THE BRISTLES OF HYBRIDS BETWEEN *DROSOPHILA MELANOGASTER* AND *DROSOPHILA SIMULANS**

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INTRODUCTION

In 1920, STURTEVANT found that hybrids from *Drosophila melanogaster* by *D. simulans* have certain bristles missing from the body that are normally present in both parent species. He discovered later (1929) that the number of bristles present (counting dorsocentrals) in these hybrids varies with the *melanogaster* stock used, and that the *simulans* male apparently produces no effect on bristle number. This suggested that the *melanogaster* egg-cytoplasm might cause the effect, but a preliminary test gave negative results.

The present paper contains the results of a detailed study of the inheritance of the differences among the stocks of the pure species, with respect to their effects on the bristles of the hybrids.

I wish to express my appreciation to Professor A. H. STURTEVANT for his direction of the work, and to Professor T. H. MORGAN and Professor TH. DOBZHANSKY for their helpful suggestions. The research was carried on at the CALIFORNIA INSTITUTE OF TECHNOLOGY, Pasadena, California.

MATERIAL AND METHODS

The various *melanogaster* stocks which were used are listed alphabetically in table 1. Stocks inbred for many generations were used, when possible, to insure a condition homozygous for any modifiers present. An at-

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TABLE 1

List of D. melanogaster stocks used in the experiments.

SYMBOL	MEANING OF SYMBOL	CHROMOSOME
$\frac{b\,g_p\,a}{C_yR}$	Black gap arc over the crossover-suppressor $d_p^2\ C_yC_{IILCy}\ p_r$-$C_{IIR}l\ p_x\ s_p$	II
$\frac{B_l}{C_y\,s_p}$	Bristle^1 over the crossover-suppressor $C_y\ C_{IILCy}\ c_n^2\ C_{IIRCy}\ s_p$	II
$\frac{c_g}{d_p^2C_y}$	Comb-gap^5 over the crossover-suppressor $d_p^2\ C_y\ C_{IILCy}\ c_n^2\ C_{IIRCy}$	II
$\widehat{ff}\,b\ p_r\,c\ \ s_e\,h$	Stock containing attached X chromosomes bearing forked, and homozygous for black purple curved and sepia hairy	I, II, III
$\frac{f_r\ s_p}{C_y}$	Fringed speck over the crossover-suppressor $C_y\ C_{IILCy}\ c_n^2\ C_{IIRCy}$	II
$\frac{f_u}{ClB}$	Fused over the crossover-suppressor $s_c\ t^2\ v\ C_I\ l\ s_l\ B$	I
$\frac{g_t\,bb''}{ClB}$	Giant^2 bobbed—11 over the crossover-suppressor ClB	I
$\frac{l_z}{ClB}$	Lozenge over the crossover-suppressor ClB	I
$\frac{p_n^2}{\widehat{yy}}$	Stock containing prune—2 males and yellow females with attached X's	I
$\frac{p_x\,b_w\,m_r\,s_p}{C_y}$	Plexus brown morula speck over the crossover-suppressor $C_y\ C_{IILCy}\ c_n^2\ C_{IIRCy}$	II
res	Homozygous stock: roughoid hairy thread scarlet peach curled stripe sooty	III
$\frac{res}{C_{FL}C_{FR}}$	"*res*" over a crossover-suppressor^5	III
$\frac{res}{D_f\,2C\,c_a}$	"*res*" over the crossover-suppressor $l\ C_{IIILP}\ D_f\ l\ C_{IIIRP}\ c_a^3$	III
$rucuca$	Homozygous stock: roughoid hairy thread scarlet curled stripe sooty claret	III
$\frac{s^2f}{ClB}$	Sable—2 forked over the crossover-suppressor ClB	I
$s_e\,h$	Homozygous stock: sepia hairy. There was also a stock $\frac{s_e\,h}{C_{FL}\,C_{FR}}$	III
$s_t\,s_r\,e^4\,r_o\,c_a$	Homozygous stock: scarlet stripe ebony—4 rough claret. There was also a stock $\frac{s_t\ s_r\ e^4\ r_o\ c_a}{C_{FL}\,C_{FR}}$	III
$\frac{s_t\ s_r\ e^4\ r_o\ c_a}{C_{IIILP}\,C_{IIIRP}l}$	Scarlet stripe ebony—4 rough claret over a crossover-suppressor	III
$\frac{t_a}{\widehat{yy}}$	Stock containing twisted-abdomen males and yellow females with attached X's	I

TABLE 1 (continued)

SYMBOL	MEANING OF SYMBOL	CHROMOSOME
thes	Homozygous stock: thread scarlet peach curled stripe sooty. There were also stocks $\frac{thes}{C_{FL}\,C_{FR}}$ and $\frac{thes}{C_{IIILP}\,C_{IIIRP}\,l}$	III
$\frac{v\,g^3\,s_l f}{ClB}$	Vermilion garnet—3 small-wing forked over the crossover-suppressor *ClB*	I
$\frac{y\,U\,c_v\,v\,f}{s_c\,c_v\,v\,f}$	Stock producing females with U-shaped X chromosome containing yellow crossveinless vermilion forked over scute crossveinless vermilion forked[4]	I
$\frac{y\,U\,c_v\,v\,f}{s_c\,e_c\,c_t{}^6\,g^2}$	Stock producing females with $y\,U\,c_v\,v\,f$ overs cute echinus cut—6 garnet—2	I
$\frac{y\,U\,e_c\,c_t{}^6\,g^2}{s_c\;\;e_c\,c_t{}^6\,g^2}$	Stock producing females with $y\,U\,e_c\,c_t{}^6\,g^2$ over $s_c\,e_c\,c_t{}^6\,g^2$	I

For a more complete description of the characters see MORGAN, BRIDGES and STURTEVANT 1925.

[1] For Bristle, see KING 1927.

[2] For giant, see MORGAN, STURTEVANT and BRIDGES 1927.

[3] For *D_f2Cc_a*, see MORGAN, STURTEVANT and BRIDGES 1928.

[4] For *yU*, see L. V. MORGAN 1926.

[5] No published data for c_g or $C_{FL}C_{FR}$.

tempt was made to keep in touch with the whole chromosome, as far as possible, by using crossover suppressors preventing the loss of modifying genes through crossing over in the female parent. All the *simulans* stocks had been inbred for many generations. (For a more complete description of all the stocks, except Pasadena, see STURTEVANT 1929. There are no published data for the Pasadena stock.) The stocks of wild-type or normal flies are named after the towns in which the flies were collected. They are Morristown (Mrstwn.) from Morristown, New Jersey, New Orleans (N. Orl.) from New Orleans, Louisiana, Pasadena (Pas.) from Pasadena, California, and St. Augustine (St. Aug.) from St. Augustine, Florida. The first chromosome stocks include homozygous yellow prune ($y\ p_n$), yellow white ($y\ w$), and a homozygous yellow stock (Metz Fla. *y*) collected by C. W. METZ in Florida. There is also homozygous black (*b*) in the second chromosome and homozygous sepia (s_e), scarlet (s_t), and scarlet peach ($s_t\,p$) in the third chromosome.

