Does degeneration or genetic conflict shape gene content on UV sex chromosomes?

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Abstract

Studies of sex chromosomes have played a central role in understanding the consequences of suppressed recombination and sex-specific inheritance among several genomic phenomena. However, we argue that these efforts will benefit from a more rigorous examination of haploid UV sex chromosome systems, in which both the female-limited (U) and male-limited (V) experience suppressed recombination and sex-limited inheritance, and both are transcriptionally active in the haploid and diploid states. We review the life cycle differences that generate UV sex chromosomes and genomic data showing that ancient UV systems have evolved independently in many eukaryotic groups, but gene movement on and off the sex chromosomes, and potentially degeneration continue to shape the current gene content of the U and V chromosomes. Although both theory and empirical data show that the evolution of UV sex chromosomes is shaped by many of the same processes that govern diploid sex chromosome systems, we highlight how the symmetrical inheritance between the UV chromosomes provide an important test of sex-limited inheritance in shaping genome architecture. We conclude by examining how genetic conflict (over sexual dimorphism, transmission ratio distortion, or parent-offspring conflict) may drive gene gain on UV sex chromosomes, and highlight the role of breeding system in governing the action of these processes. Collectively these observations demonstrate the potential for evolutionary genomic analyses of varied UV sex chromosome systems, combined with natural history studies, to understand how genetic conflict shapes sex chromosome gene content.

Introduction

On this 50th anniversary of the International Association of Bryology, we look back another five decades to the very beginnings of genetics and a remarkable period of discovery in bryology. During this period, the first sex chromosomes documented in plants were found in the liverwort *Sphaerocarpus donellii* (Allen 1917) and (Heitz 1928) coined the now ubiquitous term "heterochromatin" for the dark-staining, heteromorphic sex chromosomes in mosses. More recent work on sex chromosomes has led to key discoveries regarding fundamental genetic processes such as recombination and gene dosage (Muller 1932; Begun & Aquadro 1992). However, nearly all of this subsequent foundational work has focused on species with XY and ZW sex chromosomes like in Dipterans, Lepidopterans, Mammals, Birds, and few seed plants, organisms that do not reflect the true diversity of sex chromosomes. Many bryophytes and algae possess UV sex chromosomes, which are shaped by distinct evolutionary processes (reviewed in (Bachtrog *et al.* 2011; McDaniel & Perroud 2012; Renner *et al.* 2017; Coelho *et al.* 2018). Only in the past few years have researchers brought new experimental tools to observations first made more than a century ago to explore the untapped potential of comparative genomic analyses among haploid-dioecious organisms.

The purpose of this review is to highlight the novel insights into genome evolution that can be gained by studying UV sex chromosomes. We first present the two-locus model for the evolution of sex chromosomes in the context of a UV system. Next we describe how the symmetry of U and V sex chromosome transmission alters established expectations for several central molecular population genetic parameters, including recombination, effective population size, dosage, and the accumulation of deleterious mutations, relative to XY or ZW chromosome systems. In the third section, we focus on one of the key unanswered questions in sex chromosome evolution – what are the roles of various forms of genetic conflict (sexual dimorphism, sex-ratio bias, and parent-offspring conflict) in driving differences in the evolution of sex chromosome gene content? We conclude by highlighting how this framework provides a clear motivation for combining bryophyte genomics with systematic natural history observations and classical genetic analysis.

The evolution of UV sex chromosomes from a hermaphroditic ancestor

All eukaryotes alternate between haploid and diploid stages in their life cycle. Meiosis reduces the genome to a haploid state, while fertilization restores it to diploid. Fertilization, of course, results from the fusion of two gametes, typically called sperm and egg in anisogamous species. In species with separate males and females, the segregation of a chromosome pair often determines sex. Where in the life-cycle sexual differentiation occurs varies among lineages [BOX 1]. In organisms with dioecy in the diploid stage, the sex chromosomes are referred to as either XY or ZW, depending on which sex is heterogametic, while in haploid systems the sex chromosomes are always UV (Fig.1; (Bachtrog *et al.* 2011)). The sex chromosome systems share much in common with one another, but the differences among them can shed light on important evolutionary processes.

Sex chromosomes are widely believed to evolve from ordinary autosomes, and may first evolve in concert with dioecy. The evolution of genetically-determined dioecy from a hermaphroditic ancestor requires linked male and female-sterility mutations

(Westergaard 1958; Charlesworth & Charlesworth 1978) (but see (Akagi *et al.* 2014; Müller *et al.* 2020) for alternative routes). In the standard diploid formulation of this model, a recessive, male-sterility mutation (i.e., one that renders a hermaphrodite effectively a female) can increase in frequency in a hermaphroditic population when inbred offspring are only half as fit as outbred offspring. That is, if inbreeding is deleterious, male sterility may be favored because the increase in maternal fitness compensates for the loss of fitness through paternity. This produces a gynodioecious population containing females and hermaphrodites (Fig. 2A). Such populations are widely known in angiosperms, but to our knowledge have not been experimentally verified in bryophytes.

In a diploid gynodioecious population, a dominant, female suppressor (i.e., a proto-Y chromosome) can increase in frequency, provided that a) it has compensatory effects on male fitness and b) its inheritance is negatively correlated with the male-sterility mutation (now the proto-X chromosome). The fixation of both mutations produces a fully dioecious population with an XY sex chromosome system (Fig. 2A). The conditions under which a female-sterility mutation evolves first, leading to an androdioecious population, are more restrictive. In this case dioecy occurs following the evolution of a dominant, male suppressor (i.e., a proto-W chromosome; Fig. 2A). Recombination between the sterility factors produces some individuals that have both male and female- sterility factors. Because these individuals cannot contribute to subsequent generations, these circumstances favor the evolution of suppressed recombination between the sterility loci, completing the transformation of an autosome into a sex chromosome.

