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UV chromosomes and haploid sexual systems

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Abstract

The evolution of sex determination continues to pose major questions in biology. Sex determination mechanisms control reproductive cell differentiation and development of sexual characteristics in all organisms, from algae to animals and plants. While the underlying processes defining sex (meiosis and recombination) are conserved, sex determination mechanisms are highly labile. In particular, a flow of new discoveries has highlighted several fascinating features of the previously understudied haploid UV sex determination and related mating systems found in diverse photosynthetic taxa including green algae, bryophytes and brown algae. Analyses integrating information from these systems and contrasting them with classical XY and ZW systems are providing exciting insights into both the universality and the diversity of sex-determining chromosomes across eukaryotes.

Sex chromosomes and sex determination: variations on a theme

Meiotic sex and recombination, and the resulting alternation between haploid and diploid life cycle phases, is an ancestral, highly conserved process [1]. Meiotic recombination creates genetic variation by generating new combinations of gene variants (alleles). Many eukaryotes produce gametes of equal size (isogamy), and this is thought to be the ancestral state [2], while others have evolved to produce differentiated male and female gametes (anisogamy and oogamy). In isogamous species the distinct types of gamete are referred to as mating types, while in anisogamous/oogamous species the gametes are defined as either male (the smaller-sized gamete) or female (the larger-sized gamete). Separate male/female sexes have arisen independently and repeatedly during eukaryotic evolution, and are specified by a bewildering diversity of mechanisms ranging from purely genetic to epigenetic, or some combination of the two [3].

The sex of an individual may be determined during either the haploid or the diploid phase of the life cycle (Box 1). When sex is determined genetically in organisms with haploid-phase sex determination systems, the chromosomes that contain the sex-determining region (SDR) are referred to as U and V sex chromosomes [4]. In anisogamous and oogamous organisms, females carry a U chromosome, whereas males carry a V chromosome. UV chromosomes are relatively common among eukaryotes and arose independently in different eukaryotic groups several times during evolution (Figure 1). However, for many years research has focused exclusively on XY and ZW systems, leaving UV chromosomes and haploid sex determination largely neglected. The UV designation pertains to organisms with male and female sexes and not to those with isogamous mating types, but this distinction is somewhat artificial. For example, in volvocine algae the chromosome containing the *MT-* mating locus in isogamous species corresponds phylogenetically to the V chromosome carried by males in anisogamous/oogamous species, and the chromosome with the *MT+* locus corresponds to the U chromosome [5]. We retain the conventional usages of UV and mating-type chromosomes here, but note that theoretical predictions and empirical data support similar evolutionary processes operating in both. This review focuses on recent advances in the characterisation of haploid sex determination systems in photosynthetic eukaryotes. It is important to note, however, that many fungi have haploid sexual systems with properties similar to those of the systems described here (e.g. [6]). Several recent papers have focused on haploid mating types and sex determination in fungi (e.g.[7–9]).

Modelling the evolution of UV chromosomes

The repeated independent evolution of sex chromosomes across the eukaryotes represents a remarkable example of genomic convergence because these chromosomes share many properties. The evolution of dimorphic sex chromosomes is assumed to be driven largely by reduced recombination that arises in order to maintain tight linkage between sex-determining and/or sex-related genes (Box 2; reviewed in [4,10]). Compared with autosomes, sex chromosomes experience different mutation and recombination rates, effective population sizes and levels of sexual selection, and these differences may profoundly affect their evolution. In diploid systems, the X or the Z chromosomes experience two different environments depending on whether they are in the homomorphic state and recombination can occur (XX and ZZ) or in the heteromorphic state (XY or ZW) where recombination is blocked, thus making the evolution of the X versus Y or Z versus W chromosomes inherently asymmetric. By contrast, in haploid systems the female U and the male V