In making the crosses small mass-cultures were used, consisting of 4 or 5 *melanogaster* females with 8 to 10 *simulans* males, or 8 to 10 *simulans* females with 4 or 5 *melanogaster* males. When the combination was made in this way the cross of *simulans* ♀ by *melanogaster* ♂ caused less difficulty than had been experienced previously by STURTEVANT, MORGAN, BONNIER and others. The more frequent failure of the latter combination is due to the lower viability of *simulans* flies in wet and acid food conditions. The females may become weakened and die before laying many eggs or even before mating. To overcome this difficulty the flies were mated and kept in vials with a small amount of food for one day before transferring them to the culture bottles. The bottles were kept in an incubator set at 25.5° C until pupae had formed. The parents were then removed and the bottles kept at room temperature (20–22° C).

The chance that non-virgin females may be present increases with the number of females used in a mating. Since a large number of *simulans* females were used in each cross greater care was required in selecting virgins. There was the added difficulty that *simulans* females are sometimes fertilized a few hours after emerging (MORGAN 1929). Hybrid cultures generally consist of only one sex (see STURTEVANT 1920). This served as a check, but in addition all the crosses were made in such a way that flies which were not hybrids could be detected immediately by other characters.

In counting the bristles the four dorsocentrals and four scutellars were considered. To save time in making and recording the counts it was decided at first to include flies with more than four of the eight bristles missing in the class of "four missing." This tended to lower the computed mean number of missing bristles in cases where many bristles were absent, but did not affect the cases where a smaller number were absent. If only four of the eight bristles had been considered the low classes would have been reduced by approximately half and the differences between them would hardly be apparent. The differences between the various high classes are sufficient, as recorded, to distinguish them from one another. Recording all eight bristles would make the differences greater instead of less. In the later counts all eight bristles were recorded.

SUCCESS OF CROSSES

It is easier to make the cross using *melanogaster* females than *simulans* females. This had been found previously by STURTEVANT, MORGAN and others, but the difficulty with *simulans* females was not as great as in their experiments. This may have been due to the methods that were used. STURTEVANT (1929) and MORGAN (1929) expressed the opinion that the yellow stocks gave a greater percent of successful crosses since the females were less vigorous and offered less opposition to mating. In the present experiment the yellow *simulans* stocks gave poor results and the yellow *melanogaster* stocks gave about the average number of successful matings.

In a few cases crosses with *melanogaster* females were one hundred percent successful out of five or six matings, but in some other cases as many as fifty unsuccessful attempts at crossing were made. The figure for the success of all crosses with *melanogaster* females, 44 percent, is really not a true index since an equal number of attempts at each cross was not made. The values range from 0 percent to 86 percent for the *simulans* males used and from 0 percent to 100 percent for the *melanogaster* females. The stock which gave 100 percent included only six cultures; the next highest value is 68 percent.

The values for successful crosses with *simulans* females range from 8 percent to 100 percent for the *simulans* females and from 0 percent to 83 percent for the *melanogaster* males. The figure for all crosses, 45 percent, is again not a true index as to the success of the matings. It must be remembered that an average of ten *simulans* females were used for each culture while only five *melanogaster* females were used in the crosses.

Considering all the matings the black *simulans* stock was found to give the highest percent of successful crosses, 79 percent. The New Orleans stock came next with 68 percent. In the *melanogaster* stocks $\widehat{yy}\ C_y$ from (F) was first with 70 percent and $\frac{C_y}{+}\ \frac{s_e\ h}{+}$ from (B) second with 67 percent of successful crosses.

A summary of most of the crosses with the mean number of bristles missing is given in table 2.

TABLE 2

Mean number of bristles missing in hybrids between Drosophila melanogaster and D. simulans.

simulans STOCK ♂ AND ♀	*melanogaster* STOCK											
	$\frac{C_y}{+}\ \frac{s_eh}{++}$ ♀ FROM (A) AND (B)		$\frac{C_y}{+}\ \frac{s_eh}{++}$ ♂ FROM (A) AND (B)		$\frac{C_y}{II}\ \frac{s_eh}{+}$ ♀ FROM (D)		$\frac{C_y}{II}\ \frac{s_eh}{+}$ ♂ FROM (D)		$\widehat{yy}\frac{C_y}{II}\ \frac{s_eh}{D_f}$ ♀ FROM (C)		$\widehat{yy}$ ♀ FROM $\frac{p_n^2}{\widehat{yy}}$	$\widehat{yy}$ ♀ FROM $\frac{t_a}{\widehat{yy}}$
	C_y ♀ +		C_y ♂ +		C_y ♀ +		C_y ♂ +		C_y ♂ +		♂	♂
s_e	0.23	0.18	♂1.50 ♀0.55	.52 .21	0.27	0.15	2.06	0.62	3.04	1.44	2.28	1.83
N. Orl.	..	..	..	..	0.59	0.23	1.84	0.29	2.85	1.38	2.26	1.93
Pas.	..	..	..	..	0.19	0.07	1.60	0.41	3.04	1.55	1.81	1.89
Mrstwn.	0.40	0.28	1.25	0.13	0.85	0.45	1.20	0.15	1.51	0.54	0.78	0.74
St. Aug.	0.36	0.33	..	..	..	..	3.36	1.32	..	..	2.19	1.32
b	..	..	..	..	1.26	0.46	2.70	0.79	..	..	2.92	2.73
yw	..	..	..	..	..	..	..	..	..	..	..	2.53
yp_n	..	..	..	..	..	..	..	..	..	..	..	1.38

TABLE 3

Hybrids produced by all crosses.

TYPE OF CROSS	FEMALE HYBRIDS	MALE HYBRIDS	TOTALS
mel. ♀ × *sim.* ♂	20,388	41	20,429
$\widehat{XX}Y$ *mel.* ♀ × *sim.* ♂	3	15,045	15,048
sim. ♀ × *mel.* ♂	437	16,870	17,307
Totals	20,828	31,956	52,784

Table 3 shows the number of hybrids produced by all the crosses. The 41 males produced by regular *melanogaster* females were due to non-disjunction in females containing *ClB*. The 3 females produced by attached-X *melanogaster* females were due to separation of the attached X's in the mother.

