows the same relation is important, for it indicates that the X chromosomes of the two distinct species have essentially the same constitution. Not only are many of the genes identical, but they are arranged in the same relative positions.

The map corroborates the conclusion that the "tiny-bristles" in the two species represent different mutations, for their respective loci are on opposite sides of the garnet-carmine locus. This fact was not discovered until the negative test of allelomorphism had been completed.

COINCIDENCE

Table 6 shows the total available three-point data that can be used for calculation of coincidence, including those which can be extracted from the

[5] See the appendix of this paper for a discussion of the maps of the *virilis* and *funebris* X chromosomes, also shown in the figure.

four-point crosses. The coincidence values are close to those that have been observed for similar distances in *melanogaster*, but perhaps average a little lower. Detailed comparison is not easily made from the available data, and will not be attempted here.

NON-DISJUNCTION

Non-disjunction of the sex chromosomes occurs in *D. simulans*, and in the same way as in *D. melanogaster* (see BRIDGES 1916), so far as it has been investigated.

It has been shown, by the use of the mutant character scarlet, that the third chromosome pair is distributed as usual in females that are producing non-disjunctional exceptions.

Exceptional females have been found to produce further exceptions. Seventeen tests of exceptional yellow females, mated to not-yellow males, have given a total of 1079 not-yellow daughters, 1062 yellow sons, 39 yellow daughters, and 26 not-yellow sons. The percentage of secondary exceptions calculated from these data, 2.9, is somewhat less than the percentage (4.3) found by BRIDGES to be normal for *D. melanogaster;* but the difference is probably not significant, for in both species the percentage is a quite variable quantity.

In *D. simulans*, as in *melanogaster*, some of the regular daughters of an exceptional female produce exceptions, while others do not. No cytological examination has been made of XXY *simulans*, and the sterility of the XO males has not been adequately tested.

In general, the two species behave very similarly with respect to non-disjunction, and we may safely conclude that the mechanism demonstrated by BRIDGES for *melanogaster* is the one that is at work in *simulans*.

GYNANDROMORPHS

Seven gynandromorphs have been found in *D. simulans*. The general conclusions to be deduced from a study of them are in agreement with those reached by MORGAN and BRIDGES (1919) as a result of their examination of a large series of gynandromorphs obtained in *D. melanogaster*. Nevertheless it seems worth while to put on record the data obtained with *simulans*.

The first gynandromorph was obtained, December 13, 1919, from a mating of a female, with yellow and rubyoid in one X and tiny-bristle in the other, by two rubyoid males. This female and at least one of the males were heterozygous for the autosomal recessive eye-color scarlet.

The daughters from this mating were 46 wild-type, 47 rubyoid (disregarding scarlet) and the gynandromorph that is shown in figures 2 and 3. This specimen was a wild-type female in all respects except that the right eye was partly rubyoid, and some of the head-bristles were smaller than their mates and were therefore probably male. The left eye was wild-type, there were no sex-combs, and the individual bred as a female. Mated to scarlet males it produced 21 wild-type daughters, 20 scarlet daughters, 8 wild-type (and scarlet) sons, and 18 rubyoid (and rubyoid scarlet) sons. The female parts of the gynandromorph thus had one rubyoid (paternal) X and one wild-type X that was due to a crossover in the mother, between rubyoid and tiny-bristle. The maternal X was eliminated from a cell that gave rise to part of the right side of the head.

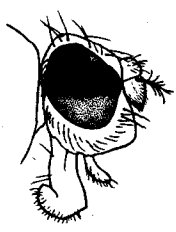

FIGURE 2

FIGURE 3

FIGURES 2 and 3.—The first gynandromorph discovered in *Drosophila simulans*.

The second gynandromorph appeared, January 17, 1920, in a mating of two yellow females by two wild-type males. The specimen was wild-type female on the right side (no sex-comb, longer wing, female abdominal pattern), and yellow male on the left side (sex-comb, shorter wing, male abdominal pattern). The genitalia, however, were entirely yellow and male. On the right side there was a narrow wild-type-colored sixth dorsal abdominal tergite, and the right half of a fifth ventral plate[6] (also wild-type in color), behind which were the male genitalia, normal in structure but yellow in color. The incomplete sixth dorsal tergite did not fuse with the fifth of the left side, but narrowed to a point near the mid-dorsal line. The internal genitalia were male, including two small pale testes.