experience largely similar and symmetrical recombination environments since they are either unpaired in the haploid gametophyte or paired heteromorphically in UV sporophyte diploids [11]. As a result, both the U and the V SDRs are expected to exhibit the degenerative effects of arrested recombination and reduced effective population size to a similar extent. Moreover, because U and V chromosomes function in the context of an extended haploid life cycle phase when only one sex chromosome is present in each cell, deleterious mutations are expected to be more efficiently purged diploid phase sexual systems where there is greater opportunity for sheltering of deleterious alleles [11,12]. Consequently, degeneration of UV chromosomes is expected to occur more slowly than for diploid phase sex chromosomes (XY or ZW). Note, however, that deleterious mutations in SDR genes can be masked if these genes function during the diploid sporophyte phase and this may allow both the U and V chromosomes to degenerate to some extent [13,14]. Unlike XY or ZW chromosomes where gene loss on the non-recombining portion of the Y or W chromosome is a prevalent long-term outcome, the fate of non-recombining genes in UV systems is more likely to be allelic differentiation between the U and V copies where neither copy can be lost, but over time, polymorphisms in either member of the gametolog pair will become fixed through a combination of drift, positive selection and/or hitchhiking. As a result, UV systems are predicted to exhibit gametolog differentiation and not gene loss as a long-term outcome of suppressed recombination [13]. It has also been suggested that changes in the size of the U or V should involve predominantly sequence gains including additions of beneficial (but not essential) genes and/or relatively neutral sequences such as repeats and transposons rather than gene loss [11]. Although U and V chromosomes are expected to evolve similarly, verbal models predict they may exhibit some asymmetry if sexual selection is stronger in one of the sexes [11]. Recent mathematical modelling predicted a gradual decrease in the amount of recombination between U and V chromosomes and addition of strata via successive inversions or rearrangements in flanking sequences, just like in diploid sex chromosome systems (Box 2). Note that the theoretical predictions described above are valid both for UV chromosomes and chromosomes carrying mating type loci (MTL) provided there is even minor differential selection between the two mating types favoring decreased recombination [13].

The empirical era – a range of haploid sexual systems revealed by next- generation sequencing

Over the last decade a growing amount of information has become available about the structure (Table 1) and evolution of UV chromosomes and MTLs, and the taxonomic breadth of haploid sexual systems under study has increased considerably. The sections below highlight some recent advances

93 in representative UV systems from the chlorophyte, bryophyte and brown algal lineages.

94 Volvocine algae

95 Overview

96 Volvocine algae are a related group of chlorophytes (green algae) that collectively form a fascinating
97 study set for the evolution of sex and sex chromosomes. Although volvocine algae are not a formal
98 taxonomic grouping, the multicellular members form a monophyletic clade including genera that
99 exhibit different degrees of sexual dimorphism from isogamy, to anisogamy and oogamy [15]. The
100 isogamous unicellular species *Chlamydomonas reinhardtii* is an outgroup that is included in the
101 volvocines due to its high degree of relatedness to the multicellular members [16]. The volvocines
102 and most other green algae have a haplontic life cycle where vegetative haploid cells or individuals
103 can reproduce mitotically, but under appropriate conditions transition to a sexual phase that involves
104 gametic differentiation and mating to form a diploid zygotic resting spore. Under favourable
105 conditions the environmentally-resistant spores reawaken and undergo meiosis to produce new
106 haploid vegetative progeny. The majority of volvocine algae are heterothallic (dioicous), and the
107 lineage as a whole appears to be ancestrally heterothallic, but homothallism (monoicy) has arisen
108 independently within the volvocines multiple times [17]. The MTLs/SDRs of volvocine algae control
109 not only mating type/sexual differentiation, but also govern uniparental organelle inheritance
110 [18,19]. Complete MTLs/SDRs sequences are currently available for five volvocine species including
111 isogamous (*Chlamydomonas reinhardtii*, *Gonium pectorale*, *Yamagishiella unicocca*), anisogamous
112 (*Eudorina* sp.) and oogamous (*Volvox carteri*) representatives [20–22]. A series of studies on volvocine
113 MTLs/SDRs, starting with the well-established model *C. reinhardtii* [23] have documented results that
114 are in agreement with predictions for UV chromosome or MTL evolution, as well as unexpected
115 findings that were not anticipated by theoretical models. The molecular-genetic basis of mating-type
116 determination and sex determination in volvocine algae is continuous throughout the lineage where
117 a conserved transcription factor gene, *MID*, is found in either the *minus* mating type of the MTL or in
118 the V (male) chromosome SDR in all dioicous species [20,22,24–26] (Box 4). A few additional mating-
119 type-linked or sex-linked genes with functions in the sexual cycle have also been described in
120 volvocine algae including the *MT+*/female gamete-fusion protein coding gene *FUS1* and the *MT-*
121 /male gene *MTD1*, though none are as universally conserved as is *MID* [18,22].

