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Segregation and pairing of compound fifth-chromosomes in *Lucilia cuprina* males

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SUMMARY

Variability in fertility in compound chromosome (CC) strains of *Lucilia cuprina* (Wiedemann) is directly correlated with the segregation properties of the CCs in those strains. In compound fifth-chromosomes, high fertility (up to 50%) is associated with high frequencies of segregation of the left element (*C(5L)*) from the right element (*C(5R)*) in males, while low fertility (up to 25%) is associated with random assortment of the CCs in males. Regular segregation of *C(5L)* and *C(5R)* chromosomes in males is associated with particular *C(5L)* elements, which contain cytologically visible duplications of *5R* chromatin. These duplications may contain a site which is normally involved in the pairing of the fifth chromosomes in males.

In females the CCs segregate from one another with a frequency of 89%. None of the *C(5R)* elements studied affected segregation in males, and neither *C(5L)* nor *C(5R)* elements had any demonstrable effect on segregation in females. Transmission of certain CC elements through one or both sexes is significantly lower than expected. This could have a variety of causes, such as meiotic drive, inviability associated with position effects, or homozygosis of deleterious mutations on homologous CC arms during meiotic crossing over in females. The CC strains released during a field trial of genetic control contained both high-fertility and low-fertility *C(5L)* chromosomes. Both types of CC were subsequently recovered from individuals which had overwintered in the field. Over a period of several generations following this recolonization one particular high-fertility *C(5L)* chromosome increased in frequency to near-fixation, despite the presence in this chromosome of deleterious mutations.

1. INTRODUCTION

The potential use of compound autosome-bearing strains in genetic control of insect pests has led to a considerable amount of research using *Drosophila melanogaster* as a model system (reviewed by Fitz-Earle & Holm, 1983) and to the construction of compound autosomes in *Lucilia cuprina* (Foster, Whitten & Konowalow, 1976; Maddern, 1981). Early research in *D. melanogaster* (reviewed by Holm, 1976) showed that compound chromosomes (CCs) usually segregated from one another in females and assorted at random in males, resulting in

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compound strain fertilities approaching 25%, but that in some cases regular segregation of left and right compound chromosomes in males led to higher fertilities. It is now reasonably well established that regular segregation of compounds in *D. melanogaster* males occurs when they share certain homologous euchromatic sequences (Gethmann, 1976; Hilliker, Holm & Appels, 1982).

In *L. cuprina*, Foster *et al.* (1976) showed cytogenetically that the compound chromosomes *C(5L)1* and *C(5R)1* assort randomly in males (although strain fertility was much lower than the predicted 25%, presumably due to factors other than segregation). Several hundred compound fifth-chromosomes have now been isolated in this laboratory (Maddern, 1981; Foster *et al.* 1985). In the course of preliminary screening and genetic manipulations aimed at preparation of strains for field trials of genetic pest control methods, single-pair crosses in which egg hatch was 40–50% were frequently encountered (Foster *et al.* 1985). This report describes a study of segregation of compound chromosomes sampled from most of the mass-reared (MR) lines used to generate the compound strains released in a field trial in 1979–81 (Foster *et al.* 1985), and contains data on genetic changes in CC strains established from flies recaptured during that trial.

2. MATERIALS AND METHODS

(i) *Mutations and strains*

The names and symbols of mutations mentioned in this report are as follows: topaz eyes (*to*, to^2), bronze body (*bz*), M1-veinless (*mv*), and stubby bristles (*sby*). The *to*, *bz* and *mv* loci are on the left arm of chromosome *5*, and the *sby* locus is on the right arm (Foster *et al.* 1980*b*).

The compounds *C(5L)1*, to^2 *bz mv*, *C(5L)2*, +, and *C(5R)1*, + were isolated by Foster *et al.* (1976) following irradiation of oocytes. *C(5L)3*, *to*, *C(5R)2*, *sby*, *C(5R)3*, *sby* and *C(5R)5*, *sby* were isolated following irradiation of spermatocytes (Maddern, 1981). *C(5L)bzd* appeared as a spontaneous dark bronze body colour mutation ('bronzoid') in a wild-type *C(5L)* induced by irradiation of spermatocytes. The wild-type *C(5L)* chromosomes numbered 101–117 and *C(5R)* chromosomes numbered 102–118 were all recovered after irradiation of spermatocytes (Maddern, 1981), and combined into a series of MR lines (Foster *et al.* 1985). For the present study individual chromosomes were isolated from the MR lines after generation 1 (Fig. 1 and see below) as follows:

MR 39: *C(5L)101*, *C(5L)103*, *C(5L)105*, *C(5R)102*, *C(5R)104*, *C(5R)106*;
MR 41: *C(5L)107*, *C(5L)109*, *C(5R)108*, *C(5R)110*;
MR 1+4: *C(5L)111*, *C(5L)113*, *C(5L)115*, *C(5R)112*, *C(5R)114*, *C(5R)116*;
MR 47: *C(5L)117*, *C(5R)118*.

After generation 3 (Fig. 1), the only unmarked chromosomes saved for further study were: *C(5L)101*, *C(5L)109*, *C(5L)111*, *C(5L)115*, *C(5L)2*, *C(5R)110*, *C(5R)116* and *C(5R)1*.

Because individual *C(5L)*s and *C(5R)*s were frequently used in more than one MR line (Foster *et al.* 1985), different numerical designations do not necessarily

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indicate independent origin. However, the records of MR-line construction (unpublished) plus the observed genetic and cytological differences (see below), indicate that the compound chromosomes chosen for more detailed study were all of independent origin.

During the field trial in 1979–81, three strains were re-colonized from trapped field-inseminated females, by combining as pupae the second-generation offspring of individual females which had proved to represent compound × compound matings (Foster *et al.* 1985). Strains *BP32D* and *BP31D* were established from 27 and 9 females trapped 26 March and 16 May 1980, respectively (i.e. in the same season as they were released). Strain *BP64D* was established from 13 females, trapped 22, 27 and 30 October 1980 (i.e. after overwintering in the field). Strain *64R1 + 2* was derived from *BP64D*, by outcrossing to recently colonized (1–4 years) wild-type strains using whole-arm *T(4;5)* translocations as a bridging system (Foster, 1982).

(ii) *Experimental plan*

The series of crosses used to generate most of the segregation data reported in the present paper is outlined in Fig. 1. For the generation-1 crosses flies were taken from laboratory stocks of *C(5L)1;C(5R)2*, *C(5L)3;C(5R)5*, *C(5L)bzd;C(5R)3* and *C(5L)2;C(5R)1*, and from 11 different MR lines. In these and all subsequent crosses broods were reared from individual females. In generation 2 individual lines of *C(5L)* and *C(5R)* chromosomes were established from single-female generation-1 crosses. In these and subsequent crosses only segregant offspring were used, (i.e. containing the maternal *C(5L)* plus the paternal *C(5R)* (ML + PR), or the paternal *C(5L)* plus the maternal *C(5R)* (PL + MR), excluding flies from cultures in which the frequency of nonsegregants was significantly higher (see below) than in other genotypically similar crosses).

