Divergent evolutionary trajectories of two derived homomorphic sex chromosome systems

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Objectives

1. Assess the extent of sex linkage and recombination suppression
2. Determine sex specific rate of recombination genome-wide
3. Explore differentiation of young, homomorphic sex chromosomes

Introduction

Sex chromosomes evolve from autosomes and are thought to follow a predictable path of progressive degeneration[1]. However, the fate of sex chromosomes is variable with some degrading, others not, and age of the sex chromosomes has little impact on these outcomes[2]. Fundamental to our understanding of sex chromosome divergence is to characterize to what extent, how long, and why recombination is suppressed in genomic regions flanking the sex determining locus. In African clawed frogs (*Xenopus*) multiple sex chromosome turnover events have occurred (Fig. 1)[3] and we assess recombination and differentiation using reduced and whole genome sequencing on lab-reared families.

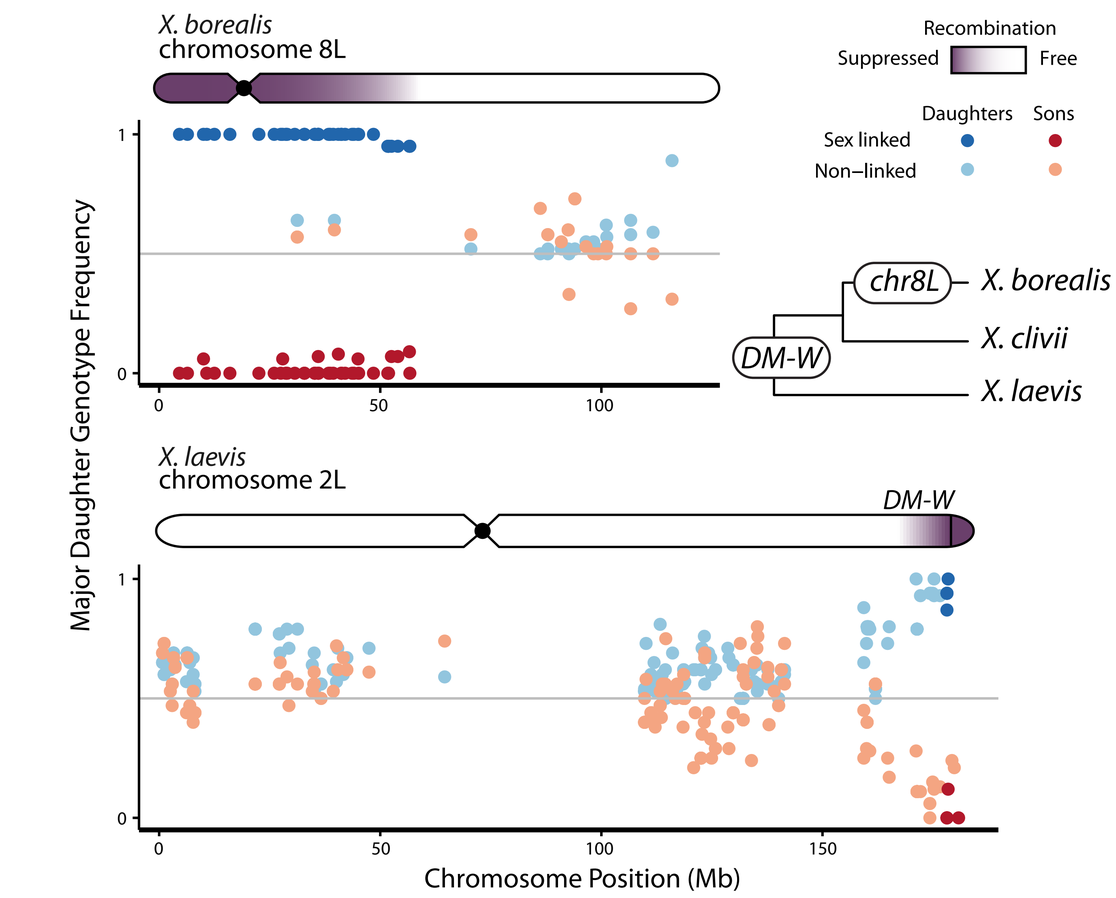

Fig. 1: Most frequent genotype in daughters of each family, and the frequency of that genotype in sons. Dark colors reflect $P < 0.05$ following FDR correction for genotype association with sex. Phylogeny from Furman and Evans (*3*).