The gynandromorph probably resulted from the elimination of a paternal X at an early division.

[6] Normal males have only five dorsal and four ventral abdominal plates aside from the genital segments; females have seven dorsal and six ventral ones (see figures in Part III of these studies). The fifth dorsal plate of the male bears two pairs of spiracles, and evidently represents two fused plates, i.e., it is homologous to both the fifth and the sixth of the female.

The third gynandromorph appeared, February 10, 1920, in a culture produced by a female with yellow and prune in one X and forked in the other, mated to three yellow prune males. The specimen was wild-type and female on the right side of the head and thorax (no sex-comb, longer wing) and in most of the abdomen. The male parts were yellow (neither prune nor forked), and included the left side of the head and thorax (sex-comb, shorter wing), and part of the abdomen. The external genitalia (ovipositor plate and anal plate) on the right side were wild-type and female, and on this side there were the six dorsal tergites of the normal female. On the left side there were only five dorsal tergites, and then followed *two* distinct male first genital tergites, both yellow in color. No anal plates were observed on this side. The presence of two male parts and one female in the external genitalia is distinctly unusual among gynandromorphs; and this specimen was also unusual in other ways. Dr. J. F. NONIDEZ dissected it, and made the drawing here reproduced (figure 4). The uterus and receptacles were normal female organs, but were connected with small testes in which Dr. NONIDEZ observed active sperm. The small bodies attached below the testes are of uncertain nature, though Dr. NONIDEZ states that they looked superficially more like ovaries than like the usual accessory glands of the male. They were, however, not studied in detail.

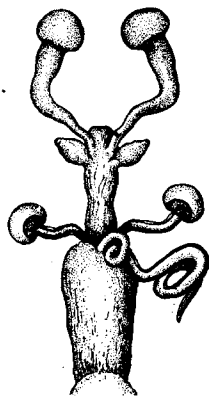

FIGURE 4.—Internal genitalia of the third gynandromorph. Dissection and drawing by Dr. J. F. NONIDEZ.

The origin of this gynandromorph presents certain difficulties. Since its father was yellow prune, but the female parts were not yellow or prune, the maternal X must have been either wild-type or forked. Furthermore, this maternal X must have been the one eliminated,—yet the male parts included an eye that was not prune, though the paternal X certainly carried prune. It seems probable that the gynandromorph received *two* maternal X's, one yellow and not prune or forked (a double crossover), and one either wild-type or forked. These X's may have been in the same nucleus, causing an XXX zygote; or, what seems more likely, they may have been in separate nuclei and fertilized by separate sperm. These two possible origins have been discussed at some length by MORGAN and BRIDGES (1919), so will not be gone into here. The fact that this gynandromorph showed extra parts in the external genitalia (and perhaps also in the gonads) may perhaps be taken as arguing for the double-nucleus origin, but is certainly not conclusive.

Another possible interpretation of this gynandromorph is based on the assumption that prune, like vermilion in *melanogaster* (STURTEVANT 1920 b), is not self-differentiating. If the color of a prune eye is determined, not by the genetic constitution of the eye pigment itself, but by that of some other portion of the body, then the present gynandromorph may be explained very simply, as being due to the elimination of a maternal X at an early division.

The fourth gynandromorph appeared, March 17, 1920, in a culture produced by a female heterozygous for yellow and for the autosomal recessive eye-color plum, mated to a plum male. The gynandromorph (figure 5) was anteriorly largely wild-type and female, but was yellow and male in part of the thorax and most of the abdomen. The head and legs were entirely wild-type and female (no sex-combs). The right side of the thorax was entirely wild-type and female, and the right wing was distinctly larger than the left. There was a streak of yellow on the left side including the left acrostical hairs, dorsocentrals, scutellars, postalars, presutural, and the posterior supraalar, but not the other thoracic bristles of the left side. The left wing was wild-type anteriorly, yellow posteriorly. Apically the dividing line, as shown in the figure, was clearly just anterior to the third vein. Basally the division was difficult to determine: the two branches of the dotted line in the figure show its possible limits, the region between the branches being impossible to identify either as wild-type or as yellow. It does not follow that this region was intermediate in character, as the differences to be seen in this region between wholly yellow and wholly wild-type wings are slight. The whole wing, though it included a female anterior margin, was approximately of the size characteristic of males. The abdomen was yellow and male, except for the right half of the first dorsal tergite, which was wild-type and female. The individual was found to be sterile as a male. It can easily be accounted for by the elimination of a paternal X at an early division.

