EXTRACHROMOSOMAL ELEMENT DELTA IN *DROSOPHILA*
MELANOGASTER. III: INDUCTION OF ONE-SIDED
GAMETE RECOVERY FROM MALE AND
FEMALE HETEROZYGOTES

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DEVIAnt segregation ratios from certain matings may be due either to differential mortality of zygotes or unequal fertilizing functions of gametes from heterozygous parents. Segregation deviation caused by the latter mechanism has been called the segregation distortion phenomenon. The Segregation-Distorter gene (*SD* SANDLER, HIRAIZUMI and SANDLER 1959) has been extensively analyzed. It is located on the second chromosome of *D. melanogaster*. A male heterozygous for *SD* produces dysfunctional *SD*⁺-bearing spermatozoa, and his *SD* progeny are recovered in great excess over his *SD*⁺ progeny. The distortion occurs only in *SD*-heterozygous males, not in *SD*-heterozygous females.

A similar phenomenon has been found in the *sc*⁴-*sc*⁸ X-chromosome line (PEACOCK 1965) and the *RD* line (ERICKSON 1965) of *D. melanogaster*; more female than male offspring are recovered in both instances. These aberrant sex ratios are observed only in the progeny of males heterozygous for the chromosome or gene, and not in the offspring of the females. Another case of sex ratio distortion has been found in the yellow fever mosquito, *Aedes aegypti*, where excess males are recovered in the progeny of *M*^D/*m*^d males and not in the progeny of females of the same genotype (HICKEY and CRAIG 1966).

The extrachromosomal element called delta in *D. melanogaster* was found and studied in our laboratory. Briefly, the main conclusions from our past studies (MINAMORI 1969a,b; MINAMORI and ITO 1970) which are relevant to the present study are the following: (1) Delta induces a segregation distortion in crosses of certain second chromosome lines. The distortion was interpreted as due to differential mortality of zygotes; namely, homozygotes or heterozygotes for a certain second chromosome or chromosomes, denoted as sensitive chromosomes, are more susceptible to the killing action of delta than heterozygotes for sensitive and insensitive chromosomes. (2) There are two kinds of sensitive chromosomes. Some of the chromosome lines have retained delta steadily, but other lines are not usually accompanied by delta. (3) Delta is transmitted through female and male parents. The amount of delta transmitted by males is considered to be lower than a certain threshold amount at and above which the killing action appears. It was found that delta could not be eliminated from a sensitive line by repeated backcrosses of the males to females of another line. (4) Delta induces frequent lethal mutations at definite regions of the second chromosome, probably acting in an embryonic stage of the carrier.

Only one kind of progeny was recovered from both male and female heterozygotes for certain sensitive chromosomes. The recovery in male heterozygotes is believed to be caused by the production of only one kind of functional spermatozoa from the heterozygote, and not by zygote mortality. A one-sided recovery of progeny or gametes occurred when the heterozygotes carried an appreciable amount of delta. However, normal recovery in a 1:1 ratio was always observed when the two kinds of progeny were recovered from the heterozygote.

MATERIALS AND METHODS

The one-sided recovery of progeny reported here was found in heterozygotes for a *Cy*-bearing sensitive chromosome and a non-*Cy* sensitive chromosome. All the progeny recovered from the heterozygote carried the *Cy* gene. The sensitive second chromosomes used were:

S-Cy: carried *Cy* (Curly wing) and a lethal gene and was not accompanied by delta; found in *Cy/L* stock (*L* Lobe eye) in 1965.

S-5, *S-16*: carried a lethal gene and retained delta steadily; isolated from natural populations in 1964 (*S-5*) and in 1966 (*S-16*).

S-7, *S-9*: normal in homozygous viability and retained delta steadily; isolated from a natural population in 1965.

The *S-Cy* heterozygotes for each of the four non-*Cy* chromosomes noted above were obtained and progeny tested by the following mating scheme, where *S* is a sensitive chromosome:

P	♀ ♀ <i>Cy/S</i> × <i>S-Cy/L</i> ♂ ♂
F ₁	♀ (♂) <i>S-Cy/S</i> × <i>cn bw/cn bw</i> ♂ ♂ (♀ ♀)
F ₂	1 <i>S-Cy/cn bw</i> : 1 <i>S/cn bw</i>

Single *S-Cy/S* F₁ males or females were crossed to four *cn bw/cn bw* females or males (*cn* cinnamon eye, *bw* brown eye genes on the second chromosome), and the Curly and non-Curly F₂ flies emerging were scored.

