HETEROCHROMATIC RECOMBINATION IN GERM CELLS OF *DROSOPHILA MELANOGASTER* FEMALES[1]

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ABSTRACT

Heterochromatic recombination in germ cells was found to occur in females of *Drosophila melanogaster* having a specific genotype. Results of the present study can be summarized as follows: (1) The frequency of heterochromatic recombination descreases consistently and markedly as the female ages. (2) The female that induces heterochromatic recombination is associated with reduced number of progeny when she is young, but as she gets older, the number of progeny increases, approaching that of the normal female. The reduction in the number of progeny is due to unhatchability of eggs produced, not to reduced egg laying. (3) Cytoplasmic factors affect the above two traits. These traits seem to be due to interaction between chromosomal and cytoplasmic elements. (4) These traits are not expressed in males. (5) The increase in recombination frequency seems to be limited to the centric heterochromatin. ——It is suggested that heterochromatic recombination is one of the traits associated with the *I-R* system of hybrid dysgenesis in *D. melanogaster*.

IT has been widely accepted that practically no meiotic crossing over occurs in the heterochromatic regions of *Drosophila melanogaster*, although mitotic recombination may take place occasionally in heterochromatic as well as in euchromatic regions of the chromosomes (WALEN 1964). During the course of a study on the Segregation Distorter (*SD*) system in *D. melanogaster*, however, the present author found that, under a certain specific genotypic condition, crossing over indeed occurred in nontrivial frequencies within the centric heterochromatin of chromosome *2* (HIRAIZUMI, MARTIN and ECKSTRAND 1980). Further studies on this subject have since been carried out in this laboratory, and the results thus far obtained strongly suggest that heterochromatic crossing over is in fact one of the traits associated with the so-called *I–R* system of hybrid dysgenesis in *D. melanogaster* (see BREGLIANO *et al.* 1980 for review).

MATERIALS AND METHODS

Strains and chromosome lines of *D. melanogaster* used in the present study are listed below.

(1) *cn bw*: a standard strain containing second chromosomes marked with the recessive eye color mutants *cn* (cinnabar eye color, *2R*–57.5) and *bw* (brown eye color, *2R*–104.5). This strain has been classified in this laboratory as *M* type in the *P–M* system and weak R type in the *I–R* system of hybrid dysgenesis.

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(2) *lt stw*^{3}: a strain containing second chromosomes marked with the recessive mutants *lt* (light eye color, *2L*–55.0; this locus is in the centric heterochromatin of *2L* and *stw*^{3} (an allele of *stw*, straw body color, *2R*–55.1). This strain has been classified in this laboratory as *M*– and *R*–type in the two systems of hybrid dysgenesis described in (1) above.

(3) *al b sp; ve st ca*: a strain containing second chromosomes marked with the recessive mutants *al* (aristaless, *3L*–0.01), *b* (black body color, *2L*–48.0) and *sp* (speck, *2R*–107.0), and third chromosomes marked with the recessive mutants *ve* (veinlet, *3L*–0.2), *st* (scarlet eye color, *3L*–44.0) and *ca* (claret eye color, *3R*–100.7). This strain has been classified in this laboratory as *M*– and *I*–type in the two systems of hybrid dysgenesis described in (1). In this report, this strain will be abbreviated as *al b sp*.

(4) *al dp b pr cn c px sp*: a strain containing second chromosomes marked with the recessive mutants, *al, dp* (dumpy wing, *2L*–13.0), *b, pr* (purple eye color, *2L*–54.5), *cn, c* (curved wing, *2R*–75.5), *px* (plexus wing vein, *2R*–100.5) and *sp*. This strain has been classified in this laboratory as *M*– and *R*– or *N*–type in the two systems of hybrid dysgenesis described in (1).

(5) *In(2LR) SM5*: a multiply inverted chromosome *2* balancer. This chromosome line has been maintained in this laboratory by repeated backcross to the standard *cn bw* females for many years. In this report, this chromosome will be referred to as *SM5*.