The fifth gynandromorph appeared, March 20, 1920, in culture 8362. The mother was heterozygous for yellow, and both parents were heterozygous for the second-chromosome recessive mutant genes plum and intersex. There were no traces of these autosomal characters in the gynandromorph, but the intersex character (see STURTEVANT 1920 a, and Part III of these studies) could have been detected only had genitalia been present on the female parts, which was not the case. The gynandromorph was wild-type and female on the left side, yellow and male on the right, throughout the body except the external genitalia. These were yellow and male on both sides. No spermathecae were present, and gonads

were not found on hasty dissection. The gynandromorph evidently arose through the elimination of a paternal X at an early division.

The sixth and seventh gynandromorphs were produced, April 1920, by the same culture, which was made up by mating two scarlet (autosomal recessive) females to three not-scarlet males. At least one of these males was heterozygous for scarlet. No sex-linked mutant genes were present, so that no analysis of the origin of the gynandromorphs is possible.

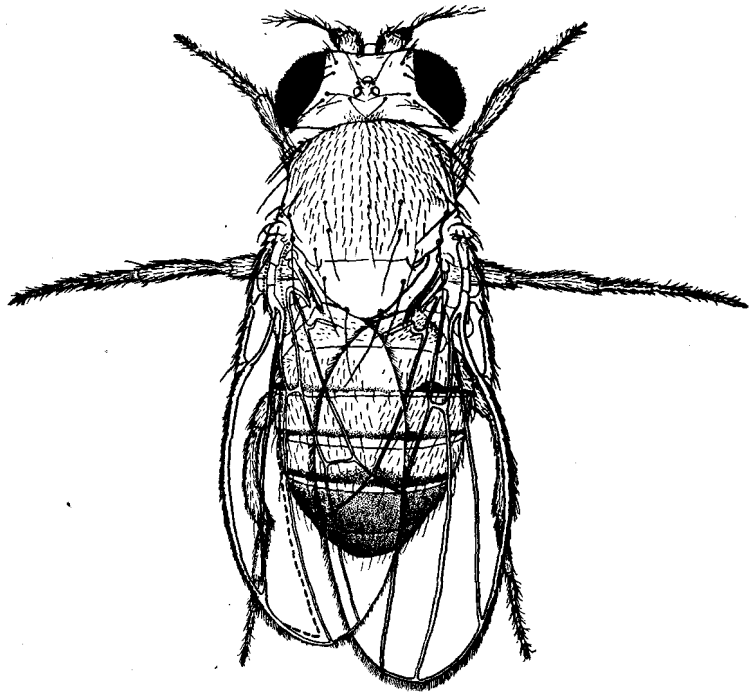

FIGURE 5.—The fourth gynandromorph. The dotted line on the left wing marks the division between the yellow and not-yellow portions.

Number six (found April 5) showed no trace of scarlet. The head, most of the thorax, both front tarsi, and the left wing were female. The right wing was male. The abdomen was female-colored on the right side, male-colored on the left. There were five dorsal abdominal tergites on each side; on the right side the fifth one was narrow and had one spiracle, on the left it was broad and had two spiracles,—the normal sexual difference. There were four ventral abdominal plates, with two more half-plates on the female side, these being behind and displaced toward the right side of the body. The external genitalia were male, and were twisted around so that the dorsal line of the first genital tergite was opposite the lower

edge of the fifth dorsal tergite on the left side. A penis, two testes, and two male accessory glands were present; there were no ovaries or receptacles.

Number seven (found April 7) was female anteriorly, with no sex-combs, and had a female right wing. The left wing was male, as was the abdomen, including testes and accessory glands. This specimen had scarlet eyes.

As stated above, these gynandromorphs do not add materially to the conclusions derived by MORGAN and BRIDGES from their study of gynandromorphs of *D. melanogaster*. They serve to bring out again the fundamental similarity of the genetic processes occurring in the two species. Aside from this their chief interest lies in two specimens,—number three, which represents a new example of one or the other of two rare types of gynandromorphs, and was unusual in having three sets of external genitalia instead of the usual two; and number four, which is the only Drosophila gynandromorph known to me that has a wing that is a mosaic of male and female parts. This last specimen is interesting in that the mosaic wing was male in size, instead of being intermediate or of abnormal shape. It indicates that the length of the anterior margin of the wing is not self-differentiating, but depends upon other factors,—presumably upon the nature of the rest of the wing.

