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Gene conversion in higher organisms: Non-reciprocal recombination events at the rosy cistron in *Drosophila melanogaster**

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SUMMARY

Analysis of a series of exceptional ry^+ half-tetrads, produced in mass matings involving rosy mutant heterozygous half-tetrads, provides rigorous demonstration of the occurrence of non-reciprocal as well as reciprocal recombination events within the rosy cistron of *Drosophila melanogaster*. Inferences about allele recombination drawn from this and other studies in Drosophila provide a strong argument that gene conversion occurs as a regular event in higher eukaryotes.

1. INTRODUCTION

Current models of gene conversion (Boon & Zinder, 1969; Hastings & Whitehouse, 1964; Holliday, 1964; Paszewski, 1970; Whitehouse, 1963) focus upon the non-reciprocal nature of intracistronic exchange events first observed in tetrad analysis in *Neurospora* (Mitchell, 1955), and subsequently confirmed in other fungal systems. In higher eukaryotes, such as *Drosophila melanogaster*, observations which may be inferred to reflect conversion events have been reported on more than several occasions (Baillie, Astell & Scholefield, 1966; Chovnick, 1958, 1961; Chovnick, Lefkowitz & McQuinn, 1956; Finnerty, Duck & Chovnick, 1970; Green, 1960; Hexter, 1963; Welshons & von Halle, 1962). Rigorous confirmation of these events as conversions has awaited the development of appropriate genetic systems for systematic investigation. Just such experimental systems have been developed in this laboratory, and have been the subject of prior reports (Ballantyne, Chovnick & Baillie, 1970; Chovnick, Ballantyne, Baillie & Holm, 1970; Chovnick, Ballantyne & Holm, 1970; Smith, Finnerty & Chovnick, 1970*a*, *b*). The present report provides additional information gathered from a study of recombination between separable mutants of the rosy cistron (*ry*: 3–52·00), clearly demonstrating the occurrence of non-reciprocal recombination events, as well as reciprocal events, within the rosy cistron.

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Fig. 1 presents a map of the proximal third of the right arm of chromosome 3 of *D. melanogaster* indicating the location of rosy, the centromere, and other markers used in the study (Lindsley & Grell, 1967). In addition, Fig. 1 presents a summary map of separable sites within the rosy cistron obtained from prior random strand mapping experiments (Chovnick, 1966). These earlier mapping experiments utilized a system which selected for survival only those progeny receiving a single (or odd-numbered multiple) meiotic exchange product between markers flanking the rosy cistron, and consequently suppressed observations on conversion.

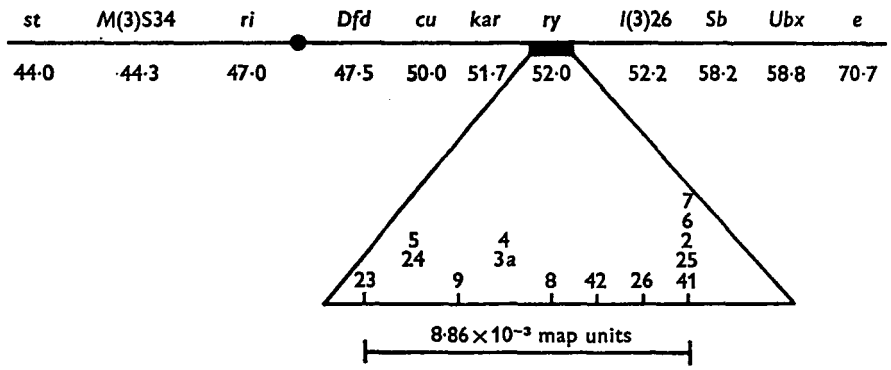

Fig. 1. A genetic map of the rosy region of chromosome 3 indicating the location of various mutants used in this study and summarizing the genetic fine structure of the rosy cistron.

