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Chromosome Replacement in Mixed Populations of Compound-2L; Free-2R and Standard Strains of *Drosophila melanogaster*

An Example of Unstable Genetic Isolation*

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Summary. Crosses between compound-2L; free-2R (free-arm) and standard strains of *Drosophila melanogaster* produce two classes of inviable aneuploid hybrids in equal proportions: monosomic 2L and trisomic 2L. The lethal period for monosomics occurs during embryogenesis while the trisomics survive to late pupae. Since the hybrids are inviable, standard and free-arm strains within a mixed population remain genetically isolated. Genetic isolation in the absence of mating isolation offers an extreme example of unstable equilibrium. Relative fitness data indicate that an unstable equilibrium will be established between free-arm and standard strains at a ratio of 2.5:1. Indeed, in three cage experiments established at initial ratios of 3:1, free arms to standards, laboratory (Oregon R) or native (Okanagan S) standard strains were completely replaced in approximately 100 days by free-arm lines derived either from laboratory or from native genetic background. In contrast, one cage established at an initial ratio of 4:1 failed to show replacement and for 92 days remained at approximately the initial ratio. Subsequent genetic analysis of flies removed from this cage identified the presence of an anomalous strain through which genetic information was transferred reciprocally between the free-arm and standard lines. The second chromosomes carried by this strain consisted of a free-2R and a standard second on the right arm of which was attached a duplication for all of 2L. While the origin of the 2L·2R+2L chromosome was uncertain, genetic and cytological examinations revealed that it represented the reciprocal crossover product expected from an exchange that generated a F(2R). Additional crosses disclosed that the transmission frequency of the asymmetrical pair of second chromosomes, as well as their right-arm crossover products, was disproportionately in favor of the short arm. Since unequal transmission was invariably greater from female parents, this phenomenon was viewed as further evidence in support of the drag hypothesis.

Key words: Compound; free-arm strains – *Drosophila melanogaster* – Unstable genetic isolation

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Introduction

The control of insects through genetic techniques has emerged during the past few years as an important and active area of pure and applied genetic research. Methods that have been investigated embrace the well-tried sterile-insect technique, hybrid sterility, inherited semi-sterility, cytoplasmic incompatibility and the more genetically complex technique of insect population replacement in combination with the introduction of controllable genetic factors (Curtis 1968; Bushland 1971; Foster et al. 1972; Wagoner et al. 1974; Whitten and Foster 1975; Fitz-Earle 1976, 1978; Fitz-Earle and Holm 1976; Robinson 1976).

Principles of the latter approach have been exemplified by studies on strains of *Drosophila melanogaster* bearing compound autosomes (see Holm 1976). Recently, compound autosomes have also been successfully generated in the commercially important sheep blowfly, *Lucilia caprina* (Foster et al. 1976). Hybrids from crosses between compound and standard strains are lethal thereby creating, in a mixed population, an unstable equilibrium (Li 1955). As such, compound lines can be used to displace standards. In addition, mutations desirable from man's viewpoint may be included in the genome of the compound strain prior to the displacement of standards. This method for insect control has been tested extensively with success in laboratory and field cages using *D. melanogaster* as a model (Childress 1972; Fitz-Earle et al. 1973, 1975; Cantelo and Childress 1975; McKenzie 1976, 1977).

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One major drawback of compound strains is their low frequency of egg hatch (e.g. 25 percent or less for *D. melanogaster*); consequently, there is a low production of surviving progeny, although the latter are as competitive as standards. Recently, attention has turned to another combination of chromosomal rearrangements that have twice the viability of compounds, yet retain their genetic isolation features. These strains, termed compound; free-arm combinations, were originally generated in *D. melanogaster* and characterized by Grell (1970). They include in their genome a compound left or right and, respectively, a pair of homologous free right or left arms (Figure 1b). For brevity, organisms carrying this combination of rearrangements will be referred to as 'free-arm' strains.

An earlier study on free-arm lines (Fitz-Earle and Holm 1978) revealed that egg hatchability was approximately 50 percent and adult recovery was approximately 40 percent that of standards. In addition, free-arm strains were shown to be genetically isolated from strains carrying standard chromosomes (as well as those bearing compound autosomes). Crosses between free-arm and standard strains produce two classes of inviable aneuploid hybrids in equal proportions: hybrids monosomic for 2L and hybrids trisomic for 2L. While the monosomic individuals die during embryogenesis, a high proportion of the trisomics survive to a late pupal stage. Preliminary cage competition studies between free-arm and standard laboratory lines revealed that some free-arm strains were able to displace standards at ratios close to the equilibrium ratio (of 2.5:1) predicted from fitness data (survival to adults), while others were not. In addition, two cages with initial ratios of 3:1 and 4:1, respectively, free arms to standards, were found to be anomalous.

