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Short Communication

Transposable elements from the *mesophragmatica* group of *Drosophila*

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Abstract

Transposable elements (TEs) are middle repetitive DNA sequences classified into families according to their sequence similarities, such elements can playing an important role in the evolutionary process of their host genomes. There are many reports on the distribution of TEs in the fruit fly genus *Drosophila*, although there is relatively little information relating to the Neotropical *mesophragmatica* group of *Drosophila*, probably the most typical cluster of species occurring almost exclusively in the Andes mountains. Dot Blot and PCR analyses was used to study the distribution of some TEs (*I, mariner, hobo, gypsy, Tom/17.6, micropia* and *P* elements) within the *mesophragmatica* group of *Drosophila*. We found *gypsy* elements in all the *mesophragmatica* group species studied and *mariner* elements were absent only from *Drosophila pavani* but *P* element homologous sequences were present only in *D. pavani* and *Drosophila gasici* and the other TEs (*I, hobo, Tom/17.6, micropia*) were not found in any of the species investigated.

Key words: Drosophila, *mesophragmatica,* phylogenetic distribution, transposable elements.

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Transposable elements (TEs) are a theme of much interest because they form a significant portion of genomes and can play an important role in the evolutionary process of their host genomes (Kidwell and Lisch, 2000).

Two major classes are distinguished by their different modes of transposition (Finnegan, 1992). Class I elements use reverse transcriptase to transpose by means of an RNA intermediate and are called retroelements. They include long terminal repeat (LTR) retrotransposons as well as long and short interspersed elements (*LINES* and *SINES*, respectively). Long terminal repeat retrotransposons are closely related to other retroelements of major interest, such as retroviruses. Class II elements transpose directly from DNA to DNA and include transposons such as the *P* and *hobo* elements in *Drosophila*. Recently, two novel groups of DNA transposons have been described. One, called helitrons, transpose by some form of 'rolling circle' replication mechanism. The other, miniature inverted-repeats transposable elements (MITEs), are very short elements which are not autonomous and normally present an elevated copy number (Poulter *et al*., 2003).

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During their "life-cycle" in the host genomes TEs seem to experience a complex evolutionary pattern and may suffer: *i*) horizontal transfer, *ii*) stochastic loss, *iii*) inactivation and subsequent sequence degeneration and, sometimes, *iv*) revival by sequence recombination. Furthermore, ancestral polymorphism with different evolutionary rates of variable copies can make it more difficult to analyze the complex pattern of TE evolution (Herédia *et al.*, 2004; Brookfield, 2005).

The fruit fly genus *Drosophila* and related species are especially useful for investigating the role of transposable elements in evolution, with 96 different TEs families having so far been found in the sequenced *Drosophila melanogaster* genome (Kaminker *et al.*, 2002). Furthermore, sequencing of the *Drosophila pseudoobscura* genome has also been finished and ten other *Drosophila* genomes are in final process of sequencing (http://rana.lbl.gov/drosophila/), which will help to further clarify the evolutionary role played by the TEs. However, to understand the origin of transposable elements and how they are lost or gained by species and the role they play in genome evolution there is a need for a wide-ranging screening program of those TEs already identified in the *Drosophila* genomes already sequenced. Some extensive analyses have been made for a number of different *Drosophila* TEs (see

the review by Biémont and Cizeron, 1999), such as the *P* element family (Stacey *et al.*, 1986; Anxolabéhère and Periquet, 1987; Daniels *et al.,* 1990a; Loreto *et al*., 1998); *I* (Bucheton *et al*., 1986; Stacey *et al*., 1986); *gypsy* (Stacey *et al.,* 1986; Heredia *et al*., 2004); *hobo* (Daniels *et al.,* 1990b, Loreto *et al*., 1998); *micropia* (Almeida *et al.* 2001; 2003); and *mariner* (Maruyama and Hartl, 1991; Brunet *et al.,* 1994).