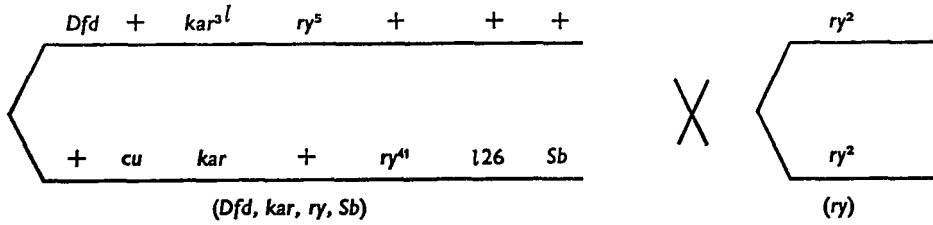

Fig. 2. The genetic composition of the half-tetrads in the cross which yielded the exceptional ry^+ progeny, the subject-matter of this report.

Recently, this laboratory turned to the use of compound-autosomes in order to re-examine recombination events between rosy mutants in half-tetrads. The feasibility of autosomal half-tetrad analysis involving mass matings has been demonstrated (Baldwin & Chovnick, 1967), and pertinent features of the meiotic behaviour of these chromosomes are described elsewhere (Baldwin & Chovnick, 1967; Holm, Deland & Chovnick, 1967; Holm, 1969). Large-scale half-tetrad experiments, involving compound-3 stocks heterozygous for separable rosy mutants as well as non-selective flanking markers, were carried out on a purine enriched selective medium (Finnerty, Baillie & Chovnick, 1970). In such medium, rosy mutant homozygotes and heterozygotes, which lack the activity of the enzyme xanthine dehydrogenase, are unable to complete development, and only pheno-

typically ry^+ zygotes survive. A detailed discussion of these experiments is presented elsewhere (Chovnick, Ballantyne, Baillie & Holm, 1970), and only those features essential to the present report are reviewed. Mass reciprocal crosses of parents of the genetic composition indicated in Fig. 2 yielded cultures rich in larval growth, but only rare phenotypically ry^+ progeny survived. Such progeny exhibit the following features: (1) They arise as unclustered products of oogenesis, and never from spermatogenesis. (2) They appear as progeny of mutant females, heterozygous for recombinationally separable rosy mutants, and not from mutant homozygotes. This point is documented by the absence of ry^+ half-tetrad derivatives of the ry^2 homozygous parent (Fig. 2), as well as homozygous controls involving the mutant alleles ry^5 and ry^{41}.

Table 1. *Genetic composition of the* ry$^+$ *half-tetrads which are non-recombinant for immediate flanking markers*

Half-tetrad genotype						No.	Diagnosis
Dfd	+	*kar*^{3l}	*ry*^{5}	+	+	10	Conversion-*ry*^{41}
+	*cu*	*kar*	+	*l26*	*Sb*		
Dfd	+	*kar*^{3l}	+	+	+	1	Conversion-*ry*^{5}
+	*cu*	*kar*	*ry*^{41}	*l26*	*Sb*		
Dfd	+	*kar*^{3l}	+	+	*Sb*	1	Conversion-*ry*^{5}
+	*cu*	*kar*	*ry*^{41}	*l26*	+		Crossover, *l26-Sb*

The ry^+ exceptional half-tetrads were subjected to detachment experiments which produced a population of 15 to 25 detached arms for each exceptional half-tetrad. Subsequent experiments were carried out on each detachment, and the analysis of each group of detachments permitted classification of the half-tetrad from which they derived. Major features of the analysis of the ry^+ half-tetrads are: (1) For each surviving ry^+ half-tetrad, a series of detached arms falls into two classes with respect to the rosy cistron, and these reflect the two strands of the half-tetrad. Invariably, one strand is ry^+ as measured by its effect on eye colour and enzyme activity, and the other is mutant. (2) Analysis of the flanking marker distribution of each ry^+ half-tetrad permits its classification into one or another of two groups. One group consists of two classes of ry^+ half-tetrads, whose flanking marker distribution suggests their origin as classical single exchanges between the two mutants, ry^5 and ry^{41}, taking place in oogenesis in the heterozygote. Fig. 3 illustrates the two classes of single exchanges which are expected to occur with equal frequency on such a model, and the resulting ry^+ survivors. Class A exchanges involve two non-sister chromatids destined to be attached to the same centromere at the completion of meiosis, while Class B exchanges involve non-sister chromatids destined to be attached to different centromeres at the completion of meiosis. These two classes of ry^+ half-tetrads did, in fact, arise in approximately equal numbers (6:5). The second group of ry^+ half-tetrads fell into three classes on the basis of flanking marker distribution, and these data are summarized