(6) *R(SD) cn-14s* a chromosome *2* line having the genotype *Sd Rsp*^{i}, where the *Rsp* locus is located in the centric heterochromatin of *2R* (for information about the elements of the *SD* system, see GANETZKY 1977; HIRAIZUMI, MARTIN and ECKSTRAND 1980). This chromosome carries the recessive marker *cn* and shows a moderate degree of segregation distortion when made heterozygous with the *cn bw* chromosome in the male. So far, no structural abnormality has been found in this chromosome. This line has been kept in this laboratory by repeated backcross to the standard *cn bw* females for more than 10 years. For the origin of this chromosome, see HIRAIZUMI and NAKAZIMA (1967). In this report, this chromosome will be abbreviated as *cn–14*.

(7) *R(++)bw-1*: a chromosome *2* line of the genotype *Sd Rsp*$^{s-s}$, marked with the recessive mutant *bw*. This chromosome was derived from a *cn-14/al dp b pr sp* female through recombination between the *pr* and *cn* loci (as a recombinant, *pr*+ *cn*+); *bw* was added later. Since then, the chromosome has been maintained in this laboratory by repeated backcross to standard *cn bw* females. More detailed information on this chromosome can be found in MARTIN and HIRAIZUMI (1979).

(8) *R(SD)cn-14-(2)* and *-(7)*: chromosome 2 lines isolated from a bottle population cage that was initiated with 50% *cn-14* and 50% *cn bw* chromosomes in 1967 and has been maintained since in this laboratory through mass transfer about every 3 weeks. *R(SD)cn-14-(2)* appears to be *Sd Rsp*^{i}; whereas, *R(SD)cn-14-(7)* is *Sd*+ *Rsp*^{s}. Both of these chromosomes carry the marker *cn*. They will be abbreviated in this report as *cn-14(2)* and *cn-14(7)*, respectively.

RESULTS

Demonstration of heterochromatic recombination: Females collected from the *lt stw*^{3} stock were mated, in four separate groups, to (1) *cn-14/SM5*, (2) *cn-14(2)/SM5*, (3) *al b sp* and (4) *R(++)bw-1/SM5* males. Then, non-*SM5* F_1 females were collected from each of the above matings and mated, at 1.0 to 1.5 days of age, to *lt stw*^{3} males 2 to 4 days old. For the F_1 females of mating types (1) through (3) above, *i.e.*, *lt stw*^{3}*/cn-14*, *lt stw*^{3}*/cn-14(2)* and *lt stw*^{3}*/al b sp* females, respectively, 2 females and 6 or 7 males were placed in a vial and kept together for 5 days, and then transferred to the second vial for another 5 days. Transfers were continued until the 5th brood. For the F_1 females of mating type (4), *lt stw*^{3}*/R(++)bw-1*, a single female, 1 to 1.5 days old, and 6–7 males, 2 to 4 days old, were placed in a vial, and the same transfer procedure was applied as shown for mating types (1) through (3). Two other genotypes of females, *lt*

stw^s/*cn bw* and *lt stw*^{s}/*al dp b pr cn c px sp*, were also examined under the similar mating scheme and transfer conditions as shown for the mating types (1) through (3), except that transfer was made only through the second before the parents were discarded. Results are summarized in Table 1.

It can clearly be seen in Table 1 that recombination between *lt* and *stw*^{s} occurred, in the first four genotypes, in much higher frequencies than in the last two genotypes (hereafter, these will be called control genotypes), which appeared to be comparable to the standard map distance of 0.0010.

There are two other points to be mentioned regarding this table. First, the frequency of recombination decreased very consistently in each of the first four genotypes as the females got older. Second, the number of progeny produced per brood was small for the first brood, but it tended to increase relatively sharply in the second and later broods. These observations suggest that there is a correlation between these two traits. Note that there was little or no reduction in progeny production in the first brood of the two control genotypes.

The data for *R*(++)*bw-1*/*lt stw*^{s} females presented in Table 1 were those pooled for 24 females tested. Then, the data were divided to show each individual female's record. The results are shown in Table 2.

Table 2 shows that the reduced progeny production in the first brood is consistent for all of the 24 females tested. The data in this table suggest that the number of progeny produced and the recombination frequency are negatively correlated. Accordingly, the correlation coefficient between them was calculated and found to have a highly significant deviation from zero (in the calculation, data for 5 broods were pooled for each female); *i.e.*, $r = -0.7434$, $df = 22$, $p < 0.01$ in parametric tests and $r = -0.7074$, $df = 22$, $p < 0.01$ in Spearman's coefficient of rank correlation after adjusting to ties. This result confirms the previous suggestion that the two traits are related in some way.

