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Meiotic pairing behavior of two free duplications of linkage group *I* in *Caenorhabditis elegans*

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Summary. In this paper we describe the meiotic pairing behavior of two free duplications in *Caenorhabditis elegans*. *sDp1* is a duplication of approximately 30 map units of the right portion of linkage group *I* including *unc-74* to *unc-54*. This duplication pairs, recombines, and apparently segregates from one of the normal homologues. A second duplication, *sDp2*, is a duplication of approximately 15 map units of the left portion of the linkage group. *sDp2* was not observed to recombine with the normal homologue but did suppress exchange between the two normal homologues in a *sDp2*/ + +/ *dpy-5 unc-35* heterozygote. Although a number of free duplications have been described previously in *Caenorhabditis elegans*, none of these have been shown to pair with normal homologues. The meiotic behavior of the duplications described in this paper can be understood assuming the existence in *C. elegans* chromosomes of pairing sites of the type described in *D. melanogaster* chromosomes (I. Sandler 1956; Hawley 1980).

Introduction

Homologue pairing and orderly disjunction is the essence of eukaryotic meiosis. The necessary features of homologue pairing are not, however, known. Recent evidence from experiments in *Saccharomyces cerevisiae* indicates that replacing a centromere with a cloned nonhomologous centromere (spindle attachment site) does not interfere with homologue recognition (Clarke and Carbon 1983). On the other hand, evidence from studies on the pairing behavior of certain translocations in *Drosophila melanogaster* (I. Sandler 1956; review by Roberts 1976; Hawley 1980) and *Caenorhabditis elegans* (Rosenbluth and Baillie 1981) indicates that chromosomal features other than DNA homology are required for homologue recognition. These features (which exist in addition to spindle attachment sites) may or may not be intimately associated with what has commonly been called a centromere.

In *D. melanogaster*, I. Sandler (1956) has proposed the existence of specific chromosomal sites which initiate pairing and allow recombination to occur. Hawley (1980) examined the boundaries of recombination suppression in translocations and suggested that these boundaries may correspond to pairing sites, which are necessary for the establishment of proper chromosomal associations for meiotic recombination. The existence of such pairing sites in *C. elegans* chromosomes could explain the meiotic behavior of the translocation, *eT1 (III,V)* (Rosenbluth and Baillie 1981). This translocation exchanges the left half of linkage group (LG) *V* with the right half of LG *III*. In *eT1* heterozygotes, one of the translocated chromosomes always disjoins from LG *V* and the other always from LG *III*. No region along the entire length of the translocated portion confers information about chromosome identity; apparently the information exists within the nontranslocated region. Evidence for the absence of pairing sites in the translocated portion comes from the fact that recombination is absolutely suppressed in this region.

Although numerous free duplications have been described in *C. elegans* (Herman et al. 1979; Hodgkin 1980; Herman et al. 1982), none have been shown to pair with their normal homologues. In this paper, we describe the pairing behavior of a free duplication of LG*I*, *sDp1*, that synapses, recombines, and apparently disjoins from its normal homologue. The occurrence of recombination between a free duplication and a normal homologue provides an opportunity to study the meiotic behavior of this free duplication and to ask which features allow it to pair and recombine. Through this approach an understanding of the mechanisms responsible for normal homologue pairing at meiosis may be achieved.

Materials and methods

Wild-type and mutant strains were maintained and mated on petri plates containing nematode growth medium (NGM), streaked with *Escherichia coli* OP50 (Brenner 1974). Crosses were carried out on 10 × 35 mm petri plates. All experiments were performed at 20° C. The wild-type strain N2 and some mutant strains of *C. elegans* var. Bristol were originally obtained from the MRC stock collection at Cambridge, England. Others were received from the Caenorhabditis Genetics Center at the University of Missouri, Columbia. The following mutant genes and alleles were used:

LG *I*: *bli-3(e579); unc-35(e259); unc-11(e47); unc-73(e936); unc-74(e883); unc-57(e406); unc-38(e264); unc-63(e384); dpy-5(e61); let-76(s80); dpy-14(e188); let-75(s101); unc-15(e73); unc-13(e51); unc-56(e403); dpy-24(s71); lev-11(x12); unc-54(e190)*
LG *II* *dpy-10(e128)*
LG *III* *dpy-1(e1); dpy-18(e364)*

