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Fungal transposable elements and genome evolution

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Abstract

The transposable elements (TEs) identified in fungal genomes reflect the whole spectrum of eukaryotic transposable elements. Most of our knowledge comes from species representing different ecological situations: plant pathogens, industrial, and field strains, most of them lacking the sexual stage. A number of changes in gene structure and function has been shown to be TE-mediated: inactivation of gene expression upon insertion within or adjacent to a gene, DNA sequence variation through excision and probably extensive chromosomal rearrangements due to recombination between members of a particular family. Moreover, TEs may have other roles in evolution related to their ability to be horizontally transferred and to capture and transpose chromosomal host sequences, thus providing a mechanism for dispersing sequences to new sites. However, the activity of transposable elements and consequently their proliferation within a host genome can be affected, in some fungal species which undergo meiosis, by silencing processes. Our understanding of the biological effects of TEs on the fungal genome has increased dramatically in the past few years but elucidation of the extent to which transposons contribute to genetic variation in nature, providing the flexibility for populations to adapt successfully to environmental changes is an important area for future research.

Introduction

Transposable elements are ubiquitous in prokaryotic and eukaryotic organisms, both plants and animals. In fungi they were first identified in the yeast *Saccharomyces cerevisiae* (reviewed in Boeke, 1989) but only very recently in filamentous fungi (see reviews by Oliver, 1992 and Dobinson & Hamer, 1993). Despite extensive investigation of molecular genetics of some species used as models for fungal genetics, exemplified by the well-studied ascomycetes *Neurospora crassa* and *Aspergillus nidulans*, no evidence for the activity of transposable elements has been revealed that might be the consequence of continuous selection for phenotypic stability. Paradoxically, most of our knowledge of TEs in fungi comes from studies on undomesticated species: plant pathogens, industrial, and field strains. Most of these species lack the sexual stage and generally exhibit a high level of genetic variation, which attracts speculation that they contain active transposons. In the last decade there has been considerable interest focused on these diverse and poorly genetically characterized species. Intensive studies of the molecular genetics of these species by using molecular tools developed in the model systems has allowed the identification of many distinct families of TEs over the last few years. The discovery that TEs are common components of the fungal genome, forming a large portion of the genome in some species, has made them objects of interest for effects they may exert on their host genomes. Fungal transposable elements have been found to cause spontaneous genetic changes that have the potential to influence many aspects of fungal genome evolution. However, little is known about the impact of transposon-induced genetic changes in natural populations and much remains to be done to have a clear view of the role that they can play in the evolution of the fungal genome.

The purpose of this review is to provide an overview of the structural and biological features of fungal TEs with particular emphasis on what is known about their activity and consequently their effects on the host