Since *stw*^{s} is located in the euchromatic region of the right arm, the region between the *lt* and *stw*^{s} loci actually includes some euchromatin. In order to see if any of the recombinants between *lt* and *stw*^{s} involved a heterochromatic exchange event, some of the *lt* and *stw*^{s} recombinants were examined for their allelic status at the *Rsp* locus, which has been mapped in the centric heterochromatin of *2R* (GANETZKY 1977). This was done by making each of the recombinant chromosomes heterozygous in males with the appropriate chromosome chosen from the group *cn bw*, *R*(++)*bw-1* and *cn-14*. As was shown by HIRAIZUMI, MARTIN and ECKSTRAND (1980), it is possible to determine the kind of alleles at the *Rsp* locus by examining patterns of segregation frequency from males of the above genotype. Based upon the result, it is possible to determine whether the exchange event occurred between *lt* and *Rsp* (*i.e.*, within heterochromatin) or between *Rsp* and *stw*^{s} (in a hetero- or euchromatic region). Results are shown in Table 3.

Table 3 indicates that approximately ½ of the exchange events between *lt* and *stw*^{s} took place between *lt* and *Rsp*, in the heterochromatic region. Considering the fact that the region *Rsp* and *stw*^{s} still includes heterochromatin, it seems reasonable to conclude that at least ½, and perhaps the majority, of recombinations between *lt* and *stw*^{s} were due, in fact, to exchange events in the hetero-

TABLE 1

Recombination frequencies between lt *and* stw^3 *in females of the 6 genotypes shown*

Genotype of female	n	Brood 1 R	Brood 1 N	Brood 2 R	Brood 2 N	Brood 3 R	Brood 3 N	Brood 4 R	Brood 4 N	Brood 5 R	Brood 5 N	Total R	Total N	θ for brood 1,2
$\frac{lt\ stw^3}{cn\text{-}14}$	16	16	1237	12	1962	5	2495	2	2123	2	2909	37	10726	0.0088
(θ)		(0.0129)		(0.0061)		(0.0020)		(0.0009)		(0.0007)				
$\frac{lt\ stw^3}{cn\text{-}14(2)}$	16	9	752	16	2831	9	2421	2	1857	1	1503	37	9364	0.0070
(θ)		(0.0120)		(0.0057)		(0.0037)		(0.0011)		(0.0007)				
$\frac{lt\ stw^3}{al\ b\ sp}$	10	0	17	3	186	4	392	4	505	3	411	14	1511	0.0148
(θ)		(0.0000)		(0.0161)		(0.0102)		(0.0079)		(0.0073)				
$\frac{lt\ stw^3}{R(++)bw\text{-}1}$	24	2	112	20	1116	19	1932	4	2083	1	1923	46	7166	0.0179
(θ)		(0.0179)		(0.0179)		(0.0098)		(0.0019)		(0.0005)				
$\frac{lt\ stw^3}{cn\ bw}$	10	0	940	2	1154	—		—		—		2	2094	0.0010
(θ)		(0.0000)		(0.0017)										
$\frac{lt\ stw^3}{al\ dp\ b\ pr\ cn\ c\ px\ sp}$	10	1	732	2	782	—		—		—		3	1514	0.0020
(θ)		(0.0014)		(0.0026)										

n: number of replications, R: number of recombinants, N: number of progeny, θ recombination frequency. In all cases, cytoplasm was from *lt* stw^3 stock.

TABLE 2

Recombination frequencies between lt *and* stw^3 *in* R(++)bw-1/lt stw^3 *females whose mothers were from* lt stw^3 *stock*