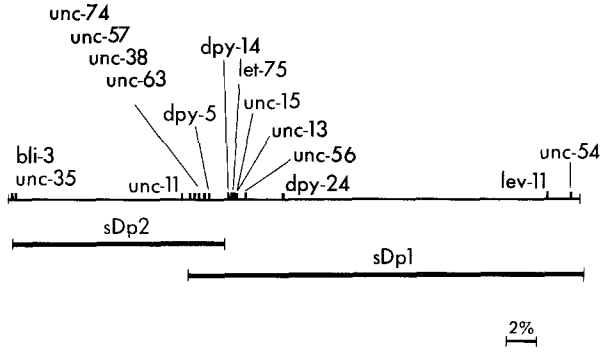

Fig. 1. Genetic map of LG *I* illustrating the duplicated regions

LG *V*: *dpy-11(e224)*
LG *X*: *lon-2(e678)*

Duplications were induced by treating N2 males with 7500 rads of gamma-radiation in a Cobalt-60 source (Gammacell, Atomic Energy of Canada). Treated males were mated to homozygous *dpy-unc (I)* hermaphrodites. The progeny of individual F1's were scored, and two individuals that gave exceptional segregation patterns were recovered. These individuals appeared to carry a suppressor of the mutant phenotypes. Analysis of strains derived from these individuals showed that each carried a duplication for LG *I* genes. These duplications have been named *sDp1(I)* and *sDp2(I)*. The extent of each duplication is illustrated in Fig. 1. Several strains carrying *sDp1* or *sDp2* were constructed and maintained in the course of this study. The canonical strains are BC159 *sDp1/dpy-5(e61) unc-13(e51)/ dpy-5(e61) unc-13(e51);* and KR16 *sDp2/unc-11(e47) dpy-5(e61)/unc-11(e47) dpy-5(e61)*. These strains were maintained by transferring the "wild type" (duplication-bearing) progeny. The chromosomes of *sDp1* and *sDp2*-carrying hermaphrodites were examined cytologically according to a modified procedure of Herman et al. (1976).

Results

As will be shown below, two overlapping duplications carrying wild-type alleles for genes on LG *I* were recovered following treatment with gamma-radiation.

sDp1. The presence of *sDp1* was shown as follows. The strain recovered from gamma-irradiated males (Materials and Methods) produced modified wild types ("Wts") and Dpy-5 Unc-13 hermaphrodites and was maintained by selecting "Wts". Each "Wt" (duplication-bearing individual) produced approximately 115 viable self-cross progeny: "Wts" and Dpy Uncs. Approximately 2% of the progeny were male compared to the expected 0.15% (Hodgkin 1974; Rose and Baillie 1979a). These males have been extensively tested and found to be sterile. A few slow developing inviable larvae and some unhatched eggs were observed. The "Wts" could be heterozygous for the *dpy unc* with a tightly linked lethal on the wild-type chromosome, or homozygous for the *dpy unc* chromosome but carrying in addition the wild-type alleles of both genes on a duplication. That the latter was the case was shown by mating "Wt" hermaphrodites to N2 males. Progeny testing the resulting F1's showed that all had received a *dpy unc* chromosome from the hermaphroditic parent. Self-cross progeny could be distinguished from out-cross on the basis of their segregation ratio. Self-cross F1's segregated less than 2 "Wts" to 1 Dpy Unc. The out-cross F1's fell into two classes. Most segregated approximately 3 "Wts" to 1 Dpy Unc. The rest segregated few Dpy Uncs indicating the presence of a duplication carrying wild-type alleles for *dpy-5* and *unc-13*. In addition to segregating reduced numbers of Dpy Uncs, individuals carrying *sDp1* exhibited a recognizable phenotype ("Wt"), body wall clarity and slow movement.

In order to determine the extent of the duplication, males heterozygous for the allele to be tested were mated to *sDp1*-carrying individuals. From this cross, F1 hermaphrodites were isolated. Only those segregating the male-derived marked chromosome were scored. One of two results was anticipated: the mutation to be tested was suppressed by the presence of a wild-type allele on the duplication, or it was not. As further confirmation that the duplication carried a wild-type allele of the gene being tested, a strain with a "Wt" phenotype and carrying two copies of the mutation was established and maintained. These experiments demonstrated that *sDp1* carried wild-type alleles of the following genes: *unc-74, unc-57, unc-38, unc-63, dpy-5, dpy-14, unc-15, unc-13, unc-56, dpy-24, lev-11* and *unc-54* (Fig. 1). Therefore, *sDp1* extends from this breakpoint to the right end of LG *I*, a distance of approximately 30 map units.