ABSENCE OF GYNANDROMORPHS AMONG THE *melanogaster-simulans* HYBRIDS

It seemed not unlikely that irregularities in cell-division might be more frequent in the *melanogaster-simulans* hybrids than in either pure species, since it is known that irregular distribution of the chromosomes does occur in many species hybrids. One type of irregularity,—viz., the elimination of an X chromosome at an early division,—occurs rarely in both species and gives rise to gynandromorphs. MORGAN and BRIDGES (1919) have shown that in *melanogaster* such elimination occurs, and causes gynandromorphs that can be detected, in about one out of each 1100 eggs fertilized by X-bearing sperm.

I have examined a few more than 1300 hybrid females, and have carefully scrutinized each one with this point in mind, but have found no gynandromorphs at all. Over 400 of these hybrids were heterozygous for yellow, a circumstance that makes the detection of gynandromorphs especially easy. Many of the others were heterozygous for other sex-linked genes that would also increase the likelihood of detection, though to a less extent. We may conclude that gynandromorphs are at most not much more frequent among the hybrids than in pure *melanogaster*. This constitutes still further evidence that the two species have essentially similar germ-plasms.

SOMATIC MUTATIONS

On two occasions variations have appeared in single individuals of *D. simulans* that were to all appearances mutations, but that were not inherited. They were probably due to mutation in the somatic tissue of the individuals that showed the new characters. The germ-cells had evidently not undergone mutation.

Culture 7863 contained two yellow carmine scarlet females (of which one at least was XXY) and three scarlet males. There were 32 sons, of which two were scarlet (due to non-disjunction), and the remaining 30 were yellow carmine scarlet as expected. The carmine scarlet eye is a clear yellow in color; but one of these males had eyes that at first appeared to be white. Closer examination showed small patches of yellow color, and also showed that the ommatidia were enlarged and somewhat flattened. Dr. C. B. BRIDGES, who examined the specimen, pronounced it intermediate between "lozenge" and "lozenge 2," allelomorphic sex-linked mutants of *D. melanogaser*. This male was mated to two forked females, of an unrelated stock. Seventy-eight daughters and 80 sons were produced, one of the sons being a non-disjunctional exception. None of these showed any trace of the unusual character of their father's eye. The non-disjunctional son, since he had a paternal X, showed either that the mutant gene was not sex-linked, or that not all (and therefore probably not any) of the germ-cells of the mutant male carried it. This latter conclusion was borne out by the fact that seven daughters of the mutant male were tested, two of them by mating to their brothers, and all failed to produce lozenge-like offspring. It follows that even if the mutation was not sex-linked, it was not inherited.

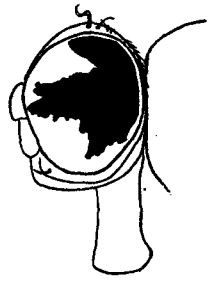

FIGURE 6.—Left eye of somatic mosaic from culture 8368. The drawing was made after the specimen was dead, and most of the hairs and bristles had been rubbed off.

Culture 8368 was made by mating a female with yellow and carmine in one X and forked in the other, to four yellow carmine tiny-bristle males. Among the 115 sons of the expected classes was one that was yellow forked, and had a wild-type right eye. The left eye (figure 6) was a mosaic of the wild-type color and white. This male was mated to three females of a wild-type stock, and produced 53 wild-type offspring. Five females from this last culture were mated individually to brothers, and produced from 35 to 116 offspring each. These included the expected classes with respect to yellow and forked, but all had wild-type eyes. The white color present in the original male was therefore not inherited.

In both the cases just described it is possible that we are dealing not with mutations but with accidents of development, due perhaps to injury. The nature of the characters concerned, and their resemblance to known mutant characters of *melanogaster*, makes it more probable that they are examples of somatic mutation.

SUMMARY

1. Seven sex-linked mutants of *Drosophila simulans* are described. All strongly resemble known sex-linked mutants of *D. melanogaster*.