Virgin females which had been protein-fed and allowed to mature their ovaries (Woodburn, Vogt & Kitching, 1978) were caged with appropriate males (usually 15 females + 5 males) for 1–2 days prior to oviposition. Females were discarded after a single oviposition attempt (whether successful or not). Under these conditions females only mate once. Thus all broods reared from single females can be regarded as single-female × single-male matings.

The terms 'segregant' and 'nonsegregant' are used in the same sense as 'segregational' and 'non-segregational', as defined by Holm and Chovnick (1975). Nonsegregant (NS) progeny contain either both paternal CC elements (i.e. they are patroclinous), or both maternal elements (matroclinous).

(iii) *Statistical analysis*

In the present study poorly-fertile broods with fewer than ten offspring were excluded from analysis.

Data from individual broods of a given cross were tested for heterogeneity of segregation frequency using the χ^2 statistic from $2 \times n$ contingency tables. Although traditionally χ^2 has been regarded as valid only if expectations in the smallest

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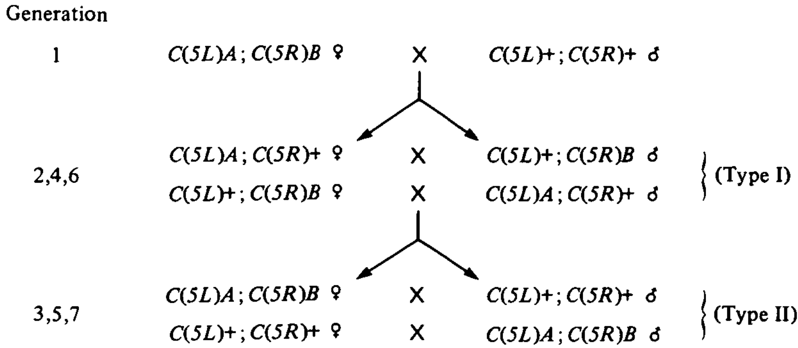

Fig. 1. Sequence of crosses used to obtain segregation data. $C(5L)A$, $C(5R)B$ indicate genetically marked compound chromosomes; $C(5L)+$, $C(5R)+$ indicate unmarked chromosomes.

classes are five or greater, some statisticians feel that this is unnecessarily conservative (Lewontin & Felsenstein, 1965; J. Wood, pers. comm.) and that χ^2 can be used with caution to test homogeneity of separate measurements (i.e. single-female broods) of the frequency of rare events such as nonsegregation of compound autosomes (Holm & Chovnick, 1975).

Generally, within-cross heterogeneity was not significant ($P > 0{\cdot}05$), and data from individual broods were pooled. Heterogeneity between crosses was then tested using the pooled cross totals. Occasionally, however, a small number of broods gave significantly higher NS frequencies than that typical for the particular cross. Such broods were excluded from the present analysis, but will be discussed in a separate report.

3. RESULTS

(i) *Segregation data*

Segregation data from the generation-1 crosses of $C(5L),+;C(5R),+$ females to genetically marked $C(5L);C(5R)$ males are presented in Table 1 (A). Within-cross NS frequencies were statistically homogeneous, except for a small number of broods with unusually high NS frequencies, which are listed separately. Excluding these cultures, between-cross heterogeneity was only barely significant ($0{\cdot}04 < P < 0{\cdot}05$), i.e. the NS frequency did not vary markedly when compound chromosomes from different MR lines were tested in females.

Segregation data from the generation-1 crosses of marked $C(5L);C(5R)$ females to $C(5L)+;C(5R)+$ males are presented in Table 1 (B). In contrast to the reciprocal crosses (Table 1 A), NS frequencies were highly heterogeneous between crosses, even after exclusion of a few cultures with unusually high NS frequencies. CCs from different MR lines thus differed considerably with respect to segregation, when tested in males, with NS frequencies ranging from 1 to 12%. It should be noted that, unlike the reciprocal crosses (Table 1 A), in which the males were genetically uniform, some of the 'within cross' heterogeneity observed in crosses with MR-line males (Table 1 B) could have reflected matings by males carrying different CCs.

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Table 1. *Segregation data from generation-1 crosses*

Cross		No. of offspring			Non-seg. freq.	Within-cross homogeneity $\chi^2(n-1)$	
♀♀	♂♂	n†	Seg.	Non-seg.			
(A) MR-line females							
MR 1+4	*C(5L)1;C(5R)2*	13	318	25	0·073	18·09	32·27***
		1	28	11	0·28	—	
MR 48	*C(5L)1;C(5R)2*	22	577	65	0·101	25·28	
MR 13+19	*C(5L)1;C(5R)2*	13	398	25	0·059	18·64	49·20***
		2	24	12	0·33	0·51	
MR 39	*C(5L)1;C(5R)2*	19	677	56	0·076	27·60	55·41***
		3	62	22	0·26	1·26	
MR 41	*C(5L)1;C(5R)2*	19	430	24	0·053	27·90	52·29***
		2	33	13	0·28	0·11	
MR 47	*C(5L)1;C(5R)2*	20	481	54	0·101	28·96	
MR 2+8	*C(5L)1;C(5R)2*	12	274	26	0·087	8·51	23·08*
		1	21	10	0·32	—	
MR 5+14	*C(5L)bzd;C(5R)3*	16	448	50	0·100	22·70	
MR 42	*C(5L)3;C(5R)5*	8	179	21	0·105	11·66	
MR 44	*C(5L)1;C(5R)2*	10	246	16	0·061	14·96	29·94**
		2	33	12	0·27	0·00	
MR 45	*C(5L)1;C(5R)2*	24	663	61	0·084	23·40	
C(5L)2;C(5R)1	*C(5L)1;C(5R)2*	10	237	20	0·078	6·37	
(B) MR-line males							
C(5L)1;C(5R)2	MR 1+4	3	197	2	0·010	1·08	20·92***
		2	27	5	0·16	0·11	
C(5L)1;C(5R)2	MR 48	23	1483	32	0·021	29·91	86·44***
		3	102	18	0·15	0·86	
C(5L)1;C(5R)2	MR 13+19	4	181	4	0·022	3·99	
C(5L)1;C(5R)2	MR 39	4	223	3	0·013	2·55	
C(5L)1;C(5R)2	MR 41	3	135	2	0·015	0·56	
C(5L)1;C(5R)2	MR 47	4	119	2	0·02	1·38	
C(5L)1;C(5R)2	MR 2+8	9	421	20	0·045	9·73	31·87***
		2	41	11	0·21	1·03	
C(5L)bzd;C(5R)3	MR 5+14	16	376	18	0·046	21·02	34·44**
		2	34	9	0·21	0·26	
C(5L)3;C(5R)5	MR 42	15	478	60	0·112	18·83	88·86***
		4	85	54	0·39	8·86*	
C(5L)1;C(5R)2	MR 44	4	78	11	0·12	1·06	
C(5L)1;C(5R)2	MR 45	14	433	52	0·107	20·28	42·31***
		2	53	24	0·31	1·07	
C(5L)1;C(5R)2	*C(5L)2;C(5R)1*	5	119	7	0·06	4·50	

* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$. Between-cross heterogeneity: A crosses – $\chi^2_{(11)} = 19·70$*; B crosses – $\chi^2_{(11)} = 152·39$***.

