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Review

The role of homeodomain transcription factors in fungal development

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ABSTRACT

The role of homeodomain (HD) transcription factors during development in animals is well established since the identification of the homeobox gene clusters. In the kingdom Fungi homeodomain genes also play a crucial role during multicellular development. They were first identified in mating type loci, which regulate sexual development. Later, other HD genes were shown to be involved in fruiting body development in several members of Ascomycota and Basidiomycota. In this review we describe recent research on HD transcription factors in fungi. An evolutionary framework is provided by reanalyzing 222 previously published fungal genomes to identify potential functions of HD transcription factors in multicellular development and fructification.

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1. Introduction

Fruiting bodies are among the most complex multicellular structures formed by Fungi and have evolved to produce and disperse spores. Although mushrooms of the order Agaricales are generally best known due to their complex macroscopic structure, fruiting bodies are formed by members of many clades of higher fungi (Ascomycota and Basidiomycota). The genetic regulation of fruiting body formation is not well-characterized, despite its potential economic impact. However, several groups of transcription factors have been identified as regulators of fructification. In the basidiomycete *Coprinopsis cinerea* the light sensing *dst1*, as well as the high mobility group transcription factor *pcc1* have been shown to be involved in fructification (Kamada *et al.*, 2010; Murata *et al.*, 1998). In *Schizophyllum commune* transcription factors containing a zinc

finger of the fungal-specific Zn(II)2Cys6 domain (*fst3*, *fst4*), the C2H2 domain (*c2h2*) or the GATA domain (*gat1*, *wc-2*) and transcription factors containing a BRIGHT domain (*bri1*) or a homeodomain (HD) (*hom1*, *hom2*) regulate various aspects of fruiting body formation (Ohm *et al.*, 2013, 2011; Pelkmans *et al.*, 2017). No functional characterization has been done in other Agaricales, although many of the previously mentioned genes are conserved across the Agaricales (Pelkmans *et al.*, 2017).

In the ascomycete *Neurospora crassa* many TF knock-out strains show aberrant perithecium formation: seven Myb-like, seven C2H2, six Zn(II)2Cys6, four GATA, three Zn(II)2Cys6/Fst, two BRIGHT, two bZIP, two homeodomain, two HLH, two HMG, one BRIGHT/Myb-like, one C2H2/Zn(II)2Cys6, one Cbf-NY-Y, one Forkhead, one HTH, Kila-N and one NDT80/PhoG-like transcription factor were shown to have

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some defect in fructification, ranging from reduced perithecium count to no perithecium formation at all (Aramayo et al., 1996; Carrillo et al., 2017; Colot et al., 2006; Degli-Innocenti and Russo, 1984; Feng et al., 2000; Li et al., 2005).

In the ascomycete *Podospira anserina* five HMG and two homeodomain transcription factors are known to be required for wild type development of the fruiting body (Ait Benkhali et al., 2013; Coppin et al., 2012). In *Aspergillus nidulans* two C2H2, two Zn(II)2Cys6, one Dopey_N leucine zipper, one GATA and one KilA-N transcription factor are identified to be involved in successful conidiophore development (Han et al., 2001; Pascon and Miller, 2000; Prade and Timberlake, 1993; Vallim et al., 2000; Vienken et al., 2005; Vienken and Fischer, 2006; Wu and Miller, 1997).

A homeodomain is a conserved DNA-binding domain of 60 amino acids that features a helix-turn-helix structure. HDs are found in transcription factors in almost all eukaryotic species, except some unicellular species (Derelle et al., 2007). HDs are classified as either TALE (three amino acid length extension) or non-TALE domains, based on the presence of an insertion in the sequence between the two helices. This split occurred before the origin of plants, animals and fungi, as both types are present in each of these kingdoms (Bharathan et al., 1997).