122 Structure and molecular evolution of volvocine MTLs/SDRs

123 In models of UV chromosome evolution, the non-recombining MTL/SDR can expand through

124 additional rearrangements or insertions of sequences that were formerly autosomal leading to
125 formation of distinct "strata" whose residence times in the non-recombining region can be estimated
126 based on divergence between gametologs (in the case of rearrangements) or between the MTL/SDR-
127 linked and autosomal copies of sequences (in the case of insertions) (Figure 3) [27,28]. It might be
128 expected that the history of volvocine MTLs/SDRs could be elucidated based on structural and
129 molecular comparisons of shared regions and/or gene content. On the contrary, the five known
130 MTLs/SDRs of volvocine algae vary greatly in size (7kb to >1Mb) with none of them sharing strata or
131 structural features; and few of their genes appear to be long-term permanent residents[22]. This lack
132 of structural continuity suggests relatively frequent turnover of volvocine MTLs/SDRs. Interestingly,
133 however, the U/V or mating type chromosome in which the volvocine MTLs/SDRs reside has
134 remained the same across the lineage, a conclusion inferred from the conservation of genes in and
135 around the MTLs/SDRs from different species [20,22]. This contrasts with some animal systems, for
136 example, where new SDRs have emerged on what were originally autosomes as a result of genes on
137 these chromosomes evolving a primary sex-determining role during evolution [29–31]. It is not
138 known what mechanisms might bias the volvocine MTL/SDR towards remaining on the same
139 chromosome when it turns over.

140 ## Recombination and gametolog divergence patterns

141 Four volvocine MTLs/SDRs (*Chlamydomonas*, *Gonium*, *Yamagishiella* and *Eudorina*) appear youthful
142 based on very low divergence between gametologs, lack of gametolog decay, and relative paucity of
143 intergenic repeats [21,22,32]. However, as in the case for some amphibian sex chromosomes,
144 youthful-appearing MTLs/SDRs may not be so young [33]. A more extensive study of gametolog
145 divergence and stratum formation in *Chlamydomonas* revealed that, although crossover
146 recombination is undetectable across the MTL and flanking pseudoautosomal region (PAR) [23] there
147 has clearly been a history of gene conversion between gametologs and between PAR genes that
148 neighbour the MTL, evidenced by extensive allele sharing between mating haplotypes [32]. Using
149 mutant or transgenic strains with reversed mating types, a test was performed for recombination
150 when the two MTLs were collinear during meiosis (i.e. *MT+/MT+* or *MT-/MT-*). Surprisingly, the
151 homozygous MTL strains behaved differently from each other, with normal rates of recombination
152 within the MTL observed after meiosis with *MT+/MT+* diploids, but no MTL recombination in *MT-*
153 */MT-* diploids (which had normal recombination outside of the MTL [32]). It was inferred from this
154 asymmetric behaviour that there may be recombination suppressor sequences in the