† n = no. of single-female broods.

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In order to remove this possibility, CCs descended from single broods were selected for further study (see Methods & Materials).

Segregation data from the generation-2 and -3 crosses are presented in Tables 2 and 3 respectively. Between-cross heterogeneity was highly significant

Table 2. *Segregation data from generation-2 crosses of*: (*A*) C(5L)1;C(5R), +♀♀ × C(5L), +;C(5R)2♂♂ *and* (*B*) C(5L), +;C(5R)2 ♀♀ × C(5L)1;C(5R), +♂♂

Cross genotype	n†	Number of offspring: Seg.	Number of offspring: Non-seg.	Non-seg. freq.	Within-cross homogeneity $\chi^2(n-1)$‡
(A) *C(5R)*, +♀ × *C(5L)*, +♂					
102 × 2	14	369	67	0·154	17·19
104 × 2	5	141	17	0·108	2·09
108 × 2	1	15	2	0·12	—
114 × 2	7	228	20	0·081	7·91 } 26·44***
	1	53	21	0·28	—
1 × 103	2	109	1	0·01	—
1 × 107	2	157	2	0·013	1·76
1 × 113	9	446	3	0·007	4·80
1 × 115	3	100	8	0·07	0·45
106 × 109	2	71	0	0	—
110 × 111	6	226	1	0·004	—
112 × 105	11	605	3	0·005	4·98
116 × 117	14	723	2	0·003	9·45
118 × 101	8	326	5	0·015	14·32*§
(B) *C(5L)*, +♀ × *C(5R)*, +♂					
103 × 1	4	93	5	0·05	3·10
107 × 1	6	189	13	0·064	8·34
113 × 1	6	141	6	0·04	1·84 } 14·92*
	1	32	9	0·22	—
115 × 1	14	536	19	0·034	11·39
2 × 102	5	118	3	0·02	4·28
2 × 104	3	58	7	0·11	6·11
2 × 108	4	100	2	0·02	3·04
2 × 114	12	307	11	0·035	11·39
117 × 116	6	146	18	0·110	4·17
101 × 118	4	50	9	0·16	5·38 } 12.35*
	1	22	16	0·42	—
109 × 106	5	145	14	0·088	5·64
111 × 110	8	245	12	0·047	13·29
105 × 112	12	419	32	0·071	15·80 } 31·97*
	1	14	7	0·33	—

*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$.

† n = no. of single-female broods.

‡ Between-cross homogeneity: $\chi^2_{(12)} = 289·31$*** for the (A) crosses; $\chi^2_{(12)} = 41·53$*** for the (B) crosses.

§ Only two cultures contained all the nonsegregants (88 offspring total); heterogeneity did not disappear if only one of these was removed.

($P < 0·001$) for each of the reciprocal cross types in both generations. Comparison of Tables 2 and 3 suggests the following generalizations. Firstly, when the male parent carried *C(5L)1*, *C(5L)2* or *C(5L)115* the NS frequency was usually greater than 3%. The two exceptions, out of 29 crosses, involved *C(5L)1*, in crosses with

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relatively small numbers of offspring. Secondly, the NS frequency was usually less than 3% in the remaining crosses. The one exception involved *C(5L)105*, which did not give consistent results between the two generations. Thirdly, the *C(5R)* chromosomes appeared to have no demonstrable effect on NS frequency. Most of the between-cross heterogeneity in Tables 2A and 3A can thus be accounted for by subdivision of the crosses into groups in which NS frequencies were low or high, as outlined above. The heterogeneity in the crosses involving *C(5L)1* males (Tables 2B, 3B) is unexplained, however, and not consistent with the largely homogeneous results of the previous generation (Table 1A), or those of similar or identical crosses in subsequent generations (see below).

Table 3. *Segregation data for generation-3 crosses of:* (*A*) C(5L)1;C(5R)2 ♀♀ × C(5L),+;C(5R),+♂♂ *and* (*B*) C(5L),+;C(5R),+♀♀ × C(5L)1;C(5R)2 ♂♂

Cross genotype	n†	Number of offspring: Seg.	Non-seg.	Non-seg. freq.	Within-cross homogeneity $\chi^2(n-1)$‡	
(A) *C(5L)*,+;*C(5R)*,+♂						
105;112	13	421	38	0·083	16·84	
111;110	13	426	6	0·014	18·99	} 26·69*
	2	56	6	0·10	0·00	
109;106	12	665	18	0·026	15·78	
101;118	8	380	5	0·013	3·38	
117;116	10	580	6	0·010	10·18	
2;104	11	249	37	0·129	16·74	
2;108	6	124	25	0·168	6·44	
113;1	14	484	1	0·002	—	} 33·84**
	1	30	3	0·09	—	
115;1	10	295	17	0·054	8·70	
(B) *C(5L)*,+;*C(5R)*,+♀						
105;112	8	194	25	0·114	4·54	
111;110	11	226	14	0·058	7·26	
109;106	8	329	17	0·049	3·22	
101;118	5	130	42	0·24	8·60	
117;116	5	69	6	0·08	2·74	
2;104	4	89	6	0·06	2·85	
113;1	5	126	18	0·125	6·05	
115;1	9	313	15	0·046	7·19	} 41·84***
	3	76	25	0·25	0·43	

*$P < 0{\cdot}05$; **$P < 0{\cdot}01$; ***$P < 0{\cdot}001$.

† n = no. of single-female broods.

‡ Between-cross homogeneity: $\chi^2_{(8)} = 194{\cdot}04$*** for the (A) crosses; $\chi^2_{(7)} = 73{\cdot}59$*** for the (B) crosses.

