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The distribution of transposable elements on X chromosomes from a natural population of *Drosophila simulans*

SERGEY V. NUZHDIN*

Department of Genetics, North Carolina State University, Raleigh, NC 27695-7614 and Institute of Molecular Genetics, Kurchatov Square, Moscow 123182, Russia

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Summary

The distribution of 13 transposable element families along 15 X chromosomes from an African natural population of *Drosophila simulans* was determined by *in situ* hybridization to polytene chromosomes. The transposable elements cloned from *Drosophila melanogaster* all hybridized with *Drosophila simulans* chromosomes. The number of copies per family was 3·5 times lower in the latter species and correlated with the copy number per family in *Drosophila melanogaster*. With the exception of *297*, the copy number per chromosome followed a Poisson distribution. Element frequencies per chromosome band were generally low. However, several sites of the distal region and the base of the X chromosome had high frequencies of occupation. Elements had higher abundance at the base of the chromosome compared to distal regions. Overall, the distribution of transposable elements in *Drosophila simulans* is similar to that found in *Drosophila melanogaster*. These data provide evidence for the operation of a force (or forces) opposing transpositional increase in copy number, and that this force is weaker at the bases of chromosomes, consistent with the idea that recombination between elements at non-homologous sites contains TE copy number. The reduction in copy number of all TE families in *Drosophila simulans* compared to *Drosophila melanogaster* can be explained by stronger selection against transposable element multiplication and/or lower rates of transposition in *Drosophila simulans*.

1. Introduction

Transposable elements (TEs) are ubiquitous components of bacterial and eukaryotic genomes (Berg & Howe, 1989). In *D. melanogaster*, for example, roughly 10% of the total DNA consists of about 50 families of moderately repeated TEs (Finnegan, 1992). Such elements are sequences capable of inserting copies of themselves into new genomic locations and are a potentially important source of mutational variation. What forces are responsible for the persistence of TEs in natural populations is an issue of considerable speculation and interest (Charlesworth, Sniegowski & Stephan, 1994).

These forces have been inferred from the distribution of TEs between and along chromosomes from natural populations of *D. melanogaster*. TE copy number does not vary much between flies or between populations (Berg & Howe, 1989). TEs are distributed randomly along distal regions of chromosomes, and each site of occupation has low frequency (Charlesworth & Lapid, 1989; Charlesworth, Lapid & Canada, 1992*a*, *b*; Biemont *et al.* 1994). The inference from these data is that the spread of TEs in natural populations is affected by two deterministic forces, TE transposition and selective elimination of TEs, rather than by drift; and there is a stable equilibrium between these two forces (Charlesworth & Charlesworth, 1983; Langley, Brookfield & Kaplan, 1983; Montgomery & Langley, 1983). Because TEs are equally abundant on X chromosomes and major autosomes, and insertions on the X chromosome should be under stronger selection than insertions on autosomes since the fitness effects of insertions are partly recessive, Montgomery, Charlesworth & Langley (1987) argued that selection against deleterious mutations caused by transpositions is not a major force controlling TE abundance on chromosomes. However, TEs are more abundant in pericentric regions of chromosomes (Charlesworth & Lapid,

* Present address: Department of Genetics, Box 7614, North Carolina State University, Raleigh, NC 27695, USA. Tel. (919)515-5811; FAX (919)515-3355; E-mail: nuzhdin@unity.ncsu.edu or nuzhdin@ncsumvs.bitnet.