Although considerable data about the distribution of TEs in *Drosophila* are emerging on the evolution of these sequences in the *Drosophila*, few data are available on the Neotropical *mesophragmatica* group of *Drosophila* which are probably the most typical cluster of species occurring almost exclusively in the Andes Mountains (Brncic *et al.,* 1971). In this group, *Drosophila pavani* has been investigated for TEs and sequences homologous to *gypsy* and *copia* (Stacey *et al.,* 1986) and *Bari*1 (Moschetti *et al.,* 1998) have been found but not *P* and *I* homologous sequences (Brookfield *et al.,* 1984; Bucheton *et al.*, 1986). Furthermore, *gypsy* sequences, but not *P* and *hobo* sequences, have been found in *Drosophila gaucha* (Loreto *et al*., 1998).

This paper provides a brief description of the distribution of *I, mariner, hobo, gypsy, Tom/17.6, micropia* and *P* element TEs in the *mesophragmatica* group of *Drosophila*.

The species of the *mesophragmatica* group of *Drosophila* studied were: *D. pavani* (Brncic, 1957); *D. viracochi* (Brncic and Koref-Santibanez, 1957); *D. brncici* (Hunter and Hunter, 1964) and *D. gasici* (Brncic, 1957). For *D. gasici* three populations (Arica-Chile, Colombia, Cochabamba-Bolivia) were analyzed. All strains employed were maintained in the laboratory by massal mating under standard conditions. Genomic DNA was prepared from approximately 100 adult flies per sample and extracted according to Jowett (1986) with minor modifications.

Polymerase chain reactions (PCR) were performed in 25 μL volumes using approximately 25 ng of template DNA, 20 pMol of each primer, 0.2 mM of each dNTP, 1.5 to 2.5 mM $MgCl_2$ and 1 unit of Taq DNA polymerase (Invitrogen) in 1x Polymerase Buffer. The PCR conditions, the used primers and also the expected fragment sizes are presented in the Table 1. For *Tom/17.6* elements the degenerated primers were designed using the alignment of *Tom* element from *D. ananassae* and 17.6 and 297 from *D. melanogaster* described by Tanda *et al.* (1988).

For *P* and *mariner* elements, after PCR the product was separated on 0.8% (w/v) agarose gel, blotted onto a Hybond N+ nylon membrane (Amersham Biosciences) and hybridized with the *P* and *mariner* probes to confirm the specificity of amplification.

The transposable elements *I, mariner* and *micropia* were investigated by Dot Blot for all species. For each strain about 2 μg of DNA was boiled for 5 min, cooled for 5 min in a freezer, applied to a Hybond N+ nylon membrane and fixed at 80 °C for 2 h before being hybridized to a random primer-labeled probe at 60 °C in 5x SSC containing 0.1% (v/v) SDS; 5% (w/v) dextran sulfate and a 20-fold dilution of liquid block. The filters were washed twice with SSC 0.2X and 0.5% SDS (w/v) for 15 min at 60 °C. Hybridization and detection were performed using Gene Images KIT (Amersham Biosciences) according to the manufacture's instructions.

The following probes were used in Dot and Southern Blot experiments: the Mos1 plasmid for *mariner* (Maruyama and Hartl, 1991); the pI786 plasmid containing a 1 kb insert derived from the internal region of the *D. melanogaster I* element (see Fawcett *et al*., 1986); the amplified PCR fragment from the *micropia* dhMiF2 plasmid (Huisjer *et al*., 1988); the PCR fragment from the *gypsy* pGGHS plasmid (Dorsett *et al.*, 1989); the amplified PCR fragment from the *P* element pπ25.1 plasmid (O'Hare and Rubin, 1983); and the amplified PCR fragment from the *Tom* element pTOM plasmid (Tanda *et al*., 1988). The primers used to amplify the probes are presented in Table 1.

The status of the species of the *mesophragmatica* group related to the presence of the *I, hobo, Tom/17.6, mariner, micropia, P and gypsy* transposable elements is presented in Table 2.

Table 1 - The PCR conditions, primers and expected size of PCR products.

