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journal homepage: www.elsevier.com/locate/fbr



Review

Contrasted patterns in mating-type chromosomes in fungi: Hotspots versus coldspots of recombination

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ARTICLE INFO

Article history:

Received 17 December 2014

Received in revised form

10 June 2015

Accepted 12 June 2015

Keywords:

Bipolar

Cryptococcus neoformans

Heterothallism

Homothallism

MAT

Microbotryum violaceum

Muller's ratchet

Neurospora tetrasperma

Podospora anserina

Tetrapolar

ABSTRACT

It is striking that, while central to sexual reproduction, the genomic regions determining sex or mating-types are often characterized by suppressed recombination that leads to a decrease in the efficiency of selection, shelters genetic load, and inevitably contributes to their genic degeneration. Research on model and lesser-explored fungi has revealed similarities in recombination suppression of the genomic regions involved in mating compatibility across eukaryotes, but fungi also provide opposite examples of enhanced recombination in the genomic regions that determine their mating types. These contrasted patterns of genetic recombination (*sensu lato*, including gene conversion and ectopic recombination) in regions of the genome involved in mating compatibility point to important yet complex processes occurring in their evolution. A number of pieces in this puzzle remain to be solved, in particular on the unclear selective forces that may cause the patterns of recombination, prompting theoretical developments and experimental studies. This review thus points to fungi as a fascinating group for studying the various evolutionary forces at play in the genomic regions involved in mating compatibility.

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1. Introduction

A decade ago an alarming hypothesis captured public imagination: men were going to become extinct within the next

5–10 million years (Marshall Graves, 2002). Behind this prediction was the degeneration of the male-specific Y chromosome. The Y chromosome, which was once an autosome carrying a sex-determining gene, has indeed experienced

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<http://dx.doi.org/10.1016/j.fbr.2015.06.001>

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repeated and expanding stages in its accumulation of mutations relative to its homologous X chromosome. Degeneration of gene content and mutation accumulation are consequences of the lack of crossing-over during meiosis, because it is through such recombination that chromosomes with fewer deleterious mutations than the minimum number in the population can be produced (Graves, 2006; Bergero and Charlesworth, 2009) (Fig. 1a). It was thus first reasoned by Hermann Muller that, in the absence of recombination, chromosomes containing the fewest deleterious mutations would be regularly lost from the population by chance, which would lead to an irreversible and increasing loss in coding capability over time (Muller, 1964; Bergero and Charlesworth, 2009) (Fig. 1b). Although extensions of this model, known as “Muller’s ratchet,” have been formulated [e.g., (Kondrashov, 1982)], they all predict a connection between the suppression of recombination and the accumulation of mutations. Furthermore, large regions united by recombination suppression prevent selection from acting independently upon variation in separate loci, causing hitchhiking of deleterious mutations together with positive

selection of a beneficial allele [i.e., Hill-Robertson interference (Gillespie, 2000)].

Suppression of recombination and the consequent molecular degeneration around genes controlling sexual compatibility is not unique to humans as it is found in other animals, plants, and in the fungi (Hood, 2002; Fraser and Heitman, 2004a,b; Whittle et al., 2011; Hood et al., 2013; Fontanillas et al., 2015). An apparent irony is found in that the very elements regulating genetic exchange between individuals are themselves largely excluded from the benefits of this recombination (Idnurm, 2011), especially because sex does not have to be determined genetically but can be through, as examples, environmental sex determination or sequential hermaphroditism (Bachtrog et al., 2014; Beukeboom and Perrin, 2014).

There may be processes that counter the trend toward degeneration and the recombinationally-inert nature of mating-type or sex chromosome regions. In one view, the nonreciprocal transfer of DNA sequence achieved through gene conversion may counter-act some of the deleterious effects of suppressed recombination (Marais et al., 2010; Trombetta et al., 2010), but this phenomenon remains rare in the regions where crossing-over frequencies are low (Bachtrog, 2013). A process of cyclical renewal of sex-determining regions has also been suggested, where new regions evolve to control the process of mating when old sex chromosomes become too degraded (Mank and Avise, 2009; Blaser et al., 2014). However, as recent studies expand both the diversity of species and the genetic tools for documenting recombination, there are some rare exceptions in which presumed dead spots of genetic exchange permit recombination.

Regions controlling mating compatibility are in some cases associated with suppressed recombination while in other cases they harbor crossing-over hotspots (Burgoyne, 1982; Yi and Li, 2005; Hsueh et al., 2006; Brick et al., 2012; Sarbajna et al., 2012; Jakociūnas et al., 2013; Bolton et al., 2014). The evolutionary drivers for these contrasted relationships between recombination and mating-type determination are still unclear. That is, the regions controlling sex determination or mating compatibility take a broad range of values in their association with either recombination suppression or enhancement.

This article outlines three contrasted situations regarding recombination associated with regions that control mating compatibility; suppressed recombination, enhanced recombination, and non-homologous or non-reciprocal exchange that may counteract molecular degeneration. We outline some of the puzzles about these relationships between mating-type determination and recombination, and we suggest possible explanations. Recent discoveries in fungi provide valuable insights into the evolutionary genomics of sexual compatibility. While previous articles have highlighted the similarities between fungal mating-type chromosomes and the sex chromosomes in other eukaryotes (Fraser and Heitman, 2004a,b; Menkis et al., 2008; Whittle and Johannesson, 2011), here we focus on the evolutionary causes for these similarities, point out the evolutionary differences, and highlight questions that remain to be answered.

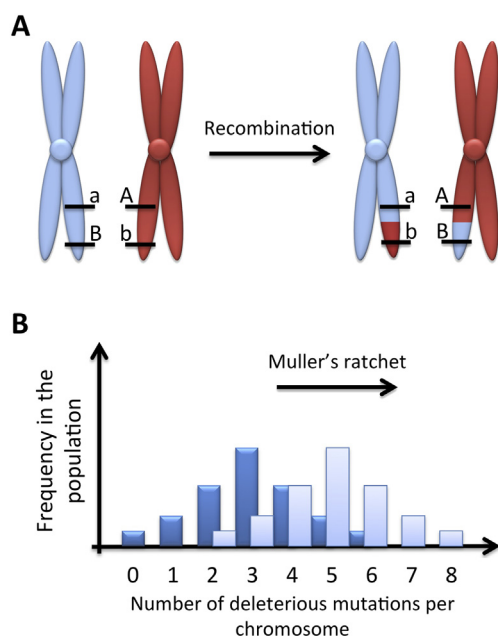


Fig. 1 – (A) Illustration of recombination as a mechanism for purging deleterious mutations. A crossing-over event between two chromosomes carrying different deleterious mutations (a and b) produces a chromosome free of deleterious mutations (A and B). (B) Illustration of the concept of Muller’s ratchet. Without recombination, the number of deleterious mutations per chromosome increases over time in the population, and the chromosomes free of deleterious mutations will be lost by chance. The dark blue shading shows a theoretical original state, with a given mean and variance for the number of deleterious alleles per chromosome in a population. The light blue shading shows the resultant state after many generations without recombination, illustrating the Muller’s ratchet effect of an increase in the mean number of deleterious mutations.

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