Genet. Res., Camb. (1987), **50**, *pp.* 125–130 *With 1 text-figure Printed in Great Britain*

Correlation of compound autosome segregation and sex-chromosome disjunction in female *Lucilia cuprina* (Wied.) (Diptera: Calliphoridae)

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(*Received 2 October 1986 and in revised form 15 April 1987*)

Summary

In *Lucilia cuprina* (Wiedemann) females, non-segregation of compound fifth-chromosomes is correlated with non-disjunction of the *X* chromosomes. Approximately two-thirds of eggs which inherit both maternal compound elements are nullo-*X*, suggesting that meiotic pairing between *X* chromosomes and compound autosomes has occurred. There was no evidence for pairing of the compounds and the *X* or *Y* chromosome in males. A limited amount of data suggests that high non-segregation frequencies may occur in the offspring of putative *X/X/X* and *X/O* females. These results suggest the existence of non-homologous (distributive) pairing in *L. cuprina* females.

1. Introduction

Although the two halves of a pair of compound autosomes share only a limited homology in the centromeric regions, it has been known for many years that compound left chromosomes regularly segregate from compound right chromosomes in *Drosophila melanogaster* females (Holm *et al.* 1967; Holm & Chovnick, 1975). E. H. Grell (1970) showed that this regular segregation was due to the compound chromosomes (CCs) virtually always being available for pairing with non-exchange chromosomes. Usually the CCs pair and segregate from one another, because in most meioses they are the only large non-exchange chromosomes. More recently, Harger & Holm (1980) have shown that non-segregation of compound autosomes in *D. melanogaster* females is frequently associated with non-disjunction of the *X* chromosomes.

In *Lucilia cuprina*, it has been estimated that 89% of the gametes produced by females carrying compound fifth-chromosomes are segregational (Foster & Maddern, 1985). This paper presents further data from the crosses of Foster & Maddern (1985), which indicate that, as in *D. melanogaster*, there is a high correlation between non-segregation of compound autosomes and non-disjunction of the *X* chromosomes in *L. cuprina* females.

2. Materials and Methods

(i) *Mutations and strains*

C(5L) 1 (Foster *et al.* 1976) and *C(5R) 2* (Maddern, 1981) are compound left and right fifth-chromosomes, genetically marked with the mutations to^2 (topaz eyes), *bz* (bronze body) and *mv* (M1-veinless) on *C(5L) 1*, and *sby* (stubby bristles) on *C(5R) 2*. Descriptions and genetic localization of these mutations are given by Foster *et al.* (1980*b*, 1981). *C(5L) 2, C(5L) 101, C(5L) 109, C(5L) 111, C(5L) 115, C(5R) 1, C(5R) 110, C(5R) 116* and *C(5R) 118* are unmarked compound chromosomes whose derivation and genetic properties have been outlined previously (Foster *et al.* 1976; Foster & Maddern, 1985). The derivation of the compound-chromosome line MR18 was described by Foster *et al.* (1985). Compound-chromosome line CA was derived by a procedure similar to that described for MR lines by Foster *et al.* (1985).

The *X*-chromosome mutation b^2 (black body) is a variegating allele of *b* (Whitten *et al.* 1975). The strain b^2/b^2; *C(5L) 1; C (5R) 2* was constructed by transferring the *X* chromosome from a chromosomally normal b^2 stock to *C(5L) 1; C(5R) 2* using the *T*(4; 5) bridging system (Foster, 1982).

(ii) *Experimental methods*

Details of rearing and statistical analysis are given in Foster & Maddern (1985). Data on sex ratio and *X*-deficiency phenotype (see below) were obtained from the progeny of the crosses performed by Foster & Maddern (1985). Details of other crosses performed are given in the Results section.

3. Results

(i) *Sex-ratio distortion in matroclinous non-segregants*

Analysis of the sex-ratio data from previously reported compound-chromosome crosses (Foster & Maddern 1985) reveals a consistent bias toward high female:male ratios (2·63:1–3·31:1) in the matroclinous non-segregant (MNS) class, but not in the patroclinous non-segregant (PNS) and segregant offspring (Table 1A). MNS sex ratios were significantly higher than those of the other classes in all the homogeneous crosses, while the sex ratios of segregant and PNS offspring did not differ significantly, except for a barely significant result in the *C(5L)+;C(5R)+* cross type ($\chi^2_{(1)} = 4{\cdot}61$, $P < 0{\cdot}05$).