We should point out two important differences between the diploid and haploid formulations of the two-locus model. First, both the androdioecy and gynodioecy pathways lead to the evolution of UV sex chromosomes (Fig. 2B). Like diploid systems, we expect that gynodioecious mating systems should be more frequent than androdioecious systems, but we know of no rigorous evaluation of the frequencies of such systems in any haploid mating species. Second, because the sexes are haploid, dioecy in a UV system can evolve without a dominant male or female suppressor, because dominance is irrelevant in a haploid system. Given that the evolution of a UV system does not depend on the occurrence of rare dominant mutations, unlike both XY and ZW systems, UV systems might evolve more readily than their diploid counterparts (McDaniel *et al.* 2013; Villarreal & Renner 2013; Laenen *et al.* 2016). Interestingly, most UV systems that have been studied to date are quite old (Ahmed *et al.* 2014; Bowman *et al.* 2017; Carey *et al.* 2020).

Symmetry in sex chromosome transmission alters evolutionary patterns

The fundamental differences between XY/ZW and UV sex chromosomes stem from the symmetrical transmission of U and V compared to the asymmetry of X and Y or Z and W (Table 1). The most obvious implications of symmetry in transition are in the expected amount of segregating variation on the sex chromosomes. In diploid systems, each mated pair has three copies of an X or Z chromosome compared to four copies of each autosome and only one Y or W. Thus, the baseline expected effective population size (N_e) for a X or Z-linked locus is ¾ of an autosome and a Y or W-linked locus is ¼ (Bachtrog *et al.* 2011). In haploid-dioecious systems, each mated pair has one U and one V for every two autosomes so both the U and the V chromosomes are expected to have ½ N_e of an autosome (McDaniel *et al.* 2013). Thus, in UV systems males and females may have similar amounts of sex-linked genetic variation on which selection can act, while in diploid systems the sexes are expected to have different amounts. We should point out that demographic realities, including differential variance in reproductive success between the sexes (Charlesworth 2009), for example due to deviations from an equal ratio of males to females, or variance in female reproductive output (Bengtsson & Cronberg 2009), may dramatically alter the patterns of N_e in sex chromosomes relative to the autosomal expectation.

Regions of suppressed recombination, like sex chromosomes, also generally have lower than expected levels of diversity due to selective sweeps and background selection, which remove variation across these linked regions (reviewed in (Sayres 2018). In XY/ZW systems, suppressed recombination is confined to the male-specific Y or the female-specific W chromosomes. In contrast, in UV systems, suppressed recombination is present on both the female-specific U and male-specific V chromosome (Table 1). Thus, both the male and female-specific chromosomes are expected to experience an equivalent decrease in nucleotide diversity as consequence of suppressed recombination, barring differences in mutation rate or the strength of selection between the sexes. In addition to reduced genetic variation, suppressed recombination can cause genes on the non-recombining chromosome to respond slower to selection (positive or negative) (Comeron *et al.* 2008; Hough *et al.* 2017). Consequently, such regions may show decreased codon bias (relative to autosomes) and an increase in transposable element (TE) abundance, which in UV systems, is expected to affect both equally, in contrast to the asymmetry in diploid systems (Table 1).

The decreased response to selection in non-recombining regions can promote the accumulation of deleterious mutations and loss of functional genes, a process referred to as degeneration (Charlesworth & Charlesworth 2000). In addition, because Y and W chromosomes are always heterozygous with the X and Z, respectively, recessive deleterious mutations are sheltered from purifying selection. In UV sex chromosomes, because the diploids are always UV (not UU or VV; Fig. 1&2) the exposure to selection is symmetrical between the male and female chromosome (Immler & Otto 2015). Indeed, since the sex chromosomes are both expressed in haploids, UV sex chromosomes overall should degenerate slower than either Y or W chromosomes (Table 1; (Immler & Otto 2015)). Of course, a haploid-expressed gene could degenerate on one of the sex chromosomes – for example, a gene specifically involved in sperm production which is incorporated into the UV non-recombining region is likely to experience strong purifying selection in males where its function is critical, but weak purifying selection on the female U chromosome if its function is superfluous (Table 1). Nevertheless, we have no a priori reason to expect that the U or V sex chromosome should degenerate more than the other. The sparse data for UV systems largely support these predictions. [BOX 2]

The lack of degeneration on UV sex chromosomes influences the potential for dosage compensation, a common feature of XY/ZW systems. In diploid systems, the homogametic sex has two copies of either an X or Z, and therefore two copies of sex-linked genes to express. The heterogametic sex, in contrast, may have only one gene copy if the Y or W-linked copies have been lost. The gene expression imbalance can cause developmental problems or a variety of genetic disorders. Such problems are averted by various forms of dosage compensation, in which one copy of many X-linked genes is silenced in females, or the expression of X-linked genes is doubled in males. In contrast, the sex chromosome composition of all life stages is balanced in the UV system - the haploids are either U or V, and the diploids are homogeneous (Fig. 1). While dosage compensation in diploid sex chromosomes is highly variable, and even may be absent or incomplete (reviewed in (Mank 2013)), there is no expectation for any such compensation in haploid systems.