All the cultures were kept in an incubator at 25°C.

RESULTS

Segregation distortion in matings between two sensitive lines: The *S-Cy* heterozygotes tested were obtained mostly from mating *S-Cy/L* with *Cy/S-5* flies. The segregation ratio in reciprocal matings of these lines is expected to be 1 *S-Cy/S-5* : 1 *Cy/L* : 1*L/S-5* since *S-Cy/Cy* is lethal. However, the frequency of *S-Cy/S-5* was greatly reduced among all progeny of the cross ♀ *Cy/S-5* × *S-Cy/L* ♂ in the presence of an appreciable amount of delta. Evidence suggested that the distortion in this mating might be due to higher mortality of the *S-Cy/S-5* zygotes caused by the killing action of delta (MINAMORI 1969a). The frequency of zygotes of the same genotype was higher than expected in the same mating employing *Cy/S-5* females which carried only minute amounts of delta or in matings in the opposite direction, ♀ *S-Cy/L* × *Cy/S-5* ♂. The segregation distortion observed in the latter two matings was interpreted as being due to a viability of *Cy/L* zygotes lower than *S-Cy/S-5* zygotes when delta was absent or present in small amount.

In Table 1, an example of segregation distortion in reciprocal matings between these lines is shown. The (*S*:Curly) ratio is the number of *S-Cy/S-5* progeny divided by the number of *Cy/L* progeny of single-pair matings, expressed in percent. This ratio is used to express the magnitude of damage caused by delta to its

TABLE 1

Segregation in the reciprocal matings between Cy/S-5 and S-Cy/L

Number of <i>S-Cy/S-5</i> offspring	Number of <i>Cy/L</i> offspring	Number of <i>L/S-5</i> offspring	(<i>S:Curly</i>) ratio*
<i>♀ Cy/S-5 × S-Cy/L ♂</i>			
0	89	75	0
2	134	96	1.49
4	90	101	4.44
4	79	108	5.06
6	102	95	5.88
<i>♀ S-Cy/L × Cy/S-5 ♂</i>			
124	87	136	142.53
157	107	153	146.73
98	63	93	155.56
102	64	112	159.38
115	71	96	161.97

* (*S:Curly*) ratio: the number of *S-Cy/S-5* progeny divided by the number of *Cy/L* progeny of single-pair matings, expressed in percent.

carriers or the amount of delta carried by the carrier. The *S-Cy/S-5* zygotes derived from the mating,

♀ Cy/S-5 × S-Cy/L ♂, are symbolized [δ] *S-Cy/S-5*.

Zygotes from the reciprocal mating,

♀ S-Cy/L × Cy/S-5 ♂, are symbolized [$\pm$] *S-Cy/S-5*.

One-sided recovery of Curly progeny from [δ] S-Cy/S-5 males and females: An example of recovery of only Curly flies and an example of recovery in a ratio of 1 Curly to 1 non-Curly from individual *S-Cy/S-5* males and females from the above reciprocal matings is shown in Table 2. The males and females were sampled individually from different broods of the matings. The (*S:Curly*) ratio in the mating employing *Cy/S-5* females was extremely low as previously noted, usually lower than 10%. The progeny recovered from a single [δ] *S-Cy/S-5* male or female were all Curly.

Such one-sided progeny recovery was similarly observed in the heterozygotes when they were crossed with males or females of several wild second chromosome lines (cf. Table 5), as in the mating with *cn bw / cn bw* flies. Accordingly, there is little doubt that the one-sided recovery may be ascribed to the [δ] *S-Cy/S-5* heterozygotes themselves. In sharp contrast, the (*S:Curly*) ratios in the reciprocal matings were higher, ranging from 125–180%, and the [$\pm$] *S-Cy/S-5* males or females from these matings produced Curly and non-Curly in a 1:1 ratio. These findings indicate that the recovery of only *S-Cy*-bearing progeny from the heterozygotes may be associated with the presence of delta.