This paper describes the genetic tests that resolved these anomalies and reports on further cage replacement experiments involving free-arm and standard chromosomes derived both from native and from laboratory strains.

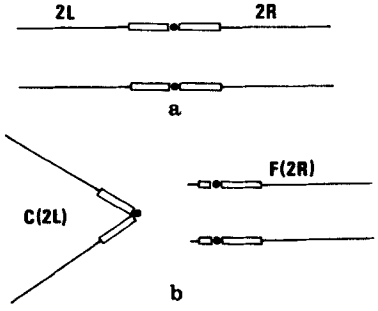

Fig. 1a and b. a Standard configuration of chromosome 2; b Configuration of a compound-2L; free-2R combination

Materials and Methods

Stocks

The lines of *Drosophila melanogaster* used in cage studies and subsequent genetic analyses are listed in Table 1. Descriptions of compound autosomes, free arms and alphanumeric codes have been given in previous reports (Holm 1976; Fits-Earle and Holm 1978) and genetic markers carried by the various strains are described in Lindsley and Grell (1968). The unmarked, native standard strain, +/+ (OK-S), represents the descendents of a single mated female, one of a number collected from a remote fruit dump in the Summerland area of the Okanagan Valley of British Columbia, Canada. All free-arm lines used in this study, including the one derived from the OK-S strain, were generated in this laboratory following procedures outlined by Grell (1970). A line of homozygous bw (brown-eyed) flies in which some portion of their genetic background contained native +/+ (OK-S) material was recovered by outcrossing +/+ (OK-S) to bw/bw, mating the F_1's and recovering the required bw/bw (OK-S) offspring from the F_2 generation.

Cage Experiments

All cage experiments were conducted in a constant temperature (24 ± 1°C) laboratory. Cages (construction and size) and medium (type, quantity and intervals of replacement) have been described in previous reports (Fitz-Earle et al. 1975; Fitz-Earle and Holm 1978). For each of the four cage competitions described, virgin females and males of the free-arm and standard lines were aged for approximately three days and simultaneously released into cages

Table 1. Free-arm and standard strains used in the experiments

Strain	Origin
C(2L)SH1,+;F(2R)VH2,bw/F(2R)VH2, bw	After Grell (1970)
C(2L)VT9,In(2L)Cy/+;F(2R)VH1,Pin/ F(2R)VH1,Pin	After Grell (1970)
C(2L)VH1,1t;F(2R)VH2,bw/F(2R)VH2, bw	After Grell (1970)
C(2L)VT1,ho;F(2R)VH2,bw/F(2R)VH2, bw	After Grell (1970)
C(2L)SH1,+;F(2R)VFE10,+(OK-S)/F(2R) VFE10,+(OK-S)	As shown in Figure 2
+/+(OK-S)	Native Okanagan-S wildtype
bw/bw	Stock
bw/bw(OK-S)	Okanagan-S background
cn bw/cn bw	Stock
lt pk cn/lt pk cn	Stock
In(2LR)bw^{V1}/In(2LR)SM1,Cy	Stock (Lindsley and Grell 1968)
Df(2L)C'	Hilliker and Holm (1975)
In(2LR)A	This paper
Dp(2L;2)	This paper

in the initial ratios entered in Table 2. Populations increased with overlapping generations. Three weeks following the initial release and usually twice weekly thereafter until fixation, a sample of approximately 1,000 flies was removed using an aspirator. Flies were anaesthetized, classified according to phenotype (brown or red eye), counted and then returned to the cage. Fixation was defined as achieved when two consecutive samplings revealed exclusively one phenotype.

Genetic and Cytological Tests

Cytological and genetic studies were carried out with flies taken from two anomalous cages. Genetic tests, which involved crosses between the aforementioned flies and strains listed in Table 1, are described in full detail in the Results and Discussion section. Cytological preparations of mitotic chromosome figures (at metaphase and anaphase) were made from ganglia removed from third-instar larvae and squashed using a standard aceto-lacto orcein staining technique (Moore 1971).