The role of genetic conflict in the expansion of UV chromosome systems

The population genetic processes that we have discussed so far suggest that sex chromosome evolution follows a well-circumscribed path. This view masks the diversity in sex chromosome size and gene content that is found among, and even within many lineages of eukaryotes (Bull 1983; Of Sex Consortium & Others 2014; Furman *et al.* 2020). Clearly degeneration may not play a major role in the evolution of gene content on UV chromosomes, suggesting that other factors, potentially related to life history, may explain variation in sex chromosome size. Surveying the UV species that have been studied so far (Box 2), the proportion of the genome residing on the sex chromosomes ranges from >1% in the brown algae *Ectocarpus*, ~1% in the green algae *Volvox*, ~2% in the liverwort *Marchantia*, and as high as 30% of the genome size in the moss *Ceratodon (Ferris et al. 2010; Ahmed et al. 2014; Bowman et al. 2017; Carey et al. 2020)*. It is possible that the variation in UV sex chromosome size is simply a consequence of different patterns of degeneration, like the accumulation of TEs. However, based on the data currently available each of these UV pairs shows a similar proportion of shared versus sex-specific genes, suggesting that the chromosomes that currently possess more genes have, in fact, also lost more genes from either the U or V. Instead, the size of the sex-limited portion of the U and V chromosomes within a species shows a remarkable correspondence with potential for new mutations to have different fitness effects in males and females, based on the life history of each species (Fig. 3).

If we consider the fate of a new mutation that increases the fitness of females more than males (i.e., a sexually antagonistic allele), that mutation has a greater chance of increasing in frequency if it is tightly linked to a U or W chromosome compared to an autosome (Rice 1987). Conversely, a female-beneficial allele is more likely to fix in a population if it is linked to a V or Y chromosome. Mutations that tighten the linkage between sexually antagonistic alleles and the sex-determining region, such as chromosomal inversions, translocations, or expansions of heterochromatin, also have a greater chance of fixing. In spite of the intuitive appeal of this mechanism to explain the evolution of sex linkage, the forces that drive the expansion of regions of suppressed recombination on sex chromosomes remain poorly understood (Ironside 2010). If sexual antagonism is a major force driving the evolution of non-recombining sex chromosomes, then species that experience more sexual antagonism should have more gene-rich sex chromosomes.

Three major forms of genetic conflict can potentially shape the evolution of genes on UV sex chromosomes, including sexual dimorphism, parent-offspring conflict, and meiotic sex-ratio distortion. Some evidence supports the action of each of these forms of conflict in species with UV systems. The prevalence of conflict is predicted to covary with the breeding system and genetic diversity, both of which vary considerably among bryophyte species. Although work on genetic conflict in UV systems is in its infancy, it is clear that the forms of conflict may act synergistically, through both increasing outbreeding levels and altering linkage patterns on the sex chromosomes. Here we specifically explore how the prevalence of genetic conflict may drive variation in sex chromosome content in bryophytes and other UV systems.

Sexual dimorphism: Perhaps the most obvious reason for sex chromosomes to grow relates to their role in sexual dimorphism. Males and females achieve fitness through different strategies (Bateman 1948; Robert 1972; Lessells & Parker 1999; Chapman 2006). Certainly genes related to sex-limited functions like sperm or egg production are likely candidates for genes that could evolve sex linkage, although the number of genes that are directly involved in gamete production may be relatively modest and is probably similar among organisms. Nevertheless anisogamy can generate selection for sexual dimorphism for a variety of additional traits between the sexes (Parker & Others 1979; Bonduriansky *et al.* 2008).

The ubiquity of sexual dimorphism suggests selection frequently favors different trait optima in males and females. For example, females of the moss *Ceratodon purpureus* produce abundant volatile organic compounds (VOCs) while males produce much less (Rosenstiel *et al.* 2012). Remarkably, the female VOCs attract moss sperm-dispersing microarthopods (mites and springtails) in laboratory choice experiments, suggesting that VOC production is part of a scent-based fertilization syndrome analogous to flowering plant-pollinator mutualisms (Rosenstiel *et al.* 2012) Shortlidge et al. submitted). Co-cultivating mosses and arthropods can increase both the number of genotypes that reproduce and the overall number of sporophytes produced (Cronberg *et al.* 2006); Shortlidge et al., submitted). The fact that males have lower VOC production, however, suggests that scent-production may be costly. Thus, a mutation that increases VOC production may be beneficial for females, but deleterious for males. This sexual antagonism can be resolved by evolving either sex-linkage (i.e., moving the genes VOC production to the sex chromosome, where they can evolve to their sex-specific optima) or sex-biased gene expression, where the genes that control VOC production may be expressed in different ways in males and females (Vicoso & Charlesworth 2006; Ellegren & Parsch 2007). Sex-biased gene expression is very common in animals, but the relative importance of sex-biased gene expression compared to sex linkage in UV systems is unknown.