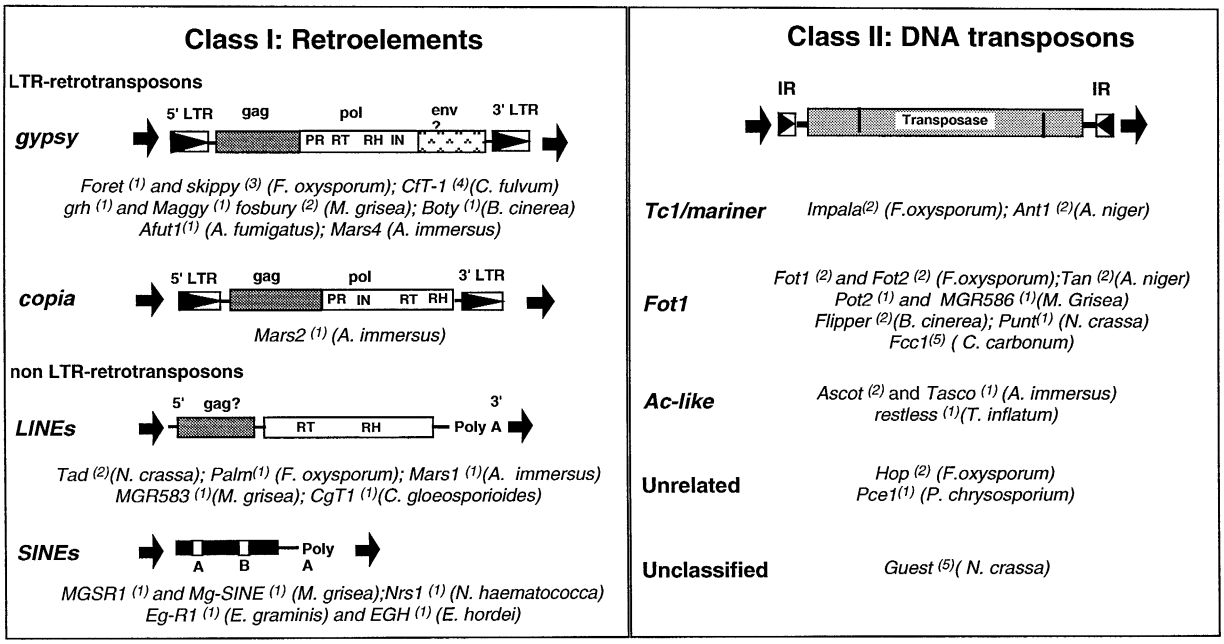

Figure 1. Transposable elements isolated from filamentous fungi. Class I elements are of two types, the LTR (long terminal direct repeats) retrotransposons that can be divided into two groups, the *gypsy*-type and *copia*-type, on the basis of the order of the *pol* products (PR, protease; RT, reverse transcriptase; RH, RNaseH; IN, integrase) and elements similar to the long and short interspersed nuclear elements described in mammals and referred to as LINEs and SINEs, respectively. Class II elements have short inverted repeats (IR) and contain a gene encoding transposase. For more details on the overall organization of these types of transposable elements see Finnegan (1989), Grandbastien (1992), Flavell et al. (1994). Numbers within brackets indicate the strategy used to identify the transposable element(1) isolated by cloning repetitive DNA, (2) isolated after transposition within the *nia* gene with the exception of *Tad* transposed into the *am* gene and *Ascot* preexisting as an insertion into the *b*2 gene, (3) isolated using a *CfT-1* heterologous probe, (4) isolated by differential screening with antibodies against RT, (5) identified through gene sequencing.

The characteristics of the transposable elements presented here can be found in the following references. For *Fusarium oxysporum* elements: *Foret* (Julien et al., 1992), *skippy* (Anaya & Roncero, 1995), *Palm* (Mouyna et al., 1996), *Fot1* (Daboussi et al., 1992), *impala* (Langin et al., 1995), *Fot2* and *Hop* (Daboussi & Langin, 1994); for *Magnaporthe grisea* elements: *grh* (Dobinson et al., 1993), *Maggy* (Farman et al., 1996a) also named *fosbury* (Shull & Hamer, 1996), *MGR 583* (Hamer et al., 1989), *MGSR1* (Sone et al., 1993), *Mg-SINE* (Kachroo et al., 1995), *Pot2* (Kachroo et al., 1994), *MGR586* (Farman et al., 1996b); for *A. immersus: Mars1, Mars2, Mars4, Tasco* (Goyon et al., 1996), *Ascot* (Colot et al., 1995); for *N. crassa: Tad* (Kinsey & Helber, 1989), *Punt* (Margolin et al., 1994) and *Guest* (Yeadon & Catcheside, 1995); in *A. niger: Ant1* (Glayzer et al., 1995) and *Tan/Vader* (Amutan et al., 1996; Nyyssönen et al., 1996); in *Botrytis cinerea: Boty* (Diolez et al., 1995) and *Flipper* (Levis et al., 1997); in *Cladosporium fulvum, CfT*-1 (Mc Hale et al., 1989, 1992); in *Aspergillus fumigatus, Afut1* (Neuvéglise et al., 1996); in *Colletotrichum gloeosporioides*, CgT1 (He et al., 1996); in *N. haematoccoca, Nrs1* (Kim et al., 1995); in *Erysiphe, Eg-R1* (Rasmussen et al., 1995) and *EGH* (Wei et al., 1996); in *Tolypocladium inflatum, restless* (Kempken & Kück, 1996); in *Phanaerochete chrysosporium, Pce1* (Gaskell et al., 1995); in *Cochliobolus carbonum, Fcc1* (Panaccione et al., 1996).

genome, their spread within and between species as well as their significance in the evolution of the fungal genome.

