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# Transmission patterns of eukaryotic transposable elements: arguments for and against horizontal transfer


## Michael P. Cummings



**Recent studies have demonstrated that several classes of transposable elements are widely distributed within eukaryotes. Horizontal transmission of these transposable elements has often been invoked in order to explain the observed variation and relationships within and between species. These same patterns of variation and relationships, however, may originate from processes that do not involve the lateral transfer of genetic material across species.**



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Transposable elements – the very name conveys movement. This theme of motion is reiterated by the names given to specific groups of transposable elements, such as *gypsy*, *hobo*, *jockey*, *mariner*, *dong* (Chinese for moving), *roo* (as in kangaroo) and *HMS Beagle*. But what is the extent of this movement? While it is clear that transposable elements move within a genome and are transmitted vertically (i.e. sexually), recent studies propose that they move horizontally (i.e. nonsexually) between species, as well[1–4]. At the outset, it should be understood that these two basic transmission patterns are not mutually exclusive.

While a heterogeneous assemblage of genetic entities is classified as consisting of transposable elements on account of crude functional similarity (i.e. they move about within a genome), the evolutionary origins of these entities and the specific mechanisms associated with their transposition are distinct. Transposable elements can be very generally divided into two categories: the Class I elements, or retrotransposons (see Box 1), and the Class II elements (see Box 2).

Several steps are required for a transposable element to become successfully transferred between species: transportation, transcription, translation, reverse transcription and increase in copy number. Transportation – the movement of the transposable element, as DNA or RNA, from one species to another – is the inaugural manoeuvre for horizontal transmission. How these transfers might be accomplished is subject to speculation, but there is some research supporting the potentiality of viruses[5,6] or mites[7] as vectors. Subsequent to the initial transfer event, the transposable element has to recognize, and be recognized by, the appropriate components of the new genetic environment. The barriers posed by transcription, translation, and where required, reverse transcription, are conditional on the particular type of element and the cellular milieu. These interactions are requisite to the increase in copy number, and hence, establishment of the elements. Arguments surrounding the issue of horizontal transmission have involved circumstantial observations, and these observations are often the subject of conflicting interpretations.


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**Box 1. Class I transposable elements**

These transposable elements are related to retroviruses, and like retroviruses their replication involves the synthesis of DNA from template RNA, a process catalysed by the enzyme, reverse transcriptase. The basic distinction between retroviruses and Class I elements is that the latter do not encode envelope proteins and, hence, are not intrinsically transmissible between cells. Although there is no universally accepted nomenclatural standard, I will refer to all transposable elements in Class I as 'retrotransposons'.

Retrotransposons are broadly classified into two categories based on structural features: (1) those with long terminal repeat sequences (LTRs); and (2) those without LTRs, which are also sometimes referred to as retroposons. The best-studied, non-LTR retrotransposons are the mammalian L1 or LINE elements, and similar elements occur in insects and plants. Retrotransposons with LTRs are, in turn, classified into two groups based on the arrangement of coding sequences, and are named after homologous elements in *Saccharomyces cerevisiae* and *Drosophila melanogaster*: the *Ty3/gypsy* group, and the *Ty1/copia* group. Based on the order of the coding sequences and on the amino acid sequence of reverse transcriptase, the *Ty3/gypsy* group appear to be more closely related to the presently known retroviruses than are the *Ty1/copia* group. The majority of the retrotransposon sequence comprises protein coding sequences and *cis*-acting sequences required for replication. Retrotransposons are extremely widespread, with both LTR and non-LTR retrotransposons occurring in animals, fungi, plants and protists.

Retrotransposons exhibit replicative transposition, i.e. transposition does not require excision of an element, but rather a new, additional copy of the element is formed. These elements do not exhibit a precise excision process, but rather appear to be lost through recombination between LTR sequences or deletion events.

The arguments are based on the distribution, phylogenetic relationships, sequence similarity and historical observations of transposable elements.