Table 1. *Positions of transposable elements along X chromosomes of* D. simulans

Line	TE family *jockey*	*2244*	*roo*	*mdg3*	*412*	*I*	*297*	*opus*	*2156*	*mdg1*	*Doc*
N1			1E, 12F, 13A, 16F, 18A, 20A			5A	18A	9A	19A		4B
N2		19C	10A, 18A, 20A	12A	19A	12F, 19A	18A			4EF	9A, 12F
N4			3C, 3E, 5A, 9E, 11C, 13D, 15D			7D	18A				
N5		3C	1F, 10C, 10D, 11C, 13C, 15A			11B, 18A	18A		3C, 19A		7E, 11C
N7	18B		1F, 9E, 11B, 19F, 20A	1B, 1D	8E, 9B, 19F		18A				6A, 7E
N13			1F, 2E, 4A, 7D, 7E, 8B, 11A, 11C, 18C, 19A		16F, 19F	19C	18A				4F
N19		10B	1E, 4B, 9E		13C	5A, 7E, 17B, 18A, 19A	19F		10B		3E, 15B
N20			1A, 3C, 6F, 9E, 11A, 19D		1D, 5D	19A	19F				4D, 11A(2), 16D, 16F
N21	10B		2E, 8E, 9A, 9E, 12F		12F	1A, 19A	18A, 19F				8D, 14B
N27			6E, 9E, 10D			4D, 13C, 19E	18A, 19C				6A, 11A, 11B
N28	9B		6A, 7A, 7D, 8E, 9E, 10C, 12E, 12F, 15D, 18C			7B, 18A					3F
N29			1E, 3C, 3D, 11E, 19E			5D, 13B, 17D	18A, 19E		2F		8E
N32			1B, 7E, 9E, 10A, 10D, 12A, 12B, 13B, 14D			13A	18A				1B
N33			3E, 7B, 7E, 10B, 11B, 16E, 18A, 19F			12F	18A				1A, 10D, 18B
N34			3F, 8F, 9C, 9E, 10A, 15C, 18A		12A		19E		19A		4E, 14B/ 4B, 4E, 12F, 14B, 15A

1989; Charlesworth *et al.* 1992*a*, *b*), on the fourth chromosome (Charlesworth *et al.* 1992*b*) and in rare inversions (Sniegowski & Charlesworth, 1994). Hence selection decreasing TE abundance appears to be weaker when recombination is suppressed. Therefore, selection against dominant deleterious chromosomal rearrangements caused by recombination between TEs situated at different positions in the genome (ectopic exchange) has been considered to be a major force opposing TE multiplication in natural populations (Golberg *et al.* 1983; Davis, Shen & Judd, 1986; Langley *et al.* 1988; Montgomery *et al.* 1991).

It is not clear whether the transposition–selection equilibrium hypothesis can be correct for TEs of any other species than *D. melanogaster*, since only fragmentary information has been collected to date. Most additional information comes from *D. simulans*. The genome of *D. simulans* carries approximately three times less middle repetitive DNA than the genome of *D. melanogaster* (Dowsett & Young, 1982), but all TE families cloned from *D. melanogaster* have also been found in *D. simulans* (Brookfield, Montgomery & Langley, 1984) (with the exception of the *P* element, that has recently invaded the genome of *D. melanogaster* (Kidwell, 1993)). It was hypothesized that *D. simulans* carries the same families of TEs in the genome but the mean number of copies per family is less in *D. simulans* relative to *D. melanogaster*. Indeed, the copy numbers of three of four TE families were lower in *D. simulans* relative to *D. melanogaster*. Unexpectedly they were frequently found at the same positions in different laboratory lines of *D. simulans* (Leibovitch *et al.* 1992). Similarity between locations of four TE families have also been found in three lines of *D. algonquin* and two lines of *D. affinis* (Hey, 1989). It is difficult to compare these data with that available for natural populations of *D. melanogaster* because so few TE families were analysed and only laboratory lines of the other species were studied. A systematic investigation of the distributions of TEs along chromosomes of species other than *D. melanogaster* is necessary.

Here I describe the distributions of 13 TE families along 15 X-chromosomes of *D. simulans* from an African natural population. The first goal of the study was to determine whether the frequency distributions of TE occupied sites would be similar in different sibling species. The second goal was to determine the distribution of TEs along the X-chromosomes to see if TEs are over-represented in the regions of restricted recombination in *D. simulans*, as they are in *D. melanogaster*. The third goal was to understand how the copy number characteristic of a given TE family would correlate between *D. melanogaster* and *D. simulans*.