Results and Discussion

Cage Experiments

Cage population competitions revealed that free-arm strains were successful in displacing standards at an initial ratio of 3:1 (Table 2). Comparably low ratios were not found for compound stains of *Drosophila melanogaster* (Fitz-Earle and Holm 1978). When laboratory free-arm lines were competed with native standards at 3:1, the free arms were successful (Cage A, Table 2), but when the same free-arm flies were matched with laboratory standards at the same ratio, the free arms were unsuccessful (Fitz-Earle and Holm 1978). In competitions between a native free-arm line and either laboratory or native standards, there was displacement of standards at the ratio of 3:1 (Cage B, C, Table 2). It might be expected that the success of laboratory free-arm strains would be restricted at low ratios, especially against native standards. However, such a prediction does not appear valid. A previous study, in which compound strains were competed with standard lines in field cages (Fitz-Earle et al. 1975) revealed that successful displacement of native standard strains would not occur unless the compound-bearing strains carried genetic material derived from the native (Okanagan-S) population. In the present study, however, under laboratory conditions, displacement of the laboratory (Oregon-R) standard strain and the native (Okanagan-S) strain was equally successful regardless of the genetic background of the free-arm lines. Evidently the native strain had been under laboratory conditions too long to maintain its competitive advantage. In any event, these cage experiments have demonstrated that for two different lines, free arms are the most effective genetic tools for cage population replacement. There were, however, anomalies in two cage populations that unfortunately cast some doubt upon the superiority of the free arm control strategy.

Anomaly 1

The frequency of wild-type flies in Cage C (Table 2) remained essentially constant at 0.996 (i.e. approximately four brown-eyed flies were found in each sample of 1000) from day 95 until day 133 when the cage was closed down. The length of time to reach this stable frequency of 0.996 was approximately that to fixation in the other two 3:1 cages (Cages A, B, Table 2). However, on day 105, one female and one male, each with the brown-eye phenotype (putative standards), were withdrawn from Cage C and crossed to mates of a known free-arm line, namely

Table 2. Results of cage competitions between free-arm and standard strains

Cage	Strain		Initial		Fixation of free-arm	Days of fixation
	Free-arm	Standard	Pairs	Ratio		
A	C(2L)SH1,+;F(2R)VH2,bw/F(2R)VH2,bw	+/+(OK-S)	120:40	3:1	Yes	108
B	C(2L)SH1,+;F(2R)VFE10,+(OK-S)/F(2R)VFE10,+(OK-S)	bw/bw	132:44	3:1	Yes	99
C	C(2L)SH1,+;F(2R)VFE10,+(OK-S)/F(2R)VFE10,+(OK-S)	bw/bw(OK-S)	75:25	3:1	Yes[a]	95 (133)[a]
D	C(2L)SH1,+;F(2R)VH2,bw/F(2R)VH2,bw	+/+(OK-S)	200:50	4:1	No[b]	92[b]

[a] This cage was shut down on day 133. However, as explain in the text, fixation in favor of the free-arm strain probably occurred about day 95

[b] Ratio remained relatively constant throughout the 92 day period. The nature of the flies in this cage was explored further (see text)

C(2L)VH1,1t; F(2R)VH2,bw/F(2R)VH2,bw. One-half of the progeny from these matings had brown eyes, the others had light-brown eyes, revealing that the two flies removed from the cage indeed carried free arms. From a subsequent sample of 1,287, four brown-eyed flies were recovered and again test crosses revealed that all four phenotypic exceptions carried free arms. Three possible explanations for these findings can be considered: (1) a spontaneous mutation to brown eye occurred in the previously unmarked original free-arm strain, or (2) triploid females were produced in which the genetic marker was transferred, through crossing over, to the free arm, or (3) a free arm was generated spontaneously in the brown-marked native, standard strain. While the most likely explanation cannot be determined at this time, the point of interest to emerge from this result is that in large populations containing genetically incompatible strains, the latter two mechanisms, albeit at low frequencies, can serve to transfer genetic information across the reproductive barrier. Consequently, the loss of any desirable genes carried by the invading strain is a distinct possibility.

Anomaly 2

The second anomaly, which proved to be the more curious, arose in Cage D (Table 2) the data for which was previously reported in Fitz-Earle and Holm (1978). In this cage the frequency of brown-eyed flies, indicative of free-arm individuals, fluctuated around the initial frequency of 0.80 (ranging from 0.68 to 0.89). Since all three 3:1 cages went to fixation in favour of the free-arm strain, the same was certainly expected to occur in this cage as well. However, after 92 days there was no indication that fixation for either strain was pending. Indeed, the data seemed to suggest that an equilibrium had been established at the initial ratio of 4:1, that is at a ratio in excess of the theoretical equilibrium for free arms against standards. Such an equilibrium had never been witnessed in over 160 previous cage-competition experiments.