## Arguments based on distribution

The distribution patterns of specific types of transposable elements across taxa have been used to infer horizontal transmission. In particular, phylogenetically disjunct distributions have been used as evidence[1,8,9]. This argument arises from studies of the distribution of a class of transposable elements across a circumscribed group of taxa whose phylogenetic relationships are at least crudely known. Apparent absence of the transposable elements under study from taxa whose closest relatives have the elements is taken as evidence for horizontal transmission. Here, it is inferred that the horizontal transmission events occurred subsequent to the divergence of the taxa, and that these events best explain the observed distribution patterns. An alternative hypothesis is that the elements have been lost in particular lineages through extinction, or are no longer recognizable under the experimental conditions used in the study. Loss of particular elements through recombination, and the process of lineage sorting (Box 3) may contribute to seemingly disjunct distributions.

Distinguishing between these hypotheses can be particularly difficult when the observations are confounded by limitations of the experimental techniques employed. In particular, experiments based on southern blot hybridizations have been shown, in some cases, to be insensitive compared to assays based on degenerate PCR (polymerase chain reactions), because of the tremendous sequence heterogeneity of some classes of elements both within and between species[10,11]. In all cases, it should be remembered that absence of evidence should not be confused with evidence of absence.

## Arguments based on phylogenetic relationships

DNA and/or protein sequences of transposable elements have been used to infer their phylogenetic relationships[3,4,10–16]. Often the inferred relationships for the elements are not in keeping with the conventionally held notions regarding the relationships of the taxa in which the elements reside. This incongruence between phylogenies for elements and the species from which they are sampled has been the basis for arguments supporting horizontal transfer of transposable elements. However, several features of transposable-element biology, combined with experimental procedures, may obfuscate phylogenetic relationships of transposable elements. These include possible recombination, lineage sorting and problems in establishing homology between elements.

The processes of recombination and gene conversion can lead to complex relationships within and between transposable elements residing within and between species. These complex relationships may not be accurately reflected in phylogenetic trees, particularly the bifurcating trees that are fundamentally assumed by most methods of phylogenetic inference, because recombination and/or gene conversion involving disparate element lineages can create situations where distinct regions of the same element may have different evolutionary histories. Very high rates of recombination have been established for retroviruses[17], and some evidence suggests that recombination has occurred between transposable elements and retroviruses, and perhaps between other retro-elements as well[18]. For example, the sequence encoding ribonuclease H of the non-LTR retrotransposons *I* and *Ingi* appear to be more closely related to those of retroviruses rather than other non-LTR retrotransposons, which is in contrast to the relationships implied by analysis of sequences encoding reverse transcriptase[19]. Another example comes from *Schizosaccharomyces pombe*, where sequence analysis of retrotransposons *Tf1* and *Tf2*[20] reveals a pattern that is consistent with recombination and/or gene conversion.

Another underlying assumption of phylogenetic inference methods – homology (see Box 4) – may be difficult or even impossible to establish in particular cases. Several studies have established a high level of heterogeneity

**Box 2. Class II transposable elements**

In this group of transposable elements (also sometimes referred to as short inverted repeat elements) transposition is directly from DNA to DNA, and does not involve an RNA transposition intermediate. Class II transposable elements comprise a broad range of elements and include *Ds*, the first transposable element discovered by McClintock[28].

Several groups of Class II elements can be distinguished based on their amino acid sequences. The *Ac/hobo* group, which include the *Ac–Ds* system of maize and relatives (*Zea* spp.), *Tam3* of snapdragon (*Antirrhinum majus*) and *hobo* of *Drosophila*. Another group that is widespread is the *Tc1/mariner* group for which representatives are found in nematodes, arthropods and vertebrates. Other examples of Class II elements, that are not yet recognized as members of widespread groups, are *P* and *FB* elements of *Drosophila*, and *Spm* and *Mu* elements of maize.

