Chromosome inversion polymorphism in a Tunisian natural population of *Drosophila melanogaster*

BY Sylvie AULARD

Laboratoire de Biologie et Génétique Evolutive
C.N.R.S., 91190, Gif-sur-Yvette, France
Université P. et M. Curie, Paris, France

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ABSTRACT

A Tunisian natural population of *Drosophila melanogaster* has been screened for chromosome inversion polymorphism. All 10 of the inversion types found are paracentric and autosomal. Five of these are cosmopolitan: common, In(2L)t and In(2R)NS, or rare, In(2R)Cy, In(3R)C and In(3R)M. The others are new endemic, with the exception of In(2L)Cy. This inversion, the break points of which are very close, both distally and proximally, to those of In(2L)t, was never formally described in a natural population before and seemed to be only a laboratory stock rearrangement. The presence of In(2L)Cy has been established unequivocally by crossing males from the Tunisian lines with virgin females from a (2L)Cy-type strain. From the results, In(2L)Cy appears to exist in at least one natural population. It is possible that this chromosome sequence might occur in another population, but described as In(2L)t because of the close similarity of these two inversions.

1. INTRODUCTION

Data on the inversion chromosome polymorphism of *Drosophila melanogaster* have considerably increased in the last ten years. The most recent results were collected from populations of USA (Stalker 1976; Langley *et al.* 1977; Mettler *et al.* 1977; Mukai and Voelker 1977; Voelker *et al.* 1978), Asia (Inoue 1979; Inoue and Watanabe 1979; Inoue *et al.* 1980) and Australia (Knibb *et al.* 1981). Nearly 300 inversions are now recorded. Considering the increasing number of natural inversions reported and in view of their distribution and abundance, Ashburner and Lemeunier (1976) and Mettler *et al.* (1977) decided to classify the inversions of *D. melanogaster* in four classes: (i) common cosmopolitan inversions; (ii) rare cosmopolitan inversions; (iii) recurrent endemic inversions; (iv) unique endemic inversions.

Apart of few exceptions, the inversions are paracentric, autosomal and simple (Lemeunier *et al.* 1986). If many populations have been sampled in U.S.A., Asia and Australia, no data are known so far about North Africa, except those in Ashburner and Lemeunier (1976) in Morocco.

The purpose of this paper is to present a description of the different inver-

sions found in a Tunisian population and to discuss the unequivocal discovery of In(2L)Cy whose existence in a natural population was previously doubtful.

2. MATERIALS AND METHODS

Wild flies were collected in the oasis of Nasr'Allah, 50 km South West of Kairouan (Tunisia) in Autumn 1981 and fertilized females were individually kept in vials to initiate isofemale lines. One male from each of 50 isofemale lines was mated with one virgin Canton-S female, homozygous for the cytologically standard sequence in all chromosome arms. The salivary gland of a minimum of six third instar larvae per parental male was examined. The break points of the inversions were identified by comparing photographs with the salivary gland chromosome maps drawn by Bridges (1935) and the photographic maps of Lefevre (1976).

3. RESULTS

Ten different inversions were detected. We named each of them by its break points in the following list:

Chromosome 2, left arm (2L)

1. In(2L)t22D3-E1; 34A8-9, common cosmopolitan
2. In(2L)Cy22D1-2; 33F5-34A1, see comments in the text
3. In(2L)30A1-2; 33A3-8, new endemic found in two isofemale lines

Chromosome 2, right arm (2R)

4. In(2R)NS52A2-B1; 56F9-13, common cosmopolitan
5. In(2R)Cy42A2-3; 58A4-B1, rare cosmopolitan
6. In(2R)45F3-8; 59B, new unique endemic

Chromosome 3, left arm (3L)

7. In(3L)69A-B; 73A, new unique endemic
8. In(3L)69A; 79E5-8, new unique endemic

Chromosome 3, right arm (3R)

9. In(3R)C92D1-E1; 100F2-3, rare cosmopolitan
10. In(3R)M86F; 100E, rare cosmopolitan.

In(2L)t, In(2R)NS, In(3L)P and In(3R)P are the four common cosmopolitan inversions of *D. melanogaster* found in most natural populations investigated. The first two have also been detected in this Tunisian population, in frequencies of 13 and 7 percent, respectively (Table 1). But none of the 50 isofemale lines has revealed the two common cosmopolitan rearrangements of the third chromosome, In(3L)P and In(3R)P. The only inversions found on this chromo-

Table 1. Nature and frequencies (%) of the inversions found in the Nasr' Allah population (Tunisia).

chromosome 2 (N=100)						chromosome 3 (N=100)		
left arm			right arm			left arm	right arm	
In(2L)t	In(2L)Cy	others*	In(2R)NS	In(2R)Cy	endemic*	endemic*	In(3R)C	In(3R)M
13	(10)	(2)	7	6	(1)	(2)	3	6

N: number of chromosomes examined

*: endemic inversions, description in the text

(): number of endemic inversions

Fig. 1. Location of the cosmopolitan and In(2L)Cy inversions of *D. melanogaster*.

some were two new unique endemic ones and two rare cosmopolitan ones, In(3R)C and In(3R)M (3 and 6 percent, respectively). The absence of In(3R)P is very surprising because it is the most frequent and cosmopolitan of the four common inversions of *D. melanogaster*, found in all natural populations so far screened.