General features of fungal transposable elements

Fungal transposable elements have been identified using a variety of strategies (Figure 1). First, by cloning dispersed repetitive sequences, different transposon-like sequences have been recognized by comparison with the known transposons from other organisms, although it is not known if these transposon-like sequences are still active. Second, and the most satisfactory way to screen for active transposons is the transposon trapping approach, which is based on spontaneous inactivation of cloned genes. This strategy is usually applied to genes whose mutant phenotypes can be positively screened for. This is the case of mutations in the nitrate reductase gene, which can be selected through resistance to chlorate (Cove, 1976). This strategy, developed in *F. oxysporum* (Daboussi & Langin, 1994) and applied to other fungal species, *Aspergillus niger* (Glayzer et al., 1995; Amutan et al., 1996),

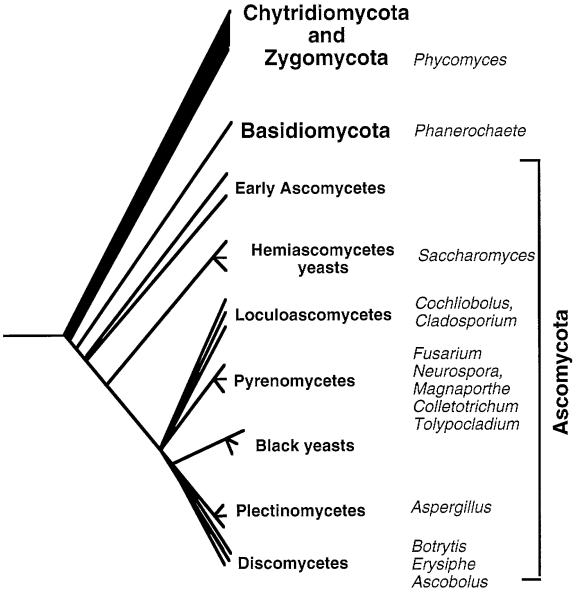

Figure 2. Phylogenetic position of fungal species in which transposable elements have been found. Diagram of phylogenetic lineages based on 18S rRNA from Taylor (1995) was slightly modified.

Botrytis cinerea (Levis et al., 1997), and *Magnaporthe grisea* (Lebrun, unpublished data) has been very successful, leading to the identification of at least eight different mobile elements. Finally, some other elements have been found using heterologous hybridization or have been discovered fortuitously through DNA sequencing.

The TEs or sets of related sequences present in the fungal genome reflect the whole spectrum of eukaryotic transposable elements (Figure 1). They are LTR retrotransposons mostly belonging to the *gypsy* group, non-LTR retrotransposons with structural features of LINEs and SINEs elements, and DNA transposons of different types. Some of them are representatives of families already described in other organisms, i.e., the *hAT* family (Calvi et al., 1991) and the *Tc1-mariner* superfamily (Radice et al., 1994; Robertson, 1995); other elements, exemplified by *Fot1*, are members of families widely dispersed in fungi and recently related to other transposons including *tigger* elements from human and *pogo* from *Drosophila* (Smit & Riggs, 1996). In addition to the elements described above, a number of less-characterized transposable elements are known which may represent new families, among them a member of the *Tourist* family (Bureau & Wessler, 1994).

An overview of the results described reveals four features: (i) TEs appear to be ancient components of the fungal genomes because, as seen in Figure 2, they are present in the major groups of Ascomycetes (species listed in Figure 1), in Zygomycetes (Avalos et al., 1996; Ruiz-Perez et al., 1996) and in Basidiomycetes (Gaskell et al., 1995), (ii) the whole spectrum of eukaryotic transposons is represented in fungi, (iii) some species of filamentous fungi, exemplified by the two plant pathogenic species *M. grisea* and *F. oxysporum* are very rich niches for these elements, and (iv) TEs have been detected mostly in undomesticated strains, most of them undergoing meiosis infrequently or apparently never.

Mechanism of transposition

Despite the wide distribution of TEs in fungal genomes, relatively little is known about the mechanism and regulation of transposition. This is probably due to the fact that many TEs appear to be remnants of transposons and because mechanisms exist in some fungal species that inactivate repeated sequences. Consequently, demonstration of transposition has been obtained only in few cases.