The possibility of a spontaneous occurrence of free arms in the native standard strain or the transfer of genetic markers through triploid females, similar to that suggested for Cage C (Anomaly 1), was suspected. Therefore, 15 wild-type males were withdrawn from Cage D (Table 2) and crossed individually to C(2L)VH1,1t;F(2R)VH2,-bw/F(2R)VH2, bw virgin females. Twelve of the 15 crosses were fertile in that pupae appeared after seven days incubation at 25°C. Of the twelve fertile matings, four produced offspring. Clearly the males of these four crosses carried F(2R) chromosomes. Three of the four crosses produced, in relatively equal proportions, offspring of four phenotypes: red eye (wild type); light-brown eyed; light eyed and brown eyed. These classes would be expected if the sampled wild-type males carried an unmarked compound 2L and F(2R)s heterozygous for brown eye. The fourth productive cross gave progeny of two phenotypes: light eyed and red (wild type) eyed. No progeny with brown eyes or the combined phenotypic expression of light and brown eyes were recovered. A backcross of phenotypically light-eyed male progeny to C(2L)VH1,1t;F(2R)VH2,bw/F(2R) VH2,bw females produced light and light-brown offspring in equal proportions. This finding is consistent with the light-eyed parents (progeny from the fourth cross) having a compound 2L marked with light and free arms heterozygous for brown eye. However, a backcross of the wild-type male progeny of the fourth cross to C(2L)VH1,1t;F(2R)VH2,bw/F(2R)-VH2,bw females gave quite different results.

This mating would be expected to give, in equal proportions, offspring of the four phenotypic classes; wild type, light-brown eye, brown eye and light eye, if the phenotypically wild-type parent (progeny from the fourth cross) carried a compound 2L without genetic markers and free arms heterozygous for brown. However, the cross produced only offspring with light-brown eyes or wild-type (red) eyes, and continued to do so for two further backcrosses. Upon mating the wild-type male and female progeny of the latter cross, a phenotypically wild-type, pure-breeding strain was established.

Since flies from this strain, when crossed to C(2L)VH1,1t;F(2R)bw/F(2R)bw, produced phenotypically light-brown as well as wild-type progeny, it was evident that it carried a F(2R) chromosome bearing the brown-eye marker. However, the genetic results implied that the wild allele of brown was carried on a right arm linked to a compound 2L. We reasoned that an intact chromosome composed of one right and two left arms could arise, through recombination, as the reciprocal product in the generation of a free 2R (as shown in Fig. 2). From none of our previous crosses designed to generate F(2R) chromosomes had we recovered the 2L·2R+2L reciprocal product. Admittedly, such crosses were few in number and were terminated as soon as two or three F(2R) chromosomes were obtained. Moreover, each new product was immediately tested and invariable verified as free arms.

We therefore assumed that possibly the native standard, +/+ (OK-S), strain used in Cage D, had carried a second chromosome with a pericentric inversion, the nature of which was similar to $In(2LR)1t^{m3}$, as shown in Figure 2. The native standard strain may thus have led to the formation of a 2L·2R+2L chromosome that would be rescued by a F(2R)-bearing sperm. Following this line of reasoning, we crossed virgin females from the anomalous (A) strain to males bearing standard second chromosomes homozygous for the genetic marker brown eye, as well as the reciprocal cross. The first of these crosses is described in Figure 3. In this cross, crossing over between the homologous regions of the 2L·2R+2L chromosome and the