Individual female	Brood 1		2		3		4		5		Total		
	R	*N*	*R*	*N*	*R*	*N*	*R*	*N*	*R*	*N*	*R*	*N*	θ
8	0	0	1	11	3	46	1	62	0	18	5	137	0.0365
3	0	10	2	37	1	33	0	10	0	0	3	90	0.0333
9	0	0	3	24	2	58	1	86	1	92	7	260	0.0269
6	0	8	1	53	4	86	0	95	0	82	5	324	0.0154
7	1	21	2	46	1	79	1	88	0	106	5	340	0.0147
11	0	0	1	8	1	61	1	80	0	100	3	249	0.0120
2	0	0	1	27	1	76	0	84	0	1	2	188	0.0106
5	1	12	2	90	0	107	0	99	0	25	3	333	0.0090
14	0	1	1	17	1	66	0	75	0	113	2	272	0.0074
21	0	0	1	41	1	83	0	98	0	114	2	336	0.0060
17	0	0	0	52	1	94	0	68	0	31	1	245	0.0041
16	0	0	0	2	1	45	0	101	0	105	1	253	0.0040
15	0	1	1	36	0	88	0	72	0	77	1	274	0.0036
24	0	3	0	28	1	63	0	101	0	88	1	283	0.0035
22	0	4	1	56	0	102	0	98	0	53	1	313	0.0032
20	0	3	0	59	1	92	0	85	0	89	1	328	0.0030
19	0	1	1	54	0	105	0	97	0	105	1	362	0.0028
13	0	0	1	60	0	110	0	103	0	110	1	383	0.0026
1	0	15	1	98	0	100	0	99	0	82	1	394	0.0025
4	0	22	0	56	0	94	0	95	0	115	0	382	0.0000
10	0	1	0	66	0	82	0	96	0	106	0	351	0.0000
12	0	0	0	42	0	76	0	96	0	99	0	313	0.0000
18	0	1	0	57	0	98	0	100	0	116	0	372	0.0000
23	0	9	0	96	0	88	0	95	0	96	0	384	0.0000
Total	2	112	20	1116	19	1932	4	2083	1	1923	46	7166	
θ	0.0179		0.0179		0.0098		0.0019		0.0005				

R: number of recombinants, *N*: number of progeny, θ: recombination frequency.

TABLE 3

Number of recombinants between lt *and* Rsp *(I) and between* Rsp *and* stw^3 *(II) generated in females of the genotypes shown*

Genotype of female	Brood 1		2		3		4–5		Total	
	I	II	I	II	I	II	I	II	I	II
$\frac{lt\ stw^3}{cn\text{-}14}$	3	7	2	3	2	1	0	1	7	12
$\frac{lt\ stw^3}{cn\text{-}14(2)}$	1	2	6	3	0	4	0	0	7	9
$\frac{lt\ stw^3}{R(++)bw\text{-}1}$	0	1	0	0	2	0	3	1	5	2
Total	4	10	8	6	4	5	3	2	19	23

chromatin. Two recombinants obtained from control females were also examined. In both cases, the exchange occurred between the *Rsp* and *stw*^{3} loci.

Influence of cytoplasm: In all of the experiments presented in the previous section, the females in parental matings were chosen from the *lt stw*^{3} stock. In order to determine if there were any effect of cytoplasmic factors characteristic of the *lt stw*^{3} stock, *lt stw*^{3} males from the *lt stw*^{3} stock were mated to (1) *R*(++) *bw-*^{1}*/SM5*, (2) *cn-14(7)/SM5*, (3) *al b sp* and, as a control, to (4) *cn bw* females. Then, non-*SM5* F_1 females were collected from each of the above matings and mated to *lt stw*^{3} males under the same conditions as shown in the mating types (1) through (3) in the previous section, except that only two broods, instead of five, were examined. Results are shown in Table 4.

As can be seen in this table, the frequency of recombination in the *lt-stw*^{3} region was reduced dramatically in the reciprocal cross. It should be mentioned also that there was little, if any, indication of sterility of young females. These results clearly support the idea that cytoplasmic factors characteristic of the *lt stw*^{3} stock play an important role in inducing heterochromatic recombination.

Since the control genotypes shown in Table 1, in which the cytoplasm came from the *lt stw*^{3} stock, did not show any significant increase in heterochromatic recombination, it can be concluded that the traits are due to some kind of inter-

TABLE 4

Recombination frequency between lt *and* stw^3 *in females of the genotypes shown*

Genotype of female	Maternal genotype	*n*	*R*	*N*	θ
$\frac{lt\ stw^3}{R(++)bw\text{-}1}$	*lt stw*^{3}	24	22	1228	0.0179
$\frac{lt\ stw^3}{R(++)bw\text{-}1}$	$\frac{R(++)bw\text{-}1}{SM5}$	24	3	4075	0.0007
$\frac{lt\ stw^3}{cn\text{-}14(7)}$	*lt stw*^{3}	24	9	500	0.0180
$\frac{lt\ stw^3}{cn\text{-}14(7)}$	$\frac{cn\text{-}14(7)}{SM5}$	16	6	1410	0.0043
$\frac{lt\ stw^3}{al\ b\ sp}$	*lt stw*^{3}	10	3	203	0.0148
$\frac{lt\ stw^3}{al\ b\ sp}$	*al b sp*	10	0	1348	0.0000
$\frac{lt\ stw^3}{cn\ bw}$	*lt stw*^{3}	10	2	2094	0.0010
$\frac{lt\ stw^3}{cn\ bw}$	*cn bw*	16	1	2335	0.0004