Transpostion of retroelements

For retroelements believed to transpose through an RNA intermediate, direct evidence of transposition has been provided for the *Tad* LINE-like element of *N. crassa* (Kinsey, 1993) and the *fosbury* retrotransposon of *M. grisea* (Shull & Hamer, 1996), which were isolated through their insertion within or adjacent to cloned genes (Figure 1). For others, indirect evidence is provided by the structural integrity of cloned elements, the presence of virus-like particles and reverse-transcriptase activity, their increase in the copy number, and the absence of polymorphism between 5′ and 3′ LTRs (McHale et al., 1989; Anaya & Roncero, 1995; Dobinson et al., 1993; Farman et al., 1996a). Demonstration of transposition by reverse transcription has been provided only in the case of *Tad* by showing that an artificial intron introduced within the coding sequence of an active *Tad* element can be removed precisely during transposition (Kinsey, 1993). These experiments have also clearly shown that *Tad* transposes through a cytoplasmic intermediate between nuclei of forced heterokaryons and is able to invade very rapidly a genome free of elements.

Transposition of DNA transposons

For DNA transposons assumed to transpose directly from DNA copies, active transposition has been deduced for most of them through their mobility (see Figure 1) or through transcriptional expression and alternative RNA splicing (Kempken & Kück, 1996). These elements can also excise and the variation in copy number and genomic positions associated to transposition events can easily be followed when elements are present in the genome in a low copy number, exemplified by *impala* in *F. oxysporum* (Daboussi & Langin, 1994). Somatic excisions of an *impala* copy inserted into the *niaD* gene, thereby inactivating this gene, were observed to be associated in the majority of the cases with its reintegration into a new genomic position. Also, this element can increase in copy number, one additional copy being observed in the mutant compared to the wild type. Maize *Ac/Ds* elements do so by transposing during chromosomal DNA synthesis and moving from replicated to unreplicated DNA (Fedoroff, 1989; Dash & Peterson, 1994). Such a conservative mechanism of transposition can explain the loss or the gain or the movement of an *impala* copy observed after transposition, depending on chromosome replication and location of the recipient site.

Effects of transposable elements on gene and genome

The ability of TEs to induce mutations depends on their intrinsic capability of transposing within their host genome. Some of them have been shown to alter genes and genomes in several ways by promoting changes in gene expression, in gene sequence, and probably in chromosomal organization.

Modification of gene expression

In most cases, insertion of a TE within or adjacent to a gene creates a null phenotype because the element blocks transcription of nearby genes or alters the pattern of transcription. In *N. crassa*, one transposition event placing the *Tad* element in a position just upstream of the *am* promoter creates an unstable allele. Reversion depends on DNA methylation within and upstream of *Tad* indicating that *am* expression is controlled epigenetically by the methylation state of the *Tad* element (Cambareri et al., 1996). Alteration of transcription of the target gene has been demonstrated in *F. oxysporum* with mutants resulting from the insertion of *Fot1* elements in an intron of the *niaD* gene (Daboussi & Langin, 1994; Deschamps et al., submitted). In the different mutant transcripts, all were observed to be shorter than the wild-type transcript. These truncated transcripts all are chimaeric, indicating that *Fot1* elements contain termination signals and a sequence that can be used as an alternative promoter. We can imagine that some insertions of *Fot1* can probably impose new patterns of gene expression that may have profound effects on the evolution of the host genome.

Alteration of gene sequence

When DNA transposable elements excise, they generally leave a footprint of few nucleotides at the donor site. The length and sequence of the footprint depends on the element but also on the constraints of the selection for revertants. In the case of the *Fot1* elements inserted into an intron of the *niaD* gene, the footprint consists often of the same 3 or 4 bp, most likely the TA duplication *plus* one or two nucleotides from one or the other end of *Fot1* (Daboussi et al., 1992). When *Fot1* exises from an exon, either no alteration or three nucleotides encoding an extra amino acid in the protein was observed (Daboussi & Langin, unpublished results). Although the precise transposition mechanism of this element is not known, given the similarities of the *Fot1* and *Tc1* systems, it is assumed that the footprints are the results of interrupted gap repair (Plasterk, 1991; Plasterk & Groenen, 1992).