The average number of Curly flies recovered from [δ] *S-Cy/S-5* males did not differ greatly from that of Curly plus non-Curly flies recovered from [$\pm$] *S-Cy/S-5* males. The average for the former males was about 250, markedly larger than one-half (about 150) of the average for the latter males. Thus it appears that all or most eggs carrying *cn bw* may be fertilized by *S-Cy*-bearing

TABLE 2

Recovery of progeny from S-Cy/S-5 males and females in matings with cn bw/cn bw
 A single random male or female from individual broods of reciprocal matings (A,B)
 was progeny tested

(S:Curly) ratio of brood	Number of progeny from males		(S:Curly) ratio of brood	Number of progeny from females	
	Curly	non-Curly		Curly	non-Curly
A. [δ] <i>S-Cy/S-5</i> from φ <i>Cy/S-5</i> $\times$ <i>S-Cy/L</i> δ					
1.53	257	0	2.11	102	0
2.02	209	0	3.13	79	0
2.11	228	0	4.04	58	0
2.44	372	0	4.17	88	0
3.21	280	0	4.54	76	0
4.17	189	0	4.78	99	0
5.17	227	0	5.17	80	0
5.57	219	0	7.05	132	0
6.62	206	0	7.78	112	0
7.20	269	0	8.43	86	0
Mean 4.00	245.6	0	5.12	91.2	0
B. [$\pm$] <i>S-Cy/S-5</i> from φ <i>S-Cy/L</i> $\times$ <i>Cy/S-5</i> δ					
124.60	154	134	125.91	74	66
125.31	129	118	136.56	84	106
143.25	195	216	137.48	72	61
149.08	155	182	150.01	66	56
151.04	157	127	154.32	56	55
156.19	161	145	158.91	63	60
159.28	113	102	159.13	137	131
165.27	159	171	168.54	99	111
170.63	160	182	169.32	62	65
180.50	105	123	171.28	94	98
Mean 152.52	148.8	150.0	153.15	80.7	80.9

spermatozoa and not by S-5-bearing spermatozoa from the $S-Cy/S-5$ males. In contrast the average number of Curly flies recovered from $[\delta] S-Cy/S-5$ females was about one-half of the average number of Curly plus non-Curly flies for $[\pm] S-Cy/S-5$ females. Hence, it seems that the one-sided recovery of Curly flies from female heterozygotes may be due to the production of functional $S-Cy$ -bearing eggs and nonfunctional S-5-bearing eggs. This interpretation was tested by egg and fly counts which will be described below.

The progeny recoveries were also examined for $[\delta] S-Cy/S-16$, $[\delta] S-Cy/S-9$, and $[\delta] S-Cy/S-7$ males and females by the same procedure used for $S-Cy/S-5$ heterozygotes (Table 3). The (S:Curly) ratios were less than 10% in the mating $\varphi Cy/S-16 \times S-Cy/L \delta$, intermediate in the mating $\varphi Cy/S-9 \times S-Cy/L \delta$, and somewhat higher in the mating $\varphi Cy/S-7 \times S-Cy/L \delta$. All the offspring recovered from $[\delta] S-Cy/S-16$ males and females were Curly. However, such one-sided progeny recovery was not observed in $[\delta] S-Cy/S-7$ males and females; Curly and non-Curly flies were recovered in a 1:1 ratio. Either one-sided recovery of Curly or normal recovery in a 1:1 ratio of Curly and non-Curly flies was found in $[\delta] S-Cy/S-9$ males and females. The results obtained seem to show that the

TABLE 3

Recovery of progeny from [δ] S-Cy/S-16, [δ] S-Cy/S-9, and [δ] S-Cy/S-7 males and females in matings with cn bw/cn bw

(S:Curly) ratio of brood	Number of progeny from males		(S:Curly) ratio of brood	Number of progeny from females	
	Curly	non-Curly		Curly	non-Curly
[δ] S-Cy/S-16					
3.09	236	0	3.09	77	0
3.57	308	0	4.35	80	0
5.20	187	0	4.56	68	0
7.98	232	0	7.98	69	0
9.02	231	0	9.02	114	0
[δ] S-Cy/S-9					
1.55	241	0	2.04	53	0
2.04	119	0	4.26	66	0
4.21	301	0	6.67	75	0
10.48	149	168	10.48	63	65
35.11	180	173	35.11	78	86
[δ] S-Cy/S-7					
25.56	123	140	25.56	81	92
36.87	156	148	36.87	89	83
37.04	172	180	37.04	57	63
41.03	133	118	41.03	62	63
90.32	115	129	90.32	47	50

one-sided recovery of S-Cy-bearing progeny also occurs in S-Cy heterozygotes for each of the sensitive chromosomes other than S-5 when the (S:Curly) ratios of the broods from which the heterozygotes were sampled were low, but not when the (S:Curly) ratios of the broods were high.