PRELIMINARY CROSSES

It was first necessary to find various *melanogaster* stocks that produced different bristle effects on the hybrids. Females from stocks containing genes in the three large linkage groups were crossed to males from various *simulans* stocks. In the case of the X and the second chromosome it was possible to use stocks containing recessive genes as well as a dominant gene with linked crossover suppressors, such as $\frac{g_t\, bb''}{ClB}$ or $\frac{b\, g_p\, a}{C_yR}$. Thus in the

TABLE 4

Preliminary crosses involving chromosome I.

melanogaster ♀	*simulans* ♂	NUMBER OF FLIES	MEAN NUMBER OF BRISTLES MISSING	
			B	+
$\frac{f_u}{ClB}$	N. Orl.	125	1.09	0.85
$\frac{g_t\, bb''}{ClB}$	Mrstwn.	31	0.00	0.52
$\frac{g_t\, bb''}{ClB}$	St. Aug.	361	2.11	2.47
$\frac{g_t\, bb''}{ClB}$	s_e	284	0.31	0.47
$\frac{l_z^4}{ClB}$	N. Orl.	838	1.02	0.73
$\frac{l_z^4}{ClB}$	St. Aug.	40	2.72	2.68
$\frac{s^2 f}{ClB}$	s_e	282	0.25	0.18

hybrids the effect on the bristles of each of the homologous chromosomes could be determined by comparing the normal hybrids with those showing the character due to the dominant gene. There was no suitable third chromosome stock containing a dominant gene which could be used since any gene affecting the bristles had to be avoided. In this case stocks were used that contained a gene or genes corresponding to the *simulans*

TABLE 5

Preliminary crosses involving chromosome II.

melanogaster ♀	*simulans* ♂	NUMBER OF FLIES	MEAN NUMBER OF BRISTLES MISSING	
			C_y	+
$\frac{b\,g_p\,a}{C_y\,R}$	Mrstwn.	58	1.00	0.80
$\frac{b\,g_p\,a}{C_y\,R}$	N. Orl.	460	1.82	1.06
$\frac{c_g}{d_p{}^2\,C_y}$	N. Orl.	394	0.73	0.99
$\frac{f_r\,s_p}{C_y}$	Mrstwn.	433	0.65	1.82
$\frac{p_x\,b_w\,m_r\,s_p}{C_y}$	Mrstwn.	363	0.82	1.96

TABLE 6

Preliminary crosses involving chromosome III.

melanogaster ♀	*simulans* ♂	NUMBER OF FLIES	MEAN NUMBER OF BRISTLES MISSING	
			s_t	+
$\frac{rucuca}{C_{FL}\,C_{FR}}$	s_t	328	0.69	0.82
$\frac{s_t\,s_r\,e^4\,r_o\,c_a}{C_{IIILP}\,C_{IIIRP}\,l}$	s_t	418	0.8	0.50
$\frac{s_t\,s_r\,e^4\,r_o\,c_a}{C_{FL}\,C_{FR}}$	s_t	147	1.86	0.93
			$s_t\,p$	+
$\frac{thes}{C_{IIILP}\,C_{IIIRP}\,l}$	$s_t\,p$	200	0.49	0.25
$\frac{thes}{C_{FL}\,C_{FR}}$	$s_t\,p$	100	0.94	0.96
$\frac{res}{C_{FL}\,C_{FR}}$	$s_t\,p$	337	0.86	0.71
			s_e	+
$\frac{s_e h}{C_{FL}\,C_{FR}}$	s_e	910	0.23	0.33
$s_e\,h$	s_e	355	0.28	..

genes. These *melanogaster* stocks were first balanced against a third chromosome crossover suppressor and then crossed to homozygous *simulans* males. The hybrids consisted of two classes and the effect of each chromosome could be observed.

The successful crosses using *melanogaster* stocks involving the X, second and third chromosomes are shown in tables 4, 5 and 6 with the mean number of bristles missing for each class. The columns headed by B, C_y, s_t, etc., represent the hybrids which showed Bar eye, Curly wing, scarlet eye, etc., but the actual *melanogaster* chromosome responsible for the effect is different in most cases as will be seen by examining the stocks used in each cross.

It is evident that the same *melanogaster* stock gave different averages with the different *simulans* males used in the crosses. This had not been expected, and further tests were made that will be described below.

CROSSES TO TEST CYTOPLASMIC DIFFERENCES IN *melanogaster* STOCKS

In order to test the effect of the cytoplasm on the bristles reciprocal matings were made between *melanogaster* stocks producing high and low numbers of missing bristles, and the F_1 females were then crossed to *simulans* males. Two stocks were obtained which could be used reciprocally since the recessive genes present would not affect the viability of the males. Females having the constitution $\frac{yU\,c_v\,v\,f}{s_c\,c_v\,v\,f}$ and $\frac{y\,U\,e_c\,c_t^6\,g^2}{s_c\,e_c\,c_t^6\,g^2}$ were crossed to males of several different *simulans* stocks, but none of the cultures produced flies. Many different numbers of males and females per culture were tried (STURTEVANT [1915] has shown there may be fighting between

TABLE 7

$$\frac{g_t bb''}{ClB}\,♀ \times \frac{c_g}{dp^2C_y}\,♂ \rightarrow \frac{ClB}{+}\ \ \frac{d_p{}^2\,C_y}{+}\,♀\ \textit{mel.} \times \textit{Mrstwn.}\ ♂\ \textit{sim.}$$

CULTURE	NUMBER OF BRISTLES MISSING															
	C_y B				C_y +				+ B				+ +			
	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3
112	86	3	2	0	77	7	3	0	62	7	1	0	55	4	1	0
121	51	10	5	0	57	5	1	0	32	5	2	1	33	4	3	0
122	30	6	1	0	27	5	3	0	22	7	1	0	33	7	1	2
Total	167	19	8	0	161	17	7	0	116	19	4	1	121	15	5	2
Mean values	0.18				0.17				0.21				0.22			

the males if two court the same female), and the wings and legs of the females were cut in the hope of making mating easier, but all the cultures failed (see STURTEVANT 1929). It is probable that mating did not take place, since many eggs were laid, but none hatched. Some of the females were dissected, but no sperm could be found in their receptacles This does not, however, prove conclusively that no mating took place, since the females were at least nine days old and the sperm may have been used up after a possible mating, but males were still alive in the bottles when the females were dissected and sperm should be found if a recent mating had occurred. These males were found to contain many sperm. Males of the constitution $y\ U\ e_c\ c_t^6\ g^2$ were crossed to *simulans* females, but again all the matings failed.

Of the second chromosome stocks $\frac{C_g}{d_p^2 C_y}$ males were crossed with $\frac{g_t\, bb''}{ClB}$ females and the $\frac{ClB}{+}\ \frac{d_p^2\ C_y}{+}$ F_1 females crossed with Morristown *simulans* males (table 7). The low values—much lower than those for either parent—are probably due to the recombination of modifiers through crossing the two stocks. The high average stock $\frac{b\ g_p\ a}{C_y\ R}$ was crossed reciprocally with the low average stock $s_e h$ and the $\frac{C_y}{+}\ \frac{s_e\ h}{+}$ F_1 flies used in crosses with sepia *simulans* males and females.