The HD was first identified in homeobox (*hox*) transcription factors in *Drosophila melanogaster* (Lewis, 1978). These *hox* genes are found in several clusters in the genome and control the body plan of an embryo along the anterior–posterior axis (Mallo et al., 2010). For example, a change in the gene order modifies the body plan and leads to the famous antennapedia phenotype, where legs grow in place of the antenna. This is caused by a dominant inversion in the bithorax complex Hox cluster and subsequent *antP* expression in the head (Frischer et al., 1986; Maeda and Karch, 2009). Phenotypical changes such as this led to the name homeodomain, after the process of homeosis, where an organ is replaced by another organ. Similar functions are found in all Bilateria, where spatial expression along the anterior–posterior axis determines segment identity by activating specific expression patterns per segment, leading to the development of these segments. As such the localized activation of *hox* genes through developmental pathways ultimately regulates the segment identity in Bilateria (Mallo et al., 2010). In plants HD transcription factors play a similarly important role in development (Hay and Tsiantis, 2010). For example, overexpression of the HD transcription factor *kn1* in *Arabidopsis thaliana* leads to lobed leaves, compared to the simple structure in WT plants (Lincoln et al., 1994).

Given their role in developmental processes in a wide range of organisms, it has been suggested that HD transcription factors are part of the genetic toolkit that allowed organisms to develop multicellularity and cell differentiation (King, 2004). In both animals and plants the HD genes expanded to over 100 genes per species (Derelle et al., 2007). In Fungi the diversification happened on a much smaller scale: HD counts range from 1 to 51 (Todd et al., 2014) (this study). Notably, in the kingdom Fungi HDs are also associated with regulating (multicellular) development, since they are involved in mating as well as fruiting body development.

This review will focus on the role of homeodomain transcription factors in multicellular development and

fructification in the kingdom Fungi. Recent literature is combined with a re-analysis of 222 previously published fungal genomes to provide a framework for studying the function of HD transcription factors.

2. Homeodomain transcription factors in Fungi

Evolutionary framework for homeodomain transcription factors

In recent years hundreds of fungal genomes have been sequenced and published, including Ascomycota, Basidiomycota and ‘early diverging fungi’ (i.e. non-Dikarya) (Cerqueira et al., 2014; Cherry et al., 2012; Grigoriev et al., 2014; Hibbett et al., 2016; Nagy et al., 2016; Riley et al., 2016; Skrzypek et al., 2017), resulting in a large number of predicted HD transcription factor genes. These previously published data were re-analyzed and the evolutionary history of fungal HD genes was reconstructed, providing an evolutionary framework for this review (Supplementary Text 1). In the case of Ascomycota and Basidiomycota the number of HD genes generally correlates with the total number of predicted genes (Fig. 1). The early diverging fungi are a clear exception to this, however, and generally have much higher counts of HD genes. This increase can be attributed primarily to the Mucoromycotina (Supplementary Table 1). Furthermore, fungi with a predominantly unicellular (yeast) lifestyle generally have fewer HD genes than fungi with a predominantly multicellular (filamentous) lifestyle (Fig. 2). This suggests that in Ascomycota and Basidiomycota the HD genes tend to be involved with multicellular development (Derelle et al., 2007), although this effect is less pronounced than in the Metazoa (de Mendoza et al., 2013). Interestingly, it was previously reported that the increase in transcription factor count resulting from genome expansion in fungi can be mostly explained by three TF families, including the HD TFs, which show a higher relative increase compared to the TFome as a whole (Shelest, 2017; van Nimwegen, 2003).

A phylogenetic analysis of all predicted HD genes allowed the identification of 12 groups of HD genes (Fig. 3, Supplementary Text 1 and Supplementary Table 1), which were mapped onto the species tree of the 222 fungi (Fig. 4, Table 1). This revealed the evolutionary history of each of these 12 groups of HD genes, which will be discussed below.

Mating type HD transcription factors

The best-studied HD transcription factors in Fungi are those belonging to the mating type locus. In many Fungi this locus is essential for the recognition of (and successful fusion with) a non-self mating partner. This is generally seen as the first step in the initiation of sexual reproduction and (depending on the organism) the associated multicellular differentiation and development (Raudaskoski and Kothe, 2010).

In the ascomycete yeast *Saccharomyces cerevisiae* the *mat* locus is either *mat-a* or *mat- α* and transcription of the locus leads to *mat-a* or *mat- α* specific cellular development (Haber, 2012). In *mat- α* cells, the HD gene *MAT α 2* is expressed.

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