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**Horizontal transfers of transposable elements in eukaryotes:
The flying genes**

*Transferts horizontaux d'éléments transposables chez les eucaryotes :
les gènes volants*

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ABSTRACT

Transposable elements (TEs) are the major components of eukaryotic genomes. Their propensity to densely populate and in some cases invade the genomes of plants and animals is in contradiction with the fact that transposition is strictly controlled by several molecular pathways acting at either transcriptional or post-transcriptional levels. Horizontal transfers, defined as the transmission of genetic material between sexually isolated species, have long been considered as rare phenomena. Here, we show that the horizontal transfers of transposable elements (HTTs) are very frequent in ecosystems. The exact mechanisms of such transfers are not well understood, but species involved in close biotic interactions, like parasitism, show a propensity to exchange genetic material horizontally. We propose that HTTs allow TEs to escape the silencing machinery of their host genome and may therefore be an important mechanism for their survival and their dissemination in eukaryotes.

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R É S U M É

Les éléments transposables (ET) sont des composants ubiquitaires des génomes eucaryotes. Leur capacité à se multiplier dans les génomes de la plupart des plantes et des animaux est en contradiction avec le fait que la transposition est très strictement et efficacement contrôlée par plusieurs voies de mise au silence agissant aux niveaux transcriptionnel et post-transcriptionnel. Les transferts horizontaux (TH), définis comme la transmission de matériel génétique au-delà des barrières de reproduction des espèces ont longtemps été considérés comme anecdotiques. Plusieurs études montrent qu'au contraire, les transferts horizontaux d'ET sont très fréquents. Même si les mécanismes de tels transferts demeurent mal connus, il semble que ceux-ci soient fréquents entre espèces ayant des relations biotiques, comme par exemple dans les systèmes hôtes/parasites. Nous proposons que les transferts horizontaux permettent aux ET d'échapper au contrôle de

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leur génome hôte et pourraient ainsi représenter un mécanisme essentiel à leur survie et à leur dissémination au sein des eucaryotes.

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1. Introduction

Transposable elements (TEs) are ubiquitous components of eukaryotic genomes. The first TEs were discovered by B. McClintock decades ago [1], as “controlling elements” involved in the variegation of kernel colour in maize. At the time McClintock was awarded her Nobel Prize in 1983, TEs had been discovered in all eukaryotic organisms where they were looked for and this has since been confirmed by the discovery that TEs are by far the major constituents of plant and animal genomes [2]. TEs are classified into two categories [3]. Class-I elements, also referred to as retrotransposons, transpose *via* RNAs intermediates, through a copy and paste mechanism. Class-II elements, the transposons, transpose through excision and reinsertions (a cut-and-paste mechanism). Class-I elements can undergo large transpositional bursts, which lead in some cases to *catastrophic* genomic amplifications. This is well exemplified in human with the LINE L1 which is present at more than 100,000 copies [4], or in rice, for which we showed that the retrotranspositional activity of only three LTR-retrotransposon families led to a doubling of genome size of the wild rice species *Oryza australiensis* in the last 2 Myr [5]. This propensity of TEs to densely populate eukaryotic chromosomes rather helped solve one of the most striking paradox in biology, *i.e.* the « C-value paradox » [6], by showing that the large extent of genome size variation in eukaryotes can be accounted for mainly by TEs, while the gene content among plants and animals remains remarkably constant (except for some variations caused by polyploidization or segmental duplications). However, while solving the paradox, this discovery led to a paradigm, built on the “*selfish gene*” theory, which classified TEs in a *non-genic* and thus *non-functional* compartment of the genome [7]. Nevertheless, the mutagenic nature of TEs has always been a “*stone in the shoe*” of some evolutionary genomicists who could not reconcile this putative negative effect on fitness (caused by the inactivation of genes) with such evolutionary success. Recent studies have suggested that transposition may on the contrary be beneficial to organisms and at the origin of major biological innovations in the course of evolution. For instance, the transpositional burst of the transposon *mer20* was shown to be at the origin of the placenta through the reprogramming of developmental genes [8] in mammals. More recently, Chuong et al. [9] showed that a similar process involving an endogenous retrovirus (ERV) was at the origin of innate immunity also in mammals. Interestingly, several cases of TE-mediated phenotypic changes have also been reported in plants, some of which being of agronomic interest, like the grape colour [10] the blood orange phenotype [11], or the Mantel abnormality in date palm [12].

2. The new paradox

Despite the fact that TEs are present in most genomes and exhibit polymorphisms in both natural populations and domesticated gene pools, which is an indirect evidence of their transpositional activity, the analysis of TE-driven genomic transgenerational changes in various organisms have shown that, in a vast majority, TEs are not transpositionally active. Over the past ten years, significant advances have been made in our understanding of how transposition is suppressed through epigenetic mechanisms. Transposition in plants and animals is notably limited through TE silencing ensured by epigenetic mechanisms [13,14]. These mechanisms include the deposition of epigenetic marks, such as DNA methylation and heterochromatic histone post-translational modifications. In addition, in-depth analysis of angiosperms genomes shows that they often harbour traces of more ancient transposition bursts, but these are in the form of short, deleted and degenerated copies of TE families [15], suggesting that TE-related sequences are eliminated over time. There are two main mechanisms of LTR-retrotransposon elimination: small deletions [16] and illegitimate recombinations between LTRs, leading to solo-LTR sequences and the elimination of circular molecules harbouring one LTR and the internal region of the element [17]. The combined actions of silencing and elimination should lead to complete elimination of TEs from most species, which is exactly the opposite of what is observed. This new paradox could only be solved with the discovery of the mechanisms allowing TEs to circumvent the silencing machinery of their host. We recently proposed a model positing that this may actually be achieved through horizontal transfers [18].

3. Horizontal transfers of transposable elements

HTs refer to the transmission of genetic material across reproductive barriers. They have been evidenced for TEs for many years [19]. However, until recently, horizontal transfers of TEs (HTTs) were essentially described in animals [20,21], with only very few cases in plants [22]. HTTs are usually detected using three criteria: phylogenetic incongruence between the host and TE phylogenies, patchy TE distributions in phylogenies, and/or a high similarity between TEs from distantly related species. In a pioneering large-scale comparative genomic survey [18], we showed that HTTs are in fact very frequent in flowering plants, with an estimation of more than two millions among monocots and dicots within the last two million years. We also showed that TEs were transpositionally active following their transfer, leading in some species to significant genomic amplification. We therefore proposed that HTTs should be a key mechanism of the evolution of eukaryotic genomes by

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