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Review

From two to one: Unipolar sexual reproduction

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ABSTRACT

While sexual reproduction is universal in eukaryotes, and shares conserved core features, the specific aspects of sexual reproduction can differ dramatically from species to species. This is also true in Fungi. Among fungal species, mating determination can vary from tetrapolar with more than a thousand different mating types, to bipolar with only two opposite mating types, and finally to unipolar without the need of a compatible mating partner for sexual reproduction. *Cryptococcus neoformans* is a human pathogenic fungus that belongs to the Basidiomycota. While *C. neoformans* has a well-defined bipolar mating system with two opposite mating types, MAT α and MAT α , it can also undergo homothallic unisexual reproduction from one single cell or between two cells of the same mating type. Recently, it was shown that, as in α - α bisexual reproduction, meiosis is also involved in α - α unisexual reproduction in *C. neoformans*. Briefly, recombination frequencies, the number of crossovers along chromosomes, as well as frequencies at which aneuploid and diploid progeny are produced, are all comparable between α - α bisexual and α - α unisexual reproduction. The plasticity observed in *C. neoformans* sexual reproduction highlights the extensive diversity in mating type determination, mating recognition, as well as modes of sexual reproduction across fungal species.

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1. Introduction

Sexual reproduction, the process of producing progeny by combining genetic material from the two parents, is pervasive and present in all of the major groups of the eukaryotic tree of life. However, while sexual reproduction is ubiquitous and conserved in core features (e.g. ploidy changes, zygote formation, mixing and segregation of parental genetic material), the detailed aspects of sexual reproduction, including how sex is determined, as well as how sexual reproduction is accomplished, are diverse (Dellaporta and Calderon-Urrea, 1993;

Goodfellow and Lovell-Badge, 1993; Heitman et al., 2013; Korpelainen, 1990; McNair Senior et al., 2015). For example, while for most animal species the sex is genetically determined by sex chromosomes, for some reptile species, sex is decided by environmental factors, such as the temperature at which the egg is hatched (Bull, 1980). Additionally, sex can change in some fish species due to changes in the social dynamics within the group of fish (Lorenzi et al., 2006), and in the ciliate *Paramecium tetraurelia*, it has been shown that a small RNA-mediated genome defense mechanism is involved in the maternal inheritance of mating types in this species (Singh

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et al., 2014). Also, while most animals and plants have only two sexes, this is far from a universal rule in many other species. In the social amoeba *Dictyostelium discoideum*, there are three mating types that are decided by different gene compositions at one *mat* locus (Bloomfield et al., 2010). More strikingly, in the ciliate protozoa *Tetrahymena thermophila* there are seven different mating types, and each mating type can undergo successful mating with individuals of any of the other six mating types, but not with individuals of its own type. The mating type of *T. thermophila* is determined by a specific chromosomal region called the mating type locus in the active somatic nuclear genome, and the presence of one of the seven different alleles at this mating type locus decides the mating type of the individual (Cervantes et al., 2013). Interestingly, it has recently been shown that the mating type locus in the *T. thermophila* germline nucleus that is dormant during vegetative growth actually contains all seven elements that are required to define the seven different mating types, and that these seven elements form a cluster at the mating type locus that is interspersed with repetitive elements. During the development of the somatic nucleus from the germline nucleus, the mating type locus undergoes repeated homologous recombination events mediated by these repetitive elements, which results in successive elimination of mating type elements until only one of the original seven elements is left, with this remaining element defining the mating type of that individual (Cervantes et al., 2013).

In fungi, it is thus not surprising that the processes of sexual reproduction also show extensive plasticity in mating type determination and the number of sexes, as well as in mating recognition, leading to different modes of sexual reproduction.

2. Mating type loci and mating recognition in fungi

In fungi, sexual identity is defined by the mating type, which is typically established by a specialized region of the genome that is termed the mating type locus (MAT) (Ni et al., 2011). Some fungi (e.g. many of the Ascomycetes) have only one MAT locus in their genome that encodes mating-type-specific transcription factors. In these species, the MAT locus is usually biallelic and defines two mating types, and mating can only occur between individuals with opposite mating types. Thus, these fungi have a bipolar mating system, because a maximum of two different mating types can be produced from one meiotic event. In some other fungal species (e.g. many of the Basidiomycetes), the mating type is established by the allelic combination of two unlinked MAT loci, where one encodes the pheromones and pheromone receptors (P/R locus) and the other encodes homeodomain transcription factors (HD locus) that activate mating specific pathways upon successful mating recognition by the P/R locus. In these fungi, successful mating can only occur between isolates with different alleles at both of the two MAT loci. Thus, these species have a tetrapolar mating system because a maximum of four different mating types can be produced through one round of meiosis (Casselton and Olesnick, 1998).

The MAT locus/loci are evolutionarily dynamic, and undergo expansions and contractions, as well as chromosomal rearrangements including translocations and inversions, even between closely related species (James, 2007). This is likely due to the fact that these regions are normally repressed for meiotic recombination and are typically enriched with transposable elements and repetitive sequences. Additionally, transitions between tetrapolar and bipolar mating systems have also been shown to occur in several fungal species (Fraser and Heitman, 2004; James et al., 2006). For example, in the mushroom *Coprinellus disseminatus*, it was shown that the extant bipolar mating system has likely evolved from the ancestral tetrapolar mating system through the loss of mating-type-specific pheromone receptor function, rendering the P/R locus no longer involved in mating recognition. Also, the human fungal pathogen *Cryptococcus neoformans* has a well-defined bipolar mating system with an unusually large MAT locus (>100 kb in size with more than 20 genes) (Fraser et al., 2004; Lengeler et al., 2002). When compared to closely related species, it is clear that this large MAT locus has evolved through some sort of chromosomal rearrangement that resulted in the physical linkage between the ancestrally separated P/R and HD locus (Findley et al., 2012). However, the detailed mechanisms by which this linkage was established have yet to be elucidated.

3. Heterothallic vs. homothallic

We mentioned that in species with bipolar mating systems, mating can only occur between individuals with different mating types; and for species with tetrapolar mating systems, only individuals that differ at both P/R and HD loci can undergo successful sexual reproduction (Raper, 1966). For these species, we say they undergo heterothallic sexual reproduction, because the two individuals involved in mating have different mating types and are most likely not genetically identical by descent. However, there are also some fungal species that do not require a mating partner to initiate and complete sexual reproduction, and can initiate and complete the sexual cycle from a single cell. We call these species homothallic, and there are several mechanisms that could enable a species to undergo homothallic sexual reproduction.

First, homothallic sexual reproduction can be achieved by mating type switching, such as in the model yeasts *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe*, which independently evolved one active mating type locus and two silenced mating type cassettes that enable gene conversion mating type switching evoked in response to recombinogenic lesions (Dalgaard and Klar, 1999; Egel, 2005; Haber, 2012; Klar, 2007, 2010). In the genome of *S. cerevisiae*, there is one active MAT locus that defines a bipolar mating system with two mating types, MAT α and MAT a . In addition, there are also two silent mating cassettes, HMR and HML, which carry epigenetically silenced copies of MAT α and MAT a alleles, respectively. So, an individual with a MAT α allele at the active MAT locus behaves as a mating type even though it carries a silenced MAT a allele at the HML locus, and vice versa. Now, *S. cerevisiae* can undergo a unique process called mating type switching, where during the G1 phase of the cell cycle in

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