in Table 1. Clearly, these 12ry^+ half-tetrads, representing approximately 1/2 of the total of exceptional ry^+ half-tetrads, defy explanation in terms of classical single exchanges within the rosy cistron. We shall refer to the process which gave rise to this second group of half-tetrads as gene conversion, and the specific product of such an event will be referred to as a convertant. For the moment, let us restrict our definition of conversion to operational terms. Thus, we are dealing with an unspecified event which leads to the 'conversion' of a rosy mutant allele to a ry^+ allele. At this point, it is distinguished from classical allele recombination only in that it takes place unaccompanied by exchange for the closely linked flanking markers. One group of 10 ry^+ half-tetrads, diagnosed as ry^{41} convertants (row 1,

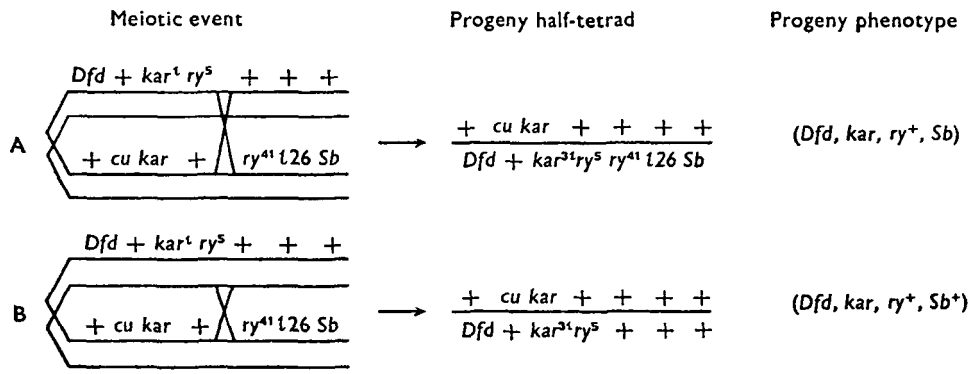

Fig. 3. Classical crossing-over between rosy mutants in half-tetrads.

Table 1) exhibits the parental distribution of all markers flanking the rosy cistron. In each half-tetrad of this group, the ry^+ chromosome bears the specific array of flanking markers originally associated with the ry^{41} bearing chromosome, while the *ry* mutant member exhibits the markers associated with the ry^5 bearing chromosome. The remaining two ry^+ half-tetrads (rows 2 and 3, Table 1) are classified as ry^5 convertants. One (row 2, Table 1) exhibits no change from the parental distribution of markers flanking the rosy region. The ry^+ bearing chromosome carries the markers originally associated with the ry^5 bearing chromosome, while the rosy mutant bearing chromosome carries the distribution of markers originally present on the ry^{41} parent chromosome. The last ry^+ half-tetrad (row 3, Table 1), also classified as a ry^5 convertant, exhibits the parental distribution of markers immediately flanking the rosy cistron, but is a recombinant with respect to the more distal flanking markers. Thus on the basis of flanking marker distribution, we have been able to classify these exceptional half-tetrads (Fig. 3 and Table 1) as either classical recombinants or convertant half-tetrads.

The present report considers the following question about these data: one arm of each exceptional ry^+ half-tetrad is mutant with respect to the rosy cistron. What are the specific mutant alleles(s) present on these arms? Thus, one wonders if the mutant bearing arms of the convertant half-tetrads of Table 1 carry one or

the other mutant allele, as suggested in the table, or might both parental mutant alleles be present on some or all of these chromosomes?

