

NEWS AND COMMENTARY

Sex chromosome evolution

A 'missing link' in the evolution of sex chromosomes

RC Moore

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Sex chromosomes have evolved independently in all major lineages of eukaryotes, and although the precise genetic mechanism for their formation may differ, it is hypothesized that these sex chromosomes began as 'ordinary' autosomes. With their publication of a genetic map for the octoploid strawberry, *Fragaria virginiana*, Spigler *et al.* (2008) have discovered a missing link in the evolution of sex chromosomes from autosomes. Before this study, sex determination in this subdioecious plant (consisting of males, females and hermaphrodites) was considered to be controlled by a single Mendelian locus. However, Spigler *et al.* (2008) found that male and female functions mapped independently and are tightly linked in a single linkage group. These findings are consistent with current models of sex chromosome evolution from autosomes and represent one of the earliest stages of sex chromosome evolution.

Sex in flowering plants is often a personal affair. The majority of flowering plants are hermaphroditic, and whereas genetic and morphological mechanisms promoting outcrossing exist, separate sexes (dioecy) are relatively uncommon. When separate sexes do evolve, they tend to do so in a step-wise manner, first with the formation of females (gynodioecy) and second with the replacement of hermaphrodites with males (dioecy). The polyploid strawberry, *F. virginiana*, is at an intermediate stage between gynodioecy and dioecy, with females, males and hermaphrodites (sub-dioecy).

Sex in polyploid strawberries was previously thought to be determined by a single Mendelian locus consisting of either a single gene or a gene complex (see Figure 1; Ahmadi and Bringham, 1991). However, Spigler *et al.* (2008) were able to tease apart the genetics of sex determination in this species by separately mapping female function ($\geq 5\%$ fruit-forming flowers) and male function (presence of pollen-filled anthers) in a mapping population derived from a cross between a *F. virginiana* female and hermaphrodite (which

served as the male parent). The separation of reproductive function is critical, as hermaphrodites can have both male and female function. In contrast to the classic genetic model for sex determination in this species, Spigler *et al.* (2008) discovered that male and female function map to separate loci. Furthermore, they found that these loci are closely linked in the same linkage group. Based on these data, the authors propose a two-locus model for sex determination in this polyploid strawberry (see Figure 1).

If this sounds familiar, it is because it is exactly what current models of sex chromosome evolution predict (Charlesworth *et al.*, 2005). In the familiar case, in which males are determined by a single dominant Y chromosome, the initial step in sex chromosome formation is an inhibition of recombination between two sex determining loci, one that suppresses female expression and one that promotes male expression. In *F. virginiana*, in which females are heterogametic, the story is similar, except there is close linkage between a locus that promotes female expression and one that represses male development (see Figure 1). One difference in *F. virginiana*, however, is that recombination is not completely suppressed between these two loci, as evidenced by the occurrence of neuters in the *F. virginiana* mapping population as well as in natural populations (Spigler *et al.*, 2008). This supports the hypothesis that the sex-determining chromosomes of *F. virginiana* are at one of the earliest stages in the evolution of sex chromosomes; they are on the cusp of becoming sex chromosomes.

The findings of Spigler *et al.* (2008) place *F. virginiana* alongside a growing number of sex chromosome systems that are at early stages of sex chromosome evolution, a number of which are plants (Ming and Moore, 2007). Of interest is that the plant models, in particular, tend to span various stages during the early events in sex chromosome evolution. For example, the sex determining loci in papaya, in which males are heterogametic, are found

in a non-recombining region of the Y chromosome (NRY) that is confined to an approximately 8 Mbp region around the centromere of a pair of homomorphic sex chromosomes (Yu *et al.*, 2007). Estimates of the age of the papaya sex chromosomes suggest that they emerged less than 2 mya (Yu *et al.*, 2008). The sex chromosomes of the white campion (*Silene latifolia*), which is a classic genetic model for sex chromosome evolution in plants, are at a later stage in the evolution of sex chromosomes; the NRY has expanded to over 90% of its heteromorphic Y chromosome. Still, the *S. latifolia* Y is upwards of only 10–15 my old (Nicolas *et al.*, 2005). Other emerging plant model systems for the early events in the evolution of sex chromosomes include asparagus and poplar (Telgmann-Rauber *et al.*, 2007; Yin *et al.*, 2008).