155 *Chlamydomonas MT-* that can act independently of sequence rearrangements. Another difference
156 between the *Chlamydomonas MT* haplotypes is the insertion in *MT+* of three autosome-derived
157 regions and of a large tandem segmental repeat which together make the *MT+* region (~396 kb)
158 significantly larger than the *MT-* (~204 kb) [32]. Whether this size asymmetry is connected to the
159 recombination asymmetry of the two *MT* haplotypes is unknown, but in any event, it represents an
160 example of a size difference arising in the SDR/MTL of a haploid system in the absence of any
161 apparent differential selection between mating types or sexual antagonism. Interestingly, genes
162 within each of the three autosome-derived regions in the *MT+* mentioned above exhibited a wide
163 range of neutral divergence rates from their autosomal counterparts and could not be reliably binned
164 into strata [32], so the relative timing of autosomal sequence additions to the *Chlamydomonas* MTL
165 is unclear.

166 In *Gonium*, *Yamagishiella* and *Eudorina* MTLs/SDR, there are no insertions of autosome-derived
167 sequences and very little neutral divergence between gametologs [21,22]. Whether this lack of
168 gametolog differentiation is due to youthfulness of the MTLs/SDR, ongoing homogenization through
169 gene conversion, or some combination of the two, is not known. On the other hand, the *Volvox carteri*
170 SDR is very different from the other four volvocine MTLs/SDR in terms of its large size (>1Mb), low
171 gene density, extensive gametolog differentiation, reduced codon adaptation, and completely
172 arrested recombination that spans several speciation events [20]. These properties of the *Volvox* SDR
173 make it conform more closely than the other volvocine MTLs/SDRs to the predicted properties of a
174 "mature" UV sex chromosome system.

175 ## Ostreococcus

176 Prasinophyte marine picoalgae in the genus *Ostreococcus* have compact genomes (13 Mb) that are
177 likely the result of genome reduction, but scans for meiotic genes and population genetic studies
178 both support the presence of a sexual cycle being retained in this group [34–37]. A recent study
179 examined a candidate mating type chromosome (Chr 2) from different *Ostreococcus tauri* isolates
180 and found two divergent haplotypes designated *M-* and *M+* with candidate MTL regions of 650 kb
181 and 450 kb respectively [34]. The genes within these candidate MTLs are suppressed for
182 recombination and have high inter-haplotype divergence that extends through one or more
183 speciation events. These results indicate that the two candidate MTL haplotypes of *Ostreococcus*
184 have persisted in the population for up to 600 MY since the origins of the class Mamiellophyceae
185 which includes the genus *Micromonas* where evidence of meiotic genes and a possible MTL have also

186 been described [38]. Interestingly, the *M-* candidate MTL haplotype has a predicted RWP-RK
187 transcription factor gene that may function in mating-type determination like the volvocine algal
188 gene *MID* (see Box 4), though the function of this gene remains to be tested. While population
189 genomics and protein-coding gene predictions provide compelling evidence for an active sexual cycle
190 in *Ostreococcus*, sex has not been directly observed in this genus, so a formal association between
191 the candidate *M-* and *M+* haplotypes with mating-type differentiation has yet to be made.

192 ## Bryophytes

193 Bryophytes (liverworts, hornworts and mosses) are an informal taxonomic grade of early diverging
194 land plants (embryophytes) which retain an ancestral gametophyte-dominant life cycle with a
195 reduced diploid sporophyte generation. Their sexual cycles are oogamous, with monoicous and
196 dioicous species found among members of all three groups [39,40] (see also Box 3). Many bryophytes
197 are amenable to cytological evaluation and surveys revealed some dioicous species with dimorphic
198 sex chromosomes that are easily distinguishable based on their sizes while others appear to have
199 homomorphic sex chromosomes [41].