2. Six of these have been tested for allelomorphism with the corresponding *melanogaster* types, by crosses.

3. Yellow, prune, rubyoid, carmine, and forked *simulans* are shown to be allelomorphic to yellow, prune, ruby, garnet, and forked *melanogaster*, respectively.

4. Tiny-bristle *simulans* is not allelomorphic to tiny-bristle *melanogaster*, though strikingly similar to it.

5. A map of the *simulans* X chromosome is based on the crossing-over relations of these sex-linked mutations.

6. The sequence of the five allelomorphic mutations in *simulans* and *melanogaster* is the same in the two species, but the amount of crossing over is not identical.

7. The coincidence values for the two species are similar.

8. Non-disjunction occurs in *simulans*. The percentage of secondary exceptions observed was 2.9.

9. Seven gynandromorphs are described. These fit in with the conclusions reached through studies on *melanogaster* gynandromorphs.

10. Gynandromorphs are at most not significantly more frequent among the *melanogaster-simulans* hybrids than in pure *melanogaster*.

11. Two somatic mutations in *simulans* are described. Each resembled a known mutation of *melanogaster*, and neither was inherited.

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APPENDIX—X-CHROMOSOME MAPS OF *virilis* AND *funebris*

METZ (1918) has published data on the sex-linked mutant genes of *Drosophila virilis* Sturtevant. Two of the mutant characters, yellow and forked, appear very similar to the characters of the same names in *melanogaster* and *simulans*. Since *virilis*, which is a very distinct species, cannot be crossed to either of these, it is not certain that we are here dealing with identical loci. However, there is much evidence that strongly suggests such to be the case. The characters are closely similar in the three species; the evidence from *melanogaster* and *simulans* shows that in those species the two loci are relatively highly mutable, so that they might be expected to mutate also in a third species; and the positions occupied by the two loci in the *virilis* map are about the same as those established in *melanogaster* and *simulans*. The data presented by METZ indicate that the yellow-forked distance is about 56,—a strikingly close approximation to the values (56.3 and 57.8) obtained for the other two species.

I have published elsewhere (STURTEVANT 1918) an account of notch, a parallel mutation in *D. funebris* Fabricius. As was pointed out in that paper, notch *funebris* and notch *melanogaster* are alike in so many respects that there can be little doubt that they are allelomorphs, even though the two species cannot be crossed. Since then I have obtained a forked mutation in *funebris*. This character is strikingly similar to the forked known in *virilis* and to those in *melanogaster* and *simulans*. Forked *funebris* and forked *virilis* agree in that the marginal hairs of the wings stand out almost at right angles to the wing-margin itself, instead of lying nearly flat along the wing margin as they do in wild-type flies. This peculiarity is also present in forked *melanogaster* and *simulans*, but is much less marked, i.e., the angle is decidedly less than 90°. It is probable that forked *funebris* is allelomorphic at least to forked *virilis*, though here again the two species cannot be crossed.

Tests of the linkage between notch and forked in *funebris* have given 931 crossovers among 3198 flies, a crossover percentage of 29.1. Allowing for about the amount of double crossing over usual in *melanogaster*, we may provisionally map the two loci about 32 units apart. Notch in *melanogaster* being a little less than 4 units from yellow, the position of forked in *funebris* becomes approximately 36, as opposed to 56.3 in *melanogaster*, 57.2 in *simulans*, and about 56 in *virilis*. There are several possibilities of error in this calculation for *funebris;* but taken at its face value it indicates much less crossing over in the X chromosome of *funebris* than in those of the other three species. This result is rather unexpected, in view of METZ'S (1916) observation that what is presumably the X chromosome of *funebris* is, cytologically, much longer in proportion to the rest of the chromatin than is the X of *melanogaster* or of *virilis*. Of course, since METZ'S observations are based on chromosomes in the contracted stage, it is possible that the finely spun-out growth-stage chromosomes do not show a disproportion in this direction. Even if they do it is quite possible that other factors act to decrease the amount of crossing over in *funebris*. In any case, speculation along these lines is rather futile until more information concerning the *funebris* map is available, i.e., until more sex-linked mutants are discovered and studied.[7]

[7] Since the above was written a mutant gene lying at least 45 units to the right of forked has been studied in *funebris*. The discussion given needs revision accordingly.