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Original article

Presence of the deleted *hobo* element *Th* in Eurasian populations of *Drosophila melanogaster*

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Summary — Molecular analysis has revealed the presence of a specific deletion-derivative *hobo* element, the *Th* element, in all current strains of *Drosophila melanogaster* examined throughout the Eurasian continent. The *Th* element is characterized by an internal deletion of 1.5 kb as compared to the complete *hobo* element. The presence of this element in natural populations raises the question of its possible role in the regulation of the *hobo* system.

***Drosophila* – transposable elements – *hobo* – populations**

Résumé — Présence de l'élément *hobo* délété *Th* dans les populations eurasiennes de *Drosophila* melanogaster. *Un élément* hobo *défectif (élément* Th*), présentant une délétion interne de 1,5 kb a été mis en évidence par analyse moléculaire. Cet élément est présent dans toutes les souches actuelles de* Drosophila melanogaster *examinées sur le continent eurasien. Sa présence dans les populations naturelles pose la question de son rôle éventuel dans le mécanisme de régulation du système* hobo.

Drosophila – *éléments transposables* – hobo – *populations*

Introduction

In *Drosophila melanogaster,* the progeny of certain out-crosses is characterized by a number of germline abnormalities, including chromosome breakage, high mutation rates, sterility, and male recombination. This syndrome has been termed hybrid dysgenesis (Kidwell *et al.,* 1977). Three independent systems of transposable elements (*I, P, hobo*) can produce these anomalies through the interaction of chromosomal, cytoplasmic, and environmental factors (see reviews by Blackman and Gelbart, 1988; Engels, 1988; Louis and Yannopoulos, 1988).

In the *hobo* system, molecular analysis has determined 2 classes of strains defined by their *hobo* elements. H strains contain 3.0-kb full-sized elements and numerous smaller derivatives, whereas E strains lack all such elements.

In most strains examined, the number of 3.0-kb elements is low, about 2–10 copies per genome, while smaller elements appear to be more numerous, from 30 to 75. These elements usually form only a few size classes, with each member of a class having the same internal deletion (Streck *et al.*, 1986; Blackman *et al.*, 1987). However, different H strains, tested from different laboratory stocks, harbor different classes of defective elements. The homogeneity of defective elements within a given strain contrasts with the heterogeneity of the size classes among different strains. The presence of identical defective elements throughout these strains has suggested the predominance of preference for the amplification of defective elements rather than complete elements (Blackman and Gelbart, 1988).

In this paper, we report the analysis of current strains collected from natural populations over the Eurasian continent and show the presence of 2 major classes of *hobo* elements, a 3.0-kb element class and one particular deletion-derivative class of elements which have accumulated in all naturally occurring strains throughout the continent.

Materials and Methods

Southern blot analyses were performed on DNA extracted from 31 strains of *D. melanogaster*, established by mass culture, from natural populations collected from France to China in 1986–87 (11 strains), and in 1981–84 (20 strains).

Standard techniques were used for DNA extraction, gel electrophoresis, blotting, hybridization, and ligation (Maniatis *et al.*, 1982). All Southern blots were hybridized and washed at I x SSC; 0.1% SDS at 65°C. Genomic DNA was digested by *Xhol* and probed by the pRG 2.6 X plasmid containing the internal 2620 bp *Xhol* fragment from a complete *hobo* element inserted into pUC8 (Fig. 1).