The broods identified in Foster & Maddern's (1985) analysis of segregation in CC males, as having either exceptionally high non-segregant frequencies, or low fertility, produced results which differed markedly from the above data. Sex ratios of MNS progeny from these two types of crosses, differed significantly from those in the homogeneous crosses ($\chi^2_{(5)} = 14{\cdot}62$, $P < 0{\cdot}05$), but did not difer significantly from one another or from those of the segregant and PNS progeny (Table 1).

(ii) *X-chromosome deficiency phenotype in MNS females*

It was noted that MNS females (but not males) often exhibited a phenotype (irregular thickening or doubling of the M_{1+2} or r-m wing veins), which is frequently seen in females heterozygous for deficiencies of the small euchromatic portion of the otherwise heterochromatic *X* chromosome (Maddern & Bedo, 1984). This phenotype was not seen in the PNS classes, and only rarely in the segregant classes. Of 246 MNS female offspring from crosses involving several different parental female compound-autosome genotypes (the generations 5–7 crosses of Foster & Maddern, 1985), 82 (33%) expressed the *X*-deficiency phenotype and are presumed to have been *X/O*. There was no correlation between the incidence of the *X*-deficiency phenotype, and non-segregant frequency, culture fertility or cross genotype.

(iii) *Crosses with genetically marked X chromosomes*

The prevalence of the X-deficiency phenotype and distortion of sex ratio among MNS offspring are consistent with the hypothesis that nonsegregation of CCs in females is correlated with non-disjunction of the *X* chromosomes, such that MNS eggs are frequently nullo-*X*. Since the *Y* chromosome is male-determining in *L. cuprina* (Ullerich, 1963; Bedo & Foster, 1985), *X/O* individuals are females. Insemination of nullo-*X* eggs by an *X*-bearing sperm

Table 1. *Distribution of sex in segregant and non-segregant offspring*

	Number of offspring						Chi-square values		
			Non-segregants					1:1 Expectation (1 d.f.)	
	Segregants		Patroclinous		Matroclinous		Homogeneity[a]	Sex ratio	
Cross type	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	(2 D.F.)	SEGS+PNS	MNS
(A) Homogeneous crosses[b]									
C(5L)+;C(5R)+ ♀♀	5304	5820	280	366	292	111	102·24***	30·79***	81·29***
C(5L)+;C(5R)2 ♀♀	2452	2506	122	146	88	33	27·64***	1·16	25·00***
C(5L)1;C(5R)+ ♀♀	3686	4161	88	78	60	19	28·50***	26·98***	21·28***
C(5L)1;C(5R)2 ♀♀	4036	4967	122	147	88	26	47·60***	98·57***	33·72***
(B) Heterogeneous crosses[c]									
All crosses	348	352	78	102	40	28	5·07	0·65	2·45
(C) Poorly-fertile crosses[d]									
All crosses	552	744	32	47	19	18	1·29	31·16***	0·03

[a] 2 × 3 contingency tables.
[b] Sex ratio of data from the crosses of Foster & Maddern (1985) (segregational data contained in their Tables 1–5), excluding the crosses with MR-line male parents, and excluding heterogeneous (high non-segregation) cultures.
[c] Summary of data from heterogeneous cultures of Foster & Maddern (1985) (see note *b*).
[d] Summary of data from low-fertility (< 10 progeny) cultures of Foster & Maddern (1985).
* $P < 0{\cdot}05$; *** $P < 0{\cdot}001$.

https://doi.org/10.1017/S0016672300023521 Published online by Cambridge University Press

would give rise to X/O female offspring, most of which should exhibit the X-deficiency phenotype (Maddern & Bedo, 1984). Insemination by a Y-bearing sperm would give rise to O/Y zygotes, which are not viable, since the X chromosome carries one or more vital loci not carried by the Y chromosome (Maddern & Bedo, 1984).

This hypothesis was tested in crosses in which the compound chromosomes were marked to enable scoring of segregation, and the paternal X chromosome was marked with the mutation b^2 In this type of cross, all viable offspring which inherit one or both maternal X chromosomes, are expected to be wild type, but those which inherited no maternal X should be black-bodied (Fig. 1). The results (Table 2) indicate a high correlation between non-segregation of the CCs and non-disjunction of the X chromosomes. Approximately half of the MNS offspring, but none of the PNS offspring, arose from nullo-X eggs. Three of the segregant offspring arose from nullo-X eggs indicating that non-disjunction of the X chromosomes can be independent, *i.e.* not necessarily accompanied by non-segregation of the CCs. The observed frequency (0·2%) of independent non-disjunction of the X chromosomes is similar to that reported by Harger & Holm (1980) in *D. melanogaster*. One of the independent non-disjunctional progeny, the black-bodied male, appears to have resulted from fertilization of a nullo-X egg by a non-disjunctional X/Y sperm. Although such sperm are rare in chromosomally normal males, they frequently are produced by males carrying chromosome rearrangements (Maddern & Bedo, 1984; Bedo & Foster, 1985).

