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Review

Evolution of sexual reproduction: A view from the fungal kingdom supports an evolutionary epoch with sex before sexes

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ABSTRACT

Sexual reproduction is conserved throughout each supergroup within the eukaryotic tree of life, and therefore thought to have evolved once and to have been present in the last eukaryotic common ancestor (LECA). Given the antiquity of sex, there are features of sexual reproduction that are ancient and ancestral, and thus shared in diverse extant organisms. On the other hand, the vast evolutionary distance that separates any given extant species from the LECA necessarily implies that other features of sex will be derived. While most types of sex we are familiar with involve two opposite sexes or mating types, recent studies in the fungal kingdom have revealed novel and unusual patterns of sexual reproduction, including unisexual reproduction. In this mode of reproduction a single mating type can on its own undergo self-fertile/homothallic reproduction, either with itself or with other members of the population of the same mating type. Unisexual reproduction has arisen independently as a derived feature in several different lineages. That a myriad of different types of sex determination and sex determinants abound in animals, plants, protists, and fungi suggests that sex specification itself may not be ancestral and instead may be a derived trait. If so, then the original form of sexual reproduction may have been unisexual, onto which sexes were superimposed as a later feature. In this model, unisexual reproduction is both an ancestral and a derived trait. In this review, we consider what is new and what is old about sexual reproduction from the unique vantage point of the fungal kingdom.

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1. Introduction

No one knows the exact nature of the LECA, but we think that this ancestor was a unicellular, aquatic, motile creature with one or two flagella. Thus, in some respects the LECA was simple. But in other ways, it was already quite complex, with a

nucleus, mitochondria, secretory apparatus, RNAi, and reproducing both asexually and sexually. Thus, when we think of where sex first evolved, it was in the water, involving swimming cells (Levin and King, 2013; Umen and Heitman, 2013). And when we think of how sex first evolved, this involved changes in ploidy and the process of meiosis, given their

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conserved nature throughout eukaryotes. And while cell–cell and nuclear–nuclear fusion play prominent roles in sexual reproduction today, there may have been an era in which endoreplication cycles followed by meiosis drove the processes of ploidy change during ancestral modes of sexual reproduction. In this view, cell–cell fusion may be ancient, but perhaps not as ancient as other features of sexual reproduction.

Why sex is so pervasive is thought to result from potential benefits conferred by sexual reproduction. These include purging the genome of deleterious mutations and shuffling the genome via independent chromosomal assortment and recombination to give rise to a diverse repertoire of meiotic progeny. Sex may also enable organisms to keep pace with or outrun pathogens, including those both external and those internal (such as transposons). There is sound experimental evidence from studies in *Caenorhabditis elegans* and in naturally occurring snails in New Zealand for this last hypothesis in which sex allows species to keep pace with their pathogens (King et al., 2009, 2011; Morran et al., 2011; Vergara et al., 2013). However, these potential benefits of sex are pitted against well-known costs of sexual reproduction: that only 50 % of a parental genome is transmitted to any given progeny, the time and energy required to locate mates, and the breaking apart of well adapted genomic configurations.

The core features of sexual reproduction are conserved in organisms as diverse as the model budding yeast *Saccharomyces cerevisiae* and humans, despite a billion years or more of evolution separating us from our last common shared ancestor. These conserved features include: 1) ploidy changes from haploid to diploid to haploid (or diploid to haploid to diploid), 2) the process of meiosis that enables meiotic recombination and halves the ploidy of the genome, and 3) cell–cell fusion between mating partners (a and α cells) or gametes (the sperm and the egg). This ubiquity of the conserved features of sex again speaks to the antiquity of the process.

Beyond the commonalities in the mechanisms of sex, there are also shared features to the modes of sexual reproduction. This includes outbreeding between genetically divergent members of the population, but also types of inbreeding that can involve the ability of the yeast *S. cerevisiae* to undergo mating type switching that allows mother cells to mate with their daughter cells. And in humans there are the examples of consanguineous marriages, resulting for example from cousin–cousin pairings, which lead to considerable inbreeding with the risk of exposure of recessive alleles in a homozygous configuration. We will return to this theme of the balance between outbreeding and inbreeding.