Element	Primers	PCR conditions	Expected size	Reference
Tom/17.6	T12A (5' AGTWTGGGCSACAAARAC 3') T12B (5'CCGTCYCTRTCYGCCTTT 3')	95 °C for 1 min; 55 °C for 45 s; 72 °C for 1min (35 cycles)	± 1 kb	
gypsy	GYP3S2 (5' AAAGGCGAYTTGGTTGACACTCC 3') GYP3AS2 (5'CARGTGGCTRGGTTGRGTGTG 3')	96 °C for 15 s; 55 °C for 30 s; 72 °C for 1 min 30 s (35 cycles)	485 bp	Herédia *et al*. (2004)
hobo	P651 (5' CACCTCCAATTTATCCCGCC 3') P1597 (5' GGATGGAATACGAAGC 3')	94 °C for 1 min; 50 °C for 45 s; 72 °C for 1 min (35 cycles)	946 bp.	Klein (2002)
micropia	MIC1777 (5' CTCCCCTTTTGCCAGTCCT 3') MIC2570 (5' TTGAGCTAGCGT CGGTGTG 3')	95 °C for 1 min; 55 °C for 45 s; 72 °C for 1 min (35 cycles)	812bp	Lankenau *et al*. (1994)
mariner	Mar-fw (5' TGGGTNCCNCAYGARYT 3') Mar-rv (5' GGNGCNARRTCNGGNSWRTA 3')	95 °C for 1 min; 53 °C for 45 s; 72 °C for 1 min (35 cycles)	473bp	Robertson and Macleod (1993)
P	2684 (5' GCTATTTGNYTNCAYACCGCNGG 3') 2687 (5' CCCAATGNATWGCANCGTCTKAT 3')	94 °C for 45 s; 50 °C for 45 s; 72 °C for 1 min (35 cycles)	± 1 kb	Lee *et al.* (1999)

Table 2 - Distribution of transposable elements in *mesophragmatica* species group.

	Transposable element presence (+) or absence (-)												
	gypsy		*P*		*hobo*		*17.6/tom*		*mariner*		*micropia*		*I*
Drosophila species	Dot	PCR	Dot	PCR	Dot	PCR	Dot	PCR	Dot	PCR	Dot	PCR	Dot
D. gasici (Arica)	+	+	-	-	-	-	-	-	-	+	-	-	-
D.gasici(Colombia)	+	+	-	+	-	-	-	-	-	+	-	-	-
D.gasici (Cocha)	+	+	-	-	-	-	-	-	-	+	-	-	-
D.brncici	+	+	-	-	-	-	-	-	-	+	-	-	-
D.pavani	+	+	-	-	-	-	-	-	-	-	-	-	-
D.viracochi	+	+	-	+	-	-	-	-	-	+	-	-	-

The *gypsy* homologous sequences were present in all the species tested. The ENV fragment amplified by PCR corresponded to the expected size (0.5 kb) and a strong band was produced (Figure 1). Homology with the *gypsy* sequence was confirmed by Dot Blot of the PCR products and also with the genomic DNA probed with the *D. melanogaster gypsy* sequence. The presence of the *gypsy* sequence in all *mesophragmatica* group species tested was expected because all *Drosophila* species so far investigated have *gypsy* homologous sequences (Stacey *et al.*, 1986, Herédia *et al.*, 2004). Some reports have suggested that the wide *gypsy* distribution in *Drosophila* could be related to the fact that *gypsy* is a retrovirus and therefore could have a high capacity to invade different genomes (Kim *et al.*, 1994; Prud'homme *et al.*, 1994; Heredia *et al*., 2004). However, to test whether the occurrence of *gypsy* in the genome of *mesophragmatica* group species is related to its presence in the ancestral genome or is a product of recent invasion, the *gypsy* related sequences from these species need to be cloned and sequenced.

Using degenerated primers we were able to amplify *P* homologous sequences in *D. pavani* and in the Colombia population of *D. gasici,* while the two other populations of this species analyzed were negative. The other species tested also lacked *P* sequences (Figure 1). The PCR product obtained with the *mesophragmatica* group species were of the expected size but the band was weak. In order to confirm the homology with the *P* element, the PCR products were transferred to a nylon membrane and hybridized to the *D. melanogaster P* element.