(iv) *Segregation in* X/O *females*

Presumptive X/O MNS females are usually sterile. The single such female so far to produce viable offspring was poorly fertile, but produced a very high frequency of nonsegregational offspring (2♀+1♂ segregants, 2♀+3♂ PNS, and no MNS offspring).

4. Discussion

The homogeneity of nonsegregation frequencies between segregant classes and paternal *C(5L); C(5R)* genotypes (Table 1 A) indicates no evidence of pairing between the compound elements and the sex

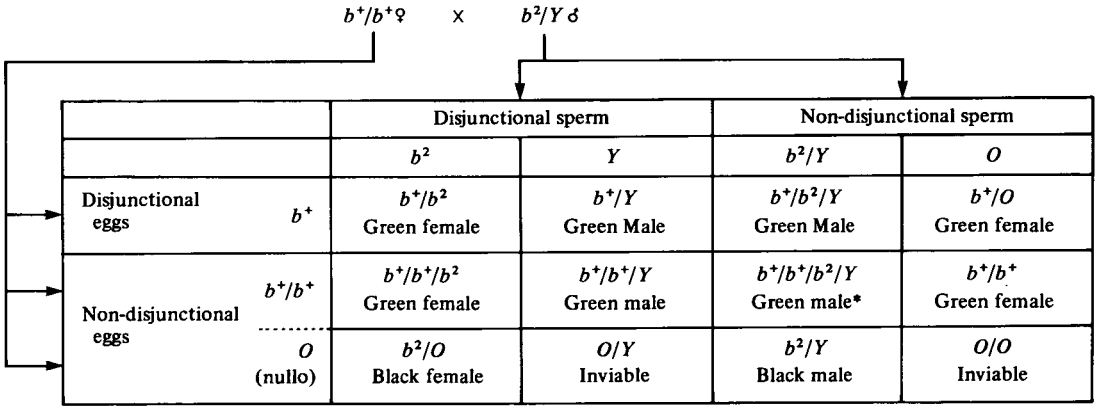

Fig. 1. Detection of sex-chromosome non-disjunction. * Assuming $X/X/X/Y$ are viable males.

Table 2. *Incidence of the black body* (b) *phenotype in crosses of wild-type compound-chromosome females mated to* b/Y; C(5L) 1; C(5R)2 *males*

	Number of each progeny class											
	Segregants				Patroclinous non-segregants				Matroclinous non-segregants			
	♀♀		♂♂		♀♀		♂♂		♀♀		♂♂	
Female genotype	+	b	+	b	+	b	+	b	+	b	+	b
MR18	180	1	182	0	7	0	5	0	8	3	5	0
CA	299	1	349	0	28	0	44	0	8	17	9	0
C(5L)115; C(5R) 1	26	0	43	1	0	0	1	0	0	1	0	0
C(5L)115; C(5R) +[a]	69	0	82	0	5	0	5	0	3	0	1	0
Totals	574	2	656	1	40	0	55	0	19	21	15	0

[a] Combined data from *C(5R) 118* and *C(5R) 110* females.

https://doi.org/10.1017/S0016672300023521 Published online by Cambridge University Press

chromosomes in males. However, the frequency of coincidence of non-disjunction of the *X* chromosomes and non-segregation of compound autosomes in females suggests that the distributive-pairing hypothesis (R. F. Grell, 1976), may be applicable at least partly to pairing and segregation in *L. cuprina* females. According to this hypothesis, distributive pairing occurs after meiotic crossing over in females between homologues (which event determines that those homologues will segregate from one another), and is restricted to chromosomes which have not been involved in crossing over with an independent homologue. Compound autosomes are always part of the postulated distributive-pairing pool, because they are mainly heterologues and thus fail to undergo meiotic crossing over with one another. Homologous or non-homologous pairing can occur between any of the chromosomes in the distributive-pairing pool; however, in *D. melanogaster* a strong size-specificity ensures that homologues usually pair with one another. Non-homologous pairing can give rise to genetically or cytologically detectable events such as non-disjunction of homologues or non-segregation of compound autosomes.