Sexual dimorphism is found in a wide variety of other traits in bryophytes, suggesting that sexual antagonistic selection may drive the evolution of sex linkage. For example, leaf size and juvenile growth in *C. purpureus* are sexually dimorphic (McDaniel 2009) as are traits in the liverwort *Marchantia introflexa* (McLetchie & Puterbaugh 2000; Fuselier 2008) and the brown algae *Ectocarpus* (Lipinska *et al.* 2015). The links between such trait variation and either male or female fitness are less clear than for VOC production, but it remains a reasonable hypothesis that more dimorphic species, or species with stronger male – male competition or female choice, may possess more sex linked genes. We should point out that the relationship between dimorphism and sex chromosome gene content may not be entirely straight-forward – for example, several species of mosses, like the genera *Dicranum* and *Homalothecium*, possess an extreme form of sexual dimorphism in which dwarf males grow epiphytically on more typical sized females (Hedenäs & Bisang 2011; Rosengren & Cronberg 2014), a form of sexual dimorphism that may actually decrease male-male competition. Detailed studies relating the breeding system of a species to levels of sexual conflict are fertile areas for research in bryophyte biology.

Parent-offspring conflict over nutrient allocation: The fact that males and females differ in the amount of resources they allocate to reproduction also sets the stage for genomic conflict (Arnqvist & Rowe 2005). Theory suggests conflict is particularly likely for species that provision offspring through vivipary (Zeh & Zeh 2000). In embryophytes (i.e., land plants), the embryo is retained on the haploid, female gametophyte and water and nutrients are provided for a time through specialized transfer cells analogous to a placenta. The males, in contrast, have no role in providing for offspring after fertilization. A better provisioned embryo (sporophyte) is likely to make more and healthier spores, increasing the fitness of both the male and female. However, in species where the female can reproduce more than once, the allocation to one sporophyte may come at the expense of other sibling sporophytes (Stark *et al.* 2009). Therefore, female fitness is maximized by equal allocation to several offspring by modulating the transfer of nutrients across the placenta (Haig 2013). In contrast, a male may not mate with the same female again (nor any other female), so male fitness increases with every additional viable spore that an offspring sporophyte produces. Thus, paternal genes in the embryo are expected to evolve to extract as much of the female’s resources as possible to promote spore production (Haig 2013)). Recent data in *C. purpureus* supports the parent-offspring hypothesis. In test crosses, the same female crossed to two different males results in differences in sporophyte height, spore production, and spore germination, suggesting the paternal genotype influences the transfer of nutrients across the placenta (Shortlidge et al., submitted). Interestingly, the difference between the interests of the maternal and paternal contributions becomes more intense as the levels of outbreeding increase (Haig 2010), again highlighting the importance of the breeding system for shaping genetic conflict.

We expect that sex chromosomes may be enriched in genes that influence the flow of nutrients across the placenta from mother to offspring. In XY systems, only the degenerate Y chromosome shows sex-limited inheritance, potentially minimizing its role in parent-offspring conflict. However, autosomal genes that influence maternal transfer may have parent-of-origin effects depending upon whether they are transferred from the mother or father, an observation termed genomic imprinting (Reik & Walter 2001). What is striking about UV systems is the unusual pattern of inheritance of the sex chromosomes accomplishes what other systems do by genomic imprinting. Because the U and V chromosomes do not recombine, their interests diverge considerably in the developing UV-heterozygous embryo, providing a highly favorable environment for the fixation of diploid-acting, sexually antagonistic alleles that influence the flow of nutrients from the maternal (U) gametophyte to the offspring (UV) sporophyte. The U-linked maternal genes within the embryo are genetically identical to its nurturing mother, and therefore share a common interest, but the V-linked paternal genes in the embryo may have different interests regarding the amount of offspring provisioning (Haig & Wilczek 2006). Formal tests linking parent-offspring conflict to the expansion of UV sex chromosomes will likely involve a combination of placental transcriptomics, classical genetics, and transgenic approaches.

Sex-biased transmission ratio distortion: A final form of sexual antagonism that is common to all dioecious species with chromosomal sex determination is meiotic sex ratio distortion. The meiotic sex ratio in a wide variety of eukaryotes deviates from the expected 1:1 segregation of males and females (Lyttle 1993). At meiosis, any allele that preferentially transmits itself to the next generation has an immediate benefit, thus selection on these loci can be very strong because such alleles consistently have higher frequency in offspring. In principle, any heterozygous locus could experience biased transmission (Haig 2010). Distorter alleles may bias transmission by a wide variety of mechanisms, but in UV systems distorters generally disable meiotic products carrying the alternate allele. Mutations that result in more female offspring are likely to arise on, or be inherited with, the U, while mutations that distorter the sex ratio in favor of males will be associated with the V.

Most meiotic sex-ratio distorter systems typically consist of multiple distinct genes. Distorter systems require a killer locus that halts development or otherwise disables the products of meiosis, and a second locus which protects the distorting chromosome from being disabled. Thus, a distorting U chromosome would have a killer allele and an allele at the second locus that disarms the killer, often termed an insensitive-responder allele. The V chromosome, in contrast, would lack the killer and would carry a linked, sensitive-responder allele. Because the killer and insensitive-responder must be inherited together, genomic regions that lack meiotic recombination, like sex chromosomes, may be more likely to evolve distorter systems simply because they contain more genes that can potentially evolve the killing and resistance functions. As a meiotic killer system spreads, one sex could become rare, conditions which favor the evolution of alleles at a third locus that suppress the killer allele, restoring fertility. Although restorer alleles can arise on autosomes, the sex chromosomes are predicted to be hot-spots for the evolution of restorer alleles, too. Thus, because they contain large regions of suppressed recombination that have sex-limited inheritance, sex chromosomes are likely to accumulate multiple genes that influence the outcome of meiosis through either spore killing or fertility restoration.