Although a diverse range of elements falls into Class II, most share the basic structural feature of a single, open reading frame (sometimes split by introns) flanked by short, inverted repeat sequences, and they also tend to create short target-site duplications upon integration. The protein product of the open reading frame is usually referred to as a 'transposase'. Some members of this class consist of autonomous and non-autonomous elements within the same genome, for example, the *Ac–Ds* system of maize and *P* of *Drosophila*. The non-autonomous elements are capable of transposition in the presence of autonomous elements through *trans* activation.

Unlike the Class I elements, excision of Class II elements appears to be a prerequisite for transposition in those cases which have been carefully studied to date. Although this coupled excision–transposition process is nonreplicative, these elements may increase in copy number within a genome through double-strand gap repair of the empty target site when an element-containing DNA strand is used as a template.

within species[3,4,10,11,15,16]. It is the source of this heterogeneity that is germane to the subject of transmission patterns of these elements. The presence of diverse elements within species demonstrates the presence of multiple transposable lineages within species lineages. Some argue that this is best explained by horizontal transmission of elements between species[2-4], although it has been argued that this pattern might also be explained by sampling processes and comparisons between elements that differ in their homology, i.e. confusion between orthologous and paralogous elements[11,16] (Box 4). Sampling associated with the evolutionary processes can lead to lineage sorting (Box 3), and this lineage sorting, alone or in combination with sampling of the experimental procedures involved, can lead to incongruent phylogenies for species and their associated transposable elements.

Correctly inferring phylogenetic relationships may prove very difficult when sequences exhibit rapid rates of changes and/or a very wide range in rates of change, as is the case for the retrotransposons. Reverse transcription, a step in the replicative transposition of retrotransposons, is highly error-prone, due to the absence of any proofreading endonuclease activity associated with reverse transcriptase. This error rate, based on data from the retrovirus HIV, is estimated to be of the order of $10^{-4}$ to $10^{-2}$ substitutions per site per year[21]; a marked contrast to the rate for most genes, which is of the order of $10^{-9}$ substitutions per site per year[22]. Specific retrotransposons integrated into the genome may be relatively quiescent, giving rise to other insertions after millions of years of no apparent activity[23]. Differences in activity of particular elements or element lineages, and therefore differences in the amount of error-prone reverse transcription, may contribute to differences in the effective rates of evolution. These differences in rates of evolution, to the extent that they lead to very different branch lengths for closely related elements, may contribute to problems inferring phylogenetic relationships[24].

## Arguments based on sequence similarity

This type of argument follows a very simple form: how does one explain the high level of sequence identity between transposable element sequences from different species except by relatively recent horizontal transmission? One problem with this is that it is not always clear what level of sequence identity constitutes a level that clearly favors a hypothesis of horizontal transmission over a hypothesis of vertical transmission. For example, the similarity of the putative transposase amino acid sequences of *hobo* from fruit fly (*Drosophila melanogaster*), *Ac* (*Activator*) from maize (*Zea mays*) and *Tam3* from snapdragon (*Antirrhinum majus*) has been explained as horizontal transfer[25]. The 19% identity between *Ac* and *hobo* was the highest level between the three elements compared. Although this level of similarity establishes these elements as members of the same group of elements, it hardly seems strong evidence for horizontal transfer. An appropriate context is provided when one considers that the distance observed between *Ac* of maize and *Ac*-like elements in another member of the grass family, pearl millet (*Pennisetum glaucum*), is not significantly different from that observed for the gene *Adh1* between the same taxa[14].