(A) $$\frac{b\ g_p\ a}{C_y R}\ ♀ \times \frac{s_e\ h}{s_e\ h}\ ♂ \rightarrow \frac{C_y}{+}\ \frac{s_e\ h}{+}\ ♀ \text{ and } ♂$$

(B) $$\frac{s_e\ h}{s_e\ h}\ ♀ \times \frac{b\ g_p\ a}{C_y\ R}\ ♂ \rightarrow \frac{C_y}{+}\ \frac{s_e\ h}{+}\ ♀ \text{ and } ♂$$

The F_1 females (A) and (B) have exactly the same chromosome constitution, but (A) females came from eggs with C_y cytoplasm and (B) females came from eggs with $s_e\ h$ cytoplasm. The males are alike except for the X and Y. The (A) males receive their X from the C_y stock and their Y from the $s_e\ h$ stock; the (B) males receive their X from the $s_e\ h$ stock and their Y from C_y. The different Y chromosomes can be seen to have no effect on the bristles of the hybrids, since the classes from both (A) and (B) crosses show practically the same values (table 8). This table also shows the hybrids from (A), and (B) females crossed with s_e *simulans* males differ from each other slightly or not at all. If the cytoplasm of the C_y stock was responsible for the high number of missing bristles we would expect the

TABLE 8

Mean number of bristles missing in crosses between s_e sim. and $C_y\ s_e\ h$ mel.

melanogaster PARENT	*simulans* PARENT									
	s_e ♂ PRODUCING ♀ HYBRIDS					s_e ♀ PRODUCING MOSTLY ♂ HYBRIDS				
	NUMBER OF FLIES	$C_y\ s_e$	C_y +	+ s_e	+ +	$C_y\ s_e$	C_y +	+ s_e	+ +	NUMBER OF FLIES
$\frac{C_y}{+}\frac{s_e h}{+}$ from (A)	3372	0.25	0.24	0.18	0.20	♂ 1.24	1.62	0.39	0.63	5078
						♀ 0.56	0.55	0.15	0.28	379
$\frac{C_y}{+}\frac{s_e h}{+}$ from (B)	1731	0.23	0.18	0.16	0.17	1.29	2.01	0.40	0.66	2436
$\frac{C_y}{+}\frac{s_e h}{+}$ from (D)	1099	0.22	0.31	0.12	0.19	1.64	2.45	0.44	0.83	2088

hybrids from (A) to show a higher number missing than those from (B). The striking difference is that between the number of bristles missing in males compared with females and the separation of these values into four classes in the case of the males. The difference is seen to be due to the sex of the hybrid, since males and females which hatched from the same cultures (A ♂ × s_e *simulans* ♀) gave decidedly different values (table 8).

One may conclude that the differences between the two *melanogaster* stocks used are chromosomal in nature, rather than cytoplasmic.

THE USE OF *melanogaster* ATTACHED-X STOCKS

Since the hybrid males have more bristles missing than the females it was decided to study them in particular and to compare the hybrid males obtained by using *melanogaster* attached-X stocks with hybrid males from *simulans* mothers. A *melanogaster* stock was made up as follows:

$$\overset{\frown}{yy}\ ♀ \text{ from } \frac{p_n^2}{\overset{\frown}{yy}} \times \frac{B_l}{C_y\ s_p}\ ♂ \rightarrow \overset{\frown}{yy}\frac{C_y}{+}\ ♀$$

$$\overset{\frown}{yy}\frac{C_y}{+}\ ♀ \times \frac{res}{D_f\ 2C\ c_a}\ ♂ \rightarrow \overset{\frown}{yy}\frac{C_y}{+}\ \frac{D_f}{+}\ ♀$$

$$\text{(C)}\quad \overset{\frown}{yy}\frac{C_y}{+}\ \frac{D_f}{+}\ ♀ \times \frac{\text{II}}{\text{II}}\ \frac{s_e\ h}{s_e\ h}\ ♂ \rightarrow \overset{\frown}{yy}\frac{C_y}{\text{II}}\ \frac{s_e\ h}{D_f}\ ♀ \text{ and } \frac{C_y}{\text{II}}\ \frac{s_e\ h}{D_f}\ ♂.$$

The stock was kept by selecting the $\overset{\frown}{yy}\ C_y\ D_f$ females and crossing to $s_e\ h$ males. Thus the stock contained the crossover suppressor including C_y over the normal second chromosome from $s_e\ h$ and the third chromosome from $s_e\ h$ over the crossover suppressor including D_f. Males and females are alike except for the X chromosome, but this does not enter into the constitution of the hybrids, since only male hybrids (with *simulans* X) will be produced when either males or females from this stock are crossed to *simulans*. Many male hybrids were obtained by using $\widehat{yy}\,\frac{C_y}{II}\,\frac{s_e\,h}{D_f}$ females, but unfortunately the crosses (thirty-eight attempts) involving $\frac{C_y}{II}\,\frac{s_e\,h}{D_f}$ males failed.

TABLE 9

Mean number of bristles missing using $\widehat{yy}\,\frac{C_y}{II}\,\frac{s_e\,h}{D_f}$ ♀ *mel.* (C).

simulans MALE USED	NUMBER OF FLIES	$C_y +$	$C_y\,D_f$	$+\,+$	$+\,D_f$
s_e	589	2.97	3.12	1.21	1.72
N. Orl.	661	2.82	2.91	1.25	1.60
Pas.	652	2.95	3.15	1.44	1.65
Mrstwn.	679	1.59	1.52	0.51	0.57

Table 9 shows the results of crosses between (C) females and males from four different *simulans* stocks. The hybrids from Morristown males are seen to give lower values than the others in all four classes. In this table the class labeled C_y+ corresponds to the $C_y\,s_e$ class of table 8. $C_y\,D_f$ corresponds to the C_y+ class, and so on, since the D_f chromosome now corresponds to the $+$third chromosome of table 8. Of course sepia appeared in the hybrids from the cross with s_e *simulans*.