A key difference between diploid and haploid mating systems is the action of a meiotic distorter most often will result in spore death. Because each spore directly contributes to forming the next generation of gametophytes, unlike sperm which contribute indirectly through fertilization of an egg, spore death causes a loss of fitness. Thus, the evolution of meiotic sex ratio distorters is likely to be held in check by the fitness cost caused by spore-killing, in addition to the reduction in mating opportunity cause by decreasing the frequency of one sex. Nevertheless, several spore killer systems segregate in fungi (e.g., (Hammond *et al.* 2012)) and variation in spore death in *C. purpureus* has a genetic basis (Shaw & Gaughan 1993; McDaniel *et al.* 2007; Norrell *et al.* 2014). Numerous questions remain regarding the true fitness costs of meiotic sex-ratio distortion, life history traits that promote the evolution of meiotic distorters, and the potential interactions among different forms of genetic conflict in shaping the gene content of the male and female sex chromosomes.

The central role of natural history in evolutionary genomics

In this review, we have argued that the wide variation in sex chromosome size and gene content may be explained by variation in levels of genetic conflict, and further that bryophytes provide the necessary variation to test this hypothesis. In UV systems, suppressed recombination is not confounded with sex-specific mutational biases, sex-specific inheritance, and sexual selection, making bryophytes well-suited for studying how conflicts affect both male and female sex chromosomes. Clearly this effort will be bolstered by sequencing additional bryophyte genomes, and we anticipate that soon we will have a clearer picture of the gene content and evolutionary history of an increasing number of sex chromosome systems. In addition, generating sex-linked markers will open numerous research avenues in many previously genetically intractable systems, enabling us to understand many sex-specific demographic phenomena (dispersal, growth, mating success, male-male competition, female choice, biased mortality, or effective population size), in addition to more effectively designing studies of sexual dimorphism, parent-offspring conflict, and meiotic sex-ratio variation.

Equally important, however, is the role that natural history and phylogenetics can play in contextualizing the results of genomic analyses. Life history features relating to patterns of mating in nature, in particular, may be central to modulating the role of genetic conflict in genome evolution. Bryophytes are one of the few terrestrial groups that contain large proportions of both hermaphrodites and species with separate sexes.

This circumstance makes bryophytes unusually well suited for linking sex chromosome history and molecular evolution to patterns of diversification. How often is speciation associated with a change in mating system? Are sex chromosomes more likely than autosomes to be exchanged among distant populations, or more likely to host loci that promote reproductive isolation? Does genetic conflict promote elevated rates of speciation (Crespi & Nosil 2013), or extinction (Price *et al.* 2010; Werren 2011), and under what conditions? Critically, bryophytes possess underexplored life history and taxonomic variation that may be used to draw general solutions to key questions regarding the long-term evolution of sex chromosomes across eukaryotes.

BOX 1: UV sex chromosomes are found in haploid-dioecious life cycles

In animals and vascular plants with genetically-determined separate sexes, sexual differentiation occurs in the diploid stage of the life cycle. Therefore, the sex of an individual is determined by the genotype at fertilization. In the XY system, the fusion of Y-bearing sperm with an X-bearing egg produces a male zygote (the heterogrametic sex), while the fusion of an X-bearing sperm with an X-bearing egg produces a homogametic, female zygote. In the ZW system, in contrast, the female is the heterogametic sex, meaning it produces Z or W-bearing eggs, which fuse with Z-bearing sperm. In these diploid systems, the non-recombining Y and W chromosomes are sex-specific (i.e., transmited only through the male or female line, respectively), while the X and Z are shared between both sexes and freely recombine, much like an autosome, in the homogametic sex. In both the XY or ZW systems, sexual differentiation is a diploid phenomenon.

In other multicellular lineages, including the Phaeophytes (brown algae), Rhodophytes (red algae), Chlorophytes (Ulvophyceae and Chlorophyceae green algae), and Bryophytes (mosses, liverworts, and hornworts), sex determination occurs in the haploid stage of the life cycle. As such, only one copy of a sex chromosome is present during sex expression, with individuals inheriting the U correlating with females and V with males. Indeed, since the sexes are already haploid, gametes are produced by mitosis not meiosis (Fig. 1). Fertilization of a U-linked egg and a V-linked sperm produces a zygote. Importantly, the zygote is monomorphic (i.e., non-sexed) and heterozygous at the sex determining factor - homogametic UU or VV individuals are never formed. At maturity the diploid individual, the U and V pair at meiosis and segregate independently into females and males (Bachtrog *et al.* 2011). Therefore, in UV systems both the U and V are sex-specific.

The U and V chromosomes are in some ways similar to mating-type (MT) loci found in fungi, algae, and other protists (e.g., (Ferris *et al.* 2010; Bazzicalupo *et al.* 2019). In these organisms, however, the gametes bearing alternate MT are not phenotypically distinct from one another (i.e., isogamous) and therefore do not have defined sexes (Fig. 3). Thus, while MT loci provide valuable systems for studying the evolution of suppressed recombination in the absence of anisogamy (Branco *et al.* 2017; Bazzicalupo *et al.* 2019), we restrict our focus here to true UV sex chromosomes.