200 The dioicous liverwort *Marchantia polymorpha* is an emerging model for early embryophyte
201 evolution and developmental studies, including sex determination [42]. Partial characterization of its
202 male (V) chromosome [43] has been followed more recently by full genome sequencing of male and
203 female strains where candidate SDRs for both U and V chromosomes (referred to as X and Y in
204 Bowman 2017 and older literature) were identified [44]. The complete *M. polymorpha* genome is
205 around 226 Mb with a V chromosome of around 10 Mb and a U chromosome estimated to be ~20
206 Mb [43]. The V chromosome has a ~4 Mb male-specific, low complexity repeat region while the U
207 chromosome has a larger, less well characterized presumed repeat region that is at least partly
208 composed of rDNA repeats [45,46]. The relatively gene-rich/high-complexity portions of the U and V
209 chromosomes encompass 4.4 Mb and 6.0 Mb respectively and will be referred to as SDRs, but it
210 should be noted that additional male-specific or female-specific genes could be contained in the non-
211 assembled repeat regions of the *Marchantia* U and V.

212 The *Marchantia* U and V SDRs contain 75 and 99 total genes, respectively, including 20 gametologs
213 that are expressed primarily in the vegetative phase and encode conserved green-lineage proteins
214 (Table 1) [43,44]. The gametologs are saturated for neutral substitutions indicating long-term
215 absence of recombination that likely extends back to the origins of the class Marchantiopsida. In
216 addition, the male and female SDRs show signs of degeneration with five-fold lower gene densities

217 compared to autosomes and abundant transposon-derived sequences. A strikingly high proportion
218 of the V-specific genes with detectable expression were expressed mainly during sexual reproduction
219 (53/62), and several of them had annotated motility functions that are likely associated with
220 spermatogenesis [43,44]. For U-specific genes a majority with detectable expression (23/39) were
221 also preferentially expressed during the reproductive phase [44], and among them may be one or
222 more feminizer loci that can dominantly determine sex in diploid *Marchantia* gametophytes, which
223 differentiate as sterile females [47]. Several MYB-family predicted transcription factors are among
224 the sex-induced U-specific genes in *Marchantia*, but they do not appear to be conserved in related
225 species. Notably, many of the sex-induced female genes were located on small scaffolds that are
226 presumably embedded in repeat regions and could not be easily assembled, and there may be
227 additional undetected U chromosome candidate feminizer genes that are not present in the current
228 U chromosome assembly [44]. Overall, the *Marchantia* UV chromosomes conform to predictions
229 regarding loss of recombination, gametolog differentiation, accumulation of non-coding repeat
230 sequences and preferential retention or acquisition of male/female specific genes on the U/V.

231 Although bryophyte sex chromosome cytology has been extensively described [41], there has been
232 little molecular characterization of UV systems outside of *Marchantia* [48]. One notable example is
233 the moss *Ceratodon purpureus* whose heteromorphic sex chromosomes are around five-fold larger
234 than the autosomes and which have been genetically mapped [49]. There is currently no published
235 genome sequence for *Ceratodon*, but several UV-linked gametologs and autosomal protein coding
236 genes were identified and characterized from a population genetic study along with their orthologs
237 from closely related sister taxa [50]. This study uncovered significantly different levels of divergence
238 between two subsets of the gametolog pairs, suggesting that at least two strata contributed to
239 formation of the present-day *Ceratodon* sex chromosome. With the addition of genome sequences,
240 including assembled U and V chromosomes, *Ceratodon* could become another very informative
241 model for understanding the evolution of UV systems.

242 ### *Ulva*

243 *Ulva partita* is a multicellular green algal species, exhibiting a typical haplo-diplontic life cycle with
244 isomorphic gametophyte and sporophyte generations (Box 1). Male and female gametophytes are
245 morphologically indistinguishable, and produce slightly anisogamous gametes with two mating types,
246 *MT*− and *MT+* [51]. Recent sequencing of the UV chromosomes of this species revealed that its MTL
247 spans 1-1.5 Mbp of highly rearranged non-recombining sequence, with 46 and 67 genes, respectively,

248 in the *MT+* and *MT-* haplotypes, of which about half are gametologs ([52]; Table 1). Suppression of
249 U/V recombination appears to have preceded the diversification of the Ulvales (about 166 Mya,
250 http://timetree.org/). Like the case in volvocine algae, no obvious strata could be detected. This could
251 be because they do not exist or because strata are no longer detectable due to extensive
252 rearrangements or divergence.

