

Horizontal acquisition of transposable elements and viral sequences: patterns and consequences

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It is becoming clear that most eukaryotic transposable elements (TEs) owe their evolutionary success in part to horizontal transfer events, which enable them to invade new species. Recent large-scale studies are beginning to unravel the mechanisms and ecological factors underlying this mode of transmission. Viruses are increasingly recognized as vectors in the process but also as a direct source of genetic material horizontally acquired by eukaryotic organisms. Because TEs and endogenous viruses are major catalysts of variation and innovation in genomes, we argue that horizontal inheritance has had a more profound impact in eukaryotic evolution than is commonly appreciated. To support this proposal, we compile a list of examples, including some previously unrecognized, whereby new host functions and phenotypes can be directly attributed to horizontally acquired TE or viral sequences. We predict that the number of examples will rapidly grow in the future as the prevalence of horizontal transfer in the life cycle of TEs becomes even more apparent, firmly establishing this form of non-Mendelian inheritance as a consequential facet of eukaryotic evolution.

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Introduction

Transposable elements (TEs) are segments of DNA able to move from one locus to another in a given genome and to replicate themselves in the process [1]. TEs are found in nearly all organisms and frequently constitute the major portion of the genome [2–6]. They can be

transmitted from one host to another in two ways: through vertical inheritance from parent to offspring, or through horizontal transfer (HT) between non-mating organisms [7,8]. HT can be viewed as a way for TEs to ensure their long-term persistence, by jumping from hosts able to suppress their transposition to naïve ones in which they can spawn new copies [9]. It is still unclear how much TEs as a whole rely on horizontal *versus* vertical transmission to propagate in eukaryotes, however it has become apparent that most known TE types have propagated horizontally at some point during their evolutionary history. Given the profound influence that TEs and their associated activities have exerted on eukaryotic genomes, it follows that the horizontal transfer of TEs (HTT) must represent an important facet of eukaryotic evolution [7]. However, cases of eukaryotic TEs for which there is robust evidence of both HT and direct functional consequences are still scarce or have remained unrecognized. Here we provide an update on the trends characterizing HTT in eukaryotes, with an emphasis on plants and animals, and we compile a list of cases whereby a given TE shows evidence of HT and has had direct evolutionary consequences for the host lineage where it was introduced. We argue that HT is likely to be a widespread mechanism ensuring the long-term persistence of TEs and that HTT should be regarded as an important source of genetic variation, whose impact on the host's biology has been underappreciated [10,11].

HTT is pervasive in plants and animals

An event of HTT is suspected when similarity between TE copies from different host species is anomalously high given the divergence time of the species. For example, copies of the *Mariner_Tbel* family of transposons from the Northern tree shrew (*Tupaia belangeri*) display up to 87% nucleotide identity over their entire length (~1300 bp) with elements found in the harvester ant (*Pogonomyrmex barbaratus*) [12]. These sequences, like most TE copies, have evolved neutrally after their insertion in the host genome. Thus, such a level of interspecific sequence identity is incompatible with their vertical inheritance since the divergence of mammals and insects, which occurred more than 550 million years ago [12]. The most likely explanation is that this TE family was introduced horizontally in one or both of these species well after they diverged from a common ancestor. Based on this type of analysis, as well as on other criteria reviewed elsewhere [13,14^{*}], no less than 2836 HTT events (retrieved from HTT-db [15^{*}] as of October 2017) have been recorded since the first unquestionable case of HTT, that of the *P*