Another *melanogaster* stock was made up as follows:

$$\text{(D)}\qquad \frac{B_l}{C_y\,s_p}\ \text{♀} \times \frac{II}{II}\,\frac{s_e\,h}{s_e\,h}\ \text{♂} \rightarrow \frac{C_y}{II}\,\frac{s_e\,h}{+}\ \text{♀ and ♂}.$$

These $\frac{C_y}{II}\,\frac{s_e\,h}{+}$ flies were like the $\widehat{yy}\,\frac{C_y}{II}\,\frac{s_e\,h}{D_f}$ flies with regard to the Y, to one third and to both second chromosomes. The male hybrids from $\frac{C_y}{II}\,\frac{s_e\,h}{+}$ *melanogaster* males would differ from the hybrids from $\widehat{yy}\,\frac{C_y}{II}\,\frac{s_e\,h}{D_f}$ females only in the chromosome containing D_f. They serve in a partial comparison of male hybrids derived from eggs containing different cytoplasm. Females from (D) were also compared with females from (A) and (B) in table 8. Little difference was expected in the comparison of the females, since they generally give low values with slight variations. The males from (C) and (D) (tables 9 and 8) differ in regard to missing bristles in each case except when Morristown male is crossed to (C) female. Considering the first three crosses it is seen that the difference in each class is consistent. Since the values for (D) males are with s_e *simulans* females, the hybrids from (C) females by s_e males alone would be more nearly comparable. Here the differences suggest that something is active during development causing one group of hybrids to have more bristles missing than the other. This comparison is not exact, however, because the hybrids from (C) contain the D_f chromosome while the others contain the normal third chromosome. Considering the four classes of hybrids produced in these crosses and comparing the ratio of D_f to s_e (2.42 to 2.11) with that of + to s_e (in the cross with [D]: 1.65 to 0.99) it appears that any effect on the bristles by D_f is in the direction of reducing the number missing, thus reducing the differences in our comparison of crosses with (C) and (D) instead of increasing them.

A more direct comparison was made by using the following stocks:

$$\text{(E)} \qquad \widehat{yy}\ ♀ \text{ from } \frac{p_n^2}{\widehat{yy}} \times \frac{b\ g_p\ a}{C_y\ R}\ ♂ \rightarrow \widehat{yy}\frac{C_y}{+}\ ♀ \text{ and } \frac{C_y}{+}\ ♂$$

$$\text{(F)} \qquad \widehat{yy}\ ♀ \text{ from } \frac{t_a}{\widehat{yy}} \times \frac{b\ g_p\ a}{C_y\ R}\ ♂ \rightarrow \widehat{yy}\frac{C_y}{+}\ ♀ \text{ and } \frac{C_y}{+}\ ♂.$$

The males and females of (E) and of (F) have the same chromosome (autosome) constitution and when crossed with *simulans* females or males should produce only male hybrids. The hybrids will have different *melanogaster* Y, but this has been shown to have no effect on the bristles (see discussion page 161, and table 8). These hybrids should be exactly alike except

TABLE 10

Reciprocal crosses.

	melanogaster STOCK					
simulans STOCK	$\widehat{yy}$ C_y ♀ FROM (E)			C_y ♂ FROM (E)		
	NUMBER OF FLIES	MEAN NUMBER OF MISSING BRISTLES		NUMBER OF FLIES	MEAN NUMBER OF MISSING BRISTLES	
		C_y	+		C_y	+
yw♂ – ♀	58	2.70	1.50	135	2.51	0.47
s_e♂ – ♀	..	..	..	286	2.81	1.18
		$\widehat{yy}$ C_y ♀ from (F)			C_y ♂ from (F)	
yw♂ – ♀	146	3.50	1.65	207	2.10	0.37
s_e♂ – ♀	78	2.95	1.78	315	2.36	1.11
		$\widehat{yy}$ C_y ♀ from (G)			C_y ♂ from (G)	
b ♂ – ♀	314	5.04±0.17	3.52±0.19	1693	2.65±0.07	1.20±0.05
		$\widehat{yy}$ C_y ♀ from (H)			C_y ♂ from (H)	
b ♂ – ♀	583	4.32±0.15	3.10±0.12	1030	3.22±0.10	1.07±0.06

that one type is developed from *simulans* egg and the other from *melanogaster* egg. Any difference between the two types should be due to the effect of the egg cytoplasm on the development. The results of the crosses are shownin table 10. This table shows that in each case hybrids developing from *melanogaster* eggs had a higher number of bristles missing than hybrids of the corresponding class developing from *simulans* eggs. The chromosome constitution of the hybrids from the two crosses is identical.

Another test was made which shows a definite maternal effect on the bristles of the hybrids. An attached-X stock was made up in such a way that the male and female flies were known to have identical Y chromosomes. A double yellow female from $\frac{p_n{}^2}{\widehat{yy}}$ was mated to a $\frac{b\ g_p\ a}{C_y\ R}$ male and an F_1 *yy* C_y female and C_y male crossed. An F_2 male was then crossed back to an F_1 $\widehat{yy}$ C_y female. This stock will be designated as (G).

$$\widehat{\mathrm{XX}}\underset{-}{\mathrm{Y}} \times \mathrm{XY}\,\frac{b\ g_p\ a}{C_y\ R} \rightarrow \widehat{\mathrm{XX}}\mathrm{Y}\,\frac{C_y}{+} \times \mathrm{X}\underset{-}{\mathrm{Y}}\,\frac{C_y}{+} \rightarrow \widehat{\mathrm{XX}}\underset{-}{\mathrm{Y}}\,\frac{C_y}{+} + \mathrm{XY}\,\frac{C_y}{+}$$

$$\text{(G)} \qquad \widehat{\mathrm{XX}}\mathrm{Y}\,\frac{C_y}{+} \times \mathrm{XY}\,\frac{C_y}{+} \rightarrow \widehat{\mathrm{XX}}\mathrm{Y}\,\frac{C_y}{+} + \mathrm{XY}\,\frac{C_y}{+}$$

A similar stock was made up using a female from $\frac{t_a}{\widehat{yy}}$ and will be designated as (H).

Reciprocal crosses were made between each of the stocks (G) and (H), and black *simulans*. The hybrids were examined and a record kept of all the dorsocentral and scutellar bristles instead of recording no more than four as was done previously. These results are included in table 10. The differences between classes are in the same direction as those found with stocks (E) and (F).

EFFECT OF *melanogaster* CYTOPLASM

The results of all the above crosses in which the hybrids from reciprocal matings have their chromosome constitution identical or nearly so are arranged in table 11. The sex chromosomes are marked Xm for *melanogaster* X and Xs for *simulans* X. The Y comes from the *melanogaster* parent in each case. C_y indicates that the hybrids contained the *melanogaster* Curly chromosome, and + indicates the presence of the not-Curly chromosome. The other chromosomes are identical in each case and are not represented. The terms low, medium, high, etc., are purely arbitrary, based on the mean values shown.

The female hybrids developing from *simulans* eggs show a slightly higher mean value than those from the reciprocal cross. However, in other

TABLE 11

Results from reciprocal crosses.