Variation in progeny recovery among heterozygotes from the same brood: [δ] S-Cy/S-5 males and females belonging to the same brood were individually examined as to their progeny recoveries (Table 4). The brood was obtained by mating a single Cy/S-5 female with S-Cy/L males; hence, the S-5 chromosomes carried by S-Cy/S-5 heterozygotes from the same brood would be identical with each other, when mutation is ignored. All the heterozygous males and females belonging to the same broods in which the (S:Curly) ratio was 1.11 and 4.17%, respectively, produced only Curly flies. In contrast, all the males and females belonging to the same brood in which the (S:Curly) ratio was 27.54% produced Curly and non-Curly flies in a 1:1 ratio. The contrast between recoveries in the former and latter types of brood was very sharp. Such contrasting recoveries were also observed among heterozygotes from the same brood in which the (S:Curly) ratio was intermediate between those noted in the former and latter cases. The progeny recovered from individual heterozygotes belonging to the same brood were either all Curly or Curly and non-Curly in a 1:1 ratio. Therefore, the one-sided progeny recovery observed in these heterozygotes appears to be an all-or-none phenomenon, as if it were induced by a single event.

Relationship between progeny recovery and the (S:Curly) ratio: The above results indicate that the one-sided progeny recovery may be connected to a lower

TABLE 4

Recovery of progeny from [δ] S-Cy/S-5 males and females of the same brood*

(S:Curly) ratio of brood	Sex of heterozygote	Number of progeny	
		Curly	non-Curly
1.11	♂	226	0
	♀	32	0
	♀	56	0
4.17	♂	189	0
	♂	119	0
	♂	206	0
	♂	80	0
	♀	42	0
12.75	♂	156	0
	♀	66	0
	♀	42	43
14.58	♂	104	118
	♀	69	0
	♀	78	75
27.54	♂	105	123
	♂	157	137
	♀	84	94
	♀	74	65

* The males and females were sampled from the same vial.

(S:Curly) ratio, with more severe damage to heterozygotes caused by the killing action of delta. The relationship was extensively examined employing S-Cy/S-5 males and females. The (S:Curly) ratios in the mating employing Cy/S-5 females were usually lower than 10%, but they were higher than 100% in the reciprocal mating employing Cy/S-5 males, and also higher in the mating employing Cy/S-5 females carrying [Cy/Pm] cytoplasm. The Cy/S-5 lines carrying [Cy/Pm] cytoplasm showed higher (S:Curly) ratios in the mating with S-Cy/L males in the initial generation of establishment, but the ratios became lower with advancing generations and reached an equilibrium of less than 10% at around the 12th generation in most lines (MINAMORI 1969b). Thus widely varying (S:Curly) ratios could be obtained in matings employing Cy/S-5 females sampled from various generations of the line. The relationship between the frequency of Curly flies among the total offspring recovered from a single heterozygous male or female and the (S:Curly) ratio of the brood from which the heterozygote was sampled is shown in Figure 1. This figure shows that one-sided recovery of Curly flies occurs in heterozygotes which belonged to broods showing low (S:Curly) ratios, whereas recovery in a 1:1 ratio occurs in heterozygotes which belonged to broods showing high (S:Curly) ratios. The upper limit of (S:Curly) ratios in which one-sided recovery occurred for members of the brood was 16.7% for male and 14.3% for female heterozygotes. The lower limit of the ratio in which normal recovery occurred was 8.7% for male and 7.1% for female

FIGURE 1.—Relationship between the recovery of Curly progeny from males and females of $S-Cy/S-5$ and the (S:Curly) ratio in the brood from which the heterozygote was sampled. The (S:Curly) ratio is the number of $S-Cy/S-5$ progeny divided by the number of Cy/L progeny of single-pair matings, expressed in percent. A single random male or female from individual broods of the mating $\varnothing Cy/S-5 \times S-Cy/L \delta$ was progeny tested.

heterozygotes. Thus it may be said that only Curly flies were recovered from the heterozygotes sampled from broods which showed an (S:Curly) ratio of less than 7%. Either only Curly flies or both Curly and non-Curly flies were recovered from heterozygotes sampled from broods which showed (S:Curly) ratios between 7 and 17%. Both Curly and non-Curly flies were always recovered from heterozygotes sampled from broods which showed (S:Curly) ratios over 17%.