For further crosses the following wild-type *C(5L)* chromosomes were saved: ***101***, ***109*** and ***111*** (low NS), and *2* and ***115*** (high NS). *C(5R)1* and three randomly-selected MR-line *C(5R)* chromosomes were saved: ***110***, ***116*** and ***118***. In generations 4–7 segregation data were collected on two separate occasions from most of the possible crosses involving these elements and the genetically marked compounds *C(5L)1* and *C(5R)2*. Except for occasional high NS cultures the results for a given cross

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genotype were statistically homogeneous between cultures and generations. The pooled segregation data from these crosses are presented in Tables 4 and 5. The total number of cultures excluded because of heterogeneous NS frequencies was small (see footnotes to Tables 4, 5).

Table 4. *Number of segregant (S) and non-segregant (N) offspring from type I crosses*

(*a*) *C(5L)*, + ;*C(5R)2*♀♀ × *C(5L)1*;*C(5R)*, + ♂♂†

Female (5L) genotype

Male (5R) genotype	*C(5L)101*		*C(5L)109*		*C(5L)111*		*C(5L)115*		*C(5L)2*		
	S	N	S	N	S	N	S	N	S	N	χ^2(D.F.)
C(5R)110	127	13	187	14	57	7	73	5	70	10	3·19 (4)
C(5R)116	89	11	88	5	134	19	284	29	17	2	3·54 (4)
C(5R)118	220	18	89	11	54	7	387	33	65	10	3·97 (4)
C(5R)1	132	17	66	3	29	0	223	23	20	1	6·41 (4)
Totals	568	59	430	33	274	33	967	90	172	23	5·43 (4)
Non-seg. freq.	0·094		0·071		0·107		0·085		0·118		
χ^2(D.F.)	1·95 (3)		3·51 (3)		3·97 (3)		1·12 (3)		1·24 (3)		17·61 (19)

(*b*) *C(5L)1*;*C(5R)*, + ♀♀ × *C(5L)*, + ;*C(5R)2*♂♂‡

Male (5L) genotype

Female (5R) genotype	*C(5L)101*		*C(5L)109*		*C(5L)111*		*C(5L)115*		*C(5L)2*		
	S	N	S	N	S	N	S	N	S	N	χ^2(D.F.)
C(5R)110	143	0	365	6	97	1	159	8	81	5	14·11**(4)
C(5R)116	415	3	620	5	195	3	267	23	48	10	90·51***(4)
C(5R)118	327	2	372	4	554	0	252	25	89	15	116·80***(4)
C(5R)1	68	0	97	0	119	0	37	0	26	4	43·29***(4)
Totals	953	5	1454	15	965	4	715	56	244	34	
Non-seg. freq.	0·005		0·010		0·004		0·073		0·122		
χ^2(D.F.)	1·46 (3)		2·61 (3)		9·52* (3)		5·88 (3)		5·15 (3)		

* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.

† Data from 91 cultures; only 2 cultures were excluded because of heterogeneous NS frequency.

‡ Data from 122 cultures; no heterogeneous cultures.

Segregation frequency was strongly dependent on the *C(5L)*, + chromosome in the male parent (Tables 4, 5). *C(5L)101*, *C(5L)109* and *C(5L)111* were associated with low NS frequencies, while *C(5L)115* and *C(5L)2* were associated with high NS frequencies. NS frequencies were significantly higher in *C(5L)*, + ;*C(5R)*, + males than in *C(5L)*, + ;*C(5R)2* males for *C(5L)109* ($P < 0·01$), and *C(5L)111* ($P < 0·05$), but not for *C(5L)101*, *C(5L)115* or *C(5L)2*. In the crosses in which *C(5L)1* was transmitted from the male parent, the data reveal no effect of *C(5R)*, + in either

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Table 5. *Number of segregant (S) and non-segregant (N) offspring from type II crosses*

(*a*) *C(5L)*, + ;*C(5R)*, + ♀♀ × *C(5L)1*;*C(5R)2* ♂♂†

Female (5R) genotype	Female (5L) genotype: *C(5L)101* S	N	*C(5L)109* S	N	*C(5L)111* S	N	*C(5L)115* S	N	*C(5L)2* S	N	χ^2(D.F.)
C(5R)110	268	20	304	19	152	11	436	58	120	9	11·57* (4)
C(5R)116	213	26	218	21	381	20	491	51	69	9	9·66* (4)
C(5R)118	360	27	157	15	309	18	810	99	54	2	13·00* (4)
C(5R)1	47	5	56	9	—	—	195	32	80	12	0·76 (3)
Totals	888	78	735	64	842	49	1932	240	323	32	
Non-seg. freq.	0·081		0·080		0·055		0·110		0·090		
χ^2(D.F.)	3·82 (3)		5·30 (3)		0·69 (2)		3·89 (3)		5·10 (3)		43·17** (18)

(*b*) *C(5L)1*;*C(5R)2* ♀♀ × *C(5L)*, + ;*C(5R)*, + ♂♂‡

Male (5R) genotype	Male (5L) genotype: *C(5L)101* S	N	*C(5L)109* S	N	*C(5L)111* S	N	*C(5L)115* S	N	*C(5L)2* S	N	χ^2(D.F.)
C(5R)110	578	10	272	7	438	8	229	13	171	21	45·71*** (4)
C(5R)116	274	0	256	7	275	1	472	51	24	1	60·70*** (4)
C(5R)118	763	8	306	9	399	6	507	62	20	4	99·08*** (4)
C(5R)1	161	1	—	—	—	—	115	14	—	—	15·39*** (1)
Totals	1776	19	834	23	1112	15	1323	140	215	26	
Non-seg. freq.	0·011		0·027		0·013		0·096		0·116		
χ^2(D.F.)	5·55 (3)		0·07 (2)		2·77 (2)		6·35 (3)		2·06 (2)		

$*P < 0·05$; $**P < 0·01$; $***P < 0·001$.

† Data from 186 cultures; 5 cultures excluded because of heterogeneity.

‡ Data from 164 cultures; 6 cultures excluded because of heterogeneity.

sex, and no consistent effect of *C(5L)*, + arms in females. In the crosses with *C(5L)*, + males, no effect of *C(5R)*, + was detected in either sex.

(ii) *Correlation of fertility with segregation frequency*

Crosses with low-NS paternal *C(5L)* chromosomes tended to be much more fertile than crosses with high-NS *C(5L)*s (Table 6). *C(5L)101*, *C(5L)109* and *C(5L)111* males differed strikingly from those carrying *C(5L)1*, *C(5L)2* or *C(5L)115*, in both range and distribution of progeny sizes. In a series of crosses (separate from those outlined in Fig. 1) in which both egg hatch and segregation were scored, the low NS compounds all yielded much higher hatch values than *C(5L)115* (Table 7).