HYBRIDS FROM *melanogaster* EGGS				HYBRIDS FROM *simulans* EGGS			
melanogaster ♀	CHROMOSOME CONSTITUTION	MEAN NUMBER OF MISSING BRISTLES		*melanogaster* ♂	CHROMOSOME CONSTITUTION	MEAN NUMBER OF MISSING BRISTLES	
$\frac{C_y}{+}\,\frac{s_e\,h}{+\,+}$	Xm Xs C_y	Very low	0.24	$\frac{C_y}{+}\,\frac{s_e\,h}{+\,+}$	Xm Xs C_y	Low	0.55
from (A)	Xm Xs +	Very low	0.19	from (A)	Xm Xs +	Very low	0.21
$\widehat{yy}\frac{C_y}{\mathrm{II}}\,\frac{s_e\,h}{D_f}$	Ym Xs C_y	High	2.97	$\frac{C_y}{\mathrm{II}}\,\frac{s_e\,h}{+}$	Ym Xs C_y	Medium	1.95
from (C)	Ym Xs +	Medium	1.46	from (D)	Ym Xs +	Low	0.52
$\widehat{yy}\,C_y$	Ym Xs C_y	High	3.19	C_y	Ym Xs C_y	Medium	2.48
from (E)				from (E)			
and (F)	Ym Xs +	Medium	1.65	and (F)	Ym Xs +	Low	0.89
$\widehat{yy}\,C_y$	Ym Xs C_y	Very high	4.57	C_y	Ym Xs C_y	High	2.86
from (G)				from (G)			
and (H)	Ym Xs +	High	3.25	and (H)	Ym Xs +	Medium	1.15

crosses using females from (A) values were obtained which approach 0.55, and in crosses with females from (D) values higher than this were obtained (see table 2). The male hybrids derived from (C) were not identical with those derived from (D) since one parent contained the D_f chromosome. As shown above the D_f chromosome influenced the bristles even less than the homologous normal chromosome. However, the best comparisons for the males are those involving the hybrids derived from (E), (F), (G) and (H). In (E) and (F) the two groups are identical in constitution

TABLE 12

Influence of simulans male on bristle number.

simulans MALE	$\widehat{yy}$ ♀ FROM $\frac{p_n^2}{\widehat{yy}}$		$\widehat{yy}$ ♀ FROM $\frac{t_a}{\widehat{yy}}$	
	NUMBER OF FLIES	MEAN NUMBER MISSING BRISTLES	NUMBER OF FLIES	MEAN NUMBER MISSING BRISTLES
b	438	2.92	552	2.73
N. Orl.	870	2.26	770	1.93
s_e	528	2.28	1409	1.83
Pas.	948	1.81	634	1.89
St. Aug.	524	2.19	532	1.32
Mrstwn.	1424	0.78	1358	0.74
y w	..	..	118	2.53
y p_n	..	..	173	1.38

except for the origin of the *melanogaster* Y as mentioned above. The differences between the mean values 3.19 and 2.48, and the values 1.65 and 0.89 are certainly significant. In (G) and (H) the two groups of hybrids are identical in chromosome constitution since the stocks were made up in such a way that hybrids from both *melanogaster* males and females would contain the same chromosomes. Here the values for each class are higher, since all eight of the bristles were recorded. A comparison of these values is shown at the bottom of table 10.

TABLE 13

Comparison of black and Morristown stocks when mated to $\widehat{yy}$ ♀ *from* $\frac{t_a}{\widehat{yy}}$.

simulans MALE	NUMBER OF CULTURES	AVERAGE FLIES PER CULTURE	NUMBER OF BRISTLES MISSING					MEAN VALUE
			0	1	2	3	4	
b	4	138	72	56	80	83	261	2.73
Mrstwn.	10	136	791	282	164	76	45	0.74

In each case the hybrids from a *melanogaster* mother have more bristles missing than those from a *simulans* mother. The differences between these classes range from 6.1 to 15.6 times the mean error.

In every cross producing males, the hybrids which developed from *melanogaster* eggs showed a higher mean value than those which developed from *simulans* eggs. The females showed a difference in only one class and that in the opposite direction, but this disagreement has been explained above, partially at least.

INFLUENCE OF *simulans* STOCKS

It has been mentioned above that different results were obtained when various *simulans* stocks were crossed to the same *melanogaster* stock. (STURTEVANT [1929] did not find this difference, possibly because the *simulans* stocks he used produced a medium effect and also because he dealt mainly with female hybrids.) While most of the *simulans* stocks gave nearly equal numbers of missing bristles, one in particular (Morristown) gave a lower mean value. This difference is not easily detected in the female hybrids, but can be seen plainly in case of the males. Further crosses were made in order to compare male hybrids from various *simulans* stocks.

Males from four different *simulans* stocks were crossed with $\widehat{yy}\,\frac{C_y}{II}\,\frac{s_e\ h}{D_f}$ females from (C) and the male hybrids compared. These values are shown in table 9.

Males from eight different *simulans* stocks were crossed with $\widehat{yy}$ females from $\frac{p_n{}^2}{\widehat{yy}}$ and $\frac{t_a}{\widehat{yy}}$ *melanogaster* stocks. The results are shown in table 12. For comparison the actual numbers are shown for the cross of $\widehat{yy}$ females from $\frac{t_a}{\widehat{yy}}$ to black and Morristown stocks (table 13).

The hybrids from *simulans* females also differ in the number of bristles missing according to the *simulans* stock used. Females from six *simulans* stocks crossed to $\frac{C_y}{\text{II}}\ \frac{s_e\ h}{+}$ males from (D) produced male hybrids which differed from each other just as in the previous crosses. The results are given in table 14.

TABLE 14

Influence of simulans female on bristle number; $\frac{C_y}{II}\ \frac{s_eh}{+}$♂ *from* (D) *used in each case.*

simulans FEMALE	NUMBER OF FLIES	MEAN NUMBER MISSING BRISTLES	
		C_y	+
St. Aug.	115	3.36	1.32
b	1270	2.70	0.79
s_e	2088	2.06	0.62
N. Orl.	844	1.84	0.29
Pas.	347	1.60	0.41
Mrstwn.	438	1.20	0.15

A comparison of the *simulans* stocks is shown in table 15. The *melanogaster* parent is listed at the top of each column and the various *simulans* stocks are arranged in the order of their effect on the bristles of the hybrids, the stock that gave most bristles missing being listed at the top of each column.

TABLE 15

Simulans stocks arranged in order of effect on the bristles of the hybrids.

EFFECT ON THE BRISTLES	$\frac{C_y}{\text{II}}\ \frac{s_e\ h}{+}$♀		$\frac{C_y}{\text{II}}\ \frac{s_e\ h}{+}$♂		$\widehat{yy}\frac{C_y}{\text{II}}\ \frac{s_e\ h}{D_f}$♀		$\widehat{yy}$♀ FROM $\frac{p_n{}^2}{\widehat{yy}}$	$\widehat{yy}$♀ FROM $\frac{t_a}{\widehat{yy}}$
	C_y	+	C_y	+	C_y	+		
Greatest	*b*	*b*	St. Aug.	St. Aug.	Pas.	Pas.	*b*	*b*
	Mrstwn.	Mrstwn.	*b*	*b*	s_e	s_e	s_e	N. Orl.
	N. Orl.	N. Orl.	s_e	s_e	N. Orl.	N. Orl.	N. Orl.	Pas.
	s_e	s_e	N. Orl.	Pas.	Mrstwn.	Mrstwn.	St. Aug.	s_e
↓	Pas.	Pas.	Pas.	N. Orl.	..	..	Pas.	St. Aug.
Least	..	..	Mrstwn.	Mrstwn.	..	..	Mrstwn.	Mrstwn.