Normal recovery in a 1:1 ratio was observed in 43 males and 35 females. The frequency of Curly flies in all these 78 recoveries ranged from 39.81 to 60.78%. However, no significant deviations from a 1:1 ratio were obtained in individual recoveries. The average frequency (weighted) of Curly flies in these recoveries was 49.24% for males and 49.40% for females. These frequencies are not significantly different from the expected 50% ($F = 0.30$, $P > 0.20$ for males; $F = 0.45$, $P > 0.20$ for females). It may be noteworthy that there were no intermediate frequencies of Curly flies between 50 and 100%, even in the recoveries from heterozygotes sampled from broods whose (S:Curly) ratios ranged from 7 to 17%.

Tests for zygote mortality: In order to test the possibility that one-sided recovery of Curly progeny could be due to inviability of zygotes carrying the $S-5$ chromosome, egg and fly counts were made for progeny of [δ] $S-Cy/S-5$ males and females. Heterozygous males and females were sampled from broods in which the (S:Curly) ratios were lower than 7%, then crossed with homozygotes

TABLE 5

Egg-fly counts for recovery of progeny from S-Cy/S-5 males and females in matings with homozygotes for a wild second chromosome

Female	Cross	Male	Number of eggs laid	Number of progeny recovered		Flies/Eggs (percent)
				Curly	non-Curly	
+/+	×* [±] S-Cy/S-5		706	258	286	77.05
+/+	× [δ] S-Cy/S-5		884	678	0	76.70
[δ] S-Cy/S-5	×	+/+	841	385	0	45.78

* Control cross.

for a wild second chromosome (symbolized 521) which was insensitive and showed normal viability in homozygous condition. The results obtained are shown in Table 5. As a control, counts were made for progeny of [±] S-Cy/S-5 males and 521/521 females. In the control, about three-fourths of the eggs laid produced Curly and non-Curly flies and the frequency of Curly among the total was about 47%, not significantly different from the expected 50% ($\chi^2 = 1.15$, $P > 0.20$). In contrast, only Curly flies emerged from about three-fourths of the eggs laid in the counts from [δ] S-Cy/S-5 males. Therefore, the percentage of flies recovered from the total eggs was similar for progeny of [δ] S-Cy/S-5 males and for progeny of control males, irrespective of whether recovery was one-sided or normal, and these percentages were not significantly different from each other ($\chi^2 = 0.014$, $P > 0.95$). Thus it may be concluded that in the recovery from [δ] S-Cy/S-5 males, all the eggs were fertilized solely by spermatozoa bearing S-Cy; the one-sided recovery was not due to inviability of progeny bearing the S-5 chromosome.

All the progeny recovered from [δ] S-Cy/S-5 females and 521/521 males were also Curly in phenotype. However, the percentage of flies recovered from the eggs laid was lower than in the reciprocal cross; nearly one-half of the eggs laid produced Curly flies. Hence, it appears that only eggs bearing the S-Cy chromosome grew up to form flies, whereas eggs bearing the S-5 chromosome did not.

DISCUSSION

The one-sided progeny recovery described in this report is an all-or-none phenomenon; the progeny recovered from S-Cy/S-5 heterozygotes were either all Curly or Curly and non-Curly in a 1:1 ratio; there were no intermediates between one-sided and normal recovery. The distortion was observed in progeny from *both* male and female heterozygotes. These findings contrast sharply with other instances reported hitherto in which a great excess of one kind of offspring is recovered from male heterozygotes and not from female heterozygotes. There is little doubt that the one-sided recovery of progeny reported here results from the production of only one kind of functional spermatozoa or eggs in heterozygous males and females. Spermatozoa carrying the S-5 chromosomes may be dysfunctional, as observed in *SD* (PEACOCK and ERICKSON 1965) and in the *sc⁴-sc⁸* X-chromosome line (PEACOCK 1965). The same interpretation may also be applied to eggs carrying the S-5 chromosome, though there remains a possi-