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2. Materials and methods

(i) Drosophila simulans *stocks*

Fifteen *D. simulans* lines carrying X chromosomes recently extracted from an African natural population were kindly provided by Dr C. F. Aquadro. Each line was obtained by crossing one male from the natural population to females of a laboratory strain carrying attached-X chromosomes marked with *y* and *w*. All male progeny of this cross inherit their single X chromosome from their father; thus males of different lines carried independently extracted X chromosomes.

(ii) In situ *hybridization*

Transposable element insertion sites were determined by *in situ* hybridization of biotin-labelled transposable element DNAs to polytene salivary gland chromosomes of third instar larvae raised at 18°, according to the procedure of Shrimpton, Montgomery & Langley (1986). The plasmids and the phage containing complete copies of the *D. melanogaster* TEs *mdg3, 297, Doc, roo, copia, I, 412, 1731, mdg1, opus, jockey* (described in Lindsley & Zimm, 1992), uncharacterized middle repetitive DNAs *2244* (Charlesworth, Lapid & Canada, 1992*a*) and *2156* (Charlesworth & Lapid, 1989) were used as probes. Probes were labelled with biotinylated dATP (bio-7-dATP, BRL) by nick translation. Hybridization was detected using the Vectastain ABC kit (Vector Labs) and visualized with horseradish peroxidase/diaminobenzidine.

Each of the 13 TEs was hybridized to polytene salivary gland chromosomes of male larvae from the 15 *D. simulans* lines. TE sites were scored only on X chromosomes because the autosomes segregated for TE sites of the laboratory line and the natural population. *In situ* hybridization reveals the sum of hybridization signals on both homologous chromosomes, so it is frequently not possible to discriminate between homozygous or heterozygous sites. Hence the TE copy number on autosomes could have been biased by an unknown and variable amount by inbreeding that occurred during stock maintenance.

The element locations along the *D. simulans* X chromosomes were determined at the level of cytological band subdivision on the standard Bridge's map of *D. melanogaster* (Lefevre, 1976), since these sibling species are cytogenetically homosequential (Lemeunier, David & Tsacas, 1986). I considered there to be no signal on the X if there was strong hybridization with the autosomal sites but none on the X. Two slides were scored per element per line if a hybridization signal was found in the first slide analysed. In all cases but one the same position(s) of the hybridization signal(s) was found in both slides. Two different patterns of hybridization were found for *Doc* in the line N34 (Table 1). I prepared three additional slides from this line and found the first pattern of sites in one larva and the second pattern in two larvae. Since only one set of sites was found in N34 for the other TE families, the heterogeneity is best interpreted as due to *de novo Doc* transpositions.

Two clones always hybridized with either 3C (*Doc*, O'Hare, Levis & Rubin, 1983) or 5A (*copia*, Dunsmuir *et al.* 1980), from which they were cloned in *D. melanogaster*. Additionally one of the plasmids and the phage showed very slight hybridization with one X chromosome site in all *D. melanogaster* and *D. simulans* lines tested. This was for *I* (3C) and *roo* (3A, the other plasmid carrying *roo* did not give hybridization with this site). These sites of hybridization were excluded from consideration as they are apparently caused by a region of restricted homology between them and the plasmid or phage used for hybridization. *2244* gave a very slight hybridization signal at 6D that was detectable only in slides with very strong hybridization. This site was also excluded from consideration since it could not be scored unambiguously.

