

BEHAVIOR OF THE GENE FOR THE MUTANT CURVED OF DROSOPHILA MELANOGASTER IN CROSSES INVOLVING GENES IN THE SAME AND OTHER CHROMOSOMES.

ROSCOE R. HYDE.

From the Department of Immunology, School of Hygiene and Public Health, Johns Hopkins University, Baltimore.

Contents.

I. Behavior of the curved winged mutant with normal wild stock.

1. Curved ♀ by $\frac{1}{2}$ wild ♂. Chromosome I.

II. Behavior of curved with bent. Chromosome IV.

1. Curved ♀ by $\frac{1}{2}$ bent ♂.

III. Behavior of curved with spineless. Chromosome III.

1. Curved ♀ by $\frac{1}{2}$ spineless ♂.
2. Spineless ♀ by curved ♂.
3. Deficiency of the double recessive, curved spineless in crowded cultures.

IV. Behavior of curved with vestigial. Chromosome II.

1. Vestigial ♀ by curved ♂.
2. Curved ♀ by vestigial ♂.
3. Back crosses between the hybrid of curved and vestigial to the parent stocks.

V. Behavior of curved with crosses involving black. Chromosome II.

1. Black ♀ by curved ♂.
2. Curved ♀ by black ♂.
3. Curved ♀ by black, purple curved ♂.
4. Black, purple curved ♂ by curved ♀.
5. Crosses involving black, purple, vestigial and curved.

VI. Summary.

VII. Literature.

A wing mutation in *Drosophila melanogaster* which has proved to be identical with curved, a mutant found by Bridges in rudimentary stock, appeared in my wild cultures in the latter part of November, 1914. The culture was one of a large number of wild stocks that were taken during the fall of 1913

in Indiana. Twelve curved of both sexes appeared simultaneously in the culture bottle. The mutant has been kept in pure culture since that time. A number of crosses with mutants known to belong to different chromosome groups are here recorded.

*I. Behavior of the curved winged mutant with normal wild stock.
Chromosome I.*

1. Curved ♀ by wild ♂.

A curved wing female bred to the normal long wing male produced 18 sons and 13 daughters,—all with wings typical of wild stock. These when inbred gave in the F₂ generation 107 curved and 348 wild type flies. Table I. Both sexes are affected. This result demonstrates curved to be a recessive, non sex-linked mutant giving a Mendelian ratio of approximately 3 to 1. It is evident that the gene for curved is not carried by chromosome I, since it does not show sex-linkage.

Table I. F₂ generation from curved ♀ by wild ♂.

Number	Normal ♂ ♂	Normal ♀ ♀	Curved ♂ ♂	Curved ♀ ♀
1	48	46	8	11
1a	52	32	21	18
1b	46	55	13	13
1c	24	45	13	10
Total.	170	178	55	52

II. Behavior of curved with bent. Chromosome IV.

1. Curved ♀ by bent ♂.

Bent is a wing mutant first described by Muller who demonstrated that its gene belongs to Group IV. The curved female by bent male gave all normal flies of the wild type in the F₁ generation. These inbred produced in F₂ the different classes given in table II.

Table II. F₂ generation from curved ♀ by bent ♂.

Wild type ♂ ♂	Wild type ♀ ♀	Curved ♂ ♂	Curved ♀ ♀	Bent ♂ ♂	Bent ♀ ♀
66	90	37	29	33	31

This cross should give a ratio of 9:3:3:1 if the gene for curved is in a chromosome other than IV. Bent is a poor character with which to contrast curved since both characters involve the wings and the double recessive cannot with certainty be distinguished. A few forms appeared, however, which I took to be curved bent. Counting the double recessive with curved and bent a ratio of 9 to 7 should result. The table gives approximately this ratio and a tentative conclusion reached that the gene for curved is borne by a chromosome which gives free assortment with IV.

III. Behavior of curved with spineless. Chromosome III.

1. Curved ♀ by spineless ♂.

Spineless, a mutant characterized by the absence of bristles on the thorax, was first described by Bridges. Its gene belongs to Chromosome III. All children from the curved ♀ by spineless ♂ were characteristic of the wild type. These when inbred in pairs gave in the F₂ generation the different classes as shown in table III.