The ease with which both normal homologues were replaced with other LG *I* marked chromosomes proved that *sDp1* was not physically linked to LG *I*. In order to investigate linkage to other chromosomes, alleles of *dpy-10(II), dpy-18(III), dpy-4(IV), dpy-11(V)* or *lon-2(X)* were each introduced from heterozygous males as markers into the strain, *sDp1/ unc-13/ unc-13*. Since the duplication is homozygous lethal, linkage would be detected by a wild type to Dpy (or Lon) progeny ratio of 2:1. By scoring the progeny of F1 outcross individuals, independent segregation of *sDp1* from all chromosomes was established. This result was subsequently confirmed by staining meiotic chromosomes with Hoechst 33258 and observing with fluorescent microscopy a fragment in addition to the normal six meiotic pairs (Fig. 2).

Evidence exists for the pairing of *sDp1* with a normal *I* homologue. In the strain *sDp1/ dpy-5 unc-54/ dpy-5 unc-54*, recombination between the duplication and either of the two normal homologues in the *dpy-5 unc-54* interval occurred frequently (Table 1). In the control, the observed ratio of Dpys to Wts across this interval was 0.17. In the *sDp1* strain, the Dpy to "Wt" ratio was 0.08, demonstrating that pairing and recombination with the normal homologue can occur efficiently. In addition to the Dpy recombinants, two Unc-54s were recovered, but they grew poorly and were sterile. Such a reciprocal Unc recombinant would carry a duplication with an *unc-54* mutation on it. It is possible that the additive effects of the duplication phenotype with the Unc-54 phenotype may have reduced this recombinant class. Recently, we have recovered viable Lev-11 recombinants of the genotype, *lev-11/ dpy-5 lev-11/ dpy-5 lev-11* (data not shown). These data clearly demonstrated that *sDp1* can synapse and recombine with its normal homologue.

In other experiments, rare Dpy-5 recombinants have been recovered from *sDp1/ dpy-5 unc-13/ dpy-5 unc-13; sDp1/ dpy-5 dpy-14/ dpy-5 dpy-14;* and *sDp1/ dpy-5 dpy-24/ dpy-5 dpy-24* individuals at frequencies in the range of 10^{-4} (Table 1). The normal recombination frequency for all of these intervals is greater than 0.01 (Rose and Baillie 1979a,

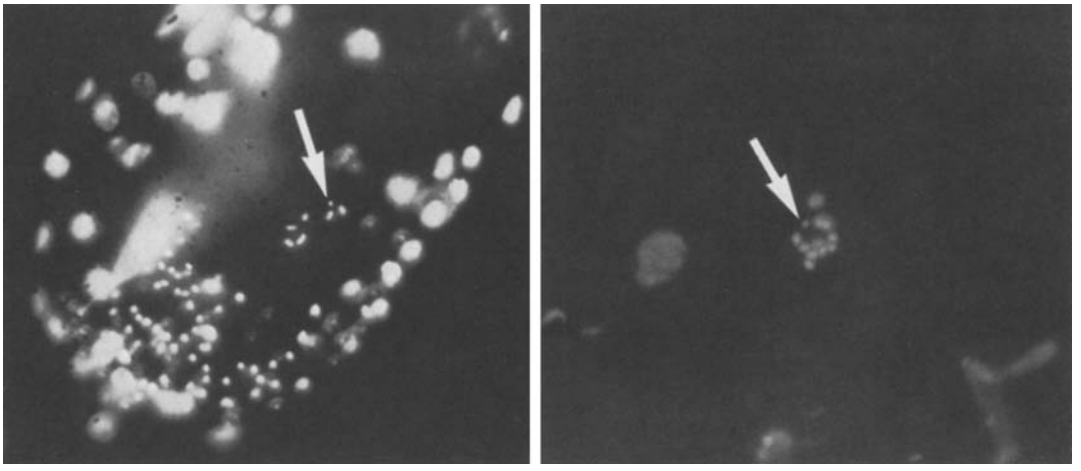

Fig. 2. Hoechst 33258 stained meiotic chromosomes in the hermaphrodite oocyte viewed by fluorescence microscopy. On the left is *sDp1* and on the right *sDp2*. A normal meiotic nucleus would contain six pairs of chromosomes. Arrows identify the additional fragment. The fluorescent nuclei of cells in the gonad and surrounding tissues can also be seen