The *P* element family is one of the best investigated eukaryote TEs, with the first studies having indicated that *P*-homologous sequences are basically confined to the subgenus *Sophophora* (Daniels *et al.*, 1990a) and that their presence in *D. melanogaster* occurs by horizontal transfer from *D. willistoni (*Kidwell, 1992). Later analysis, however, has shown a wider distribution of *P* homologous sequences, which have now also been described in other dipterans such as the blow fly (*Lucilia cuprina*; Perkins and Howells, 1992), the house fly (*Musca domestica*; Lee *et al*., 1999) and the mosquito (*Anopheles gambiae*; Sarkar *et al.,* 2003, Oliveira de Carvalho *et al*., 2004) as well as in vertebrates such as the zebrafish, chicken, pig, cow and humans (Quesneville *et al.,* 2005, Hammer *et al.,* 2005). At the moment, the dominant hypothesis sustains that the *P* element is an old component of animal genomes maintained by vertical transfer but which could also suffer horizontal transfer and domestication to new functions (Hammer *et al.,* 2005).

In our laboratory we have obtained some very divergent *P* sequences from the *tripunctata* and *cardini* groups of *Drosophila* (unpublished results). The differences observed in intensity of hybridization signal in the Southern Blots of *P* element PCR products obtained from *mesophragmatica* group species and the control *P* element from *D. melanogaster* suggest that there is little similarity between the *P* sequences from *mesophragmatica* group species and the *D. melanogaster P* element. Cloning and sequencing these sequences could contribute to elucidating the origin of the *P* element family.

The *hobo* element was initially described as present only in the genomes of some *melanogaster* group species (Daniels *et al*., 1990b, Periquet *et al.*, 1994). However, *hobo* sequences have also been described in some *D. willistoni* strains which show a weak hybridization signal with the *D. melanogaster hobo* probe (Loreto *et al*.,1998). Klein (2002) sequencing part of this *D. willistoni* element showing it is *hobo* divergent sequence. Out of *Drosophila* genus, *hobo*-like elements have been found in some species of Diptera, like *Musca domestica* (Atkinson *et al*., 1993) and different tephritids (Handler and Gomez, 1996; Torti *et al*., 2005) and, also in some species of Lepidoptera (Borsatti *et al*., 2003). However, using the primers described by Klein (2002) we have not obtained success in amplifying *hobo* related sequences in the *mesophragmatica* group.

Using the degenerated primers we were able to amplify sequences of the retrotransposons from the *Tom/17.6* families in different *Drosophila* species but no amplification occurred when DNAs of *mesophragmatica* species were used in the PCR assay, which could either mean that these retrotransposon families are not present in the *mesophragmatica* genome or the sequences are divergent in the primer region.

Using the *Drosophila mauritiana* (MOS1) as probe to *mariner,* no homologous sequences were observed in the species studied. However, Brunet *et al*., (1994) used degenerated primers to amplify *mariner* homologous sequences in some *Drosophila* species which were first thought not to contain *mariner* sequences because such sequences had not been detected by the Southern Blot technique. Our results using the degenerated primers described by Robertson and Macleod (1993) have shown that the *mariner* TE is present in *D. brncici*, *D. viracochi* and *D. gasici*, with the latter species showing an amplification fragment about 300 bp smaller than that displayed by the other species. However, *D. pavani* showed no signs of having the *mariner* sequence in its genome either by PCR or Dot Blot assay.

