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Review

Which MAT gene? Pezizomycotina (Ascomycota) mating-type gene nomenclature reconsidered

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ABSTRACT

Filamentous fungi in the subdivision Pezizomycotina (Ascomycota) display an impressive diversity of mating strategies. These mating systems are all controlled by the mating-type (*MAT*) genes, some of which are conserved, even among distantly related genera. In order to facilitate effective communication between researchers, a system was established in 2000 to name these genes and this has subsequently been widely applied. However, due to the rapid growth in the number of described *MAT* genes in the Pezizomycotina, an evaluation of the manner in which the nomenclature system has been applied is warranted and revisions should be considered. We address this challenge by doing a systematic review of the nomenclature associated with the *MAT1* locus and its associated genes described in the Pezizomycotina. Several problems in the application of the nomenclature system were identified and addressed. These included proposed revisions of the nomenclature system to provide a more accurate description of the mating-type genes. We anticipate that this review will reduce confusion and that it will be useful in future characterisation of mating-type genes.

1. Introduction

In the early part of the 20th century, Albert Blakeslee initiated a study on members of the Mucorinae and inadvertently produced the first paper concerning sexual reproduction in the fungi (Blakeslee, 1904). Although he focused on the morphology and physiology of the group, his discoveries on the behaviour of isolates during sexual reproduction have provided the cornerstone of subsequent studies on fungal mating systems. Later, the emergence of techniques such as cloning

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(Cohen *et al.*, 1973; Jackson *et al.*, 1972), PCR (Saiki *et al.*, 1988) and Sanger sequencing (Sanger and Coulson, 1975; Sanger *et al.*, 1977) provided the means to examine the molecular basis of sexual reproduction in a range of model fungi (e.g. Debuchy and Coppin, 1992; Glass *et al.*, 1988; Kang *et al.*, 1994; Picard *et al.*, 1991). More recently, whole-genome sequencing technology has allowed for a shift of focus away from studying only model organisms (Davis, 2004; Muller and Grossniklaus, 2010), where a significant fraction of previous and current genome sequencing efforts are focused on fungi (Genomes OnLine Database; Grigoriev *et al.*, 2011; Reddy *et al.*, 2015). Not surprisingly, the availability of these data has allowed for the detailed characterization of the mating-type locus from many non-model fungi (e.g. Comeau *et al.*, 2015; DiGuistini *et al.*, 2011).

The naming of mating-type genes relies on a nomenclature system developed by Turgeon and Yoder more than 15 y ago (Turgeon and Yoder, 2000). The system applies names based on shared homology, allowing a single name to be used consistently, even across diverse fungal taxa. Where a novel mating-type gene has no known homology to any gene previously described from a fungal mating-type locus, a new name is assigned following a suite of guidelines. Although very elegant, the application of these rules has in some cases proved difficult, often resulting in inconsistent and ambiguous assignment of gene names. Such discrepancies represent significant barriers to meaningful discussions on the origin, functioning and evolutionary history of the genes underlying sexual reproduction in fungi (Debuchy *et al.*, 2010; Debuchy and Turgeon, 2006; Dyer *et al.*, 2016).

In this commentary, we provide an update of the nomenclatural system used for naming the mating-type genes of filamentous Ascomycetes in the subphylum Pezizomycotina (Fig. 1). To achieve this, we first review knowledge regarding gene content and organisation of the locus underlying sexual reproduction in these fungi. The known mating-type genes are then discussed and the problems associated with naming new (and sometimes known) mating-type genes are outlined. To provide a starting point for characterising the mating-type region in the Pezizomycotina, we end with an overview of the most common strategies that are used to identify the mating-type locus and its genes. We hope that this commentary and review will not only provide clarity on the names currently used for mating-type genes, but more importantly, that it will also be useful to avoid the pitfalls associated with naming these genes in future.