2. MATERIALS AND METHODS

All mutants and chromosomes used in the present study are described in a prior report of this series (Chovnick, Ballantyne, Baillie & Holm, 1970), as well as procedures for detachment of compound-3 chromosomes, the selective system mating protocol, and test crosses to assess the distribution of recessive markers flanking the rosy cistron.

3. RESULTS

Table 2 summarizes the results of tests designed to identify the specific rosy mutant allele present on the *Dfd kar*^{3l} *ry* bearing arm of each of the ten half-tetrads classified as conversions of *ry*^{41}. If the events leading to conversion are non-reciprocal, then one expects that the rosy mutant allele present is *ry*^{5}, as indicated in Table 1. In contrast, a negative chromatid interference model for the

Table 2. *Results of rosy mutant identity tests of* Dfd kar^{3l} ry *bearing detachments from ten* ry^{41} *convertant half-tetrads*

(Each test analyses the *ry*$^{+}$ progeny of the cross *Dfd kar*^{3l} *ry/cu kar ry*^{41} *l26 Sb UBx* × *ry*^{2}/*ry*^{2} *males*.)

		Analysis of *ry*$^{+}$ chromosomes						
Dfd kar^{3l} *ry* detachment chromosome no.	Total *ry*$^{+}$ progeny	*cu kar ry*$^{+}$	*cu kar ry*$^{+}$ *l26 Sb*	*Dfd kar*^{3l} *ry*$^{+}$	*cu kar ry*$^{+}$ *l26*	*kar*^{3l} *ry*$^{+}$	*kar ry*$^{+}$ *l26*	Total progeny *N*
VIII-C-16-4	4	1	1	—	2	—	—	169000
VIII-A-30-1	3	2	—	1	—	—	—	110000
VIII-B-25-18	1	1	—	—	—	—	—	136000
VIII-A-15-11	4	—	3	1	—	—	—	129000
VIII-D-9-3	6	1	5	—	—	—	—	197000
VIII-B-7-8	3*	2	—	—	—	—	—	223000
IV-B-21-2	2	1	1	—	—	—	—	140000
XI-C-15-26	3	1	2	—	—	—	—	104000
IV-A-3-1	6	1	1	—	1†	—	1	135000
VIII-B-4-11	2	—	1	—	—	1	—	106000

* Includes one sterile female.

† One member of a cluster of three *ry*^{41} convertants, the other two being *cu kar ry*$^{+}$ *l26 Sb*.

origin of these exceptional half-tetrads predicts that these chromosomes would be double rosy mutants, *ry*^{5} *ry*^{41}. For each half-tetrad to be tested, large scale test crosses of free-third females, heterozygous for a detached *Dfd kar*^{3l} *ry* arm and a chromosome carrying *cu kar ry*^{41} *l26 Sb Ubx*, were carried out and progeny were reared on purine enriched selective medium. Exceptional *ry*$^{+}$ progeny were recovered from each of the ten crosses and the subsequent analysis of flanking

markers of the resulting ry^+ chromosomes is presented in Table 2. Thus, the first row of Table 2 presents the analysis of the test cross involving *a Dfd kar*^{3l} *ry* chromosomal detachment (VIII-C-16-4) from one of the ten exceptional half-tetrads (VIII-C-16) originally classified as a ry^{41} convertant on the basis of flanking marker distribution (Table 1, row 1). Females heterozygous for this chromosome and a *cu kar* ry^{41} *l26 Sb Ubx* chromosome were crossed to ry^2/ry^2 males, and four ry^+ progeny survived on the purine selective medium in a total estimated sample of 169,000 zygotes. Analysis of the flanking markers of the ry^+ chromosomes of the four survivors indicated that one was a recombinant, while the remaining three were ry^{41} convertants.