In each cross except one the values for the Morristown stock were the lowest. The discrepancy in this one case may be due to the small number of hybrids obtained. Black produced the greatest effect in all except one case where a small number of hybrids from St. Augustine stock showed a higher value. The other stocks were distributed at random between the highest and lowest values which suggests that they are practically equal in their effect on the hybrids. It is surprising that the black and Morristown stocks should differ so widely, since they are the most closely related of all the stocks used. The black mutation was found in the Morristown stock (STURTEVANT 1929) and the strain has never been out-crossed. Some change in one or both of the stocks must have taken place since then, or else the black mutation affects the bristles also. To test the second possibility, pair matings were made of black *simulans* flies, and the bristles counted. Of 391 offspring not one had less than four dorsocentral and four scutellar bristles, while some had extra scutellars. The mean number of bristles was 8.67 ±0.04. It is probable that this excess of bristles is not directly related to the absence of them in the hybrids since here only the scutellars are duplicated while in the hybrids both dorsocentrals and scutellars are decreased in number.

The Morristown stock was then tested to see if a definite chromosome was the cause of the low bristle effect on the hybrids. It was compared with black to test the second chromosome and with sepia to test the third. A *melanogaster* stock ($\overset{\frown}{ff}\ b\ p_r\ c\ s_e\ h$) was made up which had attached-X chromosomes bearing forked and was homozygous for the second chromosome characters black, purple, curved, and for the third chromosome characters sepia and hairy. Reciprocal matings were made between Morristown and b and Morristown and s_e, and the F_1 males in each case crossed to $\overset{\frown}{ff}\ b\ p_r\ c\ s_e\ h$ *melanogaster* females. This allowed a comparison of the normal second chromosome of Morristown with the b chromosome in one case, and of the normal third chromosome of Morristown with the s_e chromosome in the other. The effect of the Morristown X was tested in both cases. In these crosses all eight of the bristles were recorded. The results are shown in table 16.

The third chromosome of the Morristown stock does not differ from the s_e chromosome in its effect on the bristles of the hybrids since the values for these two classes are equal. The second chromosome of the Morristown stock is very little different from the b chromosome, since the values are nearly equal. In one case the difference between the black and normal classes is 0.77 ±0.23 or 3.3 times the mean error, while in the other case it is only 0.56 ±0.30 or 1.9 times the mean error. But both these differences

TABLE 16

Tests of Morristown stock.

TYPE OF CROSS	MEAN NUMBER MISSING BRISTLES	
	b	+
Mrstwn. ♀ × b ♂ → + ♂ *sim.* × $\widehat{ff}$ $b\,p_r c\ \ s_e h$ ♀ *mel.*	2.59±0.18	1.82±0.14
b ♀ × Mrstwn. ♂ → + ♂ *sim.* × $\widehat{ff}$ $b\,p_r c\ \ s_e h$ ♀ *mel.*	3.82±0.23	3.26±0.19
Difference	1.23±0.29	1.44±0.24
	s_e	+
Mrstwn. ♀ × s_e ♂ → + ♂ *sim.* × $\widehat{ff}$ $b\,p_r c\ \ s_e h$ ♀ *mel.*	2.10±0.16	2.26±0.19
s_e ♀ × Mrstwn. ♂ → + ♂ *sim.* × $\widehat{ff}$ $b\,p_r c\ \ s_e h$ ♀ *mel.*	3.56±0.18	3.48±0.19
Difference	1.46±0.24	1.22±0.27

are in the same direction, so it is possible that these two chromosomes differ slightly in their effect on the hybrids. The greatest difference between the Morristown and b and s_e stocks is due to the X chromosomes. The values from the reciprocal crosses differ in each class and show that the X chromosomes of the b and s_e stocks cause more bristles to be missing in the hybrids than the Morristown X chromosome. The differences are 4.2 and 6.0 times the mean error for the b stock and 6.1 and 4.5 times the mean error for the s_e stock.

BRISTLES OF THE PARENT SPECIES

Bristles were missing from some of the flies of every hybrid culture, regardless of the stocks which were used in the cross. Some *melanogaster* stocks gave higher numbers of missing bristles and some lower; also, different results were found to be due to the presence of different chromosomes. The chromosome containing Curly produces a greater effect than its homologue and the sepia hairy chromosome seems to produce less effect than its homologue. If specific genes acting on the bristles cause this effect in the hybrids, it would be suspected that the Curly chromosome contains more of these, or else certain ones producing greater effect than those in the sepia hairy chromosome. In that case the Curly chromosome might be expected to affect the bristles in *melanogaster* cultures. To test this $\frac{B_l}{C_y\ s_p}$ *melanogaster* females were mated to normal *melanogaster* males and 683 offspring examined. The mean number of bristles present for Curly flies was 8.01 ± 0.001 and for normal flies was 8.02 ± 0.008. Only one fly had less than eight bristles and in that case it looked as though the bristle had been present but was broken off. Homozygous stock of sepia hairy would be expected to have some of the bristles absent, since it would be homozygous also for the genes causing the missing bristles in the hybrids. The bristles of 304 sepia hairy flies (from pair matings) were examined and the mean number of bristles present was found to be 8.64 ± 0.04. Not one fly had less than eight bristles and none had extra dorsocentrals. The extra bristles were scutellars and in most cases anterior scutellars. Duplication of these bristles was found to be one manifestation of the gene for hairy (MOHR 1922). The black *simulans* stock was tested in the same way, and the mean number of bristles present was found to be 8.67 ± 0.04. Hybrids from black *simulans* crossed to *melanogaster* flies showed the greatest number of missing bristles.

If specific genes cause missing bristles in the hybrids they do not produce a noticeable effect on *melanogaster* flies either when in heterozygous or in homozygous condition. The black *simulans* flies that were examined had extra bristles, while hybrids from these had many bristles missing.

DISCUSSION OF RESULTS

The effect on the bristles is not strongly correlated with other developmental abnormalities that appear in the hybrids. Many females appear to be abnormal in one way or another, but few bristles are missing. Males usually have a normal appearance, but have many bristles missing. The hybrid females often have rough eyes (especially those from certain *simulans* stocks) while the eyes of the hybrid males are normal or practically so. Hybrid females hatching from the same culture with males have rough eyes and the eyes of the males appear perfectly normal. At high temperature (29°C) female hybrids rarely develop past the pupal stage, while males emerge and appear normal. Males emerging at 29°C have fewer bristles missing than those emerging at 22°C. The abdomen of the females is more often abnormal than the abdomen of the males, and flies with abnormal abdomens may have all the bristles present.