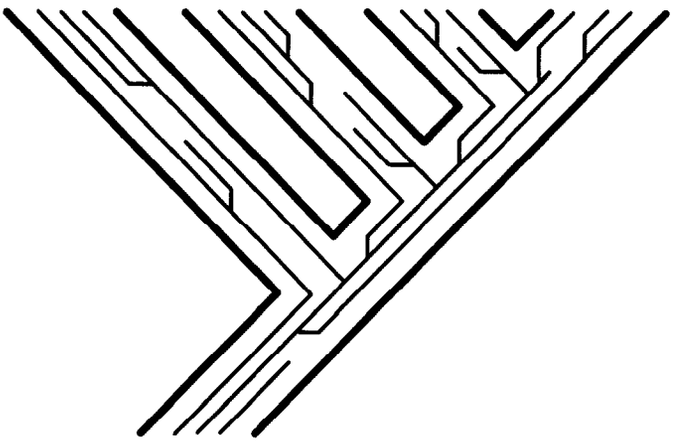
However, other cases of more-striking similarity among transposable elements from different species have been observed and offer compelling evidence in support of recent horizontal transmission. Examination of interspecific sequence variation of *P* and *hobo* elements in *Drosophila* demonstrate this quite well. For example, DNA sequencing reveals that two *P* elements from *D. melanogaster* and *D. willistoni*, species thought to have previously shared a common ancestor over at least 20 million years ago, differ in only one nucleotide over the entire 2907 bp element[26]. Additionally, *hobo* element sequences from *D. melanogaster*, *D. simulans* and *D. mauritiana* exhibit a remarkably small number of nucleotide differences compared to other genes from the same species[27]. Although the interspecific similarity for some elements may appear significant, the lack of knowledge about the evolutionary dynamics of particular groups of transposable elements precludes the objective establishment of critical values for sequence similarity to test hypotheses regarding horizontal and vertical transmission.

## Arguments based on history

Specific episodes of horizontal transmission are historical events, and often, these events must be inferred based upon some of the types of observations described above. However, sometimes specific historical information can provide strong evidence in support of horizontal transmission of transposable elements. In one case in particular, that of *P* elements in *D. melanogaster*, there is

### Box 3. Lineage sorting

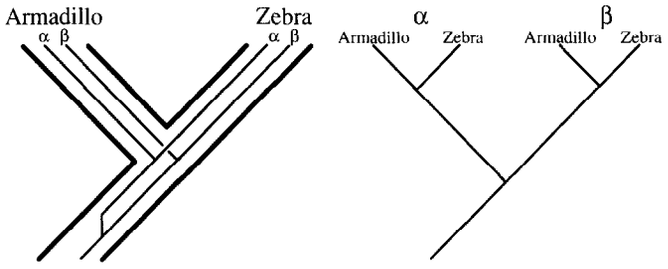
The history of any sample of transposable elements has a complex hierarchical structure, and present-day transposable elements are descendents that represent lineages that have been sampled at many levels of this hierarchy. At the lowest level of the hierarchy, the transposable elements within a cell constitute a population whose members represent individual lines of descent. For any two specific elements, these lines of descent go back to their most-recent common ancestor. That common ancestor may have arisen in the previous cell generation, in the previous generation at the organism level, in the immediate ancestral species, or, perhaps, back even further. One can therefore view transposable elements as lineages within the bounds of cell lineages, which are themselves within the bounds of lineages of individuals, and so on. This is depicted diagrammatically in the figure below, where thicker lines demarcate the lineages at a level in the hierarchy, and the thinner lines represent lineages at a lower inclusive level.



Certain evolutionary genetic phenomena, such as genetic drift, can be conceptualized as the consequence of stochastic sampling events. Similarly, the vagaries of stochastic sampling influence the sorting of transposable-element lineages. In combination with mutation, the processes of differential radiation and extinction of particular transposable-element lineages develop heterogeneity. As these and other processes, such as cell division, speciation and species extinction, continue, heterogeneity within a level of the hierarchy (e.g. within a cell) becomes heterogeneity between members at the next level (e.g. between cells), and this continues up through to the higher levels (e.g. between species). Therefore, the tens to hundreds of thousands of elements that constitute the population of elements within a genome can differ greatly in the degree of their relatedness to each other and to transposable elements in different species[3,4,10,11,16,31]. Superimposed on this evolutionary–genetic sampling is the experimental sampling, which may involve examination of only a few of the large number of element lineages.