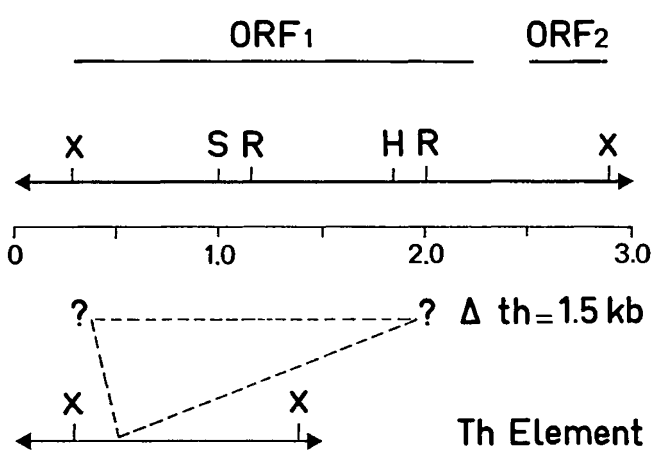

Fig. 1. Structure of the *hobo* elements, with the cleavage sites of the endonucleases : *Xho* I (X), *Sal* I (S), *Eco* RI (R), and *Hind* III (H).

Results

The results of Southern blot analyses are shown in Fig. 2a for natural strains collected in 1986–87, and in Fig. 2b for the 1981–84 sampling. About 4 μg of each drosophila genomic DNA was digested with *XhoI* and probed with pRG 2.6 X. The presence of full-sized 3.0-kb *hobo* elements gives rise to a 2.6-kb *XhoI* fragment with this probe. Any other bands are due to the presence of *hobo* deletion-derivatives which either have a deletion between the *XhoI* sites or have lost a *XhoI* site.

All strains contain sequences homologous to the probe. However, in the Paris strain the 2.6-kb band was not detected, and in the other strains strong differences in the intensity of this band were observed, reflecting variations in the number of full-sized elements present in each strain. More strikingly, all 31 of the Eurasian strains tested show a marked band of hybridization at 1.1 kb. This band appears to be derived from several copies of a particular class of deleted *hobo* element, in turn derived from a 3.0-kb element by an internal deletion of about 1.5 kb located between the 2 *XhoI* sites (Fig. 1). We refer to this element as the *Th* element as it was first detected from the French Tours (82) strain. The presence of this element was also detected in current populations of the United States and Mexico, but not in the early collected strains: Oregon-R^s (USA, 1920–30) Paris (1945), and Marseillan (France, 1965).

Discussion

Our survey of natural populations shows that the 3.0-kb *hobo* element and its deletion-derivative *Th* element are present in all Eurasian populations examined. No other derivative *hobo* elements have been accumulated to such a great extent, in terms of either geographic distribution or copy-number.

Hobo elements have been implicated as determinants of genetic instability, but their contribution to hybrid dysgenesis remains to be determined (Blackman and Gelbart, 1988; Louis and Yannopoulos, 1988). The *hobo* system has genetic analogies with the *P-M* system, although the molecular sequences of the elements are different. In the *P-M* system, genetic instability is clearly promoted by complete 2.9-kb *P* elements which encode for a transposase (Rio *et al.*, 1986; Engels, 1988). Other smaller and defective *P* elements are also present in the *Drosophila* genome, either associated with complete *P* element or alone.

The distributions of the *P* and *hobo* elements in the Eurasian population show striking similarities. In the *P-M* system, molecular and genetic analysis has revealed a specific *P* deletion–derivative, the *KP* element, present in all naturally occurring strains in Europe–USSR (Black *et al.*, 1987) and China (Anxolabehere *et al.*, unpublished data). The *KP* element appears to be implicated in the regulatory mechanisms of *P*-induced hybrid dysgenesis (Black *et al.*, 1987). These authors suggested that the accumulation of *KP* elements in natural populations is due to the selection of individuals with the highest numbers of *KP* elements, in which *P* hybrid dysgenesis is suppressed.