3. Results

(i) *Distribution of elements among chromosomes and frequency distributions of element frequencies in* D. simulans

TE DNAs of 13 different families of TEs cloned from *D. melanogaster* were hybridized with polytene salivary gland chromosomes of 15 *D. simulans* lines. Hybridization in the 1A–20A region of the X chromosome was found in at least one *D. simulans* line for 11 of the TEs (Table 1). Multiple hybridization signals with the autosomes of all lines were found for all TEs except *mdg1*, including *1731* and *copia*, which did not show hybridization for X chromosome sites. *mdg1* hybridized in autosomes only to the pericentric regions. Numbers and positions of autosomal sites were not determined. Thus all 13 tested TEs cloned from *D. melanogaster* were found in *D. simulans*. Some of these TEs have previously been found in *D. simulans* (Brookfield, Montgomery and Langley, 1984: *copia* (*cDm5002*), *412* (*cDm2042*), *jockey* (*cDm2161*), *opus* (*cDm2217*), *2244* (*cDm2244*), *2156* (*cDm2156*) and *mdg1* (*cDm2181*); and Leibovitch *et al.* 1992 (*mdg3*)).

The means and variances of TE copy numbers and occupancy profiles for the 1A–20A region of the X chromosome for each TE family are given in Table 2. With the exception of *297*, the mean is about the same as the variance, consistent with the Poisson distribution expected when elements have a low frequency at each site and there is linkage equilibrium between sites (Charlesworth & Charlesworth, 1983). The difference between the mean and the variance of *297* is caused by the high frequency of occupation at 18A (11 of 15 chromosomes). Despite this exception, it is clear from inspection of the occupancy profiles that TEs tend to be present at low frequencies at sites of

Table 2. *Means, variances and occupancy profiles of TEs on X chromosomes of* D. simulans

Copy number			Occupancy profiles 1A–18C/18D–20A										
TE	Mean	Variance	1	2	3	4	5	6	7	8	9	10	11
jockey	0·20	0·17	3										
2244	0·20	0·17	3/1										
roo	6·20	5·46	30/2	9/1	7	1/1					1		
mdg3	0·20	0·31	3										
412	0·73	1·03	8/2	0/1									
I	1·67	1·80	12/1	2	1	0/1							
297	1·13	0·27	0/1	0/1	0/1								1
opus	0·07	0·07	1										
2156	0·4	0·4	3		0/1								
mdg1	0·07	0·07	1										
Doc	1·97	1·59	20	5	3								
copia	0												
1731	0												

the distal sections 1A–18C of the X chromosomes. For reasons described by Charlesworth & Lapid (1989) the frequency distribution of site frequencies in pericentric sections may be more strongly perturbed by drift, hence only distal sections were taken into consideration as previously done for TEs on the X chromosomes of *D. melanogaster*.

The frequency distribution of element frequencies may be quantified by the parameter θ (Kaplan & Brookfield, 1983). When the number of sites available for transposition is very large compared to the number of occupied sites, the probability density of element frequency x is proportional to $x^{-1}(1-x)^{(\theta-1)}$; where θ is equal to $4N_e(v+s_{\hat{n}})$, N_e is the effective population size, v is the rate of excision per TE, and $s_{\hat{n}}$ is the rate of elimination of a TE from a site by selection when this TE has an average $\hat{n}$ copies per individual (Charlesworth & Charlesworth, 1983; Kaplan & Brookfield, 1983). For the majority of TE families (*jockey, 2244, mdg3, 412, opus, 2156, mdg1, copia* and *1731*), all sites had an occupancy of one or zero, so θ is infinite (see Charlesworth & Lapid, 1989 for detailed explanations). Finite estimates of θ were obtained by Methods A and C of Biemont *et al.* (1994) for *roo* (Table 3), *I* (θ(A) = 13·7, θ(C) = 24·6) and *Doc* (θ(A) = 10·5, θ(C) = 15·7).