Table 1. Recombination Data. Self-cross progeny from hermaphrodites of the stated genotype were scored

Parent	Wts	Dpys	Uncs
dpy-5 unc-54/ + +	1421	241	171
sDp1/dpy-5 unc-54/ + +	563	39	24
sDp1/dpy-5 unc-54/dpy-5 unc-54	513	41	2 sterile
sDp1/dpy-5 unc-13/dpy-5 unc-13	$>10^4$	1	0
sDp1/dpy-5 dpy-14/dpy-5 dpy-14	$>10^4$	1	0
sDp1/dpy-5 dpy-24/dpy-5 dpy-24	$>10^4$	1	0
dpy-5 unc-35/ + +	3329	268	177
sDp2/ dpy-5 unc-35/ + +	1007	19	11
sDp2/ dpy-5 unc-35/ dpy-5 unc-35	$>10^4$	0	0

1979b, and Fig. 1). *Dpy-5* recombinant chromosomes from the *sDp1* experiments were studied. We were able to establish strains homozygous for each recombinant chromosome, indicating that the *sDp1* fragment does not carry any lethal loci to the right of the crossover site. The reduction in recombination is pronounced in the *dpy-5 unc-13* interval. Here we observed at least a hundred-fold reduction. The severe effect on the regions close to *dpy-5* may have resulted from the fact that these intervals are very near the duplication breakpoint.

The effect of *sDp1* on the frequency of exchange between the two normal homologues has been studied (Table 1, line 2). In this experiment, approximately half of the recombinants would be missed because they segregated with the duplication. The Unc recombinants resulted only from exchanges between the normal homologues. The observed ratio of Uncs to Wts in the control was 0.12 but when the duplication was present was 0.09. This difference although not significant was in the direction expected if pairing between the normal homologues were disrupted by the presence of the duplication.

sDp1 was observed to induce nondisjunction of the normal homologues. This was demonstrated by crossing *unc-11 dpy-5/ + +* males to *sDp1/ dpy-5 dpy-14/ dpy-5 dpy-14* hermaphrodites and scoring the F1 out-cross progeny. The presence in the F1 of Unc-11 individuals indicated that a Unc-11 Dpy-5 sperm had fertilized a gamete having only *sDp1*. In two separate experiments, a total of 265 Wt, 180 Dpy and 5 sterile Uncs were observed. The Unc individuals moved backwards with a characteristic jerkiness taken to be diagnostic of the Unc-11 phenotype, indicating these individuals were *sDp1/ unc-11 dpy-5*, carrying a deletion for the left third of LG *I*. In the self-cross progeny of *sDp1*-carrying individuals, sterile adults are observed; but from *sDp1/dpy-5 dpy-14/ dpy-5 dpy-14* parents these steriles never exhibited the jerky phenotype. It is possible that the nondisjunction of the two normal homologues induced by *sDp1* was the result of *sDp1* having paired with one of the homologues.

From the above experiments, we can draw certain conclusions regarding the meiotic pairing behavior of *sDp1:* 1) *sDp1* pairs, undergoes meiotic exchange and apparently segregates from its normal homologue; 2) the frequency of crossing-over is greatly reduced in the *dpy-5* region; 3) *dpy-5* chromosomes generated by recombination with the duplication are homozygous viable, implying *sDp1* carries all essential loci to the right of *dpy-5*.

sDp2. This duplication was maintained by selecting "wild types" from the strain *sDp2/ unc-11 dpy-5/ unc-11 dpy-5*. The strain produced approximately 180 viable progeny per hermaphrodite, "wild types" (duplication-bearing individuals) and Dpy Uncs (887 "Wts" to 560 Dpy Uncs from 8 parents). The visible phenotype of *sDp2*-carrying individuals cannot be reliably distinguished from wild type, although *sDp2* individuals take longer to mature. The frequency of males was not above the expected for normal *X*-chromosome nondisjunction (Hodgkin 1974; Rose and Baillie 1979a). The rare males that did occur can mate but had reduced fertility. In addition, a few very slow developing individuals were observed. These individuals exhibited a range of phenotypes; they arrested development at a larval stage, reached adulthood but were sterile, or, rarely produced one or two "wild-type" progeny. These "wild-types" behaved exactly like the original grandparental *sDp2*-carrying individuals; that is, they segregated "Wts" and Dpy Uncs. Possibly the very slow developing individuals were homozygous for the duplication. The range of phenotypes observed may have been a result of one copy of the duplication having been lost from somatic tissues