Table III. F₂ generation from curved ♀ by spineless ♂.

Number of Mating	Wild type	Normal wing spineless	Normal spines curved	Curved Spineless
1	75	21	22	5
2	57	14	11	4
3	57	17	19	8
4	58	18	13	8
5	89	16	22	2
6	58	15	14	4
7	61	22	13	5
8	9	2	2	0
9	39	14	8	4
10	55	1	11	1
11	42	2	12	0
12	77	24	20	10
13	63	2	14	0
14	35	9	9	4
15	82	25	24	5
16	46	13	14	6
17	78	20	18	8
18	87	25	28	8
19	49	1	24	0
20	48	11	14	5
21	60	23	14	4
22	48	18	8	4
23	40	2	13	0
24	47	17	13	1
Total.....	1360	332	360	96

2. Spineless ♀ by curved ♂.

The reciprocal cross in which the spineless ♀ is paired to the curved ♂ is given in table IV. All the F₁ were like the wild type.

Table IV. F₂ generation from spineless ♀ by curved ♂.

Number of Mating	Wild type	Normal wing spineless	Normal spines curved	Curved spineless
1	72	31	27	10
2	82	23	22	2
3	79	3	26	0
4	70	22	18	8
5	50	17	18	7
6	79	23	19	6
7	72	8	20	0
8	73	17	27	1
9	83	19	16	2
10	72	17	28	3
11	76	29	27	11
12	73	15	15	5
13	82	8	23	1
14	75	15	24	2
15	61	16	21	8
16	72	22	24	11
17	13	1	7	1
18	21	7	7	5
19	68	37	8	6
20	80	15	11	4
21	78	21	25	7
22	42	20	17	1
23	20	3	10	2
24	62	15	17	10
Total	1546	404	457	113

Tables III and IV give evidence of free Mendelian assortment of curved and spineless since the classes approximate a ratio of 9:3:3:1. We conclude that the gene for curved is borne by a chromosome other than III.

3. *Deficiency of the double recessive curved spineless in crowded conditions.*

These combinations have been made many times with the same result except that when the cultures are crowded there is a marked suppression of the double recessive. Table V gives an F₂ count from crowded conditions. It is to be noted that only approximately half the number of double recessives appear under unfavorable conditions.

Table V. F_2 generation from spineless ♀ by curved ♂.

Number	Normal wild type	Normal wing spineless	Normal spines wingless	Curved spine- less
1	34	5	0	0
2	197	43	44	11
3	250	28	59	7
4	253	56	56	8
5	264	50	67	10
6	242	66	71	12
7	216	35	29	5
8	50	27	11	5
Total ²	1496	310	337	58

The F_1 were made up in mass cultures July 10, 1916, transferred to new bottles July 16. The final count was made July 24, 1916.

IV. *Behavior of curved with vestigial. Chromosome II.*

Vestigial, a member of group II, was described and the linkage of the gene reported by Morgan and Lynch. The double recessive does not appear among the offspring on mating the F_1 from a cross involving two simple recessives whose genes are allocated in the same chromosome. This is due to the fact that in this species there is no crossing over in the male.

1. Vestigial ♀ by curved ♂.

The F_1 from this combination had long wings typical of wild stock. Table V gives the different classes that appeared in the F_2 .

Table VI. F_2 generation from vestigial ♀ by curved ♂.

Number	Wild type		Curved		Vestigial	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀
1	46	32	16	13	11	9
1a	40	55	29	26	27	26
Total . .	86	87	45	39	38	35

²Six flies in this group were minus one eye.

2. Curved ♀ by vestigial ♂.

All the F₁ generation from this combination have long wings of the wild type as is the expectation. These when inbred produced the different classes as given in tables VII and VIII.

Table VII. F₂ generation from curved ♀ by vestigial ♂.