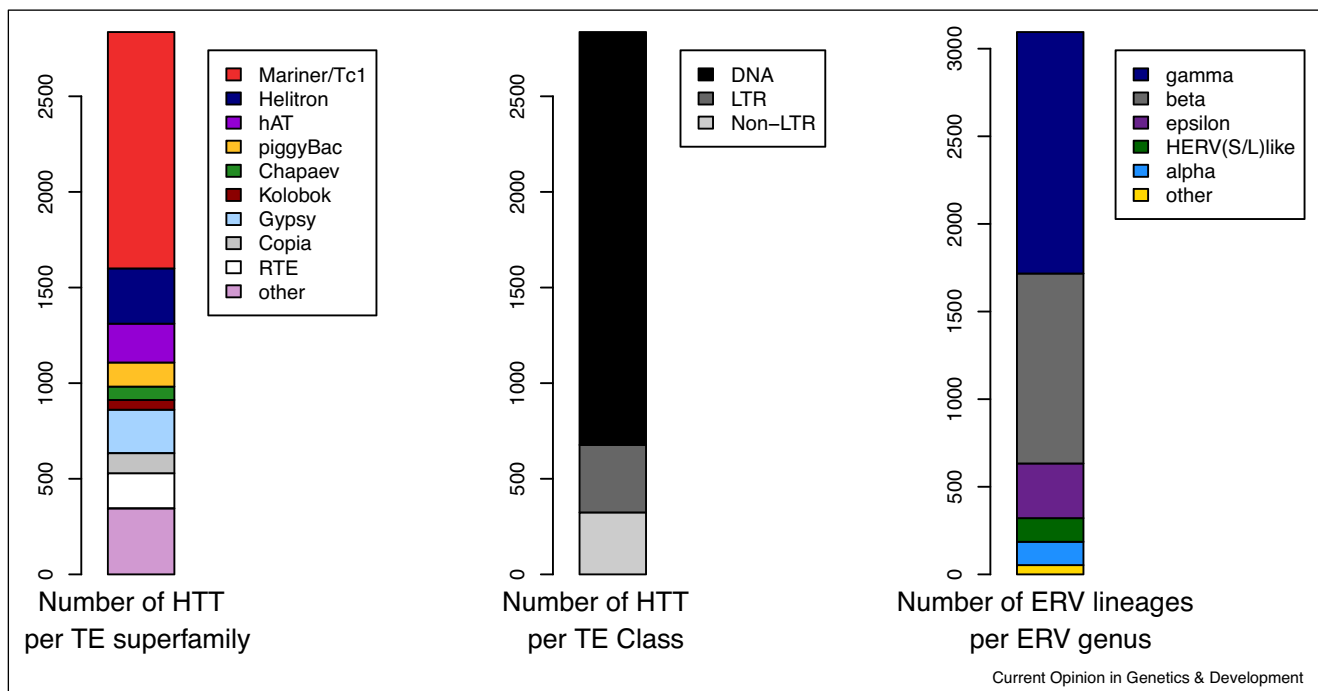
element in *Drosophila melanogaster*, reported in 1990 [16] (Figure 1). Among the many HTT stories documented over the past few years, one achieved an unprecedented level of precision in the timing of an HTT event, which again involved the *P* element but this time invading *Drosophila simulans*, a species sister to *D. melanogaster*. Population sequencing revealed that this transposon occurs only in *D. simulans* populations sampled after 2010, and that its presence in this species is best explained by a single, very recent HTT event of one particular *P* element variant from *D. melanogaster* [17**]. This HTT event, which was nearly ‘caught in the act’ provides an outstanding opportunity, together with experimental evolution studies [18], to characterize the first steps of TE invasion and the host response in natural populations.

Another recent study took advantage of the large number of whole genome sequences available in public databases to perform a systematic survey of HTT among 195 insect species [19**]. More than 2000 HTT events were inferred to explain the distribution of TEs in these insects. This is by far the highest number of HTT inferred in a single study, and it suggests that the actual number of HTT that occurred over the entire evolutionary history of insects is orders of magnitude higher [19**]. Comparable

projections were made based on a systematic search for HT of long terminal repeat (LTR) retrotransposons among 40 plant species [20**]. Non-LTR retrotransposons (notably those of the RTE clade) also appear to have transferred repeatedly during eukaryotic evolution [21**]. The pervasiveness of HTT was also apparent from a recent study focusing on the distribution of DNA transposons of the *mariner* family across 20 *Drosophila* genomes, in which almost all *mariner* lineages tested (24 out of 26) were found to have transferred horizontally, often repeatedly [14*]. These findings are in line with a seminal study quantifying HTT among three *Drosophila* species, which estimated an average rate of 0.04 HTT per TE family per million years [22]. Thus, a plethora of HTTs punctuates the evolutionary history of TEs in a variety of eukaryote lineages. To these can be added another common form of HT in eukaryotes, which involves the acquisition of viral sequences also known as endogenous viral elements (Box 1). Some EVEs such as the endogenous retroviruses (ERVs) of vertebrates can be readily affiliated with TEs and, like them, are capable of spreading vertically and horizontally (Box 1; Figure 1).

In comparison to the multiplicity of reports on HTT, evidence for the long-term vertical persistence of TEs is scarce. The best-documented cases involve non-LTR

Figure 1



Numbers of horizontal transfers of transposable elements and vertebrate endogenous retroviruses. The barplots show the numbers of HTT events per TE superfamily (a) and per TE class (b) as taken from HTT-db in October 2017 (Dotto *et al.* [15*]). The barplot in (c) shows the number of clusters of related ERV sequences for each ERV family unearthed from 65 vertebrate genomes by Hayward *et al.* [96**]. The presence of >3000 ERV lineages in vertebrates, each inferred to descend from a discrete endogenisation event [96**], suggests that this form of HTT has been pervasive during vertebrate evolution.

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