(ii) *Distribution of elements along X chromosomes*

The procedure of Langley *et al.* (1988) and Charlesworth & Lapid (1989) was used to examine the distribution of elements along the X chromosomes of *D. simulans*. Only the distributions of *roo, I, 297, Doc* and all families taken in total were analysed; copy numbers of the other TEs were too low for this analysis. The polytene chromosome map was subdivided into three sections – the tip, middle and base – corresponding to the regions between 1A–3A, 3B–18C and 18D–20A, respectively. The total numbers of TEs belonging to a given family (or all families jointly) that were found in these regions in the sample of 15 chromosomes were compared with the numbers expected if the numbers in each region were equal to the product of total number of TEs of a given family (or all families jointly) on the X chromsome and the proportion of polytene X chromosome DNA in the region (Charlesworth & Lapid, 1989). The significance of deviation from expectation was tested by χ^2. Accumulation in the tip of the chromosome was tested by pooling the middle and base sections and comparing observed and expected numbers by χ^2. Similarly accumulation in the base was tested by pooling the middle and tip sections. The only significant deviation from the random distribution was the overabundance of *I* ($\chi^2_1 = 11{\cdot}1$), *297* ($\chi^2_1 = 20{\cdot}9$) and all TEs taken jointly ($\chi^2_1 = 14{\cdot}0$) at the base of the X chromosome.

Additionally, there were several cases of hybridization with 20BC that were not included in Table 1 because hybridization signals were only slightly above the background level, and precise determination of cytological position was very difficult: *412* hybridized with this region in all lines, *I* in 13 lines, *297* in 4 lines, *jockey* in 12 lines, *mdg1* in 3 lines, and *roo* in 8 lines. The signal of hybridization of *opus* with 20BC was very weak and only detectable when hybridization was extremely strong. Overall, there was an obvious tendency of TEs of *D. simulans* to accumulate at the bases (two-fold) but not the tips of X chromosomes.

(iii) *TE copy number per family is three times less in* D. simulans *compared to* D. melanogaster, *and copy numbers per family correlate significantly in sibling species*

Copy numbers of nine TE families on *D. simulans* X chromosomes could be compared to those determined

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Table 3. *θ parameter of the probability distributions of TE frequencies for the distal sections of X chromosomes and entire genomes of* D. simulans *and* D. melanogaster

Species/region of the genome	Parameter estimated	*roo*	*mdg1*	*mdg3*	Reference
X chromosome					
D. simulans	θ(A)	6·3	∞	∞	This study
	θ(C)	8·0	∞	∞	
D. melanogaster	θ(A)	4·8	15·4		Charlesworth & Lapid, 1989[1]
	θ(C)	8·4	59·6		
D. melanogaster	θ(A)		11·5	19·9	Biemont *et al.* 1994
	θ(C)		18·7	31·2	
Entire genome					
D. simulans	θ(A)		4·0	6·5	Leibovitch *et al.* 1992[1]
	θ(C)		3·8	8·5	
D. melanogaster	θ(A)	4·9	13·8		Charlesworth & Lapid, 1989[1]
	θ(C)	8·8	52·8		Charlesworth, Lapid & Canada, 1992*a*[1]
D. melanogaster	θ(A)		9·9	21·1	Biemont *et al.* 1994
	θ(C)		13·4	30·8	

[1] Parameters were estimated as in Biemont *et al.* (1994) from the original data.

Table 4. *Comparison of transposable element copy numbers in X chromosomes of* D. simulans *and* D. melanogaster

Transposable element	X chromosome copy number	
	D. simulans	*D. melanogaster*[1]
opus (*2217*)	0·2 (0·11)[2]	1·79 (0·32)***[3]
roo	6·2 (0·60)	11·36 (0·56)***
412	0·73 (0·26)	2·29 (0·43)**
297	1·13 (0·13)	4·43 (0·59)***
jockey (*2161*)	0·07 (0·07)	4·07 (0·62)***
2156	0·4 (0·16)	0·5 (0·2)
mdg1 (*2181*)	0·07 (0·07)	1·21 (0·19)***
copia	0	1·21 (0·24)***
1731 (*2158*)	0	0·21 (0·11)
Total copy number	7·8	27·07

[1] Data from Charlesworth & Lapid (1989).
[2] Standard errors are given in parentheses.
[3] Copy numbers in *D. simulans* and *D. melanogaster* are different with significance level $P < 0·01$ (**) or $P < 0·001$ (***).