Following this logic, examination of Table 2 reveals the following: (1) The markers present on all ry^+ chromosomes clearly identify them as products of the heterozygous female parent. (2) With one exception, all ry^+ progeny appeared as rare single individuals, distributed at random among the matings. This observation is consistent with the conclusion drawn earlier (see Introduction) that the event(s) giving rise to the exceptional ry^+ chromosomes take place during oogenesis. (3) The exception consists of one cluster of three ry^+ individuals which appeared in the four broods of a single mass mating involving the IV-A-3-1 detachment chromosome. As indicated in Table 2, the flanking marker analysis of the cluster would classify them as conversions of ry^{41}. In view of (*a*) the exceedingly low frequency of ry^+ progeny resulting from this cross, and (*b*) the classification of all members of the cluster as ry^{41} conversions, the simplest explanation of the origin of this cluster would point to a premeotic gonial event. It should be noted that one member of the cluster also had a subsequent exchange between *126* and *Sb*. (4) Since a control experiment sampling 800000 progeny of ry^{41} homozygous females failed to yield ry^+ exceptional progeny (see footnote, Table 3), it is concluded that the ry^{41} mutant allele is not present on any of the ten *Dfd kar*^{3l} *ry* detachment chromosomes. Moreover, since the only other rosy mutant allele which might be present is ry^5, it is inferred that the mutant bearing arms of the ten ry^{41} convertant half-tetrads, in fact, are non-reciprocal products of the conversion event, and are genetically *Dfd kar*^{3l} ry^5. (5) This conclusion is further supported by a comparison of the data of Table 2 with the prior half-tetrad analysis (see Introduction), as well as a control cross of ry^5/ry^{41} free-third heterozygotes (Table 3). The specific features to be noted in comparison of the ry^+ chromosomes produced in each experiment are: (*a*) the direction of marker recombination among the ry^+ recombinants; (*b*) the relative frequency of recombinants to convertants; and (*c*) the relative frequency of the convertant classes. Thus, in the prior half-tetrad analysis, a 10:2 ratio of ry^{41} to ry^5 convertants was seen. In Table 2, an 18:3 ratio of ry^{41} to ry^5 convertants obtains if one considers the cluster as a single event. The control ry^5/ry^{41} experiment of Table 3 indicates a similar frequency inequality or polarity. The phenomenon of polarity is under investigation and will be reported separately.

Clearly, the experiments described above demonstrate the non-reciprocal nature of the events which gave rise to the half-tetrads previously classified as convertants on the basis of absence of recombination for the immediately flanking markers.

In the original half-tetrad experiment (see Introduction) approximately one half of the ry^+ exceptionals carried half-tetrads whose flanking marker distribution suggested their origin as classical single exchanges between the two mutants, ry^5 and ry^{41} (Fig. 3). According to classical notions about recombination, the Class A exchanges of Fig. 3 should have mutant strands which are double rosy mutants, $ry^5\ ry^{41}$. A detached rosy mutant bearing arm (I-B62-16) of one such half-tetrad (I-B62), carrying the markers *Dfd kar*^{3l} *ry l26 Sb*, has been tested, and the results,

Table 3. *Test of detachment I-B26-16,* Dfd kar^{3l} ry 126 Sb, *involving crosses of the indicated females to homozygous mutant males of either* ry^1/ry^1 *or* ry^2/ry^{2*}

Female parent	Total ry^+ progeny	Analysis of ry^+ chromosomes: *cu kar* ry^+	*cu kar* ry^+ *l26 Sb*	*Dfd kar*^{3l} ry^+	*cu kar* ry^+ *l26* Sb^+	Total progeny *N*
I-B62-16 / ry^5	0	—	—	—	—	975000
I-B62-16 / *cu kar* ry^{41}	0	—	—	—	—	1050000
Dfd + *kar*^{3l} ry^5 + + + + / + *cu kar* + ry^{41} *l26 Sb Ubx*	13	5	5	2	1	440000

I-B62-16 = *Dfd kar*^{3l} ry^5 ry^{41} *l26 Sb*

* No ry^+ exceptions arose in 800000 chromosomes sampled in progeny of homozygotes of *cu kar* ry^{41}/*cu kar* ry^{41}, nor did any arise in 1070000 chromosomes sampled in progeny of ry^5/ry^5 homozygotes.