Another interesting finding is the discovery of In(2L)Cy, with a frequency of 10 percent. This inversion was supposed not to exist in any natural populations (Ashburner and Lemeunier 1976). A great similarity exists between the common cosmopolitan inversion In(2L)t whose break points are 22D3-E1 and 34A8-9, and In(2L)Cy (22D1-2 and 33F5-34A1) (figure 1). In(2L)Cy was detected genetically by Ward (1923) as a crossover inhibitor, associated with the dominant Curly mutation. It was found in a stock composed of flies collected in Ann Arbor, Michigan, in September 1918. In(2L)Cy was thought to be only a laboratory stock rearrangement. In fact, in spite of the great number of natural populations screened, there were only very few reports of

Fig. 2. Results of crosses between males from Nasr'Allah population (Tunisia) and females from a 2LCy-type strain.

- a. Heterozygous $\text{In}(2\text{L})\text{t}/\text{In}(2\text{L})\text{Cy}$
- b. Homozygous $\text{In}(2\text{L})\text{Cy}/\text{In}(2\text{L})\text{Cy}$. Distal end of the left arm of the second chromosome.
- c. Homozygous $\text{In}(2\text{L})\text{Cy}/\text{In}(2\text{L})\text{Cy}$. Proximal end of the left arm of the second chromosome.

In(2L)Cy. When this inversion was reported, with drawings or photographs published, it was in fact In(2L)t (Ashburner and Lemeunier 1976). These confusions can be easily explained by the great similarity of these two inversions.

To confirm the existence of In(2L)Cy and In(2L)t in our natural Tunisian population, males from involved lines were crossed with virgin females from a (2L)Cy-type strain, originated from the Department of Genetics of the University of Göteborg (Sweden). The results are shown in figure 2. The presence of In(2L)t can be seen in the heterozygous larvae In(2L)t/In(2L)Cy by a non pairing of the homologues at the distal and proximal ends of the inverted segment. Figure 2b-c shows the full homology of the left arm homologues of both the (2L)Cy-type strain and Tunisian strain. This confirms unequivocally the existence of this arrangement in this Tunisian natural population. It can be further added that this inversion was found alone without the Curly mutation.

On the same chromosome, we have also detected In(2R)Cy that was declared as rare cosmopolitan by Mettler *et al.* (1977) and has been for the first time described genetically by Ward (1923), as crossover suppressor, in the same stock as In(2L)Cy. The frequency of this arrangement is similar to that of the common cosmopolitan In(2R)NS (table 1).

4. DISCUSSION

The chromosomal inversion polymorphism of the Tunisian natural population of *D. melanogaster* presents different interesting aspects. First, in spite of the great number of analysed lines, the In(3R)P inversion was not found. In(3R)P is known to be the most common of the cosmopolitan inversions of this species. Even if we supposed that In(3R)P was not revealed because of its very low frequency in the natural population, this would constitute in itself a peculiarity of this population as the frequencies of the common cosmopolitan In(2L)t and In(2R)NS are quite significant.

Another interesting finding relates to In(2L)Cy. The crosses carried out with the (2L)Cy-type strain show that this inversion occurs together with In(2L)t in this Tunisian population. Hence, this provides the first clear evidence of the existence of In(2L)Cy in a natural population. Whether or not it occurs in other natural populations is still unclear although some of the In(2L)t mentioned in the literature might be In(2L)Cy as well (or the reverse).

It is also of interest to focus attention on In(2R)Cy. It is worth emphasizing that this inversion, that appears at a 6% frequency, is always detected in our observations in a chromosome 2 bearing in the left arm either In(2L)Cy or In(2L)t. A significant linkage disequilibrium exists between In(2L)Cy and

In(2R)Cy, but not between In(2L)t and In(2R)Cy (Aulard and Lemeunier 1985). In(2R)Cy was described as crossover suppressor by Ward (1923) from the same stock and in the same chromosome as In(2L)Cy. It can be assumed that both inversions were present in the natural population from which the stock was initiated. In(2R)Cy was found previously in the Lincoln population (Nebr.) by Mettler *et al.* (1977) with In(2L)t, but without evidence of In(2L)Cy and might also occur in USSR (Dubinin *et al.* 1937; Grossman 1967). Data are still lacking to assess whether or not In(2R)Cy is closely associated, or even co-adapted, with In(2L)Cy or whether the co-occurrence of these two rearrangements has appeared repeatedly at random in the 1918-American and 1981-Tunisian populations. Their association might be due to the closeness of their proximal break points therefore preventing frequent recombination between them.

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