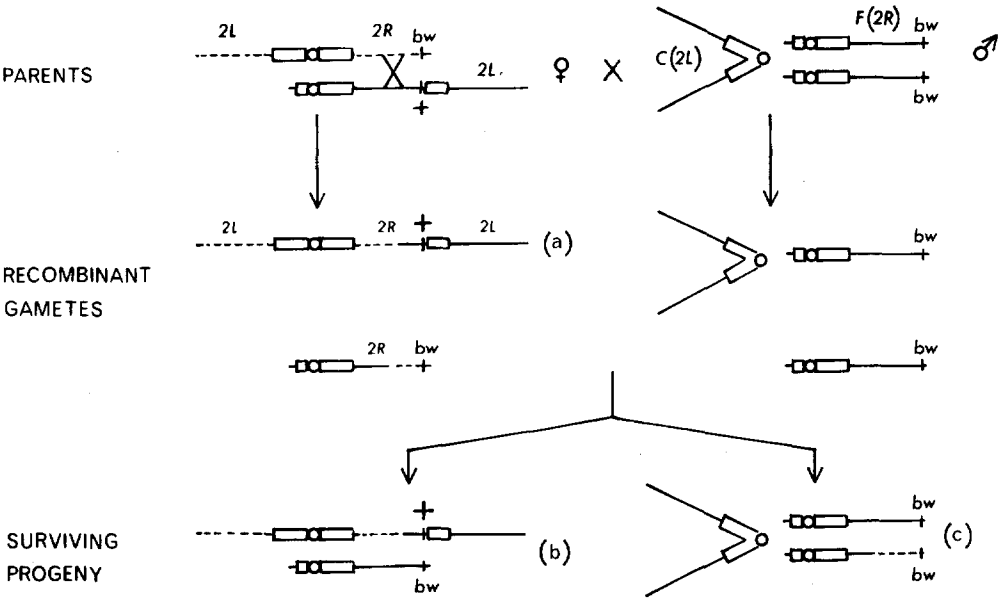

Fig. 2. Model for the formation of the Dp(2L;2)/F(2R) strain. (a) The Dp(2L;2) recombinant chromosome; (b) Dp(2L;2)/F(2R) heterozygous progeny; (c) Compound-2L;free-2R progeny

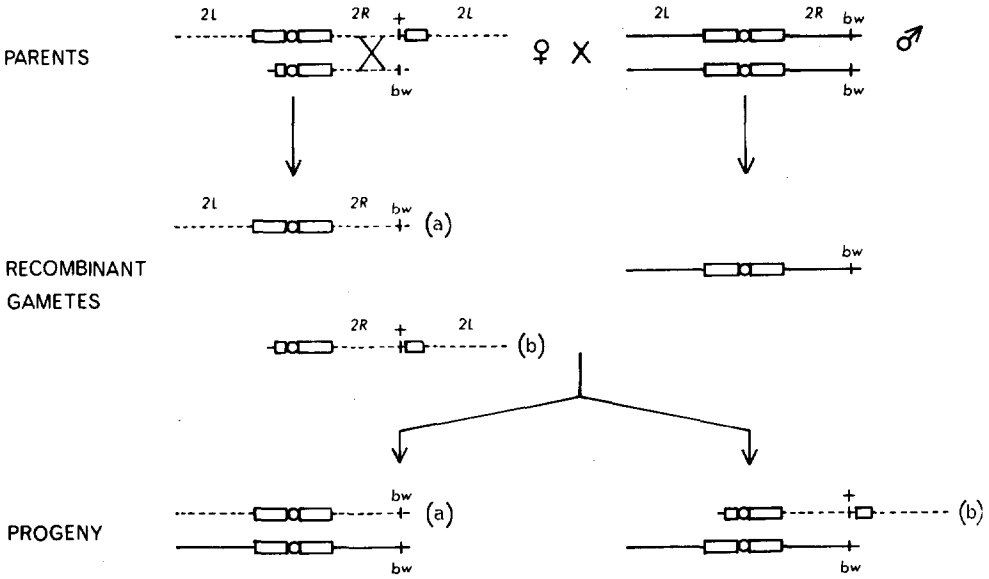

Fig. 3. The recovery of structurally acrocentric (pericentric inversion) and metacentric standard chromosomes from a cross between Dp(2L;2)/F(2R) heterozygous females and standard males. (a) Standard metacentric recombinant product; (b) structural acrocentric (pericentric inversion) recombinant product

F(2R) would be expected to yield products each composed of a 2L and a 2R: a metacentric standard chromosome carrying the brown marker and a structurally acrocentric (pericentric inversion) chromosome carrying the wild allele for brown (Fig. 3a, b, respectively).