Result 1: Widespread sex linkage in a younger system

In the younger sex chromosomes of *X. borealis*, $\approx 50\%$ was completely sex linked. A single recombination event is evident in the daughters at the end of the region, defining the boundary of strongly suppressed recombination (less clear is a similar event in sons). In contrast, very few SNPs on the sex chromosomes of *X. laevis* were sex linked, though the region of reduced recombination is evident by an increasing bias in parental genotype inheritance towards the end of the chromosome.

Conclusion

Suppressed recombination can rapidly encompass large portions of derived sex chromosomes, and this may only be associated with modest differentiation (*X. borealis*). Conversely, suppressed recombination may not expand, even after millions of years (*X. laevis*). Together, these closely related species demonstrate that sex chromosome differentiation lead by recombination suppression may not be a progressive process.

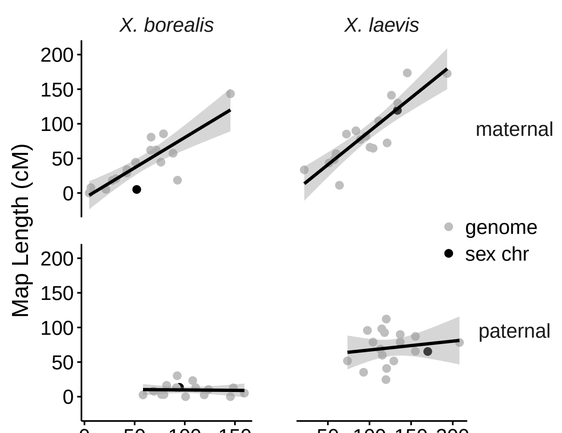

Fig. 2: Summary of sex specific linkage maps for each chromosome of both species, positioned on the *X. laevis* genome.

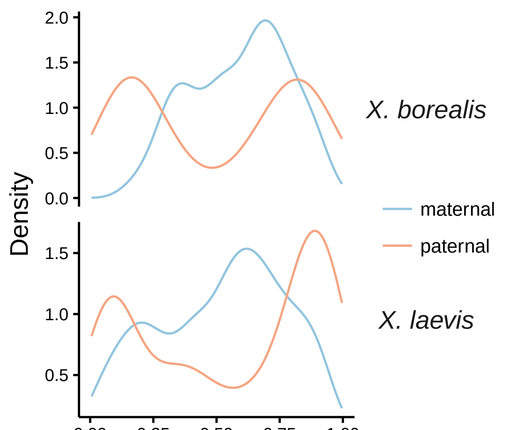

Fig. 3: All chromosomes' lengths scaled between 0–1. Density plots reveal locations of crossover events.

Result 2: More recombination in the heterogametic sex; crossover locations are sex-specific

Female maps were longer than male maps (*X. laevis* = 1572/1275 cM; *X. borealis* 719/165 cM), despite spanning less of the genome overall (Fig. 2), with *X. laevis* maps covering 2x more of the genome. As seen for many other species, crossovers in females were biased to the middle of chromosomes and in males towards the ends (Fig. 3), likely resulting in female maps positively scaling with Mb covered, unlike male maps.