Records for the first and second broods were pooled. *n*: number of replications, *R*: number of recombinants, *N*: number of progeny, θ: recombination frequency.

action between element(s) characteristic of the responsible chromosomes *2*, and cytoplasmic factors or states characteristic of the *lt stw*^{3} stock.

Sterility of young females: Young female sterility was clearly demonstrated in the previous section, but, since no egg counts were conducted, it was not clear whether the reduced number of progeny produced was due to the reduced number of eggs layed or to reduced hatchability of eggs. The following experiment was conducted to clarify this point. Reciprocal parental matings for two mating types, *R(++)bw-1/SM5* × *lt stw*^{3} and *cn-14(7)/SM5* × *lt stw*^{3}, were made, and non-*SM5* F_1 females were collected from each of the four matings. Then, each of these F_1 females, 1 to 1.5 days old, was mated single to three *cn bw* males, 2 to 4 days old, kept in a vial for one day, and then transferred to the second vial for another day for the second brood. This transfer procedure was continued until the fourth brood. Although exact records were not kept, matings appeared to occur in nearly the same frequencies among the four sets of matings. The total number of eggs layed and progeny emerged for each vial were recorded, and the results are shown in Table 5.

Clearly, young female sterility is due to unhatchability of eggs produced, not to reduced egg laying. It should be noted here that, in practically all cases, the color of the unhatched eggs remained white for a period of over 1 week, suggesting that no cleavage divisions occurred in those eggs.

Influence on recombination frequency outside the lt-stw^3 *region*: It was of special interest to find out if the increase in recombination frequency was restricted to centric heterochromatin, or if regions outside the *lt-stw*^{3} region were affected also. The following experiment was conducted to answer this question. Females of the genotype *al dp b pr cn c px sp/R(++)bw-1* were mated to *al dp b pr cn c px sp/SM5* males, from which one recombinant, *R(al*$^+$ *dp b pr cn c px sp)*, was isolated. This recombinant, upon testing after several generations of backcrossing to the standard *cn bw* females, was found to induce recombination between *lt* and *stw*^{3} in a frequency (0.0180 for two broods combined) comparable to that induced by the *R(++)bw-1* chromosome (0.0179 for two broods combined). Accordingly, *R(al*$^+$ *dp b pr cn c px sp)/SM5* males were mated to *lt stw*^{3} females to obtain *lt stw*^{3}*/R(al*$^+$ *dp b pr cn c px sp)* F_1 females. These females, 1 to 1.5 days old, then were mated to *al dp b pr cn c px sp/SM5* males, 2 to 4 days old, and their non-*SM5* progeny were scored for recombination frequency in each marked region. A control mating was also made by replacing the *R(al*$^+$ *dp b pr cn c px sp)* with the original *al dp b pr cn c px sp* chromosome. Parents were kept in a vial for 5 days, transferred to the next vial for another 5 days, and then discarded. Results for the two broods pooled are summarized in Table 6.

Although the number of progeny scored was not very large, Table 6 indicates that the frequency of recombination in each corresponding region (other than that of *lt-stw*^{3}, of course) along the entire chromosome *2* remained comparable between control and experimental genotypes. Thus, the effect on increased recombination frequency is mainly restricted to the heterochromatic region.

Influence in males: Males, 1 to 1.5 days old, of the genotype *R(++)bw-1/lt stw*^{3}, whose mother was *lt stw*^{3}, were individually mated to six young *lt stw*^{3}

TABLE 5

Results of hatchability test for females of the genotypes shown

Genotype of female	No. of females tested	Maternal genotype	Brood 1 E	Brood 1 A	Brood 2 E	Brood 2 A	Brood 3 E	Brood 3 A	Brood 4 E	Brood 4 A	Total E	Total A	A/E
$\frac{lt\ stw^3}{R(++)bw\text{-}1}$	10	*lt stw*^{3}	182	0	212	0	120	4	114	5	628	9	0.014
$\frac{lt\ stw^3}{R(++)bw\text{-}1}$	10	$\frac{R(++)bw\text{-}1}{SM5}$	120	97	121	99	94	75	104	91	439	362	0.825
$\frac{lt\ stw^3}{cn\text{-}14(7)}$	9	*lt stw*^{3}	160	0	98	0	96	0	93	0	447	0	0.000
$\frac{lt\ stw^3}{cn\text{-}14(7)}$	9	*cn-14(7)*	113	86	113	99	116	104	110	100	452	389	0.861

E: number of eggs layed, *A*: number of adult progeny recovered.

