MUTANTS AND CROSSING OVER IN THE DOT-LIKE CHROMOSOME OF *DROSOPHILA VIRILIS*

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In the oogonial metaphase of *Drosophila virilis*, we find five pairs of the rod-shaped chromosomes similar in length and one pair of the dot-like chromosomes. Hence, in this species, there should be six linkage groups besides the Y chromosome linkage, and one of them is expected to contain fewer genes and to have very low frequency of crossing over.

In the course of genetical investigations with the Japanese stock of *Drosophila virilis*, we have discovered a considerable number of genes which are assigned to six linkage groups (CHINO 1929, 1930 and unpublished data). Of the approximately one hundred genes (the number of genes including multiple allelomorphs in the six linkage groups of *D. virilis:* (X) 35, (II) 19, (III) 11, (IV) 13, (V) 17, (VI) 6) thus far found, the following six are to be assigned to the sixth linkage group in our map.

(1) plain (p_l): (March, 1929, CHINO) Recessive, somewhat yellowish body color; dark streak on thorax indistinct; this stock was lost before other genes were discovered.

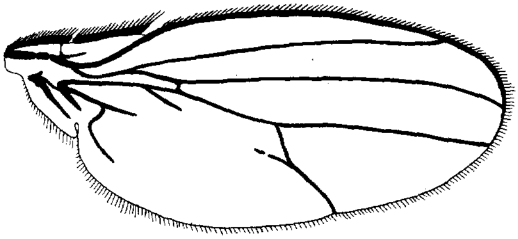

FIGURE 1.—Gap wing of *Drosophila virilis*.

(2) Gap (G_p): (January, 1931, CHINO) Dominant, lethal when homozygous; fifth longitudinal vein almost obliterated between the two crossveins; veins near anterior crossvein somewhat disarranged (figure 1).

(3) stubby (s_t): (April, 1931, CHINO) Recessive; bristles on thorax and scutellum rather shortened, but not attenuated.

(4) stubby-2 (s_{t2}): (April, 1931, CHINO) Recessive; only posterior scutellars shortened and distorted, allelomorph of stubby.

(5) lethal-VIa (l_{VIa}): (February, 1932, CHINO) Discovered in the stubby stock; this makes balanced lethal with the Gap gene.

(6) glossy (g_l): (discovered by American authors) Ommatidia irregular; surface of eyes with oily lustre; eye color reddish. (The material with this

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character was originally sent us by Doctor M. DEMEREC. After a linkage test, it has been found that this character is to be assigned to the VI chromosome in our map, though it had been located on the IV chromosome in the American map by METZ, MOSES and MASON [1923].)

Besides these six genes, METZ (1923) and DEMEREC (unpublished data) have reported several genes which belong to their sixth chromosome, namely Net, Minute, bent and Pale. But, as the results given later indicate, the genes which are assigned to the sixth linkage group in our map undoubtedly belong to the small chromosome, so that it seems to be desirable to change the original nomenclature published by METZ, etc., and call their IV linkage group the VI linkage group, if it is proper to name the small chromosome the VI chromosome, as METZ and his associates seem to consider (METZ, MOSES and MASON 1923, pp. 77–78).

CROSSING OVER EXPERIMENTS

Owing to the dominant character of the Gap gene and the phenotypic clearness with which all the genes express themselves, crossing over experiments on this chromosome can be readily performed. The result of our first experiment to combine Gap with glossy is given in table 1.

TABLE 1

Progeny of Gap/glossy×glossy (July 1931).

NUMBER OF CULTURE	GAP	GLOSSY	GAP, GLOSSY	+	TOTAL
1941	146	145	2	4	297
1942	140	144	4	3	291
1943	120	149	0	0	269
1944	157	163	2	0	322
1945	147	151	1	2	301
1946	139	161	0	1	301
Total	849	913	9	10	1781

Crossing over, 1.06 percent

As this table shows, the two parental combinations in the non-crossover class are approximately equal as are the two new combinations in the crossover class. The frequency of crossing over between these two genes is only 1.1 percent. From these facts, we may infer that crossing over has actually occurred in this chromosome, even though the frequency is very small.

From culture No. 1942 we were able to make one stock combining Gap and glossy in the same chromosome. The result of the unsuccessful second experiment to combine this stock with stubby is given in table 2.

Here, if the frequency of crossing over were about 1.1 percent as pre-

TABLE 2

Progeny of Gap, glossy/stubby×glossy (October 1931).

NUMBER OF CULTURE	GAP, GLOSSY	+	GLOSSY	GAP	TOTAL
2002	134	142	0	0	276
2003	124	133	0	0	257
2004	153	128	0	0	281
Total	411	403	0	0	814

Crossing over, 0.0 percent

viously observed, about eight crossovers would be expected among the total of 814 flies. As the cause of the discrepancy between the results of these two experiments the following possibilities may be considered: (a) the genic difference between the stocks used in these experiments, (the frequency of crossing over varies in *D. virilis* according to the strain used); (b) the possible difference in the frequency of crossing over between the cases of coupling and repulsion; and (c) the variation due to external influence, such as temperature, since the first experiment (table 1) was carried out during the summer, while the second (table 2) was performed during the autumn.

In order to solve the above question, we performed the following experiment. Larvae having s_t, G_p/g_l constitution derived from the same

TABLE 3

Progeny of Gap, stubby/glossy×glossy, at 30° C and 25° C.