BOX 2: Genomic analyses of UV systems

A growing number of genomic analyses of UV sex chromosomes systems (reviewed in (Coelho *et al.* 2018)) provide a foundation for comparative analyses between haploid and diploid sex chromosome systems (Table 1). One of the best genomically studied UV systems to date is the brown algae *Ectocarpus sp.* An ancestral-state reconstruction of sexual condition in brown algaes found dioecy evolved near the origins of this lineage (Luthringer *et al.* 2014) and molecular evidence indicate *Ectocarpus* and the kelps (Laminariales) may share a common UV system that evolved at least ~80-110 million years ago (MYA) (Lipinska *et al.* 2017) The U and V chromosomes in *Ectocarpus sp*. are relatively small (0.93 and 0.92 megabases (Mb) of the 205 Mb genome, respectively); (Ahmed *et al.* 2014). The non-recombining portions of the U and V have similar numbers of genes at 22 and 20, respectively, and share 11 homologous genes (Ahmed *et al.* 2014). Avia et al. (2018) found the *Ectocarpus* U and V-linked loci had an N_e about ½ the autosomal average, suggesting these chromosomes experience levels of selection similar to autosomal loci (Avia *et al.* 2018). As a result of suppressed recombination, the sex chromosomes show decreased codon bias (Lipinska *et al.* 2017) and increased TEs relative to autosomes in both sex-determining and pseudoautosomal regions (Ahmed *et al.* 2014; Luthringer *et al.* 2015). Consistent with the effects of degeneration, Lapinska et al. (2017) found evidence of gene loss from the ancestral brown algae sex chromosome, in addition to gene gain and gene movement to the autosomes (Lipinska *et al.* 2017).

Within the chlorophyte green algae, at least two UV sex chromosome systems evolved independently. Dioecy and MT loci evolved in the ancestor of the volvocine algae, including *Gonium pectorale*, *Volvox carteri,* and *Chlamydomonas reinhardtii* at least 200 MYA (Herron *et al.* 2009; Hamaji *et al.* 2016). Although, strictly speaking, only *Volvox* possess anisogamy and therefore true UV sex chromosomes, we mention the other species because the MT chromosomes and UV sex chromosomes are clearly homologous. The *Volvox* U and V are 1.51 and 1.13 of the 131 Mb genome and also have similar numbers of genes at 55 and 60, respectively, 50 of which are homologs between the two (Ferris *et al.* 2010). Consistent with the effects of suppressed recombination, the *Volvox* sex chromosomes have accumulated TEs (Ferris *et al.* 2010) and comparisons between *Gonium, Chlamydomonas,* and *Volvox* found evidence for gene loss (Hamaji *et al.* 2016). A second UV sex chromosome evolved in the lineage including *Ulva partita (Yamazaki et al. 2017)*. The 1.5 Mb *Ulva* U (referred to as MT+) and 1.0 Mb V (referred to as MT-) have some asymmetry in gene numbers with 67 and 46 genes, respectively, and share 23 homologs. While the size of the *Ulva partia* genome is currently unknown, the recent *Ulva mutabilis* genome is 98.5 Mb and *U. partia* may be similar (De Clerck *et al.* 2018). The discovery of sex-linked PCR markers in red algae (Guillemin *et al.* 2012), suggests that UV sex chromosomes independently evolved in this group, too, but genomic analyses are currently lacking.

Within the bryophytes, more than half of the approximately 20,000 described species are dioecious. Heteromorphic sex chromosomes have been observed using cytological methods in 16 unrelated genera (Allen 1945; Renner *et al.* 2017) and sex-linked molecular markers have been tested in several additional species (McLetchie & Puterbaugh 2000; McDaniel *et al.* 2007; Korpelainen *et al.* 2008; Baughman *et al.* 2017). Ancestral-state reconstructions of sexual condition first showed that bryophyte sex chromosomes may have ancient origins (McDaniel *et al.* 2013; Laenen *et al.* 2016) and emerging phylogenomic data support in liverworts they evolved at least 400 MYA and in mosses 300 MYA (Carey *et al.* 2020).

To date, the best studied bryophyte UV sex chromosomes are in the liverwort *Marchantia polymorpha*. The 4.37 Mb U chromosome contains 74 genes and the 6 Mb V contains 105 genes, with 20 shared homologs between the U and V, suggesting some asymmetry in size and gene number between the sexes (total genome size 225.8 Mb; (Okada *et al.* 2001; Yamato *et al.* 2007; Bowman *et al.* 2017). The gene density in the U and V-linked regions is ~5x lower than the autosomes, consistent with the accumulation of TEs due to suppressed recombination (Bowman *et al.* 2017). Early data in the moss *Ceratodon purpureus*, suggested the U and V sex chromosomes were large, and the recent chromosome-scale genomes found they are each ~110 Mb of the 360 Mb genome and harbor hundreds over 3400 genes. (Voglmayr 2000; McDaniel *et al.* 2007; Szövényi *et al.* 2015; Carey *et al.* 2020). Although, in contrast to *Ectocarpus (Avia et al. 2018)*, sex-linked genes in *C. purpureus* exhibited lower nucleotide diversity than an panel of autosomal loci (McDaniel *et al.* 2013), suggesting selection or demographic processes may shape these chromosomes.