In the *hobo* system, all 3.0-kb elements found in nature are not necessarily functional, as other analyses have revealed microheterogeneity in this class of elements for labora-

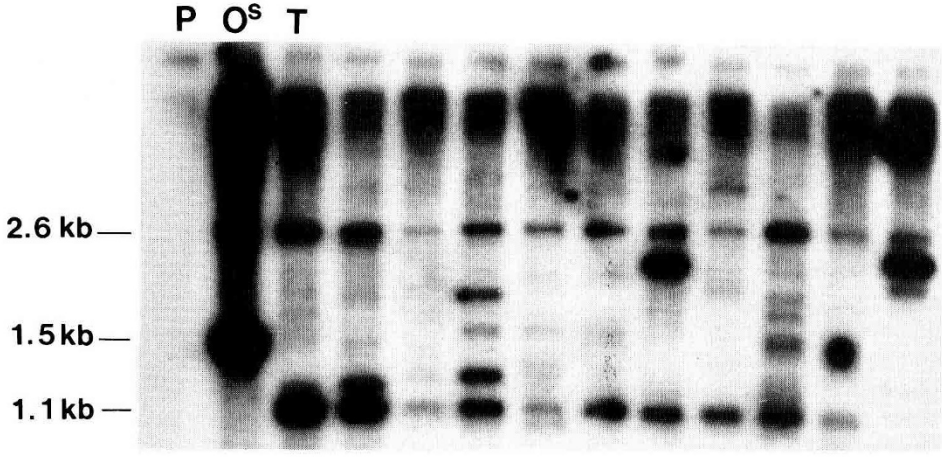

Fig. 2a.

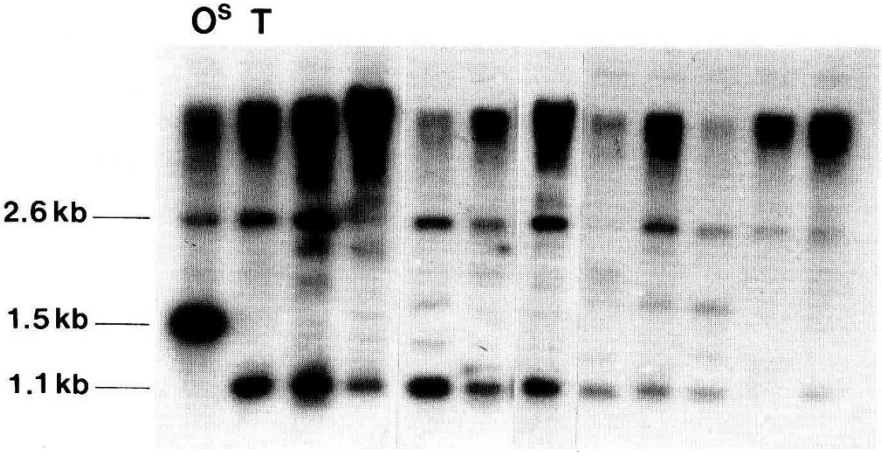

Fig. 2b.

Fig. 2. Southern blot analysis of *hobo* elements in natural populations. The 2.6-kb XhoI fragment derived from complete *hobo* elements and the 1.1-kb band from the *Th* elements are indicated. Populations tested are presented from left to right. **Fig. 2a.** Paris 45, Oregon R^s, Tours 82 (France), Tubingen 86 (FRG), Slankamen 86 (Yugoslavia), Uzhgorod 86 (USSR), Uman 87 (USSR), Nalchik 87 (USSR), Samarkand 86 (USSR), Tongza 87 (PRC), Raleigh 82 (USA), Saltillo 87 (Mexico), Marseillan 65 (France). **Fig. 2b.** Oregon R^s, Tours 82, Tubingen 83, Gomel 81 (USSR), Tashkent 81, Alma-Ata 81 (USSR), Tulufan 83 (PRC), Dunhuang 84, Jinan 82, Zhenjing 82, Quindao 84, Chougmin 83 (PRC).

tory strains (Blackman and Gelbart, 1988). However, the induction of genetic instabilities by strains isolated from a natural Greek population suggests that intact *hobo* elements are present in the wild and may express their dysgenic properties (Yannopoulos *et al.*, 1987). According to this hypothesis, the presence of the *Th* element may be interpreted as a contribution to the regulatory mechanisms of the *hobo* system. Moreover, their absence in some old laboratory strains raises the question of their putative recent origin and expansion.

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