bility that they could be fertilized, but all the zygotes would be inviable. The cause of the production of dysfunctional gametes recognized in this study may be a single event, and the same event may occur in the germ-cell lines of both male and female heterozygotes, possibly before the sex differentiation occurs. This interpretation seems to be substantiated by the finding that the upper limit of (S:Curly) ratios in which a one-sided recovery occurred was closely similar in male and female heterozygotes. It is difficult to see how such an all-or-none phenomenon could result from recurrences of the same event, without fail, in all the germ cells in the gonads. In *Drosophila*, germ cells originate from the pole cells. At the stage of blastoderm formation, more than one nucleus penetrates into the polar plasm in the posterior end of the embryo; later they become the pole cells (SONNENBLICK 1950). Hence the event probably arises only once at an early stage before the invagination of the nuclei into the polar plasm. However, there remains some possibility that the event could occur recurrently in all the nuclei in the polar plasm.

Results presented here show clearly that one-sided recovery of gametes is induced by the extrachromosomal element delta. Recovery of only *S-Cy*-bearing progeny was induced when the killing action of delta for the heterozygotes was severe, i.e., when the (S:Curly) ratio of the brood was less than 17%. It is possible that the magnitude of the killing action of delta may be a measure of the amount of delta carried by heterozygotes. Then it could be that one-sided gamete recovery is induced when the amount of delta attains some threshold at and above which delta damages the *S-5* chromosome in such a manner that the gametes which receive this chromosome become dysfunctional.

MINAMORI and ITO (1970) [cf. MINAMORI *et al.* (1970)] reported that delta induced frequent lethal mutations on the second chromosome at an early embryonic stage of the carrier; the earliest period in which the mutation was induced was estimated to be the stage between the third and fourth nuclear division of the germ-cell line. Thus it could be that the action of delta against chromosomes changes at an early stage of pole-cell formation. Before or immediately after the migration of nuclei into the polar plasm, delta is able to damage only *S-5* chromosomes; after that period, delta can damage any second chromosome so that some recessive lethal mutations are induced. Gamete recovery has been examined in *S-Cy* heterozygotes for each of the sensitive chromosomes other than those discussed here, and the same result was obtained. One-sided recovery of Curly flies was observed in more than 100 instances, but no one-sided recovery of non-Curly flies. Therefore, the recognition by delta of *S-Cy* and other sensitive chromosomes seems to be very specific. A specificity also seems to be true with regard to the induction of lethal mutations in definite regions of the second chromosome. The nature of such a strict recognition and an accurate conversion in behavior of a chromosome at a definite period in an early developmental stage might be helpful for studies of cellular differentiation.

In the mosquito, *Culex pipiens*, it has been found that hybrids from one of the sex-reciprocal crosses between local races are inviable, while those from the reciprocal mating are viable. LAVEN (1957, 1967) performed successive back-

crosses of females of the viable hybrids to the paternal race and concluded that since the unidirectional inviability was not eliminated, it was due to a difference in extrachromosomal elements and that these elements were genome independent. Although LAVEN's conclusion assumed normal recovery of gametes from the viable hybrids, McCLELLAND (1967) proposed the possibility of a one-sided recovery of gametes carrying maternal chromosomes from the viable hybrids. He suggested the chromosomal genome of the maternal race might not have been substituted by the genome of the paternal race by successive backcrosses; hence he considered that the extrachromosomal elements could still be genome dependent. YANDERS *et al.* (1968) found certain bacteria or rickettsiae in the *sc^t-sc^s* X-chromosome line; however, they could not discover any causal association between sex ratio distortion and the microorganism. There is also no evidence for some extrachromosomal element taking part in the segregation distortion phenomenon observed in the *SD* and *RD* lines of *Drosophila* or in the sex ratio distortion in *Aedes*. However, it would be desirable to examine the possibility of extrachromosomal elements in these lines as well as McCLELLAND's proposal for *Culex*.

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SUMMARY

Males and females heterozygous for the *Cy* chromosome and certain other non-*Cy* second chromosomes produced only *Cy*-bearing progeny when the heterozygotes carried an appreciable amount of the extrachromosomal element delta. This was concluded from the fact that in the broods from which they were derived, most of their sibs of the same genotype were killed by delta. Results indicate that the one-sided recovery may be due to production of only *Cy*-bearing functional gametes, and not to inviability of progeny bearing the non-*Cy* chromosome. It is suggested that delta may cause damage to the chromosome at an early embryonic stage in heterozygotes of both sexes in such a manner that the gametes receiving this chromosome may become dysfunctional.

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