The missing bristles are evidence of imperfect coördination of the genes of the two species. Genetic differences between the species were shown also in the appearance in the hybrids of the dominant *melanogaster* characters Bar and Lobe (MORGAN 1929) and Delta (STURTEVANT 1929). In respect to facet number Bar differs only slightly from normal eye in the hybrids and Lobe cannot be distinguished at all. The larger eye of *simulans* is probably responsible for part of this difference. The Delta character due to the *melanogaster* gene is less extreme in the hybrids than in pure *me-*

lanogaster, and that due to the *simulans* Delta gene is more extreme in the hybrids than in pure *simulans*.

Differences between hybrids from reciprocal species crosses have been attributed to the effect of the cytoplasm of the egg. In the present work hybrids developing from eggs containing *melanogaster* cytoplasm have more bristles missing than hybrids developing from eggs with *simulans* cytoplasm, even though the chromosomes in each case are identical. This may be interpreted as meaning that the chromosomes in the *melanogaster* egg have produced some effect on the cytoplasm before fertilization. Development might then be slightly different from that of a similar gene complex developing in a *simulans* egg. Whether the cytoplasm itself (independently of the chromosomes) causes any difference in development cannot be tested, since the hybrids have been found to be completely sterile (STURTEVANT 1920). Purely cytoplasmic inheritance is not probable, however, since the results show that the differences among the *melanogaster* stocks can all be accounted for in terms of chromosomes.

A "prematuration" (maternal) effect was considered by MORGAN (1912, 1915) as a cause of irregularities in the inheritance of rudimentary wing in *Drosophila melanogaster*. Miss LYNCH (1919) found this to be a cause of the partial sterility of homozygous rudimentary or fused females. Miss REDFIELD (1924, 1926) reported a sex-linked lethal effect which acted only when the mother was homozygous for a second chromosome gene. The females died chiefly in the egg stage due to the influence of the maternal genetic composition on the eggs before they left the mother's body. GABRITSCHEVSKY and BRIDGES (1928) found an enhancer of giant which showed a maternal effect on the eggs of females homozygous for the enhancer. STURTEVANT (1923) explained the inheritance of coiling in Limnaea as being due to the genetic complex of the unreduced egg regardless of the constitution of the offspring. DIVER, BOYCOTT and GARSTANG (1925) and BOYCOTT, DIVER, GARSTANG and TURNER (1930) have shown this to be the case since the coiling is delayed a generation in inheritance.

SUMMARY

1. In crosses between *Drosophila melanogaster* and *D. simulans* about 50 percent of the hybrids have bristles missing that are present in both parents. Bristles are missing from some of the hybrids of every cross.

2. The *melanogaster* stocks differ in their effect on the number of missing bristles in the hybrids. These differences are chromosomal rather than cytoplasmic in inheritance.

3. The *simulans* stocks differ in their effect on the hybrids. Black pro-

duced the greatest effect and Morristown the least. The other stocks that were tested gave generally the same values for missing bristles and are considered to be practically equal in their effects on the hybrids.

4. The difference between the black and Morristown stocks was found to be due chiefly to the X chromosomes of the two stocks.

5. The effects of the various *simulans* stocks on the bristles of the hybrids appear in hybrids from *simulans* mothers and in those from *simulans* fathers.

6. Male hybrids show the bristle effect more than do female hybrids. This difference cannot be due to external conditions since males and females hatching from the same culture have different numbers of missing bristles.

7. Male hybrids from attached-X *melanogaster* females were compared with male hybrids from *simulans* females. Those developing from *melanogaster* eggs had more bristles missing than hybrids developing from *simulans* eggs, although the chromosome constitution of the hybrids was identical. This maternal effect may be due to the influence of the chromosomes on the cytoplasm of the egg before the egg leaves the mother's body.

LITERATURE CITED

Boycott, A. E., Diver, C., Garstang, S. L., and Turner, F. M., 1930 The inheritance of sinistrality in *Limnaea peregra* (Mollusca, Pulmonata). Philos. Trans. **219:** 51–131.

Diver, C., Boycott, A. E., and Garstang, S., 1925 The inheritance of inverse symmetry in *Limnaea peregra*. J. Genet. **15:** 113–200.

Gabritschevsky, E., and Bridges, C. B., 1928 The giant mutation in *Drosophila melanogaster*. II. Physiological aspects of the giant race. The giant "caste." Z. indukt. Abstamm.-u. VererbLehre. **46:** 248–284.

King, R. L., 1927 Origin and description of Bristle in *Drosophila melanogaster*. Biol. Bull. **53:** 465–468.

Lynch, C. J., 1919 An analysis of certain cases of intra-specific sterility. Genetics **4:** 501–533.

Mohr, O. L., 1922 Cases of mimic mutations and secondary mutations in the X chromosome of *Drosophila melanogaster*. Z. indukt. Abstamm.-u. VererbLehre. **28:** 1–22.

Morgan, L. V., 1926 Correlation between shape and behavior of a chromosome. Proc. Nat. Acad. Sci. Washington **12:** 180–181.

Morgan, T. H., 1912 A modification of the sex ratio, and of other ratios, in Drosophila through linkage. Z. indukt. Abstamm.-u. VererbLehre. **7:** 323–345.

1915 The infertility of rudimentary winged females of *Drosophila melanogaster*. Amer. Nat. **49:** 240–250.

1929 Experiments with Drosophila. Pub. Carnegie Instn. **399:** 201–222.

Morgan, T. H., Bridges C. B., and Sturtevant, A. H., 1925 The genetics of Drosophila. Bibl. genet. **2:** 1–262.

Morgan, T. H., Sturtevant, A. H., and Bridges, C. B., 1927 The constitution of the germ material in relation to heredity. Yearb. Carnegie Instn. **26:** 284–288.

1928 The constitution of the germinal material in relation to heredity. Yearb. Carnegie Instn. **27:** 330–335.

REDFIELD, H., 1924 A case of maternal inheritance in Drosophila. Amer. Nat. **58**: 566–569.

1926 The maternal inheritance of a sex-limited lethal effect in *Drosophila melanogaster*. Genetics **11**: 482–502.

STURTEVANT, A. H., 1915 Experiments on sex-recognition and the problem of sexual selection in Drosophila. J. Anim. Behav. **5**: 351–366.

1920 Genetic studies on *Drosophila simulans*. I. Introduction. Hybrids with *D. melanogaster*. Genetics **5**: 488–500.

1923 Inheritance of direction of coiling in Limnaea. Science **58**: 269–270.

1929 The genetics of *Drosophila simulans*. Pub. Carnegie Instn. **399**: 1–62.