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(iii) *Cytogenetic examination of compound chromosomes*

Examination of the trichogen-cell polytene chromosomes of the compounds studied in the final series (generations 4–7) of crosses revealed that all were basically reversed metacentric compound chromosomes, but that several contained visible euchromatic deficiencies or duplications. These presumably result from the translocation-like origin of compound chromosomes (reviewed by Holm, 1976), and arose at the time of induction. Of the *C(5R)* elements, only *C(5R)1* contained a visible anomaly, being heterozygous deficient for all of region 74 A–B (Plate 1*a*). *C(5L)1*, *C(5L)2* and *C(5L)115* contained no visible duplications or deficiencies

Table 6. *Correlation of fecundity with paternal left compound elements*

(Proportion of cultures in each progeny-size range.)

Paternal left compound	Total number of cultures*	Size range (number of offspring) 1–20	21–40	41–60	61–80	81–110
High-NS						
C(5L)1	733	0·53	0·32	0·13	0·01	0
C(5L)2	113	0·58	0·34	0·05	0·04	0
C(5L)115	120	0·49	0·28	0·22	0·01	0
Low-NS						
C(5L)101	102	0·31	0·25	0·27	0·13	0·03
C(5L)109	88	0·32	0·32	0·17	0·10	0·09
C(5L)111	91	0·33	0·32	0·22	0·10	0·03

* Includes cultures with 1–9 offspring which were excluded from segregation data.

Table 7. *Correlation of egg hatch with segregation in males*

(Number of single-female egg masses in each size range in crosses of *C(5L)1;C(5R)116*♀♀ × *C(5L), + ;C(5R)2*♂♂.)

Paternal left arm	Egg hatch range (%) 1–10	11–20	21–30	31–40	41–50	Proportion of non-segregants	*N**
C(5L)101	1	3	4	9	2	0·014	713
C(5L)109	1	3	2	6	1	0·025	326
C(5L)111	2	3	3	11	0	0·008	593
C(5L)115	1	4	8	0	0	0·102	274

* *N* = number of adults scored to determine frequency of nonsegregants.

Plate 1

Polytene chromosome preparations of the proximal ends of compound chromosomes. Numerals and letters A–C correspond to standard *L. cuprina* polytene map regions (Foster *et al.* 1980). Arrows indicate break points. Insets: ——, 5L chromatin; ---, 5R chromatin; —O—, centric heterochromatin (not condensed) + centromere. (*a*) *C(5R)1* showing heterozygous deficiency for region 74 A–B; (*b*) *C(5L)2*; (*c*) *C(5L)115*; (*d*) *C(5L)101* with duplicated region pairing with *C(5R)116*; (*e*) *C(5L)109*; (*f*) *C(5L)109* with duplicated region pairing with *C(5R)116*; (*g*) *C(5L)111* pairing with *C(5R)116*; (*h*) *C(5L)111*; (*i*) *C(5L)64R* pairing with an unidentified *C(5R)*; (*j*) standard polytene map positions of the right-most break points of rearrangements carrying duplications or deficiencies.

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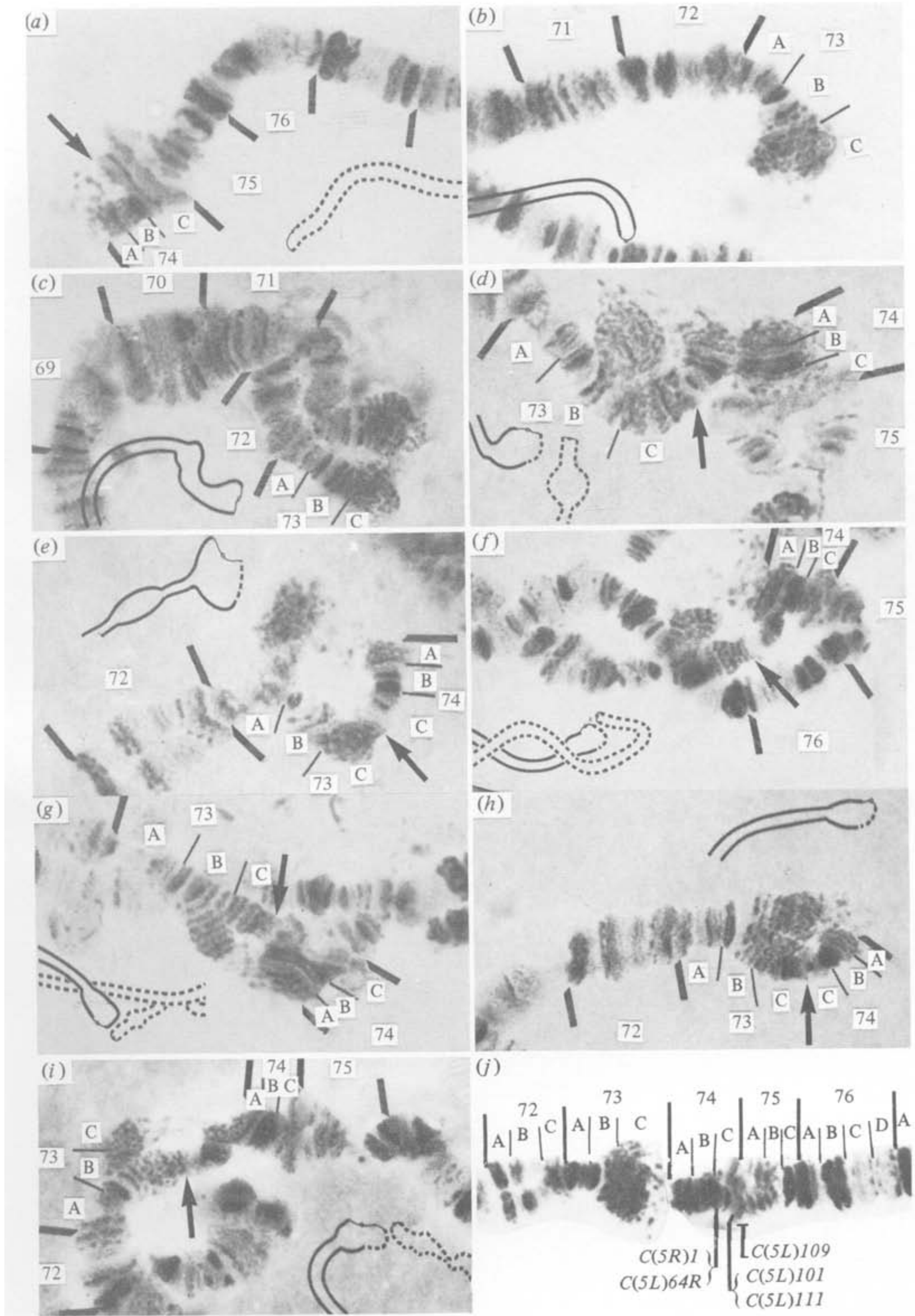