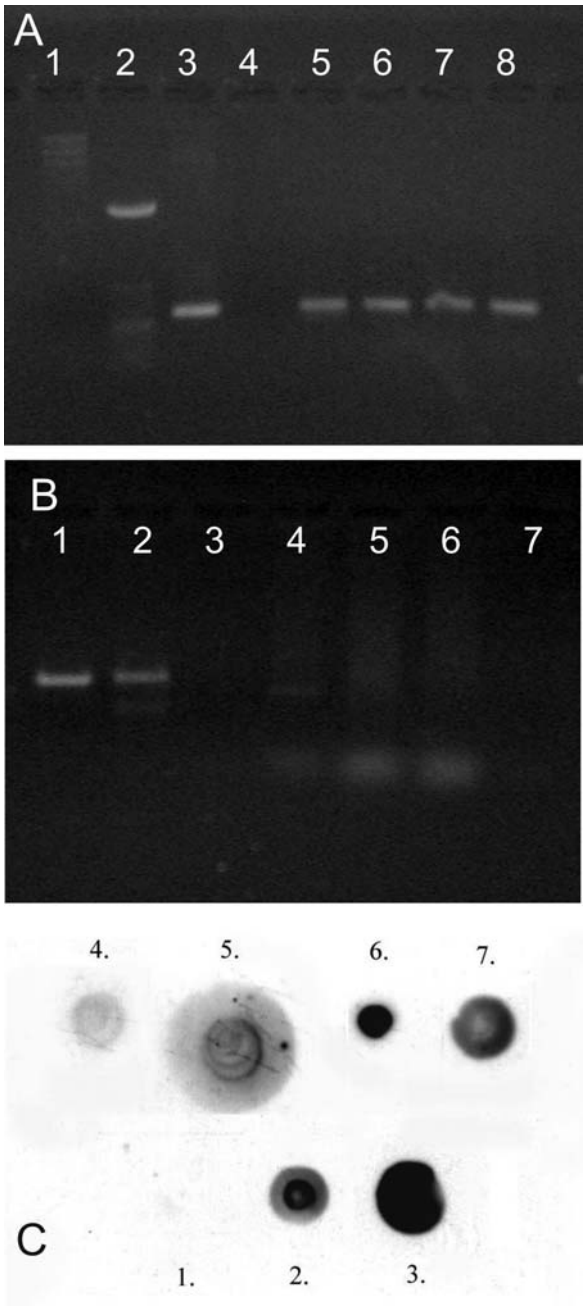

Figure 1 - A) PCR amplification of *gypsy* element: 1 = λHind III fragments; 2 = 1 kb Invitrogen DNA Ladder; 3 = positive control (pGGHS plasmid); 4 = negative control (5 - *D. gasici*); 6 = *D.* brncici; 7 = *D. pavani*; 8 = *D. viracochi.* B) PCR amplification of *P* element: 1 = pp25.1 plasmid; 2 = *D. gasici* (Colombia); 3 = *D. gasici* (Arica); 4 = *D. viracochi*; 5 = *D. brncici*; *6* = *D. pavani*; 7 = negative control. C) Dot blot of genomic DNA from mesophragmatica species probed with gypsy element: 1 = negative control (pUC 18 plasmid); 2 = positive control (pGGHS plasmid); 3 = *D. pavani*; 4 = *D. gasici* (Colombia); 5 = *D. gasici* (Arica); 6 = *D. brncici*; 7 = *D. viracochi.*

The *micropia* TE is a representative of a family of transposable elements discovered as constituents of the Y-chromosomal fertility genes of *Drosophila hydei* (Huijser, *et al*., 1998). Several members of the *micropia* family have been recovered from *D. melanogaster* and, recently, from *saltans* (Almeida *et al*., 2001) and *repleta* (Almeida *et al*., 2003) group species. However, using degenerated primers to *micropia* we obtained no amplification using *mesophragmatica* species DNA as the PCR template. Also, the Dot Blot was negative for the presence of *micropia* homologous sequences in the genomic DNA from all the species tested.

The *I* element was also absent from the *mesophragmatica* genome as indicated by Dot Blot experiments. This retrotransposon element has its distribution restricted to the *melanogaster* group, which has been reported by other authors (Bucheton *et al.*, 1986, Stacey *et al.*, 1986, Loreto *et al*., 1998).

Studies on the presence and distribution of TEs in the genus *Drosophila* have shown discrepancies between phylogenetics trees of TEs and their host. Some intriguing horizontal transfer cases have initially been indicated by wide screening analyses of TE distribution (Daniels *et al.,* 1990a; Loreto *et al*., 1998, Herédia *et al*., 2004, Almeida and Carareto, 2005). Studies on the phylogenetic distribution of TEs lead to a better understanding of the evolution of such elements and their influence on the host genome. This paper provides some information on the distribution of TEs in *mesophragmatica* group species and poses questions which may stimulate further research on the evolution of *gypsy, mariner* and *P* element in this group.

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