### Box 4. Types of homologous relationships

One of the basic assumptions of phylogenetic inference is that the entities being analysed are **homologous**, i.e. they owe their similarity to common ancestry. However, there are several ways that molecular sequences within and between species may be homologous. Sequences may be **orthologous**, i.e. their homology is due to their being derived from a single sequence in a common ancestral species, and subsequent copies were generated as a consequence of speciation. This can be seen in the amino acid sequences for the hemoglobin multigene family of vertebrates. An example is the armadillo (*Dasypus novemcinctus*) α-hemoglobin gene and the zebra (*Equus zebra*) α-hemoglobin gene. Conversely, sequences may be **paralogous**, i.e. they are homologous because they arose through duplication events. For example, the armadillo α-hemoglobin gene and the armadillo β-hemoglobin gene are paralogous.




These distinctions are more than pedantic semantics; phylogenetic relationships of paralogous and orthologous sequences may lead to difficulties in interpretation if the nature of the homology is not understood. Indeed, the α-hemoglobin genes from armadillo and zebra are more closely related than are the α- and β-hemoglobin genes within either species. These distinctions, and their phylogenetic implications, are especially important if one is to propose that a sequence may be homologous to another, not through duplication within a lineage or lineage splitting (speciation), but through horizontal transmission. This latter type of homologous relationship is termed **xenologous**. In the absence of sufficient understanding, sampling and subsequent phylogenetic analysis of members of a multigene family, such as the hemoglobins, lead to inferred relationships that on cursory examination can be interpreted as evidence for horizontal transmission. The vertebrate hemoglobin multigene family represents a relatively simple case in comparison to that of transposable elements.

some historical information regarding possible horizontal transmission[1,8]. Collections of *D. melanogaster* generally lacked *P* elements (*M* strains) before about 20 years ago, and over time, the proportion of collections with *P* elements (*P* strains) has increased to the point where *P* strains constitute all recent collections. This historical association between the date of collection and the presence of *P* elements is consistent with the suggestion that *P* elements were recently transferred horizontally from *D. willistoni*.

## Promising future research

Transposable elements were initially discovered through their effect on phenotypic traits in genetic studies[28], and this is still an important way in which they are found[29]. Also, several transposable elements have been discovered through the characterization of repetitive sequences[30]. However, with increasingly detailed study of genomes, in particular DNA sequencing, many transposable elements have been discovered by 'accident'. In terms of establishing the distribution of particular classes of transposable elements, the future looks quite bright. Several recent studies which had the goal of assessing the distribution of particular classes of transposable elements using degenerate PCR have been extremely successful and have greatly expanded the known distribution for these elements[4,11,31]. Future, inadvertent discovery of new transposable elements, or previously known element classes in new taxa, is sure to yield new information as well. Initial results from the yeast (*Saccharomyces cerevisiae*) and nematode (*Caenorhabditis elegans*) genome projects[32,33] have resulted in the discovery of transposable elements previously unknown in both these species (Ref. 34; and see annotations in GenBank accession M98552). Additionally, careful and refined computer analyses of sequences have established the relationships between previously discovered elements[12,13,35], and the identification of previously discovered, repetitive sequences as transposable elements[34,36].