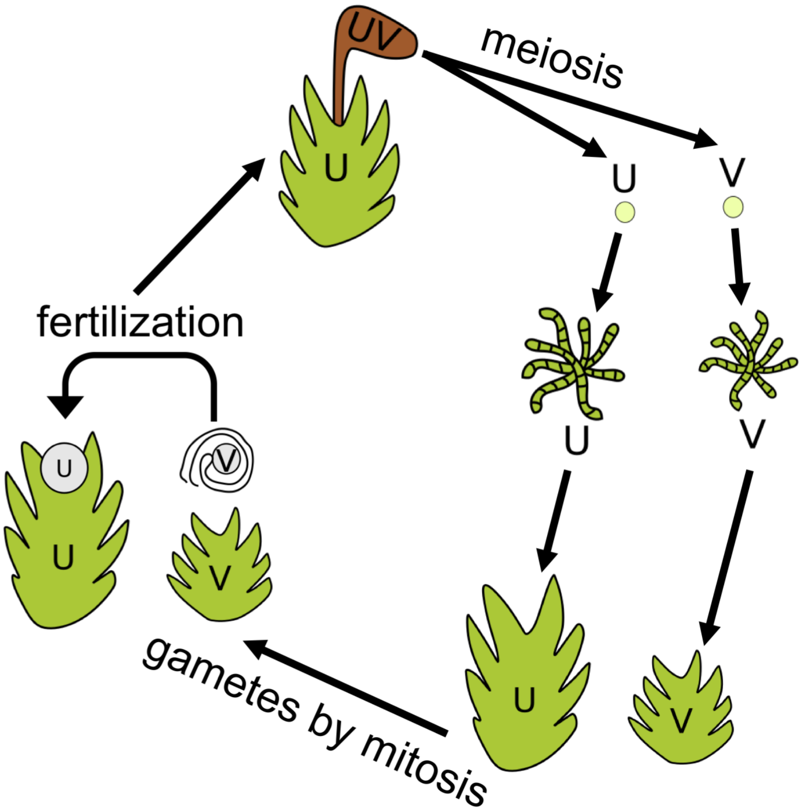

Figure 1. Life cycle of a dioecious moss. In mosses, the products of meiosis are haploid spores. For dioecious species, meiosis also segregates the U and V sex chromosomes in females and males, respectively. The spores germinate and produce protonemal filaments, upon which gametophores will develop. Because they are haploid, the male and female gametophores will produce gametes by mitosis. A V-containing sperm fuses with a U-containing egg, undergoing fertilization, and a diploid embryo (sporophyte) will develop on the maternal plant. The sporophyte embryo has both U and V sex chromosomes, but is considered a non-sexed stage, and within which the spores are produced.

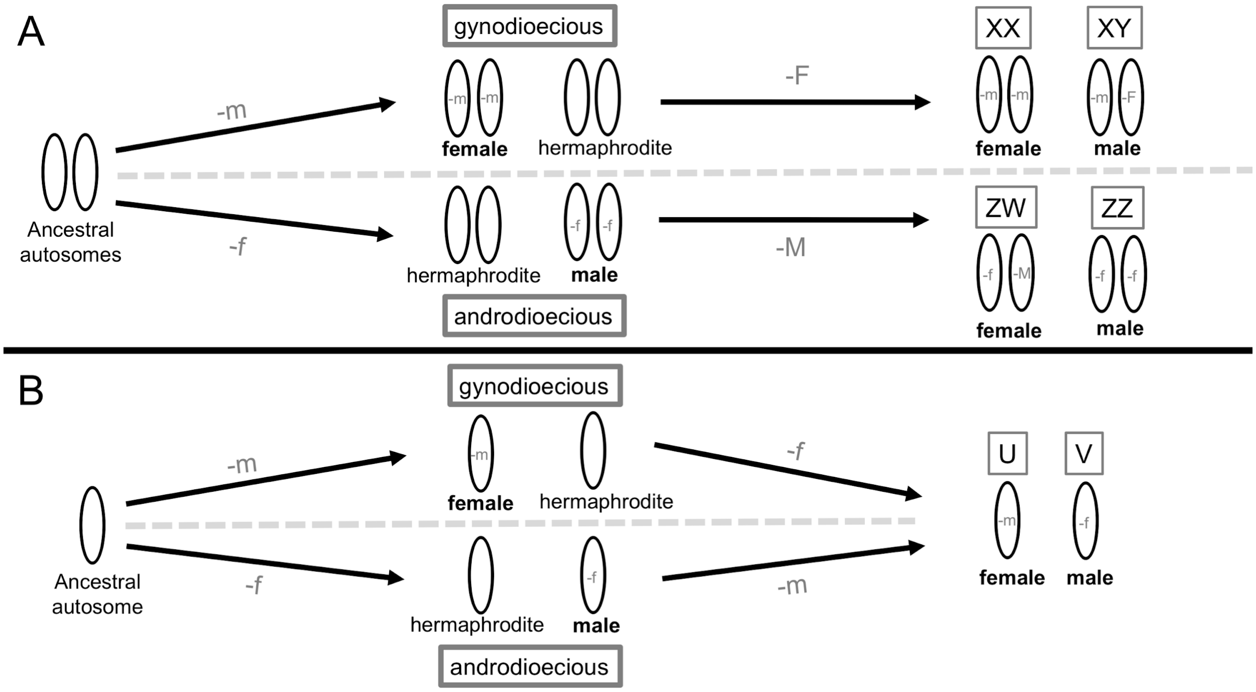

Figure 2. Two-locus model for the evolution of XY, ZW, and UV sex chromosomes. For diploid sex chromosomes (A) that originate from an ancestral pair of autosomes, a recessive male-sterility mutation (-m) first evolves, making a gynodioecious population (females and hermaphrodites). From the gynodioecious population a dominant female-sterility mutation (-F) arises making males. Once recombination is suppressed between these sex-determining loci, sex chromosomes are formed. This pathway leads to an XY sex chromosome system. If from an ancestral autosomal pair, a recessive female-sterility mutation (-f) evolves first, making an androdioecious population, followed by a dominant male-sterility mutation (-M), the result is a ZW sex chromosome system. In contrast in haploid sex chromosome evolution (B), if a male or female-sterilty mutation evolves first, followed by sterility mutation of the opposite sex, the result is always a UV sex chromosome.