2. Position and architecture of the Pezizomycotina MAT1 locus

Despite utilizing diverse reproductive strategies (Billiard *et al.*, 2011, 2012), almost all described Pezizomycotina have a bipolar mating system where sexual reproduction is controlled by a single genetic locus (Debuchy *et al.*, 2010; Giraud *et al.*, 2008). The concept of a single mating-type locus was established in the authoritative review of Whitehouse (1949) and subsequently confirmed through sequence-based characterization of the mating-type locus of *Neurospora crassa* (Glass *et al.*, 1990; Staben and Yanofsky, 1990). The locus was later formally defined as the single position in the genome responsible for controlling mating (Turgeon and Yoder, 2000; Yoder *et al.*, 1986) and named the *MAT1* locus (Fig. 2; Turgeon and Yoder, 2000). Here the numeral “1” is used to indicate that only a single *MAT* locus is present in most Pezizomycotina studied to date (Turgeon and Yoder, 2000), although it does not exclude the possibility of additional loci that might be identified and would then be named *MAT2*, *MAT3*, and so forth (Turgeon and Yoder, 2000).

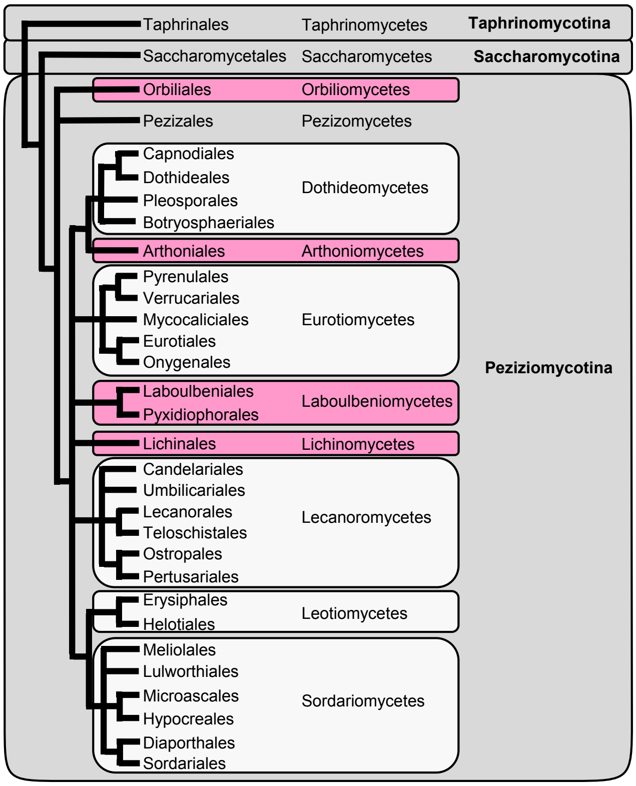

Fig. 1 – A schematic phylogeny of the subphyla in the Ascomycota. Shown are the classes that make up the subphylum Pezizomycotina, as well as representative orders within each class. The classes shown in red have no known published mating-type gene sequences. Phylogeny after Hibbett *et al.* (2007).

In all but one of the cases described (Cisar and TeBeest, 1999), the *MAT1* locus of all heterothallic Pezizomycotina species studied thus far have two “versions” (Debuchy *et al.*, 2010). These “versions” co-locate with the mating factors that were initially identified in *N. crassa* and shown to be linked to a putative mating-type chromosome (Lindegren, 1936a). Later work showed that the mating factors actually represent large chromosomal sections conferring mating specificity (Bistis, 1998; Lindegren, 1936b). Also, the two “versions” of these chromosomal sections are markedly different as they are maintained through the suppression of recombination between them (Dyer *et al.*, 2016) and the genes they encode are highly divergent (Butler, 2007; Debuchy *et al.*, 2010). Because the “versions” of the *MAT1* locus do not conform to what is generally expected for true alleles (i.e. orthologous but alternative forms of a gene/marker at a locus; Griffiths *et al.*, 2010), the term