2. Mechanisms of sex determination

Sex in humans and many other animals is determined by the X and Y sex chromosomes, in which individuals with XX karyotype are female and those with XY are male. The two sex chromosomes are dramatically different in size, and are referred to as heteromorphic sex chromosomes. A single gene resident on the Y chromosome, SRY, is sufficient to direct male fate and transferring this single gene from the Y to the X chromosome suffices to cause sex reversal in both

humans and in mice. But in other plants and animals, there are different mechanisms of sex determination. Some species, such as the plant Papaya and the fish Medaka, have sex chromosomes in which the sex specific region is small and the two sex chromosomes are the same size, so called homomorphic sex chromosomes (Kondo et al., 2004; Liu et al., 2004; Myosho et al., 2012). Chickens and other birds have a completely different type of sex chromosome, called Z and W, and in these lineages it is the heterogametic ZW pattern that specifies female and the homogametic ZZ the male (Zhou et al., 2014). In some animals, including turtles and crocodiles, the temperature at which an egg hatches determines sexual identity and this is called Environmental Sex Determination (ESD) to distinguish it from Chromosomal Sex Determination (CSD) (Barske and Capel, 2008). Yet other species appear to be hybrids of the two with features of both environmental and chromosomal sex determination. Finally in some lines of the zebra fish *Danio rerio* sex appears to be a quantitative trait, in which genes on multiple different chromosomes come together in allelic combinations that favor either female or male fate (Anderson et al., 2012; Bradley et al., 2011; Liew et al., 2012; Liew and Orban, 2014). This quantitative sex determining system has been termed polygenic sex determination (PSD). Recent studies of wild *D. rerio* reveal a sex determining region on one end of chromosome 4 that may be consistent with a WZ/ZZ sex chromosome system, suggesting loss of a sex determinant or recent origin of a novel one during domestication (Wilson et al., 2014). To summarize, in simple terms the ways in which sex is determined are plastic and diverse.

What about fungi? Relatively few fungi have large size dimorphic sex chromosomes, but there are a few well studied examples such as *Neurospora tetrasperma*, *Podospora*, and *Microbotryum* (Ellison et al., 2011; Fraser et al., 2004; Fraser and Heitman, 2004; Grognet et al., 2014; Hood et al., 2013; Menkis et al., 2008; Whittle et al., 2015). Most fungi have relatively smaller regions of their genome, called mating-type loci, or MAT for short, that dictate their mating type (Fraser and Heitman, 2003). The paradigmatic example is *S. cerevisiae* in which a relatively small region of the genome, less than a thousand base pairs, expresses in the alternate mating types one or two key cell fate determinants, all of which are transcription factors responsible for orchestrating both haploid cell type specificity (a or α) and the diploid zygote fate (a/α). Two are homeodomain proteins of the HD1 and HD2 class that form a heterodimer, $a1/\alpha2$, which is necessary for the diploid zygote fate. The other factor, $\alpha1$ from MAT α , encodes an alpha domain transcription factor necessary for turning on genes required for the α cell fate, while $\alpha2$ represses a genes to further enforce the α cell haploid fate. The a haploid cell type is the default, and is not actively specified by the MAT locus. This type of mating-type system is called bipolar to reflect the two mating types, a and α . When the two mating types are in balance in the population, bipolar mating systems enable 50 % outcrossing and 50 % inbreeding.

But other fungi have much more exotic sex lives, and have a more complex mating-type determining system in which there are literally thousands and thousands and thousands of different mating types (Brown and Casselton, 2001; Casselton, 2002, 2008; Heitman et al., 2007; Raper, 1966). In these species there are two loci that lie unlinked on different

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