Chromosomal structural changes

Transposable elements have been found at the origin of numerous types of chromosome rearrangements (Boeke, 1989; Montgomery et al., 1991; Sheen et al., 1993; Lim & Simmons, 1994), which may explain the extensive karyotype variation observed in several plant and human pathogens (reviewed by Skinner et al., 1991; Kistler & Miao, 1992). Differences are both in chromosome size and number, involving translocations and large deletions. An example of such karyotypic variation is provided by *F. oxysporum* strains originating from the same clone (Davière et al., 1996) and illustrated in Figure 3. The precise mechanism for the observed variation is currently not understood. However, considering the numerous families of transposable elements in some strains, exemplified by *F. oxysporum* and *M. grisea* (Figure 1), each family represented by many highly conserved copies (Daboussi

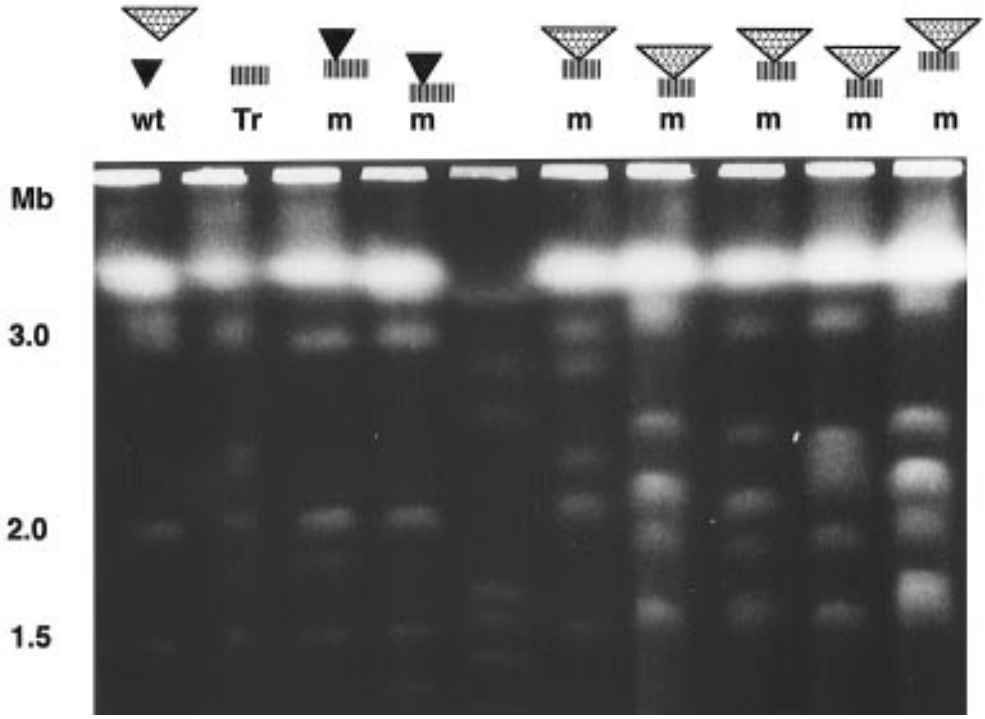

Figure 3. Chromosome size polymorphism in CHEF electrophoretic karyotypes of strains of *Fusarium oxysporum*. All the strains originated from the same wild–type strain (wt) containing different families of TEs, among them *impala* (black triangles) and *Fot1* (dotted triangles); from one transformant (Tr) carrying the *niaD* gene (hatched boxes), different mutants resulting from the transposition of *impala* or *Fot1* have been selected. The electrophoretic conditions used allowed only the separation of small chromosomes ranging in size from 1.5 to 3 Mbs.

& Langin, 1994), we favour the idea that inter- and intrachromosomal ectopic exchanges between these elements and the subsequent chromosomal rearrangements could account for the exceptional karyotypic variation observed. Data on the distribution of TEs on the chromosomes of *F. oxysporum* as well as the reconstitution of the physical map of a polymorphic chromosome by contigs may provide information on which repeated elements are involved and how frequently.

Evidence for horizontal transfer

Transposable elements can act as insertional mutagens and can cause chromosomal rearrangements, but they may also have other roles in evolution with respect to their ability to invade new populations, thus providing a mechanism for dispersing sequences to new sites. Analyses of the distribution of fungal transposons and in some cases extensive sequence analyses have revealed situations indicative of horizontal transmission of fungal transposons.