TEMPERATURE	GAP	GLOSSY	GAP, GLOSSY	+	TOTAL
30° C	95	82	0	0	177
	67	81	0	0	148
	47	74	1	0	122
	49	55	0	0	104
	64	75	1	0	140
	82	76	1	0	159
Total	404	443	3	0	850
25° C	82	90	0	0	172
	76	105	0	0	181
	94	92	0	0	186
	91	100	0	0	191
	68	67	0	0	135
	83	109	0	0	192
Total	494	563	0	0	1057

Crossing over at 30° C, 0.34 percent
Crossing over at 25° C, 0.00 percent

parent were divided into two groups and they were bred at 30°C and 25°C respectively. After their emergence, only the females showing Gap character were selected and mated to glossy males, and were bred, as before, at 30°C and 25°C respectively. The results are given in table 3.

As this table shows, each of the three cultures among the six at 30°C gave rise to one crossover individual, whereas no such crossover was found among the six cultures at 25°C, in spite of the greater total number of flies than in the former case. It is, therefore, very likely that high temperature raises the frequency of crossing over between these two genes, even if we admit the other two possibilities, especially the one mentioned under (a). Further details on these points are left for a future study.

The same relation seems to hold also for the region between Gap and stubby, although we have not yet made any detailed study of this matter. Several experiments completed thus far have given the following result in the case of $G_p/s_t \times s_t$ matings: Gap, 1228; stubby, 952; Gap, stubby, 3; wild, 6. The frequency of crossing over here is 0.41 percent.

The locus of lethal-VIa has not been found as yet, but, judging from the fact that it makes a balanced lethal with Gap, it can be assumed that the gene is located near the three genes described before.

Thus both the data concerning the number of mutants and that concerning the frequency of crossing over suggest that those genes belong to the small chromosome in this species and form the sixth linkage group. This conclusion is strongly supported also by the fact that the crossing over in our IV linkage group is high. For instance, the percentage of recombination between plexus and dachsous is 46.3, between plexus and irregular is 53.5, and that between dachsous and irregular is 22.1 (CHINO 1929, 1930 and unpublished data). This proves that the IV linkage group in our map belongs to one of the longer chromosomes.

HAPLO VI IN *Drosophila virilis*

KIKKAWA, one of the authors, found a female (December 1931) with glossy eyes among the F_1 progeny of glossy×wild mating. This fly was about $\frac{2}{3}$ of the normal fly in body size, and had small, slender bristles, blunt and slightly spread wings, and looked weaker than normal. This fly represents probably haplo VI or diminished in *D. virilis*, or the deficiency at the glossy locus. Unfortunately it was sterile.

DISCUSSION

In the fourth linkage group in *D. melanogaster*, the following six characters have hitherto been reported: bent, shaven, eyeless, Minute IV, dominant eyeless and rotated abdomen (MORGAN, BRIDGES, STURTEVANT 1925, 1926, MULLER 1930, PATTERSON and MULLER 1930, BELIAJEFF

1931). But, in *D. virilis*, no similar mutant has been found except bent previously reported by METZ, etc. (Very recently CHINO discovered a mutant, rotated abdomen, which seems to correspond to the similar mutant in the IV chromosome of *D. melanogaster*. After a linkage test, it was found that the mutant belongs to the VI chromosome in our map. However, no certain case of crossing over between it and Gap has been found as yet).

Lately, BOLEN (1931) found in the study of X-IV translocations in *D. melanogaster* that the eyeless gene is located at a point distal of the bent gene. However, before this discovery of BOLEN, it has been assumed that the orders of these genes can not be determined from crosses since the crossing over does not occur in this chromosome, and that the cases of apparent crossovers previously reported were probably due to non-disjunction or phenotypic overlapping of genotypic classes (MORGAN, STURTEVANT, BRIDGES 1926, PATTERSON and MULLER 1930).

But, in the dot-like chromosome of *D. virilis*, as our experimental result has proved, crossing over does actually occur, although there is suspicion that some of the cases given before are nothing but the result of non-disjunction. If the glossy and the stubby genes can be put into the same chromosome, we shall be able to decide the orders of arrangement and also the relative distance of these two recessive genes from the Gap gene by a crossing over test. Such an attempt is now underway.

The discrepancy noted between the two species of Drosophila concerning the crossing over in the dot-like chromosome may be accounted for to some extent as follows. The X chromosomes seen under the microscope do not show much difference, either in shape or length, between the two species; the genetical maps of this chromosome, however, show a rather considerable difference, comprising about 182 units in *D. virilis* (CHINO 1929), but only 66 units in *D. melanogaster*, (MORGAN, BRIDGES and SCHULTZ 1931, the ratio being 2.8 to 1.

A similar relation is found between the autosomes in the two species. Thus, it may be assumed that crossing over on the whole occurs more frequently in *D. virilis* than in *D. melanogaster*. If so, it is not very surprising if a few cases of crossing over should be found in the dot-like chromosome of the former species.

This fact seems to justify the view that every species has an *a priori* frequency value of crossing over as a whole which is independent of the length of the chromosomes. As a matter of fact, TANAKA (1925) has reported a case in the silkworm where the frequency of recombination exceeds 45 percent notwithstanding the oval shape of all the chromosomes, and HUXLEY (1923) advances a similar view in his work on *Gammarus chevreuxi* where the chromosomes have similar shape.

SUMMARY

1. Six factors, located in the dot-like chromosome of *D. virilis*, are described: plain, Gap, stubby, stubby-2, lethal-VIa and glossy.

2. Crossing over was found to occur between Gap and glossy, and also between Gap and stubby, the frequency being about 0–1 percent in both cases. The frequency seems to be increased by high temperature.

3. One female probably lacking one dot-like chromosome (haplo VI) was described.

4. A plausible explanation is given for the question as to why the crossing over is found in the dot-like chromosome of *D. virilis*, while it is not found in the similar chromosome of *D. melanogaster*.

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