The reciprocal cross, in which A males had been crossed to standard females, in contrast, would be expected to produce two classes of lethal aneuploid progeny: haplo-2L/diplo-2R and triplo-2L/diplo-2R. The latter class, which also arises from mating free-arm strains to standards, has been shown from earlier studies (Fitz-Earle and Holm 1978) to survive to late pupae. The results of the reciprocal crosses support the predictions with respect to the types of progeny obtainable from products of recombination in A females carrying 2L·2R+2L/F(2R) (Table 3a, b) and the lack of offspring from the nonrecombinant

Table 3. Genetic tests of the prediction that the anomalous (A) strain carried a 2L·2R+2L chromosome

Cross	Parental genotype		Number of				Mean[b]	95%[b]
	Female	Male	Crosses	Progeny[a]				
				bw	+	Total	%bw	C.I.
a	A	bw/bw	20	452	124	576	80.2	76.1 – 84.0
b	A	bw/bw	34	725	188	913	79.5	76.4 – 82.5
c	bw/bw	A	36	+	+	+	–	–

+ Survival of progeny to the pupal stage of development

[a] bw = brown-eyed progeny: putative metacentric standard chromosome
+ = phenotypically wild-type progeny: putative In(2LR)A (structurally acrocentric) chromosome

[b] Mean and 95% confidence intervals recorded in Tables 3 through 5, inclusive, were calculated from arcsin transformed values of individual results

products of males from the same strain (Table 3c).

To verify that the chromosome marked by the recessive brown-eye mutation was a standard metacentric and the unmarked chromosome was an acrocentric (analogous to In(2LR)lt^{m3}) the following tests were made. Females carrying the putative metacentric chromosome were mated to C(2L)SH1,+,F(2R)bw/F(2R)bw males, but their progeny developed only to the pupal stage, as predicted by previous results (Fitz-Earle and Holm 1978). Males heterozygous for the putative acrocentric chromosome were crossed to C(2L)VT1,ho;F(2R)bw/F(2R)bw females, and again only pupae were recovered. In contrast, when females heterozygous for the putative acrocentric (designated as In(2LR)a) were crossed to two different free-arm lines (see Table 4, crosses a-c), two classes of progeny were recovered: those inheriting a newly-generated free-2R chromosome and those inheriting the putative 2L·2R+2L chromosome, as depicted in Figure 2c and b, respectively. Since, as noted above, previous recoveries of F(2R) chromosomes from In(2LR)lt^{m3} heterozygotes had not included 2L·2R+2L recombinant products, we tested In(2LR)lt^{m3} over a standard second chromosome marked by lt pk cn from which a significant fraction of the products were identified genetically as 2L·2R+2L (cross d in Table 4).

While this combination of rearranged seconds, that is 2L·2R+2L/F(2R), represents a 2;2 translocation, since the free 2R has been symbolized previously by Grell (1970) as F(2R), we chose to designate such strains as Dp(2L;2)/F(2R). Cytologically, this strain should posses a chromosome that is 50 percent longer than a normal second. Brain squashes, using a standard staining technique, reveal this to be the case, as shown in Figure 4.

Table 4. Regeneration of 2L·2R+2L and F(2R) chromosomes as crossover products from In(2LR)A and In(2LR)1t^{m3} heterozygous females

Cross	Parental genotype		Number of				Mean %	95% C.I.
	Female	Male	Crosses	Progeny				
				ho or bw[a]	+[b]	Total	F(2R)	
a	In(2LR)A/bw	C(2L)SH1,+; F(2R)bw/F(2R)bw	11	218	96	314	69.7	60.8 – 77.8
b	In(2LR)A/bw	C(2L)VT1,ho; F(2R)bw/F(2R)bw	23	174	84	254	67.4	59.5 – 74.8
c	In(2LR)A/1t pk cn	C(2L)VT1,ho; F(2R)bw/F(2R)bw	24	130	63	193	64.2	53.1 – 74.5
d	In(2LR)1t^{m3}/1t pk cn	C(2L)VT1,ho; F(2R)bw/F(2R)bw	23	99	41	140	77.0	62.1 – 89.1

[a] Genetic markers ho or bw indicate recovery of newly generated F(2R)

[b] Wild-type progeny are those who inherit a newly generated 2L·2R+2L chromosome