The data suggest that in *L. cuprina* females the *X* chromosomes frequently pair with the compound chromosomes, creating situations in which the CCs assort independently of one another while they are segregating from the *X* chromosomes. This gives rise to the high observed incidence of simultaneous non-disjunction of the *X* chromosomes and non-segregation of the CCs (*i.e.* the black-bodied MNS females – Table 2). However, as in *D. melanogaster* (Harger & Holm, 1980), the two events can also occur independently in *L. cuprina* (Table 2).

Among the 24 *X*-chromosome non-disjunctional progeny, 3 were segregational for the compounds, giving a frequency of independent non-disjunction of the *X* chromosomes of 13% (Table 2). While this estimate is based on a small sample size, it is significantly lower ($\chi^2_{(1)} = 8{\cdot}74$, $P < 0{\cdot}01$) than that reported (43%) in *D. melanogaster* (Harger & Holm, 1980).

Several estimates of the frequency of associated non-disjunction (*i.e.* simultaneous with non-segregation) among all non-segregational events are available from the data. The incidence of the *X*-deficiency phenotype among MNS females gives an estimate of 33%. The frequency of *b*/*O* MNS females (Table 2) gives an estimate of 53%. However, both these estimates are likely to be low, since the penetrance of the *X*-deficiency phenotype is incomplete (Maddern & Bedo, 1984) and the viability of *X*/*O* females is likely to be less than that of *X*/*X* females because they are heterozygous-deficient for approximately 3% of the total euchromatic genome (Bedo, 1982). By multiplying the number of MNS females by the ratio of males to females (1·123) among the non-MNS progeny (Table 1A), the number of *Y*-bearing MNS zygotes can be estimated at 593. The difference between this and the observed number of MNS males (*X*/*Y* zygotes) gives an estimate of 404 *O*/*Y* zygotes, *i.e.* a frequency of associated non-disjunction of 68% among non-segregant offspring. This is similar to their frequency (64%) in *D. melanogaster* (Harger & Holm, 1980).

The overall incidence of MNS females was 86% relative to that of PNS females in the homogeneous crosses (Table 1A). If it is assumed that these two classes should be equally frequent, this suggests that on average 14% of MNS females are inviable. However, the data do not permit apportionment of the inviability between the two probable causes, *i.e.* the *X*/*O* condition or homozygosis of deleterious mutations (Foster & Maddern, 1985). In males, the incidence of MNS to PNS offspring was 26%, suggesting that mortality of MNS male zygotes from all causes is 74%. Subtracting the estimated frequency of *O*/*Y* zygotes, 68%, leaves an estimate of 6% mortality from other causes.

The high incidence of nullo-*X* gametes among MNS eggs suggests that the reciprocal egg type (nullo-CC) should frequently be *X*/*X*. Thus PNS offspring should frequently be *X*/*X*/*X* or *X*/*X*/*Y*. Bedo (1982) has confirmed that certain lines derived from PNS males are *X*/*X*/*Y*. The sex-ratio data from certain high non-segregation cultures could possibly be due to occasional *X*/*X*/*X* females in the CC crosses (see below). However, since segregant offspring were selected as parents for the next generation (Foster & Maddern, 1985), the origin of this class of *X*/*X*/*X* females would have been independent of non-segregation.

The possibility exists that *X*/*X*/*X* and *X*/*X*/*Y* zygotes are less viable than their *X*/*X* and *X*/*Y* counterparts. Eurchromatic autosomal duplications of a similar size to that of the *X* euchromatin can reduce survival in *L. cuprina* (Konovalov *et al.* 1983). However, it is also possible that dosage compensation in *X*/*X*/*X* females and *X*/*X*/*Y* males (Bedo, 1982) may tend to pre-empt any mortality due to aneuploidy in zygotes containing an additional *X* chromosome.

If the *X* chromosomes of *L. cuprina* were always part of the non-exchange pairing pool, and pairing between them and the CCs always random (assuming 2:2 pairings), such that a given *X* chromosome were equally likely to pair with the other *X* chromosome or either of the CCs, the frequency of non-segregation of the CCs should be 33%, and non-segregation should always be associated with non-disjunction of the *X* chromosomes. The data clearly indicate that neither prediction is true. As noted above, both independent non-disjunctional and non-segregational progeny occur, and the frequency of non-segregation in females has been estimated at 11% (Foster & Maddern, 1985). The recovery of such 'independent' products could still result from competitive pairing of the *X* chromosomes and the CCs if the 2:2 segregation assumption is relaxed, possibly through trivalent formation, but it would be difficult to account for the

three-fold reduction in the total non-segregant frequency by this mechanism. If associations which resulted in 3:1 segregations were random the frequency of independent nonsegregant and non-disjunctant progeny should be equal. The small amount of data (Table 2) suggests that this is not so. The data thus suggest that either the *X* chromosomes are not always part of the distributive pairing pool, or, if they are, some other mechanism for pairing of non-recombinant elements exists in *L. cuprina females*.