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Table 8. *Recovery of arms in segregant offspring of crosses with paternal* C(5L), + *arms: total numbers of each segregant type*

	$C(5L)+♂$													
	101		109		111		115		2		Totals†			
$C(5R),+$	ML + PR	PL + MR	ML + PR	PL + MR	ML + PR	PL + MR	ML + PR	PL + MR	ML + PR	PL + MR	ML + PR	PL + MR	$X^2_{(4)}$ (Het.)	$X^2_{(1)}$ (1:1 exp.)
(Type I crosses)‡														
110 ♀	80	63	186	179	44	53	69	90	40	41	419	426	5·72	0·06
116 ♀	218	197	321	299	100	95	147	120	28	20	814	731	1·58	4·46*
118 ♀	157	170	185	196	308	254	136	116	50	39	836	775	6·67	2·31
(Type II crosses)‡														
110 ♂	298	280	142	134	226	212	123	106	99	72	888	804	2·60	4·17*
116 ♂	133	141	122	134	157	118	238	234	15	16	665	643	6·02	0·37
118 ♂	418	345	146	160	211	188	245	233	11	9	1031	935	4·78	4·69*
Totals†	1304	1196	1102	1102	1046	920	958	899	243	197				
$\chi^2_{(5)}$ (Het.)	6·73		2·67		5·40		6·82		2·42					
$\chi^2_{(1)}$ (1:1 exp.)	4·67*		0·00		8·08**		1·87		4·81*					

$*P < 0{\cdot}05$; $**P < 0{\cdot}01$.

† $\chi^2_{(4)}$ = (marginal column totals) = 10·76*, $\chi^2_{(5)}$ = (marginal row totals) = 5·59.

‡ In type I crosses ML+PR are *to*^{2} *bz mv sby* and PL+MR are + + + +. In type II crosses ML+PR are *to*^{2} *bz mv* + and PL+MR are + + + *sby*.

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Table 9. *Recovery of arms in segregant offspring of crosses with maternal* C(5L), + *arms: total numbers of each segregant type*

	$C(5L)+♀$													
	101		109		111		115		2		Totals†			
$C(5R)$, +	ML + PR	PL + MR	ML + PR	PL + MR	ML + PR	PL + MR	ML + PR	PL + MR	ML + PR	PL + MR	ML + PR	PL + MR	$\chi^2_{(4)}$ (Het.)	$\chi^2_{(1)}$ (1:1 exp.)
(Type I crosses)‡														
110 ♂	62	71	77	110	24	41	38	35	36	34	237	291	5·59	5·52*
116 ♂	36	53	48	40	55	79	159	125	6	19	304	316	18·88***	0·23
118 ♂	106	134	41	48	20	43	181	206	26	39	374	470	5·58	10·92***
(Type II crosses)‡														
110 ♀	119	154	122	182	55	97	195	241	55	61	546	735	5·33	27·89***
116 ♀	105	116	100	118	167	222	276	232	35	33	683	721	12·66*	1·03
118 ♀	160	203	73	84	125	190	404	406	18	36	780	919	14·00**	11·37***
Totals†	588	731	461	582	446	672	1253	1245	176	222				
$\chi^2_{(5)}$ (Het.)	1·77		7·26		4·43		14·45*		10·61					
$\chi^2_{(1)}$ (1:1 exp.)	15·50***		14·04***		45·69***		0·03		5·32*					

*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$.

† $\chi^2_{(4)}$ (marginal column totals) = 37·10*** (excluding 115), $\chi^2_{(3)} = 6·58$.

‡ In type I crosses ML+PR are + + + + and PL+MR are *to² bz mv sby*. In type II crosses ML+PR are + + + *sby* and PL+MR are *to² bz mv* +.

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(Plate 1*b, c*; Fig. 4 of Foster *et al.* (1976)). The low NS *C(5L)* chromosomes *C(5L)101*, *C(5L)109*, *C(5L)111* and *C(5L)64R* (see below), all contained duplications of 5R region 74 A–B, in addition to two virtually complete copies of 5L (Plate 1*d–i*). Although variable condensation of chromatin in the region of the breakpoints (e.g. Plate 1*g, h*) at times made interpretation difficult, three different 5R breakpoints can be discerned among the four low-NS *C(5L)* chromosomes. All have a 5L break in the proximal part of 73C, and a 5R break distal to 74B. *C(5L)64R* appears to have a break point proximal to the prominent band in region 73C (Plate 1*f*). The break points of *C(5L)101* and *C(5L)111*, which cannot be distinguished from one another, are distal to this band (Plate 1*d, e, g*). The break point in *C(5L)109* appears to be still more distal, in the region of the 74C/75A junction (Plate 1*h, i*). The positions of the breaks of the duplication/deficiency compound elements are summarized with respect to the standard polytene map in Plate 1*j*.

(iv) *Transmission of compound chromosomes in segregants*

Recovery of the different compound chromosomes among the segregant offspring of the generations 4–7 crosses is summarized in Tables 8 and 9. There appear to be significant differences in recovery of particular elements. On the basis of an expected ratio of 1 ML+PR:1 PL+MR, *C(5L)115* is recovered in the expected frequency when transmitted through either sex. On the other hand, *C(5L)109* was recovered with lower-than-expected frequency when transmitted through females but not through males, and *C(5L)101*, *C(5L)111* and *C(5L)2* are recovered in lower-than-expected frequencies from both sexes. Transmission through females was significantly lower than through males for *C(5L)109* ($P < 0{\cdot}01$) and *C(5L)111* ($P < 0{\cdot}001$), but not for *C(5L)101* or *C(5L)2*. The data reveal no effect on recovery attributable to the genetic markers used.

Crosses involving *C(5R)1* did not fit consistently into the above pattern. Crosses involving this chromosome in either parent were frequently poorly fertile, and tended to produce fewer *C(5R)1* offspring than expected, although not invariably. This may have reflected low viability attributable to the heterozygous deficiency for region 74 A–B.