TABLE 6

Recombination frequencies in marked regions of chromosome 2 in females of the genotypes shown

Genotype of female	No. of progeny	Marked regions						
		al–dp	dp–b	b–pr	pr–cn	cn–c	c–px	px–sp
lt stw^3 / *al dp b pr cn c px sp*	929	133 (0.143)	295 (0.318)	45 (0.048)	17 (0.018)	183 (0.197)	258 (0.278)	70 (0.075)
lt stw^3 / *al*$^+$ *dp b pr cn c px sp*	625	—	197 (0.315)	26 (0.042)	15 (0.024)	115 (0.184)	146 (0.234)	47 (0.075)
From standard map		0.130	0.355	0.060	0.030*	0.180	0.250	0.065

Maternal parents of the tested females were from the *lt stw*^{3} stock.
* Standard map distance for this region is 3% but, in several laboratories, the actual distance has been found to be in the range of 1.0–1.5%.

females, kept in a vial for 7 days and then discarded. A total of 50 matings were made, producing a total of 2014 progeny. All of those were parental type, and there was no recombinant between the *lt* and *stw*^{3} loci. Thus, the effect seems to be restricted to females only, with no effect seen in males.

DISCUSSION

When heterochromatic recombination was first noted (HIRAIZUMI, MARTIN and ECKSTRAND 1980), it was thought that it could be a trait associated with either one of the elements in the *SD* system of *D. melanogaster*. The present study clearly ruled out this possibility, since heterochromatic recombination could be induced without any of the elements in the *SD* system. The observations described in this report seem to suggest, rather, that the phenomenon in question is one of the traits associated with the *I–R* system of hybrid dysgenesis in *D. melanogaster*. As shown in Table 1, the F_1 females of the mating *lt stw*^{3} *(R;M)* female × *al b sp (I;M)* male showed increased frequencies of recombination between the *lt* and *stw*^{3} loci, and this suggested that heterochromatic recombination is a trait associated with the *I–R* system of hybrid dysgenesis, although the other system, *P–M*, may have a similar effect. This possibility could be examined critically if a strain of *R;P* type were available, but such a strain has not yet been found. An alternative and perhaps easier way might be to construct a heterozygous female of *I;M* type containing a chromosome *2* marked with the *lt* and *stw*^{3}. This subject is left for future studies.

Although a detailed experiment to map the position of the element or elements that interact with cytoplasm and cause heterochromatic recombination has not yet been completed, it is obvious that the element(s) should be located in chromosome *2*. The fact that the *R(al*$^+$ *dp b pr cn c px sp)* recombinant from *R*(++) *bw-1/al dp b pr cn c px sp* females induced almost the same frequency of recombination between *lt* and *stw*^{3} as was induced by the original *R*(++)*bw-1* chromosome suggests that one element is located somewhere between the *al* and *dp* loci, although information available at present cannot rule out the possi-

bilities that there can be additional elements located outside of the *al* and *dp* region or that the *al*$^+$ *dp b pr cn c px sp* chromosome gained its ability to induce heterochromatic recombination through some mechanism other than crossing over, such as chromosome contamination (PICARD 1976).

Whether heterochromatic recombination is of meiotic or premeiotic origin is an interesting question, but the amount of information at hand does not allow a definite conclusion.

Certainly, information obtained thus far is limited. Many questions on the phenomenon of heterochromatic recombination reported in this study and questions on "hybrid dysgenesis" in general remain wide open for future studies. The present author hopes that further investigations on heterochromatic recombination and its modifying system will provide some insight toward understanding the genetic basis of hybrid dysgenesis—breakdown in the genomic (chromosomal and cytoplasmic) balances of two differently co-adapted populations through hybridization—which, in turn, will provide information on how co-adapted systems develop in a population.

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