for the same families by Charlesworth & Lapid (1989) for 14 X chromosomes of *D. melanogaster*. The average copy numbers of TEs in 1A–20A regions of the X chromosome for both species are shown in Table 4. Copy numbers of all TEs were lower in *D. simulans* relative to *D. melanogaster*, as found previously for *mdg1*, *copia* and *mdg3* (Leibovitch *et al.* 1992). For seven of the nine TE families this difference was highly significant. The average copy number in Xs for all nine TE families in total was 7·8 for *D. simulans* and 27·1 for *D. melanogaster*, hence TEs were 3·5 times less abundant in *D. simulans* relative to *D. melanogaster*. However, copy numbers of different families of TEs were highly correlated in *D. simulans* and *D. melanogaster* (Pearson correlation coefficient = 0·94, $P = 0·0002$; Spearman correlation coefficient = 0·72, $P = 0·03$).

4. Discussion

(i) *The distributions of TEs among X chromosomes of* D. simulans

The distribution of TEs on X chromosomes of *D. simulans* was similar to that reported by Charlesworth & Lapid (1989) for *D. melanogaster*. TE copy numbers were Poisson-distributed, as expected for low frequencies and linkage equilibrium between sites (Charlesworth & Charlesworth, 1983). Low frequencies of insertion sites have been interpreted as indicating that random drift is a minor force relative to TE multiplication and selection against TE insertions in natural populations (Charlesworth & Charlesworth, 1983; Langley, Brookfield & Kaplan, 1983). However, in *D. simulans* a high frequency was noted for three of 14 *mdg1* sites found in 12 laboratory lines, three of six *copia* sites found in nine laboratory lines (Leibovitch *et al.* 1992), and one of four *297* sites found in the 15 X chromosomes analysed here, reflecting a stronger effect of drift on TE distribution in this species compared to *D. melanogaster*.

It is generally assumed that the stable copy number of TEs results from a balance between TE multiplication and natural selection against multiplication (Charlesworth, Sniegowski & Stephan, 1994). The three-fold reduction of TEs in the genome of

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D. simulans relative to *D. melanogaster* could originate either from stronger selection against TE multiplication in the former species or from higher transposition rates in the latter species ($u_{simulans} < u_{melanogaster}$). At equilibrium $u = s_{\hat{n}} = \theta/(4N_e)$, and θ can be inferred from the frequency distribution of insertion frequencies (Kaplan & Brookfield, 1983). Because estimates of N_e are available for *D. simulans* and *D. melanogaster*, the hypothesis that $u_{simulans} < u_{melanogaster}$ can be tested.

Finite estimates of θ were obtained for these *D. simulans* data only for *roo* (Table 4), *I*, and *Doc*. Estimates of θ for *mdg1* and *mdg3* can be obtained from the data of Leibovitch *et al.* (1992) for the distribution of these TEs along the distal regions of chromosomes of *D. simulans* laboratory lines of independent origin (Table 3). The 18D–20A region of the X chromosome and the three most proximal divisions of autosomes were omitted from this analysis (Charlesworth & Lapid, 1989; Charlesworth, Lapid & Canada, 1992*a*). The estimates of θ for *roo, mdg1* and *mdg3* in *D. simulans* can be compared to estimates of θ for these TEs in *D. melanogaster* (Table 3). The estimates for *roo* were comparable in the two species, whereas the estimates of θ for *mdg1* and *mdg3* were somewhat lower in *D. simulans* than in *D. melanogaster* (Table 3). Since the effective population size of *D. simulans* is higher than that of *D. melanogaster* (Aquadro, 1992), and θ for *roo, mdg1* and *mdg3* is not higher in the former species, it follows that the rate of transposition $u = \theta/(4N_e)$ is lower in the former species for these TEs. This conclusion is subject to the caveat that estimates of θ have high standard errors (Charlesworth & Charlesworth, 1983; Biemont *et al.* 1994).