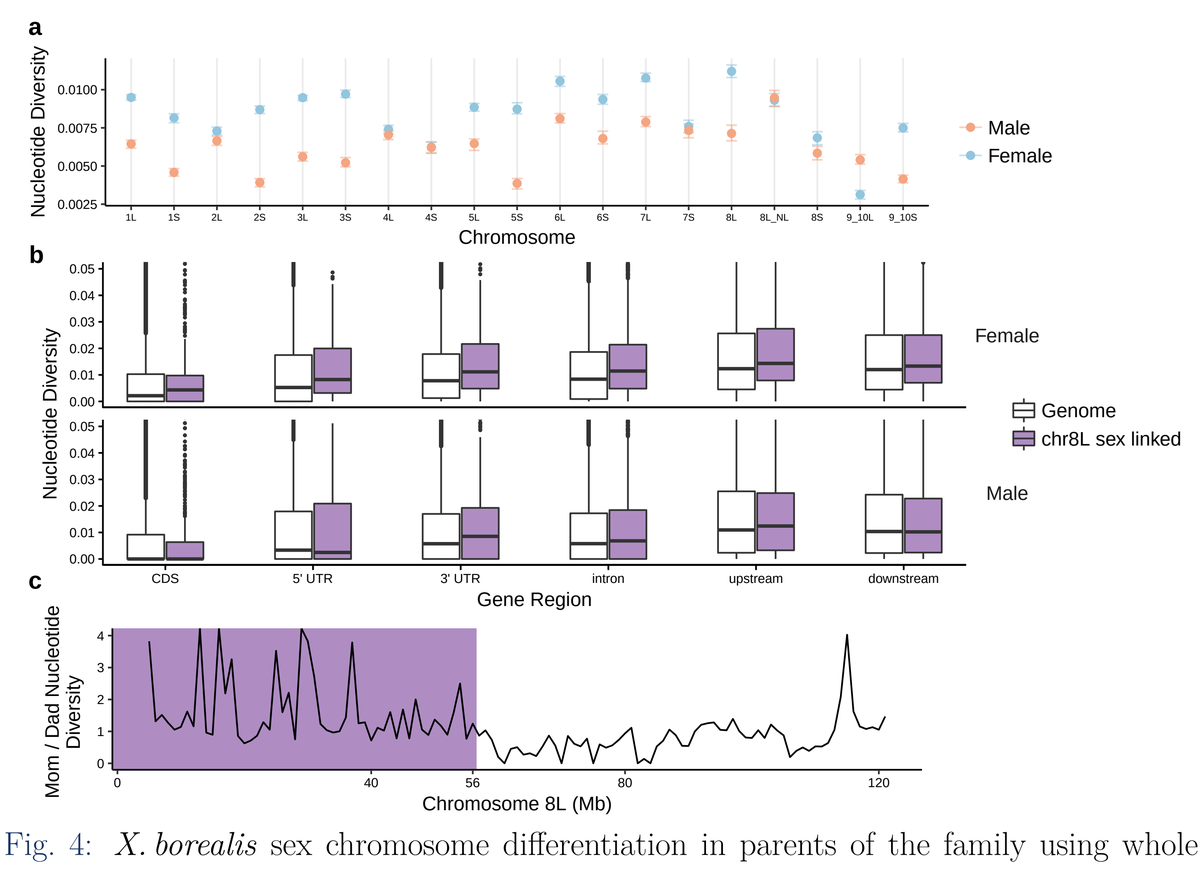

Fig. 4: *X. borealis* sex chromosome differentiation in parents of the family using whole genome sequencing. a) chromosome-wide π (95% confidence intervals). b) π measured in and around genes. c) π in the mother divided by π in the father in 1 Mb windows. Purple indicates the sex linked region defined by SNP inheritance (Fig. 1)

Result 3: Modest sex chromosome differentiation

The modest increase in nucleotide diversity on the *X. borealis* mother's sex chromosomes (Fig. 4a,b) indicates that recombination has been consistently suppressed in the sex linked region, but not for very long. There may be evidence of early strata formation, indicated by an attenuation of divergence at the end of the sex linked region (Fig. 4c). Recombination was detected near this end, and it may be that boundaries of recombination remain fluid until firmly established.

References and Acknowledgements

1. B. Charlesworth *et al.*, *Science* **251**, 1030–1033 (1991).
2. A. E. Wright, R. Dean, F. Zimmer, J. E. Mank, *Nature Communications* **7** (2016).
3. B. L. S. Furman, B. J. Evans, *G3: Genes/Genomes/Genetics* **6**, 3625–3633 (2016).

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