If the *X* chromosomes in *L. cuprina* females are not always part of the distributive pairing pool, then by inference meiotic exchange between the *X* chromosomes may be fairly common. Unfortunately the existence of only one reliable visible mutation on the largely heterochromatic *X* chromosome has so far precluded demonstration of whether or not crossing over occurs in this linkage group. Observations involving certain *X*-chromosome rearrangements suggest that exchange events involving the *X* chromosome may occur frequently in females (unpublished). However, evidence that rearrangements involving the sex chromosomes may cause chromosomal instability (Foster *et al.* 1980*a*) suggests caution in the interpretation of such observations.

If the *X* chromosomes in *L. cuprina* females do not undergo regular meiotic exchange, some other mechanism must exist to account for their non-random behaviour in CC females. As noted earlier, chromosome size is important in determining the pairing relationships of non-exchange elements in *D. melanogaster* females. Comparison of the *X* chromosomes and the autosomes in mitotic preparations of *L. cuprina* (Whitten *et al.* 1975; Bedo, 1980), and the relative sizes of *C(5L)* and *C(5R)* elements (Foster *et al.* 1976) suggests that the *X* chromosomes are similar in size to the CCs. More specifically, the normal *X* is approximately equivalent in size to *C(5L)*s, and double the size of *C(5R)*s. Thus a test of whether size-specificity also operates in *L. cuprina* should be possible, using altered (*i.e.* partially deleted) *X* chromosomes (Maddern & Bedo, 1984).

One of the predictions of the distributive-pairing hypothesis is that an odd number of chromosomes in the distributive-pairing pool should markedly increase the frequency of nonsegregation of the CCs in females, as occurs for example in *X/X/Y* or triplo-*4 D. melanogaster* females (Grell, 1976). In *L. cuprina* this condition should exist both in *X/X/X* and *X/O* females. There are no data from confirmed *X/X/X* females, but the MNS sex-ratio data from the crosses with exceptionally high frequencies of non-segregation (Table 1 B) are consistent with this hypothesis, if it is assumed that some of the female parents of these crosses were *X/X/X*. Since virtually all eggs produced by *X/X/X* females are likely to contain at least one *X* chromosome, the sex ratio of MNS offspring of *X/X/X* females should not be distorted due to the production of inviable *O/Y* zygotes. The sex ratio of MNS progeny in the high non-segregation (mean frequency 26%) crosses did not differ from a 1:1 expectation (although it also did not differ significantly from that in the homogeneous crosses). Thus some of the heterogeneous cultures may have had *X/X/X* mothers. Since the MNS sex ratio in the poorly fertile crosses (Table 1C) was also 1:1, it is possible that these cultures (at least those which produced non-segregant offspring) also had *X/X/X* mothers. We have attempted to investigate the influence of an extra *X* chromosome on non-segregation more directly, by appropriate crosses involving PNS females, a large proportion of which should be *X/X/X*. So far, however, we have not been able to demonstrate genetically the existence of three *X* chromosomes in fertile PNS females. Thus it seems probable that such flies are frequently infertile. The amount of data on nonsegregation in *X/O* females is small, because *X/O* CC females are usually sterile. The one such female to produce offspring, however, yielded a high proportion of non-segregants, in agreement with the predictions of the distributive-pairing hypothesis.

There remain two observations for which there appears to be no adequate explanation. Firstly, the overall excess of male offspring in most CC crosses (Table 1) is not associated consistently with genotype. Crosses involving *C(5L) 1* and *C(5R)+* together in males did not deviate from the expected 1:1 ratio, whereas males carrying these arms in other combinations produced significant excesses of male progeny. Secondly, the reason for increased *X–Y* nondisjunction in CC males remains obscure, especially in view of the lack of evidence of pairing between CCs and the sex chromosomes in males. This could reflect a type of interchromosomal effect caused by rearrangement of the fifth chromosome, similar to the observation that translocations involving the fifth chromosome cause increased levels of recombination in *L. cuprina* males (G. M. Clarke & G. G. Foster, unpublished).

Supported by funds from the Australian Meat Research Committee, Project CS13S/14S.
We thank Drs George Miklos and Max Whitten for critical reading of the manuscript.

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