summarized in Table 3, stand as a control in contrast to the results of Table 2. Large scale test crosses involving free-third females heterozygous for the I-B62-16 chromosome and a chromosome bearing either ry^5 or ry^{41} were carried out following the purine selective system protocol. As indicated (Table 3), these experiments failed to yield ry^+ in approximately 10^6 chromosomes assayed from each heterozygous genotype. Moreover, a control experiment on the frequency of ry^+ chromosomes (both convertants and recombinants) produced by free-third heterozygous ry^5/ry^{41} females provides dramatic support for the conclusion that the I-B62-16 chromosome is a double mutant, $ry^5\ ry^{41}$.

Utilizing the I-B26-16 chromosome, a compound-3 chromosome was constructed which possessed arms of the genotype,

$$\frac{Dfd + kar^{3l}\ \ ry^5 + ry^{41}\ \ l26\ \ Sb.}{+ cu\ kar\ \ + ry^{42} +\ \ +\ \ +}$$

A three-point intracistronic half-tetrad experiment was then carried out. This experiment, described in detail in a prior report (Chovnick, Ballantyne, Baillie & Holm, 1970), succeeded in yielding five ry^+ exceptional progeny which were confirmed to be ry^{42} conversions. Each half-tetrad possessed a ry^+ arm bearing the

specific array of flanking markers originally associated with the ry^{42} bearing chromosome, as well as a rosy mutant bearing arm carrying all of the flanking markers originally associated with the I-B62-16 parental chromosome.

It is pertinent to question the rosy mutant composition of the rosy mutant bearing arms of each of these five convertant half-tetrads. If the events leading to the production of these ry^{42} convertant half-tetrads are non-reciprocal, as suggested by the results described above, these strands should be $ry^{5} + ry^{41}$. In contrast, the model of high negative interference would predict that they be $ry^{5}\ ry^{42}\ ry^{4}$.

Table 4. *Results of rosy mutant identity tests* Dfd kar^{3l} ry 126 Sb *bearing detachments from five* ry^{42} *convertant half-tetrads*

(Each test analyses the ry^{+} progeny of the cross *Dfd kar^{3l} ry l26 Sb*/ry^{42} females × ry^{2}/ry^{2} males.*)

Detachment chromosome number	Total ry^{+} progeny	Analysis of ry^{+} chromosomes			Total progeny sampled
		+ + ry^{+} + +	*Dfd kar^{3l} ry^{+} l26 Sb*	+ *kar^{3l} ry^{+} l26 Sb*	
IX-A-5-18	2	2	—	—	164000
IX-B-16-15	2	2	—	—	303000
IX-A-24-14	1	—	1	—	199000
IX-A-15-1	1	1	—	—	301000
IX-A-4-23	3	1	1	1	199000

* No ry^{+} exceptions arose in 1376000 chromosomes sampled in progeny of homozygotes of *cu kar* ry^{42}/*cu kar* ry^{42}, nor did any arise in 1910000 chromosomes in progeny of ry^{2}/ry^{2} homozygotes.

Large scale test crosses were carried out on a rosy mutant bearing arm of each of the five exceptional ry^{42} convertant half-tetrads. Free-third females, heterozygous for a detached rosy mutant bearing arm, *Dfd kar^{3l} ry l26 Sb* and a chromosome carrying ry^{42}, were mated to ry^{2}/ry^{2} males and progeny were reared on purine enriched selective medium. Exceptional ry^{+} progeny were recovered from each of the five crosses, and the subsequent analysis of flanking markers of the ry^{+} chromosomes is presented in Table 4. Following the logic used in analysis of the previous identity tests, the results of Table 4 confirm the conclusion drawn above, that the events giving rise to the convertant half-tetrads are non-reciprocal in nature. One additional point emerges from these three-point intracistronic experiments. Three of the nine ry^{+} chromosomes recovered and analysed bear the flanking markers (*Dfd*|*kar^{3l} ry^{+} l26 Sb*) originally associated with the double mutant, $ry^{5}\ ry^{41}$ (Table 4). Applying the logic that has been followed throughout this report, these ry^{+} exceptionals would seem to be double convertants.