Table 1. Comparison of XY, ZW, and UV characteristics. Males (M); females (F); Effective population size (N_e); Transposable elements (TE)

Characteristic	**X**	**Y**	**Z**	**W**	**U**	**V**
Inheritance pattern	M and F	M	M and F	F	F	M
Hemizygosity	M	M	F	F	diploid phase	diploid phase
Expected Ne, relative to autosomes	3/4	1/4	3/4	1/4	1/2	1/2
Suppressed recombination	NA	Yes	NA	Yes	Yes	Yes
TE content, relative to autosomes	similar	higher	similar	higher	higher	higher
Gene density, relative to autosomes	similar	lower	similar	lower	lower	lower
Gene-content bias	NA, F, or M-biased	M-biased	NA, F, or M-biased	F-biased	F-biased	M-biased

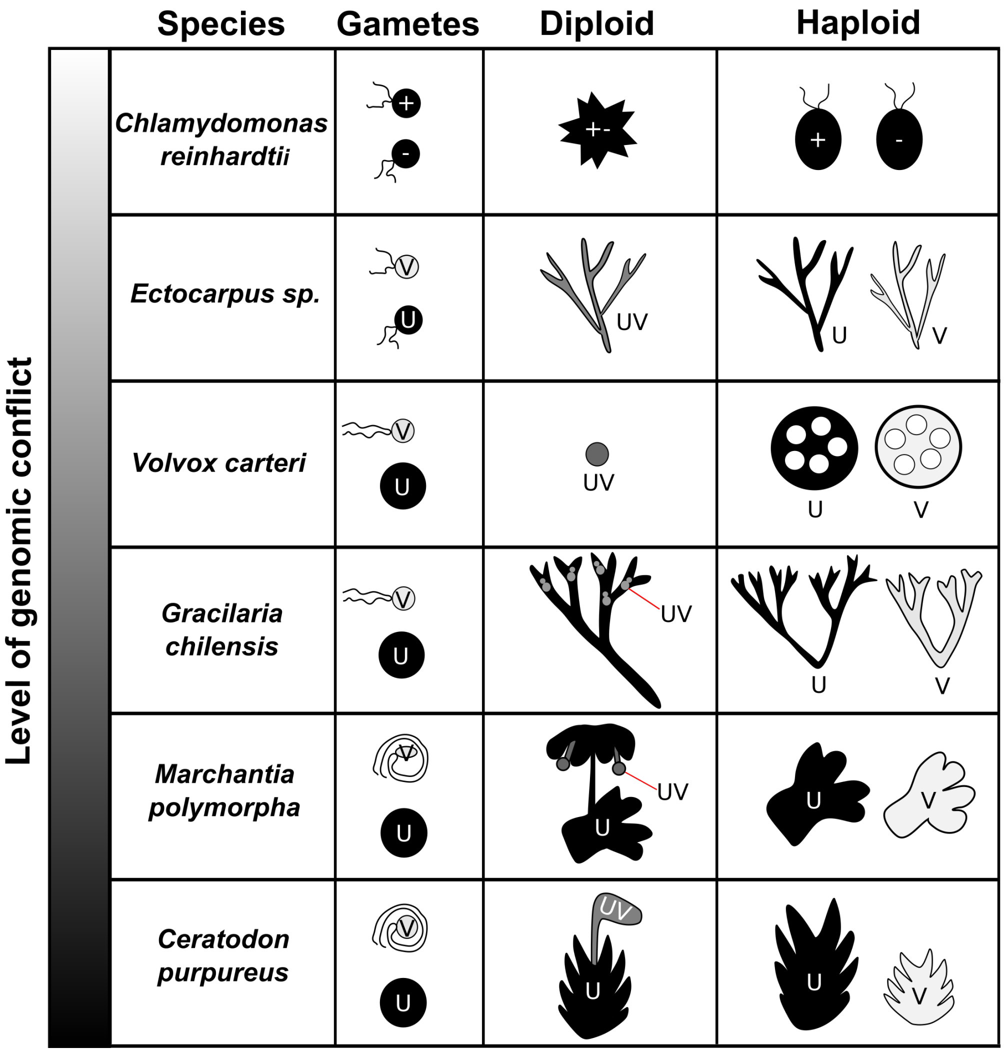

Figure 3. Predicted intensity of genomic conflict among UV systems. The level of genomic conflict is lower in mating-type loci because they do not have separate sexes, so cannot be sexually dimorphic, have parent-offspring conflict, or sex-ratio distortion. Across UV systems, the level of genomic conflict increases as the number or intensity of conflicts increases. Sexual dimorphism tends to be low in algaes and is generally greater in magnitude in bryophytes. Parent-offspring conflict depends on the amount of time the embryo remains nutritionally dependent on the maternal plant, which tends to be longer in bryophytes. Sex-ratio distortion is possible is all systems, except perhaps in

mating-type loci. Although we note there are limited studies on these metrics across UV systems and other closely-related species may have higher or lower levels of these genomic conflicts.

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