First, the sporadic distribution of an element among species, exemplified by the *grh* element found exclusively in a subgroup of *M. grisea* infecting *Eleusine* (Dobinson et al., 1993), may reflect the recent acquisition of this element. Second, the high similarity between elements in distant species is illustrated by *Fot1* in *Fusarium*. The distribution of *Fot1* in species of the *Fusarium* genus whose relationships have clearly been established by Guadet et al. (1989) appears to be discontinuous. It is widely distributed in the *F. oxysporum* species, and absent in the most closely related species, *F. moniliforme*, but it can be detected in some strains of the distant species *F. solani*. The sequence divergence of *Fot1* between these distant species is low (around 2%) compared to that observed for non-transposable sequences among the same species, 11% and 25% for the rRNA and *nia* genes, respectively (Daboussi & Langin, to be published). The discontinuous distribution of *Fot1* within the *Fusarium* genus associated with the extremely low level of divergence of the *Fot1* element between the two distant species suggest that this element could have been transferred

horizontally through a rare interspecific cross or by a parasitic vector of unknown origin.

Another situation worth mentioning is the one presented by the *Ant1* element of *A. niger*, which was found to be mobile and to carry genomic sequences (Glayzer et al., 1995). It showed how genes or part of genes might be amplified and dispersed in genomes. If horizontal transmission of such a transposon occurs, the potential exists for host genes to be transmitted between species.

Silencing processes as control of transposon activity

Genetic changes due to transposition of elements can have wide ranging effects on the biology of the organism, but in some species, their activity can be limited by silencing processes. The processes called RIP (repeated-induced point mutation) in *N. crassa* (Selker & Stevens, 1985; Selker et al., 1993) and MIP (methylation induced premeiotically) in *A. immersus* (Goyon & Faugeron, 1989; Rhounim et al., 1992) inactivate duplicated sequences, linked or unlinked, native or foreign, at a specific period of the sexual cycle between fertilization and karyogamy. This inactivation is associated with heavy cytosine methylation of the duplicated sequences. Although RIP and MIP share many features, they differ dramatically in their outcomes. RIP results in numerous base changes from C-G to T-A and is thus irreversible. MIP inactivates genes reversibly by C-methylation only. RIP and MIP have been envisioned as processes ensuring genome stability. First, because they might control the mobility of transposons by inactivating them and hence limiting the number of repeats and second, because RIP causes rapid divergence of repeated sequences which may prevent gross chromosomal rearrangements (Kricker et al., 1992; Rossignol & Faugeron, 1995). Consistent with this interpretation, no active *Tad* transposon has been detected in the laboratory strain of *N. crassa* but only relics (Kinsey et al., 1994), and in *A. immersus* the only mobile element identified, *Ascot*, has escaped the MIP probably because of its very short size (Colot et al., 1995). Thus, RIP and MIP may be defence mechanisms aimed at transposable elements but they may not be common to all fungi because many types of active transposons have been identified. However, one should keep in mind that most of the species in which they have been found lack the sexual stage, or it is rarely operant in nature. Consequently repeated sequences can be safe from RIP and MIP, if they exist, so long as they do not go through a cross.

Concluding remarks

The discovery that the genomes of all carefully investigated fungal species contain TEs or sets of related sequences has changed our perception of the fungal genome structure. Most of our knowledge comes from species found in nature, demonstrating that the diversity of research organisms still offers opportunities for fundamental discoveries. A number of changes in gene structure and function has been shown to be TE-mediated. These changes have the potential to influence many aspects of fungal genome evolution and might provide the flexibility for populations to adapt successfully to environmental conditions. However, elucidation of the extent to which transposons contribute to genetic variation in nature is an important area for future research. TEs have been shown to be factors of genomic instability, playing an important role in the dynamics of the eukaryotic genome. Some fungal species that undergo meiosis have developed silencing mechanisms possibly used to maintain genome stability after the amplification of repeated sequences. It will be interesting to discover how widely they are conserved. On the other hand, fungi found in nature have a considerable degree of plasticity compared to laboratory strains used as models for fungal genetics, likely because meiosis, which is a process that selects against many aberrations that lead to detectable polymorphism, occurs infrequently or apparently never.

The past few years have seen significant advances in our perception of the novel mechanisms for genetic change in fungi due to the discovery that TEs are important components of fungal genomes and the future holds promise for important new insights.

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