(v) *Genetic changes in mass-reared CC strains*

In order to obtain data on changes in the frequencies of high-NS and low-NS CCs in mixed colonies, the segregation properties of CCs in strain *C18* and strains recovered from field collections, were investigated. Segregation in males from strains *BP32D*, *BP31D*, *BP64D* and *64R1+2*, was examined by crossing individual males to several virgin *C(5L)1*;*C(5R)2* females and scoring the offspring, approximately 25, 23, 17 and 26 generations after recapture, respectively. The results, along with similar data from strain *C18* (Foster *et al.* 1985), obtained 20 generations after the final release, are summarized in Table 10. These results suggest the presence of both high NS and low NS chromosomes in *BP31D*, *BP64D* and *64R1+2*. There was no evidence of low NS elements in *BP32D*, and no evidence of high NS elements in *C18*. From the records of strain construction (Foster *et al.*

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1985) and the data in Tables 1–5, *C(5L)101*, *C(5L)111*, *C(5L)115*, and other high-NS and low-NS *C(5L)*s, were used in the construction of C18. From the release records (Foster *et al.* 1985) and trapping data for this strain, *BP32D* must have been derived entirely from *C18*, yet it appeared to contain mainly (if not only) high-NS CCs when assessed later (Table 10). Thus if *BP32D* originally contained low-NS chromosomes, they evidently were not at a selective advantage compared to the high-NS chromosomes in this strain. On the other hand, when *C18* was assessed at a similar time (Table 10), there was no evidence of high-NS chromosomes, suggesting that low-NS elements had been selected. Fixation of low-NS CCs had

Table 10. *Segregation in recolonized strains and strain* C18

Strain	Generation†	No of individual males tested	Total offspring Seg.	Total offspring Non-seg.	Non-seg. frequency	Heterogeneity χ^2(D.F.)	
BP32D	25	11	1714	206	0·107	17·78 (10)	
BP31D	23	4	508	7	0·014	4·46 (3)	11·70 (4)*
		1	114	7	0·06	—	
BP64D	17	12	2091	27	0·013	15·80 (11)	119·4 (19)***
		8	1028	88	0·079	9·64 (7)	
64R1+2	26	19	1858	4	0·002	15·67	96·06***
		2	115	8	0·065	1·43	
C18	20	11	1501	6	0·004	12·60 (10)	

† See text.

not occurred by generation 25 in *BP31D*, although the little data available (Table 10) suggests that low-NS chromosomes may have been more frequent than high-NS chromosomes in this strain. In the *BP64D*–*64R1+2* line, 12 of 20 males tested at generation 17 were low-NS, whereas nine generations later, 19 of 21 were low-NS. Thus the evidence suggests that in this line the high-fertility CCs were at a selective advantage.

A further line of evidence suggests that a single low-NS compound element (designated *C(5L)64R*) predominated in strain *64R1+2*. All the paternal *C(5L)* offspring of one of the low-NS *64R1+2* males (Table 10), exhibited a dark-eye (*da*) phenotype. Subsequent tests confirmed that *da* bred true and was carried on the *C(5L)* element. In the course of tests on the *C(5L)*, + ; *C(5R)2* progeny of 11 other *64R1+2* males, it was observed that 9 of the 10 low-NS *C(5L)* elements generated *da* offspring when carried maternally (frequency = 0·103, N = 939) but not when carried paternally (the single low-NS family which failed to yield *da* only produced 10 non-*C(5L)1* offspring, i.e. insufficient to establish statistically the absence of *da*). The one high-NS *C(5L)* element tested did not yield *da* offspring when transmitted maternally (N = 58).

Segregation was also examined in the male *C(5L)*, + ; *C(5R)2* and *C(5L)1*; *C(5R)*, + progeny of 11 of the low-NS males (Table 10). In each case the low-NS property was inherited with the *C(5L)*, + element. None of the *C(5R)*, + elements had any demonstrable effect on segregation.

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4. DISCUSSION

Foster *et al.* (1976) concluded from cytological evidence that *C(5L)1* assorted randomly from *C(5R)1* in males. The similarity of NS frequencies in crosses in which the paternal left compound was *C(5L)1*, *C(5L)2* or *C(5L)115*, suggests that the latter two elements also assort randomly in males, regardless of the accompanying *C(5R)* element. Assuming this to be true, the proportion of NS offspring in crosses involving males carrying these chromosomes, should be a measure of the frequency of nonsegregation in females. This group of males produced 19592 segregant and 1823 nonsegregant offspring (NS frequency 0·0851) (Tables 1–5). However, there is evidence of considerable mortality of MNS zygotes (unpublished data). Thus a better estimate of the frequency of NS zygotes can be obtained by doubling the PNS class. Of the NS offspring from these crosses, 1203 were PNS. Doubling these gives an estimate of 0·1094 for the frequency of NS in females. Thus the frequency of segregation of compound chromosomes in *L. cuprina* females is 0·8906. In *D. melanogaster*, the frequency of segregation of compound third chromosomes in otherwise structurally-normal females has been estimated at greater than 95% (Holm & Chovnick, 1975). In other words, the frequency of nonsegregation in *L. cuprina* females is at least double that in *D. melanogaster* females.

The genetic data indicate that the high fertility of crosses involving males carrying *C(5L)101*, *C(5L)109*, or *C(5L)111*, is due to non-random segregation of *C(5L)* from *C(5R)* in these males. Because the number of NS zygotes is proportional to the product of the frequencies of nonsegregation in males (Fm) and females (Ff), Fm can be estimated from the relationship $\mathrm{Fm}\,.\,\mathrm{Ff}/(1-\mathrm{Fm})\,(1-\mathrm{Ff}) = N_{NS}/N_S$, where N_S is the number of segregants and N_{NS} is the number of non-segregants (corrected for inviability of MNS zygotes). The Fm values thus estimated, using the data for generations 4–7, were 0·087 for *C(5L)101* males, 0·229 and 0·100 for *C(5L)109;C(5R)+* and *C(5L)109;C(5R)2* males respectively, and 0·127 and 0·043 for *C(5L)111;C(5R)+* and *C(5L)111;C(5R)2* males respectively.

The correlation of regular segregation with the existence of duplications of 5R euchromatin in certain *C(5L)* elements is similar to the findings of Gethmann (1976) and Hilliker *et al.* (1982). These authors found that regular segregation of compound second-chromosomes in *D. melanogaster* males carrying certain *C(2R)*s was associated with duplications of 2L euchromatin in those chromosomes. They concluded that these duplications contain a site normally involved in second-chromosome pairing during meiosis in males. By direct analogy, the results with *L. cuprina* suggest that a site involved in fifth-chromosome pairing is located in the proximal 5R euchromatin. The failure to find any *C(5R)* chromosomes associated with low NS in males suggests either (1) that no such pairing sites are located in proximal 5L euchromatin, or (2) if they are, then *C(5R)* chromosomes carrying duplications of such sites are either not recovered or have lowered fitness, or possibly the pairing function could be lost through position effects in such elements.