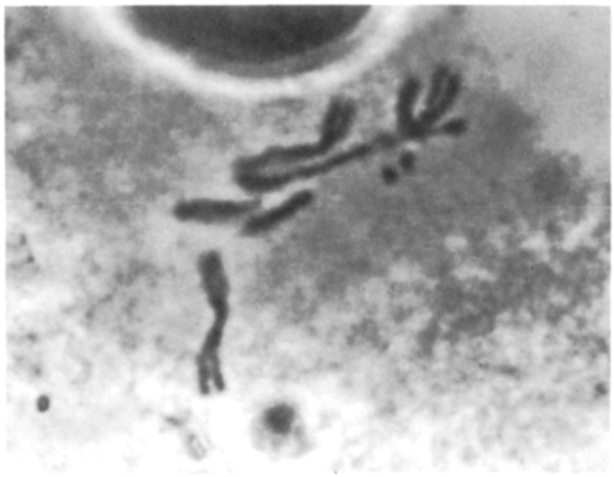

Fig. 4. Photomicrograph of a stained preparation of mitotic prometaphase chromosomes in a ganglion cell from a Dp(2L;2)/F(2R) heterozygous, third-instar, male larva. In this preparation the Y chromosome curves across the distal third of the long 2L·2R+2L chromosome and the F(2R) lies in proximity with the X

Origin of the Dp(2L;2)/F(2R) Strain

All findings to this point clearly implied that Dp(2L;2) originated as a recombinant product of In(2LR)lt^{m3} or a chromosome of almost identical configuration. Since, as previously mentioned, the native (OK-S) strain was derived from a single native female and since previous cages involving this strain had not contained mixed populations at apparent stable equilibrium, it seemed questionable that the OK-S line contributed the pericentric inversion. Nevertheless, we examined, from 40 individuals, 160 second chromosomes for crossing over in the right arm. This test failed to identify inversions as did cytological examinations of polytene chromosomes from a number of third-instar larvae. Upon examining polytene squashes from larvae of the Dp(2L;2)/F(2R)bw strain, a distal break in 2R at band position 60D was identified. This breakpoint was identical to that found for In(2LR)lt^{m3} as reported by Hessler (1958) and confirmed in this laboratory. Moreover, anaphase figures of the In(2LR)A chromosome, derived through recombination between Dp(2L;2) and F(2R)bw, revealed an arm length twice that of a metacentric.

In addition to cytological tests, we compared the phenotype of In(2LR)A to that of In(2LR)lt^{m3} when heterozygous with a large deficiency that includes the marker light (lt), namely Df(2L)C′ (Hilliker and Holm 1975) and also with In(2LR)bw^{V1}, a chromosome that also expresses a light-mottled phenotype in combination with lt. Both In(2LR)A and In(2LR)lt^{m3} showed reduced viability in combination with the deficiency and expressed the same short, droopy wing abnormalities. Neither expressed a light mottling, although a few progeny in both cases showed dark patches on the eye. In combination with In(2LR)bw^{V1}, again viability was reduced and both heterozygotes expressed a strong light mottling of the eye.

Even though the only In(2LR)lt^{m3} stock in this laboratory is heterozygous for In(2LR)SM5,Cy, a chromosome that carries the dominant Curly-wing marker, and in over 10,000 flies sampled from cage D (Table 2) no Curly-winged individual was recognized, with the lack of evidence to the contrary, we must assume that the Dp(2L;2) chromosome most likely arose as a contaminant, i.e. from an In(2LR)lt^{m3} chromosome. While it seems that we are not dealing with the product of a novel chromosome, these findings have been of considerable impact in drawing attention to a possible mechanism whereby natural strains could respond to the invasion of free-arm lines, creating a situation that not only suppresses the attempt to displace standard chromosomes, but also adds a new dimension for genetic exchange between apparent, genetically isolated strains. If natural populations did, in fact, possess rearranged chromosomes of the nature of In(2LR)lt^{m3}, their selective recovery would be provided through the use of compound; free-arm strains.

Nonrandom recovery of reciprocal products of recombination: The entries in Tables 3 and 4 reveal that the structurally dissimilar reciprocal products of recombination, In(2LR)A and the standard metacentric second in Table 3, and in Table 4, (2L·2R+2L) and F(2R), are recovered in considerably unequal proportions. From both crosses, the recombinant chromosome most frequently recovered (by a factor of 2 to 4) is that in which the right arm is shorter by one half the reciprocal products, owing to the relocation of 2L. Since the homologous arms (2R) giving rise to these products are of unequal length, single or three-strand double exchanges create pairs of asymmetric dyads that segregate to opposite poles at anaphase I. Preferential recovery of shorter chromatids from asymmetric dyads has been demonstrated in a number of studies (Novitski 1951; Zimmering 1955, 1976; Novitski and Sandler 1956; Mark and Zimmering 1977). Novitski (1951) suggested that 'the cause appears to be nonrandom disjunction at the second meiotic division when two structurally dissimilar chromatids compete for inclusion in the functional egg nucleus'. In reference to the products obtained from crossing over between a pair of X chromosomes of unequal length, Novitski (1967) pointed out that as the chromosomes separate from the crossover configuration, the longer sister chromatids 'drag' relative to the shorter ones. Consequently, the orientation of the centromeres can be such that the shorter chromatids occupy the more polar positions. Since the products of meiosis are arranged linearly, with one of the two outermost destined to be the egg pronucleus, the orientation of the exchange products should favour the recovery of the shorter chromatids from the asymmetric dyad. While it is