253 A particularly interesting feature of *Ulva* is that the gametophyte and sporophyte generations are
254 isomorphic and therefore likely to require expression of similar genes in both life cycle phases. As a
255 result, the majority of the genome may be exposed to haploid purifying selection and its MTL should
256 evolve under similar constraints as in haploid-dominant UV systems. Consistent with this idea, the
257 *Ulva* MTL showed signs of weak degeneration, evidenced by relaxed codon usage for a subset of
258 genes, decreased expression of haplotype-specific genes and lower gene density, although
259 transposable element density was comparable with that of autosomes. Intriguingly, the *Ulva partita*
260 *MT-* contains a gene of the RWP-RK family (*RWP1*) that exhibits an expression pattern consistent with
261 a role in reproduction. The relationships between *RWP1*, the volvocine algal *MID* clade (see Box 4)
262 and other *RWP* genes from the green lineage were not clearly resolved in phylogenetic
263 reconstructions leaving open the question of whether *RWP1* is *a MID* ortholog or was convergently
264 recruited for a putative (but still untested) role in *Ulva* sex determination.

265 ## Brown algae

266 The filamentous brown alga *Ectocarpus* has a haplo-diplontic life cycle. Gametophytes and
267 sporophytes are slightly dimorphic and there is a small but significant difference in size between male
268 and female gametes [53]. The *Ectocarpus* UV sex chromosome SDRs exhibit low gene density and
269 accumulation of repeated DNA (Table 1). The U and V SDRs have similar sizes and each contains a few
270 dozen genes, about half of which are members of gametolog pairs [54]. Many of the *Ectocarpus* SDR
271 genes have autosomal copies, and in some cases sex-specific genes appear to have moved into the
272 SDR very recently [54,55]. Both the male and female SDR show clear signs of degeneration, despite
273 the predicted action of purifying selection during the haploid phase of the life cycle. *Ectocarpus*
274 gametophytes and sporophytes are morphologically dimorphic [56], thus U- or V-specific genes that
275 are expressed during the diploid sporophyte phase are expected to be sheltered and are therefore
276 free to degenerate [11,57]. Consistent with this prediction, genes belonging to gametolog pairs that
277 have a role during *Ectocarpus* gametophyte development have largely escaped degeneration and
278 conversely, a subset of genes that are expressed during the diploid phase show signs of greater

279 degeneration. Interestingly, most female-specific SDR genes are weakly expressed and many are
280 pseudogenised. This is consistent with the male sex being dominant, and suggests that female fate
281 may be engaged in the absence of the master male sex-determining factor [54]. Interestingly, in
282 another brown alga with UV chromosomes (*Undaria pinnatifida*), genetically male (V-bearing)
283 individuals in certain field populations may develop both male antheridial and female oogonial
284 structures on the same individual (i.e. are monoicous [58]). Taken together these findings suggest
285 that the U SDR is not necessary for an individual to become a functional female. Note however that
286 decreased fitness was observed in these monoicous strains, suggesting that some of the genes in the
287 female SDR increase female fitness [58].

288 Comparative analysis of the U and V SDRs of several brown algal species has indicated that
289 recombination between these two regions halted more than 100 Mya [54]. At least 26 genes are
290 estimated to have been present in the ancestral SDR, and although a set of six SDR genes have been
291 consistently sex-linked over the 100 MY period, there has been a remarkable level of gene traffic in
292 and out the SDR, much the same as in volvocine algae (see above). Conserved sex-linked genes
293 include two pairs of gametologs and a male sex-specific gene, which is strongly upregulated at fertility
294 in *Ectocarpus* [55]. This male-specific gene is a predicted HMG-domain transcription factor.
295 Interestingly, HMG-domain protein coding genes are also involved in mating-type and sex
296 determination in fungi and mammals [59,60]. Given the dominance of male sexual differentiation in
297 *Ectocarpus* UV diploid gametophytes, this gene is a strong candidate for the sex-determining gene,
298 but confirmation of this hypothesis awaits functional validation. Currently no method is available to
299 generate stable gene knockouts in *Ectocarpus*, although RNAi is an effective method for transient
300 gene knockdown [61]. Naturally occurring strains, such as the monoicous *U. pinnatifida* strains
301 described above [58], represent a potentially interesting resource for such mechanistic analyses if
302 they use the same sex-determining gene as *Ectocarpus*.