(ii) *Distribution of elements along X chromosomes of* D. simulans *and* D. melanogaster

Recombination between homologous TEs situated in different positions of the genome could control TE multiplication (Davis, Shen & Judd, 1986). If this hypothesis is true, TEs should be more abundant in regions of chromosomes with suppressed recombination (Langley *et al.* 1988). Recombination is suppressed in tips and bases of the X chromosome of *D. melanogaster* (Lindsley & Zimm, 1989), and this appears to be the case in *D. simulans*, although the details are unknown (Ashburner, 1989). Charlesworth & Lapid (1989) observed a higher abundance of retrotransposons in bases but not in tips of *D. melanogaster* X chromosomes. Likewise, retrotransposons in *D. simulans* tended to accumulate in bases (18D–20A) but not in tips (1A–3A) of the X chromosome. The data for both species are only in partial agreement with the expectation of the hypothesis.

However, no data are available for the distribution of the rate of ectopic exchange along chromosomes. It has been assumed that ectopic exchange is suppressed when recombination is suppressed (Langley *et al.* 1988), based on the observation that ectopic exchanges between duplicated fragments of X chromosome occur in females but not in males of *D. melanogaster* (Sturtevant, 1925), which correlates with the suppression of recombination in *Drosophila* males (Lindsley & Zimm, 1989). Thus it is possible that ectopic exchange does control TE copy number, but the rate of recombination and the rate of ectopic exchange are not perfectly correlated.

The overabundance of TEs and recombination suppression in the base of chromosomes can possibly be explained from a completely different perspective. Recombination rates for the same chromosomal region are highly variable among different lines of *D. melanogaster*, and responses to artificial selection for higher or lower recombination rate in a particular region of a chromosome are easily obtained (moreover responses may be uncorrelated or even opposite in different regions), therefore the genome contains multiple modifiers of the rate of recombination in a chromosomal region (Korol & Iliadi, 1994). Perhaps TE insertion sites can be such modifiers. The presence of a TE at a site in one but not both homologous chromosomes could partly suppress recombination, as has been shown for suppression of recombination between homologous regions of mammalian cell culture chromosomes with and without an insertion (Godwin & Liskay, 1994). In this case the more abundant TEs are, the more strongly recombination should be suppressed. Thus, recombination could be suppressed as a result of higher abundance of middle repetitive DNA in bases (due to TE accumulation) and tips (due to accumulation of *He-T* and related sequences, Beissmann *et al.* 1992). Although the correlation between strong overabundance of middle repetitive DNA and recombination suppression can be explained in this way, the observed slight accumulation of retrotransposons in low-frequency inversions (Sniegowski & Charlesworth, 1994) still needs to be explained by suppression of ectopic exchange.

(iii) *Correlation between TE copy number per family in* D. simulans *and* D. melanogaster

Different TE families have different and characteristic copy numbers in *D. melanogaster*. For example, *gypsy* usually has 2–8 copies per haploid genome (Leibovitch *et al.* 1992), but *roo* has about 100 copies (Charlesworth & Lapid, 1989; Charlesworth, Lapid & Canada, 1992*a*, *b*). Copy numbers of nine TE families on 15 X chromosomes of *D. simulans* were highly significantly correlated with those determined by Charlesworth & Lapid (1989) for 14 X chromosomes of *D. melanogaster*.

The between-family difference in TE copy number could be due to unequal transposition rates or unequal

frequencies of ectopic exchange. Significant differences between transposition rates of different TE families were found in a highly inbred line of *D. melanogaster* (Nuzhdin & Mackay, 1994, 1995), indicating that the former explanation may be true. However, transposition rates measured in highly inbred laboratory lines may not correlate with the rates of transposition characteristic for natural populations. In theory, the majority of TE copies in flies should be defective (Kaplan, Brookfield & Langley, 1986). If active copies of some TE families are lost and active copies of the other TE families are fixed in the course of inbreeding, estimates of transposition rates would be biased. Clearly, more data are necessary on frequencies of ectopic recombination for different TE families as well as transposition rates in natural populations.

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