Number	Wild type		Curved		Vestigial	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀
1	208	203	89	82	69	90
1a	81	97	38	40	30	32
2	154	130	74	69	62	56
2a	89	112	30	34	9	17
3	156	124	61	64	63	78
3a	128	139	61	53	36	36
4	104	88	51	39	49	48
4a	70	83	21	37	17	24
5	193	208	76	96	78	87
5a	84	105	15	19	7	9
6	40	51	22	20	16	10
6a	36	39	17	22	17	19
7	41	49	9	9	15	12
7a	52	47	16	8	17	19
8	64	78	40	34	41	39
8a	71	93	22	16	23	29
9	93	75	35	26	38	35
9a	58	64	27	24	20	27
Total . .	1722	1785	704	692	607	667

3. Back crosses between the hybrid of curved and vestigial to the parent stocks.

The genetic relation between curved and vestigial was studied in various combinations of back crosses between the hybrids and the parent stocks. Tables VIII—XV shows the different combinations made and the classes realized.

Table VIII. Hybrid ♀ (curved ♀ by vestigial ♂) by curved ♂.

Number	Wild type		Curved	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀
1	87	84	53	62
1a	116	160	101	84
2	104	125	63	74
2a	3	11	2	0
3	87	107	66	77
Total	884		582	

Table IX. Hybrid ♂ (curved ♀ by vestigial ♂) by curved ♀.

Number	Wild type		Curved	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀
1	155	141	103	98
2	83	93	61	94
Total	472		356	

Table X. Hybrid ♀ (curved ♀ by vestigial ♂) by vestigial ♂.

Number	Wild type		Vestigial	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀
1	82	92	43	58
2	55	53	54	38
3	90	91	35	33
4	45	28	29	29
Total	536		319	

Table XI. Hybrid ♂ (curved ♀ by vestigial ♂) by vestigial ♂.

Number	Wild type		Vestigial	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀
1	45	41	34	34
1a	89	87	44	48
2	26	18	19	11
2a	10	7	4	2
3	95	118	92	83
3a	72	87	37	45
Total	695		453	

Table XII. Hybrid ♀ (vestigial ♀ by curved ♂) by vestigial ♂.

Number	Wild type		Vestigial	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀
	85	101	35	31
Total	186		66	

Table XIII. Hybrid ♂ (vestigial ♀ by curved ♂) by vestigial ♀.

Number	Wild type		Vestigial	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀
	74	87	32	22
Total	161		54	

Table XIV. Hybrid ♀ (vestigial ♀ by curved ♂) by curved ♂.

Number	Wild type		Curved	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀
	14	18	15	24
Total	32		39	

Table XV. Hybrid ♂ (vestigial ♀ by curved ♂) by curved ♀.

Number	Wild type		Curved	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀
	50	68	43	52
Total	118		95	

It is evident that in order to bring out the linkage value the double recessive vestigial curved should be used in the back crosses.

V. Behavior of curved with crosses involving black. Chromosome II.

Black, a body color mutation, was found by Morgan. Its linkage shows it to belong to Group II. The contrast between the two characters makes black a good character against which to test curved.

1. Black ♀ by curved ♂.

The gray (wild type color) curved ♂ mated to the straight (wild type wing) black ♀ gave 12 wild sons and 13 wild daughters. These inbred produced an F₂ generation classified in table XVI.

Table XVI. F₂ generation from straight black ♀ by gray curved ♂.

Number	Straight gray	Straight black	Curved gray	Curved black
1	80	39	20	0
2	114	30	36	0
3	219	104	67	0
Total	413	173	123	0

2. Curved ♀ by black ♂.

The reciprocal cross in which the curved ♀ is mated to the black ♂ gave all wild type in the F₁ generation. These inbred gave results as given in table XVII. These results show very clearly that there is linkage between black and curved since the double recessive does not appear in F₂.

Table XVII. F₂ generation from gray curved ♀ by straight black ♂.