Table 2. Genetic Characteristics of *sDp1* and *sDp2*

	sDp1	*sDp2*
linkage	free	free
size in map units	30	15
phenotype of *Dp/dpy-5/dpy-5*	slow movement, clear body wall	slow developing
frequency of self-cross males	0.02	0.001
male fertility	sterile	reduced
self-cross fertility	115 progeny	180 progeny
"Wt" to Dpy self-segregation	1.4 to 1	1.6 to 1
recombines with LG*I*	yes	not detectable
suppresses recombination on LG*I*	yes	yes
induces nondisjunction of LG*I*	yes	not detectable

during development. Duplication loss which occurred in gonadal stem cells could explain the reversion to the grandparental phenotype.

The region of LG *I* that was duplicated on *sDp2* was investigated (Fig. 1). Alleles of the following genes were found to be suppressed: *unc-35, bli-3, unc-11, unc-74, dpy-5, let-76,* and *dpy-14*. Three other genes, *let-75, unc-15* and *unc-13*, were tested and not suppressed. Thus, the breakpoint must lie between *dpy-14* and *let-75* an interval of 0.2 map units. The organization of genes in this region has been described previously (Rose and Baillie 1980).

sDp2 is not physically linked to any chromosome. This was demonstrated by Hoechst staining (Fig. 2) and genetic analysis. Independent segregation from *dpy-5(I), dpy-10(II), dpy-18(III), unc-22(IV), dpy-11(V),* and *lon-2(X)* was demonstrated.

sDp2 can be transmitted through either egg or sperm. In one experimnt + *dpy-5/ unc-11* + males were mated to *sDp2/ unc-11 dpy-5/ unc-11 dpy-5*. The wild type males from this cross, all of which must carry the duplication, were fertile. Taken together these observations indicate transfer of *sDp2* in both gametic lines.

We have not observed either the induced nondisjunction of, or recombination with, normal homologues. In separate experiments *unc-15/* + and *unc-13/+* males were mated to the *sDp2* strain. No Unc progeny were observed in the F1, although these deletion-carrying individuals may have been inviable due to the extensive region deleted.

sDp2 did not recombine with its normal homologue (Table 1). It might, however, disrupt pairing for recombination between normal homologues. To test this *sDp2/ dpy-5 unc-35/ dpy-5 unc-35* individuals were mated to wild-type males and the progeny of the F1 heterozygotes scored. Those Fl's that segregated 3 Wts to 1 Dpy Unc were used to calculate the control recombination frequency. In the control, the Dpy to Wt ratio is 0.08. In the presence of *sDp2*, the Dpy to "Wt" ratio is 0.02 (Table 1). Since half the Dpys will be missed because of the presence of the duplication the expected Dpy to Wt ratio will be approximately half that of the control. We observed a statistically significant reduction in recombination, indicating that the duplication did interfere with pairing between the normal homologues. Thus, *sDp2* may pair with a normal homologue but may not contain sufficient chromosomal information to accomplish recombination.

The properties of *sDp1* and *sDp2* are compared in Table 2. These two duplications apparently cover the entire LG *I*, overlapping for a region of approximately three map units between *unc-74* and *dpy-14* inclusive (Fig. 1). Currently, we do not know if *sDp2* complements all lethal mutations to the left of *unc-11* although we do know that *sDp1* complements all lethal mutations to the right of *unc-13*.

Discussion

We have investigated the meiotic behavior of two free duplications of LG *I*. One of these, *sDp1*, synapses, recombines, and apparently subsequently disjoins from its normal homologue. The other, *sDp2*, disrupts pairing between the normal homologues but does not recombine with a normal homologue. Both these duplications share extensive DNA homology with LG *I*. We would expect that if only DNA homology were required during pairing for recombination that both duplications would recombine with LG *I*. Since they do not, we conclude that factors other than DNA homology are required for recombination to occur. This conclusion is in agreement with the findings of others who have studied the pairing behavior of duplications and translocations in *D. melanogaster* (I. Sandler 1956; Roberts 1976; Hawley 1980) and *C. elegans* (Rosenbluth and Baillie 1981). Hawley (1980) investigated the suppression of crossing-over by certain translocations and suggested that sites where normal homologous pairing is established or reestablished are required for normal levels of exchange to occur in the interval between sites, as proposed by I. Sandler (1956). Furthermore, supplying an extra copy of only one of these pairing sites, by introducing the site on a duplication, resulted in a disruption of exchange in the interval between sites in the normal homologues (Hawley 1980). Rosenbluth and Baillie (1981) investigated suppression of crossing-over by the reciprocal translocation, *eTl*, which exchanges the left half of LG *V* with the right half of LG *III*. Recombination is absolutely suppressed for the left half of LG *V* (*unc-60* to *dpy-11*) and for the right half of LG *III* (*sma-2* to *unc-64*). These findings are consistent with the possibility that specific sites required for pairing and recombination exist in *C. elegans* chromosomes.