303 The study of brown algal UV chromosomes has also shed light on the evolution of the PAR, a genomic
304 region that has been largely understudied even in diploid systems. Recent studies of the *Ectocarpus*
305 sp. PAR revealed an accumulation of physically linked clusters of genes with increased expression in
306 the sporophyte (i.e. silenced in the gametophyte) in the *Ectocarpus* PAR. A mathematical modelling
307 approach indicated that the PAR of UV systems is a favourable location for genes with an advantage
308 for the sporophyte (provided there is a difference in the strength of selection when they occur in
309 male or females [62]). These results highlighted the potential impacts of life cycle features on the

evolution of UV sexual systems.

Concluding remarks and future perspectives

Our understanding of UV sex chromosomes has progressed rapidly in recent years. Bringing together information from the diverse systems currently under study, some general conclusions can already be drawn. UV sex chromosomes exhibit many of the unusual features identified in XY and ZW systems such as the presence of often extensive non-recombining regions characterised by low gene densities and at least some evidence of gene degeneration. Specific theoretical predictions, such as symmetric evolution of the U and V SDRs and a tendency for at least some gene function to be conserved within the SDR due to haploid selection, have been partially confirmed. However, not surprisingly, the reality is more complex than theoretical predictions. The analyses of UV systems have even provided some novel insights in areas that have not been looked at in detail using XY or ZW systems. These include, for example, gene traffic in and out of the SDR, structural and evolutionary features of the PAR and the evolution of sex chromosomes from mating type loci.

Despite these impressive beginnings, a lot still remains to be learned about UV sexual systems. There are marked differences between patterns and rates of evolution of different UV systems and the role of factors such as the degree of gamete and/or sporophyte/gametophyte dimorphism in influencing these differences needs to be investigated. Evolutionary strata have been detected in UV SDRs but it is not yet clear whether they are a general features of UV systems and why such regions do not always stably persist across related taxa. Sex chromosomes are known to play an important role during speciation (e.g. [31,63,64]) but this is another feature of UV systems that has not yet been investigated. Importantly, more information is needed about how genes on UV chromosomes function in sex determination. A related question is the extent to which sexually antagonistic loci play a role in UV chromosome evolution (see Outstanding Questions). Sex-determining genes have been identified, or strong candidates are available, for several UV systems but further work is needed in this area to obtain a general picture of UV sex-determining genes and the pathways they control. The finding that RWP-RK encoding genes are linked to MTLs or SDRs in different green algal taxa poses the possibility of deep homology for sex determination in the chlorophytes, and the finding of an HMG encoding gene as a possible brown algal sex determining gene suggests a potentially intriguing convergence with fungi and metazoans. Another unknown aspect of sex determination for most UV systems is the degree to which both the U and the V are actively involved in determining sex and, in instances where this is not the case, whether this might lead to asymmetry between the

341 patterns of U and V chromosome evolution. A related question involves the mechanism by which UV
342 systems and epigenetic sex determination systems transition back and forth. Finally, the origins of
343 UV chromosomes and their relationships to more ancestral mating systems remains unexplored in
344 most taxa. On a broader evolutionary scale, the fucales within the brown algae and some bryophyte
345 species provide opportunities to understand how ancestral UV systems might have evolved into XY
346 or ZW chromosomal systems. More extensive genome characterisation among key taxa coupled with
347 functional analyses are expected to provide important insights into all these exciting questions in the
348 coming years.