Number	Straight gray	Straight black	Curved gray	Curved black
1	131	41	31	0
2	139	45	31	0
3	104	58	34	0
Total	374	144	96	0

3. Curved ♀ by black purple curved ♂.

Tables XVIII and XIX give additional data in which curved was crossed to the triple recessive black purple curved obtained from Morgan in the fall of 1918. The curved ♀ by the black purple curved ♂ gave 200 gray red eyed curved sons and 218 gray red eyed daughters. The fact that all the F₁ had curved wings is conclusive proof that Morgan's curved stock and mine are identical. The independent change affecting the germ plasma had changed identical genes. Matings were made from the F₁ with the results recorded in table XVIII.

Table XVIII. F₂ generation from curved ♀ by black, purple curved ♂.

Number	Gray red curved	Black purple curved	Black red curved	Gray purple curved
1	128	35	6	6
1a	180	35	10	7
2	199	45	10	8
2a	116	32	5	2
3	123	30	7	8
3a	119	32	1	2
4	165	43	2	5
4a	44	14	1	3
Total	1074	276	49	42

4. Black purple curved ♀ by curved ♂.

The F₁ from the reciprocal cross to that in 3 gave 202 gray red eyed curved sons and 231 gray red eyed curved daughters. These inbred gave in F₂ the different classes in table XIX.

Table XIX. F₂ generation from black, purple, curved ♀ by curved ♂.

Number	Gray red curved	Black purple curved	Black red curved	Gray purple curved
1	248	52	6	25
2	273	59	14	11
3	313	77	11	7
4	263	59	13	6
Total	1097	247	44	49

The fact that all the flies in the F₁ and F₂ are curved shows that the two mutants are identical. The last two tables give data on the linkage of purple and black. There are 184 cross overs in a total of 2878 a linkage of 12.8.

5. The Black, purple vestigial was crossed to a new wild stock from Arlington, Md. Over 500 sons and daughters were like the wild type. Since crossing over does not take place in the males, F₁ females whose composition was (b p v B P V) were back crossed to black purple vestigial (b p v). The

females produce non-crossover gametes (b p v) and (B P V) and crossover gametes of the composition b P V—Bpv—bpV—BPv—bPv and Bpv. The males to which they are mated produce gametes of the composition b p v. The different classes realized are given in table XX.

Table XX. Classes realized on back crossing the bpv ♂ to the hybrid ♀ of composition bpv BPV.

No.	Vestigial				Long			
	Black		Gray		Black		Gray	
	Purple	Red	Purple	Red	Purple	Red	Purple	Red
	bpv	bPv	Ppv	BPv	bpV	bPV	BpV	BPV
1	95	2	15	23	16	13	1	119
2	62	4	6	5	8	14	2	78
3	111	4	14	9	15	16	2	89
4	179	2	12	26	62	36	4	301
Totals.	447	12	47	63	101	79	9	587

VI. Summary.

The independent origin of curved, a wing mutant identical with the one reported by Bridges, is here given. The data obtained with the various crosses is in agreement with the great mass of evidence which shows that the chromosome conception of inheritance offers the only rational basis upon which such data can be interpreted. Genes carried by different chromosomes give free assortment with Mendelian ratios, those in the same chromosome show linkage with no crossing over in the male.

It is evident that the factor grouping of a new mutant can be determined by the failure of the double recessive to appear in the F₂ generation. Morgan has made use of black-pink flies for testing a new mutant type. Black is in the second group and pink in the third. If the new factor belongs to either of these groups it will fail to show the double recessive among the grandchildren from the cross. The sex relations from such an experiment will readily determine whether or not it belongs to the sex-linked group. If it belongs to none of these groups it is by exclusion placed in the fourth group.

VII. Literature.

1. Morgan, Sturtevant, Muller, Bridges. The Mechanism of Mendelian Heredity. 1915. New York.
2. Plough, H. H. The effects of temperature on crossing over. J. Exp. Zool. 1917. 24.
3. Contributions to the Genetics of *Drosophila Melanogaster*. Morgan, Bridges, Sturtevant. Carnegie Institution of Washington. 1919. Publication No. 278.
4. Muller, H. J. A Gene for the Fourth Chromosome of *Drosophila*. J. Exp. Zool. 1914. 17.
5. Sturtevant, A. H. Zeit. für induktive Abstammungs und Vererbungslehre. 1915. 13, 234-287.