The pairing behavior of the two duplications described in this study is consistent with the existence of three pairing sites in LG *I*. If *C. elegans* chromosomes were to behave like those of *D. melanogaster*, then *sDp2* might contain one (but not two) pairing sites, thus suppressing exchange between the normal homologues but not entering into exchange events. *sDp1*, on the other hand, might contain two pairing sites and thus be able to crossover with a normal homologue. For these two proposals to be consistent, it is reasonable to suggest that both pairing sites in *sDp1* are located to the right of the *sDp2* duplicated region. Hence, the leftmost portion of *sDp1* might fall in an interval between two pairing sites. According to the Sandler-Hawley predictions, this interruption of an interval between sites would result in suppression of meiotic exchange. The observation that suppression in fact occurs suggests that *sDp1* lacks the pairing site *sDp2* retains. More extensive analysis of exchange suppression between LG *I* homologues might identify a boundary for the exchange suppression which would correspond to the position of one of the pairing sites.

In the self-cross progeny of *sDp1*, "Wt" males occurred with a frequency of approximately 0.02. Although other

free duplications have been observed to segregate from an unpaired *X*-chromosome of the male (*XO*) (Herman et al. 1979; Herman et al. 1982), no evidence for their mispairing with *X*-chromosomes in *XX* individuals has been reported. Two possible explanations for the increased hermaphroditic *X*-chromosome nondisjunction are that male production is a consequence of altered gene dosage in the *sDp1* strain, or that the unpaired duplication occasionally pairs with and disjoins from one of the *X*-chromosomes in the hermaphrodite. *sDp1* has not been analysed with regard to the *X*-chromosome except to demonstrate independent segregation from *lon-2(X)*. Further investigation might reveal some contribution by the *X*-chromosome to *sDp1*. In the absence of evidence for homologous pairing between the duplication and the *X*, it is possible that non-homologous distributive pairing (Grell review 1976) involving the *X*-chromosome is occurring. This may be a consequence of either the duplication or the normal LG *I* being left as a univalent after pairing for exchange has occurred.

In addition to the contribution these duplications have made to our understanding of chromosome pairing in *C. elegans*, they have practical aspects. The failure of *sDp2* to recombine is useful for balancing lethal strains. A strain such as *sDp2/ dpy-14 let-76 unc-13/ dpy-14 let-76 unc-13*, for example, has been established. It should be possible, therefore, to maintain mutations in essential genes using the *sDp2* strain. Used this way, *sDp2* would provide a balancer for the left third of chromosome *I*, a region for which previously no balancer was available. *sDp1* has been used to position genes on the genetic map. For example, *unc-73* has been separated from and to the left of *unc-74*. These two genes had not previously been separated. As well, *sDp2* has been used to map the position of a DNA restriction fragment length difference (RFLD) that exists between the Bristol and Bergerac strains of *C. elegans*. *sP1(ps18)*, which maps to LG *I* (Rose et al. 1982), has been mapped relative to the extent of *sDp2* (Rose and Mawji, unpublished results). The *sDp2* breakpoint has been precisely mapped between *dpy-14* and *let-75* to the left of *unc-15*. Thus, *sDp2* breaks within 0.2 map units to the left of *unc-15*. Currently, the *sDp2* breakpoint is one of the closest genetic markers to the left of *unc-15*. It is anticipated that the duplication breakpoint will be a useful tool for positioning on the genetic map cloned DNA fragments from the *unc-15* region of LG *I*.

The existence of a duplication in *C. elegans* that pairs and recombines with its normal homologue provides an opportunity to investigate those features of this duplication which facilitate meiotic exchange. Several lines of evidence argue that DNA homology is not sufficient. We suggest the possibility that localized pairing sites are required for recombination to occur. It may be possible by means of more extensive analysis of the meiotic behavior of *sDp1* to characterize more fully the mechanisms involved in homologue pairing, recombination and segregation in *C. elegans*.

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