It will be of interest to see if the genomic region harboring linked sex-determining loci in *F. virginiana* exhibit other hallmarks of sex chromosomes, such as the degeneration of genes, the accumulation of repetitive elements and low gene density (Ming and Moore, 2007). Furthermore, it is not known whether the sex-determining chromosomes in *F. virginiana* harbor sexually antagonistic and/or sex-specific loci as has been documented in other plant sex chromosome systems (Scotti and Delph, 2006). Answering these questions will be helped by increasing the marker density of the *F. virginiana* genetic map and genomic sequencing efforts.

Finally, *F. virginiana* serves as an important model in studying the ecological and genetic mechanisms involved in transition to separate sexes in plants. Selection against recombination between the two sex determining loci leading to neuters could lead to the establishment of dioecy in *F. virginiana*; indeed, its polyploid sister species, *F. chiloensis*, is dioecious. However, recombination can also lead to the production of hermaphrodites, which tend to have high fruit set (as observed both in natural populations and in the mapping population). This could counter negative selection against neuters, hindering the formation of a non-recombining sex determining region. Alternatively, hermaphroditism could be maintained by other mechanisms such as selection for self-fertilization. Ecological studies of *F. virginiana* and comparative genomic studies with dioecious *F. chiloensis* should shed light on such questions.

In conclusion, the discovery of 'incipient' sex chromosomes in *F. virginiana*

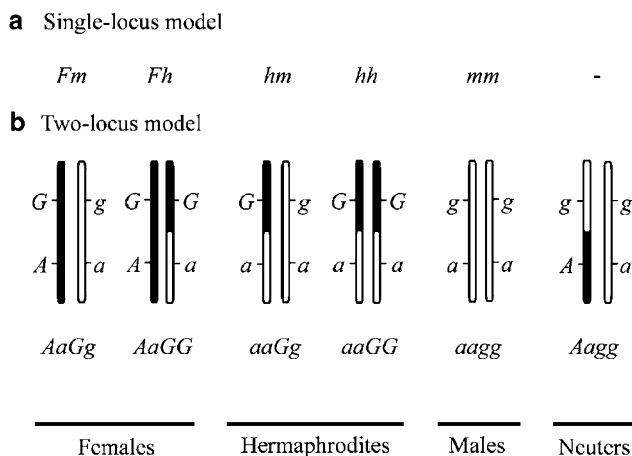


Figure 1 Genetic models for sex determination in the octoploid strawberry, *Fragaria virginiana*. (a) In the classic single-locus model, there is a feminizing allele (*F*) that is dominant to a hermaphroditic allele (*h*), which is dominant to a female-sterility allele (*m*). Females are heterogametic (*Fh* or *Fm*), whereas males are homogametic (*mm*) and hermaphrodites are either *hm* or *hh* (Ahmadi and Bringham, 1991). (b) In the two-locus model proposed by Spigler *et al.* (2008), two sex determining loci are closely linked: a dominant female-fertility allele (*G*, for gynoeceium); and a dominant male-sterility allele (*A*, for androecium). Females are heterogametic (*AaGg* or *AaGG*), hermaphrodites are either *aaGg* or *aaGG*, and males are homogametic (*aagg*). This model accounts for observed neuters (*Aagg*).

provides a necessary link in the study of sex chromosome evolution, while helping to solidify the usefulness of plants as model systems for studying the early events in sex chromosome evolution.

Dr RC Moore is at the Botany Department, Miami University, 316 Pearson Hall, Oxford, OH 45056, USA.

e-mail: moorerc@muohio.edu

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