The evolutionary histories of transposable elements are complex, and well-supported inferences about specific events in these histories are sometimes difficult to establish. Consensus within the field has not developed in many specific cases, and indeed often, the same patterns or data have been used to reach different conclusions[11,31]. The evolutionary histories of transposable elements most certainly include vertical transmission. It is the number, frequency and timing of episodes of horizontal transmission that might be superimposed on the vertical transmission patterns that require determination. The implications of horizontal transmission of transposable elements for concepts of genomic integrity within species lineages depends on one's view. The status quo is maintained if one subscribes to the view that horizontal transmission, or the successful realizations of this process, are very rare events. Conversely, the large and indeterminate number of successful realizations of horizontal transmission tacitly indicated, together with the huge number of undetected events implied in some studies, lead to a view of substantial interspecific exchange – a relative revolution with respect to genomic integrity within species. Horizontal transmission of transposable elements may one day find a place alongside other processes, such as hybridization, and become a well-established and recognized means of mixing genetic material among eukaryotic species, or, as has been suggested for some transposable elements, among eukaryotic kingdoms[12,25].

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# Terrestrial plant tolerance to herbivory

**J.P. Rosenthal and P.M. Kotanen**

**Damage to plants by herbivores is ubiquitous and sometimes severe. Tolerance is the capacity of a plant to maintain its fitness through growth and reproduction after sustaining herbivore damage. Recent physiological and ecological work indicates that tolerance mechanisms are numerous and varied. Some of the plant traits involved may reflect selection by herbivores, while others are likely to be by-products of selection for other ecological functions. Similarly, some tolerance mechanisms may participate in trade-offs with plant defence, while many do not. Regardless of its ultimate origin or physiological relationship to plant defence, tolerance often may influence the evolution of plant defence and the composition of plant communities.**

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Resistance of terrestrial plants to attack by herbivores may take two basic forms. Plants may avoid damage via defence or escape in time and space, or they may tolerate herbivore damage (see Fig. 1). While the term 'compensation' is sometimes used synonymously with tolerance to herbivory, we consider tolerance to be a broader trait, in that it may include traits other than the regrowth response that compensation frequently[1,2] implies.

Given the ubiquity of insect and mammalian herbivores and the improbability of complete escape from their feeding, tolerance to herbivory probably plays at least as great a role in the ecology and evolution of plant–herbivore interactions as does defence. However, until recently, there have been few explicit and synthetic analyses of mechanisms of tolerance to herbivory and their ecological and evolutionary significance. Like defence, tolerance may provide plants with a successful strategy for coping with herbivory, but tolerance and defence have different implications for the ecology and evolution of plant–animal interactions, and are not necessarily simple alternatives. Here, we briefly examine the major factors which affect plant tolerance to both insect and vertebrate herbivory, and summarize some developing ideas about the adaptive significance of tolerance, its evolutionary relationship to plant defence, and its importance in community structure.

## Mechanisms and the expression of tolerance

Tolerance to herbivory is a complex trait involving the interaction of both intrinsic and extrinsic factors[1]. Intrinsic factors are those determined genetically or developmentally by the plant itself. Extrinsic factors include a broad range of variables such as the availability of resources in the environment to support regrowth, the type of herbivory experienced and its spatial distribution within a plant. Here we focus primarily on intrinsic factors. They include physiological components such as growth rate, storage capacity and the flexibility of photosynthetic rates, allocation patterns and nutrient uptake. Equally important are some morphological components, such as vulnerability and number of plant meristems, and developmental plasticity (Table 1). Other intrinsic factors, such as phenological stage and growth status, also commonly affect tolerance to herbivory and may interact with the above-mentioned plant features.

Among the physiological components of tolerance, intrinsic growth rates have long been considered fundamental[3]. Coley *et al.*[4] have indicated that slower growth rates make it more difficult for a plant to replace damaged tissue. They hypothesized that, as a consequence, the high defence levels found in plants adapted to low-resource environments are, in part, an evolutionary result of their slow growth rates and the importance of protecting themselves in the face of herbivore attack.

Storage reserves of fixed carbohydrates and nutrients have frequently been discussed as important resources for regrowth after damage[1,5–8]. However, accumulating evidence from physiological studies indicates that carbohydrate reserves are often either insufficient or fail to be mobilized after the plant's initial response to damage[9–11]. While mobilization of carbon reserves to active meristems is often important in the first few days, its contribution to


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