Although the *C(5R)* elements which were tested extensively did not by themselves cause low nonsegregation in males, the data did reveal a consistent association between *C(5R)2* and lower NS frequencies in the presence of *C(5L)109* and

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C(5L)111, but not the other *C(5L)* elements (Tables 2–5). This suggests that regular pairing or random assortment between left and right compound elements in males may not be determined simply by the presence or absence of a pairing site on both elements. The data suggest that *C(5L)109* and *C(5L)111* may differ in some way from the other low-NS element, *C(5L)101*, and that *C(5R)2* differs from the other *C(5R)* elements studied. These observations may help explain the observation that males with *C(5L)105* gave a much higher NS frequency with *C(5R)112* than with *C(5R)2* (Tables 2, 3). Unfortunately, neither *C(5L)105* nor *C(5R)112* was examined cytologically, nor saved for further genetic crosses. However, it can be speculated that *C(5L)105* may have contained a defective pairing site whose possession was sufficient to enable it to pair with *C(5R)2* but not with *C(5R)112*. Alternatively, *C(5R)112* may have lacked a pairing site carried by the other *C(5R)* elements. The data do not permit a choice between these two alternatives.

The occurrence of dark eyes in the progeny of *C(5L)64R* females, but not from males, is probably due to crossing over between the mutation *da*, carried on one of the homologous compound arms, and the centromere. Meiotic crossing over is rare or absent in *L. cuprina* males (Foster, Maddern & Mills, 1980*a*). Such crossovers should result in homozygosis of the *da* or da^{+} alleles half of the time (Baldwin & Chovnick, 1967). Since the da^{+}/da^{+} homozygotes cannot be distinguished from the da/da^{+} noncrossovers, the observed frequency of dark eyes (10·3 %) suggests that *da* is situated 20·6 map units to the left of the chromosome 5 centromere. The observation that at least 9 of the 10 tested *C(5L)* elements were in fact *da*/+, suggests strongly that this single compound element was proceeding toward fixation in strain *64R1*+*2*.

The data in Tables 8 and 9 suggest that segregation properties are not the sole determinant of CC strain fecundity. The lower-than-expected recoveries of *C(5L)101*, *C(5L)109* and *C(5L)111* could thus tend to offset the selective advantages conferred on these chromosomes by non-random segregation in males. Low recovery could be caused either by unequal transmission (i.e. meiotic drive) or by poor viability. The latter could in turn be caused by position effects, the duplications, or lower viability associated with particular mutations (see below) carried on the compound chromosomes. Although there are insufficient data to distinguish firmly between these alternatives, the last hypothesis seems to be the most plausible.

Although euchromatic duplications ranging in size from 2 to 3 % of the genome have been shown to reduce viability in *L. cuprina* by 4–19 %, particularly when particular mutations are homozygous (Konovalov, Foster & Whitten, 1983), the present data, involving smaller duplications (approximate size 0·7–1 %) cannot be explained solely by inviability due to segmental trisomy. Firstly, *C(5L)2* contained no visible duplications, yet was recovered with lower-than-expected frequency from both sexes. Secondly, *C(5L)109* (approx. size 1 %) was recovered in the expected frequency from male parents. Finally, the data (heterogeneity chi squares, Tables 8, 9) reveal no influence of the presence of *C(5R)2* (homozygous for *sby*) on the recovery of the *C(5L)*, + elements, regardless of whether or not they carried duplications.

The lower recovery of *C(5L)109* and *C(5L)111* from females compared to males

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could reflect homozygosis of deleterious mutations due to meiotic crossing over within the compound elements in females (Baldwin & Chovnick, 1967; Foster *et al.* 1976). Indeed, the evidence suggests that selection of *C(5L)64R,da*/+ occurred in strain *64R1+2* in spite of this sort of handicap. The mutation *da* itself is somewhat less viable than wild-type (unpublished observation), and homozygotes are probably less competitive than wild-type in cages. More interestingly, data from the cross *C(5L)64R,da*/+ ;*C(5R)2* × *C(5L)1*;*C(5R)*+ and its reciprocal show that the *C(5L)64R* element is recovered with a much lower frequency from females than from males (0·543 from males, $N = 4164$; 0·460 from females, $N = 2571$; $\chi^2_{(1)} = 44{\cdot}18^{***}$).

The correlation of fertility with segregation behaviour and compound chromosome structure and composition has implications for the selection of compounds for use in strains intended to be released for genetic control purposes. In colonies containing a number of independently isolated elements, the frequency of duplication-bearing *C(5L)*s would thus be expected to increase, provided that their higher fertilities were not counteracted by some other genetic property. However, the recovery of both high-NS and low-NS compound chromosomes from the field (Table 10) suggests that, despite the selective advantage of low-NS CCs in cages, the segregation properties of a particular compound have no dramatic effect on the ability of individuals to survive, mate or overwinter in the field. Furthermore, recent studies have shown that both *BP32D* and *BP64D*, and the strains derived from them, are severely debilitated, relative to non-CC strains, under field conditions (R. J. Mahon & G. G. Foster, unpublished; Smith & Morton, 1985).

The foregoing results suggest strongly that the procedures used to construct CC strains for use in genetic control programmes require alteration. The strains released at Brindabella were constructed by pooling a large number of independently isolated *C(5L)* and *C(5R)* elements (Foster *et al.* 1985). However, the present data suggest that the fitness of particular CCs in the rearing colonies may have little relevance to the field performance of the released insects. It may thus be preferable to construct strains containing a single *C(5L)* and *C(5R)*. This approach might enable the selection of individual rearrangements, whose properties were likely to be advantageous to the genetic control programme, both in the rearing colony and the field.

Probably one of the main causes of the poor field performance of CC strains is homozygosis of deleterious mutations by crossing over between homologous arms. This possibility is currently being evaluated in a series of laboratory and field experiments. One possible approach to this problem would involve the construction of appropriate inversions and their incorporation into CC arms. A hunt for paracentric inversions has yielded two which greatly suppress crossing over on the left arm of chromosome 5. We are now attempting to incorporate these into *C(5L)*s. No inversions on the right arm of chromosome 5 have yet been discovered. A second approach to the problem of crossing over would be to restrict a compound chromosome to the male sex, by insertion of the male-determining gene or region. This approach would relegate CC strains to a sterile-male role, and would not be appropriate if the goal were replacement of a population through negative heterosis, which requires both sexes to be functional in the field.

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The segregation behaviour of the CCs in a strain would be an important factor in mass-rearing for a field release programme, since both the cost of buildings and equipment and the cost of maintaining the egg-production colony would be inversely related to strain fecundity. Thus, from this point of view, it may be desirable to select a CC strain which contains, in addition to inversions, a duplication that ensures regular segregation in males. Unfortunately, the possible adverse effects of the large number of chromosomal break-points contained in such a strain are not easy to predict beforehand. It may be prudent, therefore, to ensure that field performance is not adversely affected by potential component rearrangements, such as inversions, prior to their inclusion in a compound chromosome. The next step would be to demonstrate that the composite rearrangements were both stable and free of deleterious effects (whether due to position effects of the rearrangements, or the effects of segmental trisomy) before their use in a control programme.

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