4. DISCUSSION

The present report completes the analysis of a series of exceptional ry^{+} half-tetrads produced in mass matings involving rosy mutant heterozygous half-tetrads, and together with prior reports from this laboratory (Ballantyne *et al*

1970; Chovnick, Ballantyne, Baillie & Holm, 1970; Chovnick, Ballantyne & Holm, 1970) provides rigorous demonstration of the occurrence of non-reciprocal, as well as reciprocal recombination events within the rosy cistron.

The present study analyses the ry^+ half-tetrads resulting from mutant heterozygotes involving ry^5 and ry^{41} located at opposite ends of the rosy cistron (Fig. 1). In this system, all conversion events, originally diagnosed on the basis of absence of flanking marker recombination, are non-reciprocal events in terms of the analysis of the mutant strand of each half-tetrad. Moreover, examination of one of the ry^+ half-tetrads which exhibited flanking marker exchange revealed that its mutant strand was the reciprocal double mutant expected on the model of classical recombination. The concordance of the half-tetrad diagnosis based upon flanking markers with that based upon questioning the reciprocality of the event for the rosy cistron mutants stands in contrast to the observations seen in a parallel study of recombination involving maroon-like cistron mutants. In the latter case, a random strand analysis of recombination between maroon-like cistron mutants revealed that approximately half of the *ma-1*$^+$ exceptions exhibited exchange for the flanking markers. Utilizing the flanking marker recombinants, a unique internally consistent, linear, map of the *ma-1* cistron was constructed which corresponds precisely with a complementation map (Finnerty, Duck & Chovnick, 1970). However, a half-tetrad analysis questioning the reciprocality of recombination events in heterozygotes for the most distant *ma-1* alleles revealed that all of the events are non-reciprocal (Smith *et al.* 1970*a*). We suggest that the difference in results observed with the rosy mutants in the present study compared to the maroon-like results reflects upon the length of the genetic interval between the markers under study in each investigation. The recombination map length of the rosy cistron is at least an order of magnitude greater than the maroon-like cistron map length. This comparison is based upon recombination studies involving rosy mutants in standard chromosomes (Chovnick, 1966), while the maroon-like map length is based upon recombination data collected in a homozygous inversion system, specifically used to remove the maroon-like region from any possible centromere effect that might reduce recombination (Finnerty, Duck & Chovnick, 1970). A further observation in support of this argument stems from efforts to produce mutants in both cistrons with X-rays. Although controlled comparative mutation studies were never carried out, our efforts to produce maroon-like mutants free of rearrangements were a dismal failure compared to similar experiments which produced large numbers of rosy mutants.

The following additional inferences about conversion may be drawn from the *Drosophila* work on allele recombination: Like recombination; (1) Conversion occurs in mutant heterozygotes, and not in homozygotes (Chovnick, 1961; Chovnick, Ballantyne, Baillie & Holm, 1970). (2) In addition to demonstrating the occurrence of these events as regular products of meiosis in females, and not in males (Chovnick, Ballantyne, Baillie & Holm, 1970), the present data (Table 2) provide evidence that it occurs in premeiotic, oogonial, mitoses as well. (3) It may be suppressed by heterozygous rearrangements with breaks flanking the immediate

region of interest (Chovnick, 1961). (4) The population of wild-type alleles generated by conversion in various mutant allele heterozygotes are identical to each other and indistinguishable from classical wild-type recombinants as well as a control stock wild-type allele in terms of gene product function (Chovnick, Ballantyne, Baillie & Holm, 1970; Finnerty, Duck & Chovnick, 1970). From this discussion, it is apparent that conversion in *D. melanogaster*, a representative higher eukaryote, is identical to conversion in fungal systems. Indeed, that conversion events are reflexions of the mechanism of recombination, a long standing premise of the fungal investigations, is perhaps most strongly demonstrated by the *Drosophila* work summarized above.

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