Table 5. Percent recovery of the metacentric second chromosome from standard crosses in which one of the parents is heterozygous either for In(2LR)A or for In(2LR)1t^{m3}

Cross	Parental genotype		Number of				
	Female	Male	Crosses	Progeny			
				Total	cn bw[a]	Mean % cn bw	95% C.I.
a	cn bw/cn bw	In(2LR)A/cn bw	28	1775	1016	56.7	53.9 – 59.4
b	In(2LR)A/cn bw	cn bw/cn bw	29	1069[b]	744	70.4	66.8 – 73.8
c	In(2LR)A/cn bw	cn bw/cn bw	13	819[b]	570	69.0	65.2 – 72.6
d	In(2LR)1t^{m3}/cn bw	cn bw/cn bw	15	579[b]	397	67.7	63.8 – 71.6

[a] Standard metacentric second chromosomes with the right arm bearing the proximal recessive marker, cn and the distal marker, bw
[b] Included in these progeny were the following double recombinants: Cross b, 8 cn and 5 bw; Cross c, 1 cn; and Cross d, 1 cn and 1 bw. Progeny testing revealed that all double exchanges flanked the proximal marker, cn, i.e. cn was recovered on the inverted chromosome, bw on the standard metacentric

clear that the longer chromatids are not always excluded, the 'drag' hypothesis serves as a possible explanation for the disproportionate recoveries witnessed in the present study.

Support for this point of view was obtained by examining the relative recovery of the two meiotic products from C(2L);F(2R)/F(2R) males. If the transmission of sperm carrying C(2L) plus one F(2R) were significantly greater than the transmission of reciprocal F(2R) products, it would be reflected as a reduced recovery of newly generated Dp(2L;2) chromosomes. However, from four crosses in which males and females carried differentially marked C(2L) and F(2R) chromosomes, reciprocal products were recovered in equal numbers. From this we must assume that equal proportions of the two types of sperm are available to fertilize eggs.

Considering that reduced recovery of the longer Dp(2L;2) chromatid may occur owing to causes other than 'drag', reciprocal crosses were made between Dp(2L;2)/F(2R)bw and C(2L)VT9,Cy;F(2R)Pin/F(2R)Pin individuals. While our findings reveal that indeed the longer chromosome is transmitted by males less frequently than is the shorter F(2R) chromosome (64 percent or 861 of 1375 progeny inherited free-2R) the disproportionate transmission of these two chromosomes by females is exceptional (as 78 percent or 541 of 695 progeny inherited the smaller of the two chromosomes). From the latter cross, chromatids arising as products of recombination in 2R would not be recovered. However, following a single exchange in 2R, the nonexchange F(2R) chromatid would also be included in an asymmetric dyad. Consequently, in keeping with the 'drag' hypothesis, a disproportionate recovery of the nonexchange chromatids would also be expected. Moreover, it would be expected that similar results would arise from females heterozygous for In(2LR)A or In(2LR)lt^{m3} and a standard, metacentric second chromosome when crossed to standard males. Again, only chromatids non-recombinant (or double recombinant) for 2R would be recovered. The results of these crosses (Table 5) demonstrate that although the transmission by heterozygous males of the long-armed (structurally acrocentric) chromosome is less than 50 percent, this deviation from the expected 1:1 ratio is unparalleled by the highly disproportionate recovery of the structurally heterozygous second chromosomes from females. Furthermore, as indicated in the footnote to Table 5, the number of double exchanges encompassing the proximal marker, cn, suggests that little or no interference with crossing over is experienced between the right arms of the inversion heterozygote. Accordingly, the majority of the nonexchange chromatids recovered would be products of a tetrad in which recombination took place in 2R. Therefore, we suggest that, at least in part, the 'drag' hypothesis serves as a frame of reference within which these findings may be explained.

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