349 **Box 1. Life cycles and sex determination**

350 A typical eukaryotic sexual life cycle involves alternating phases with diploid to haploid transitions
351 occurring through meiosis, and haploid to diploid transitions through syngamy (i.e., fusion of two
352 haploid gametes) (see Figure I). Life cycles can be defined as diplontic, haplontic or haplo-diplontic
353 depending on whether mitotic divisions (cell proliferation or multicellular growth) occur during the
354 diploid phase, during the haploid phase or during both phases, respectively. For diplontic organisms
355 (e.g. humans), sex determination occurs during the diploid phase while in haplontic organisms (e.g.
356 the green alga *Volvox*), sex determination is in the haploid phase. For an organism with a haplo-
357 diplontic life cycle, however, sex can be determined during either the diploid (e.g. *Silene latifolia*) or
358 the haploid (e.g. *Marchantia polymorpha*) phase of the life cycle. Different terminologies are used to
359 clearly distinguish between diploid and haploid phase sex determination systems. For example, for
360 diploid phase systems, organisms are monoecious if the same individual produces gametes of both
361 sexes (e.g. *Zea mays*) and dioecious (or gonochoric) if individuals produce either male or female
362 gametes, but not both (e.g. *Silene latifolia*). For haploid phase sexual systems, however, the
363 equivalent terms are monoicous (i.e. individuals produce both gamete types, e.g. mosses) and
364 dioicous (i.e. sperm and eggs are produced by genetically distinct male or female individuals, e.g.
365 *Marchantia polymorpha*).

366 **Box 2. Models for the evolution of UV systems compared with XY/ZW systems**

367 In the commonly accepted model for sex chromosome evolution, sex chromosomes evolve from
368 autosomes, initially by the acquisition of a sex-determining locus. Emergence of sexually antagonistic
369 alleles at loci in close proximity to the sex-determining locus selects for recombination suppression
370 between the X and Y (or Z and W) chromosome, resulting in formation of a first stratum, which

371 undergoes heterochromatinisation. Once recombination is arrested on the Y or W chromosome,
372 genes without sex-specific benefits often become pseudogenes. The non-recombining region can
373 expand with the acquisition of additional sexually antagonistic alleles and further recombination
374 suppression, leading to additional strata (spatial clusters of XY or ZW gametologs with similar degrees
375 of divergence). Strata have been observed in mammals, birds, fish and plants; reviewed in [3]. The
376 lack of recombination leads to accumulation of repetitive DNA, which can lead to a short-term
377 increase in the size of the Y or W, but which typically results in large-scale deletions, a large reduction
378 in physical size of the sex-limited chromosome, and highly heteromorphic sex chromosomes.

379 Figure I shows possible mechanisms involved in the evolution of the non-recombining sex or mating
380 type determining regions on UV or haploid mating type chromosomes (B-D) compared with diploid
381 sex chromosome systems (A). Note that a XY system is illustrated, but similar processes are expected
382 to occur in ZW systems. Sexual antagonism has been proposed as a main driving force for the
383 expansion of the SDR in diploid systems (reviewed in [27]). In UV systems, the Otto and Immler model
384 predicts that reduced recombination is also favoured as long as different alleles have different levels
385 of fitness in males and female backgrounds. Note that Immler and Otto's theoretical predictions are
386 valid both for UV chromosomes that carry sex-determining regions and chromosomes with mating
387 type loci [13]. In isogamous and near-anisogamous organisms, forces other than sexual antagonism
388 may contribute to the expansion of the non-recombining region ([6]). These include for instance the
389 capture and shelter of deleterious alleles in a permanently heterozygous state, or the fixation of
390 neutral rearrangements by drift in one gametolog [6]. The non-recombining region can expand
391 symmetrically on the U and the V (B and C) but expansion can also occur independently in only one
392 of the haplotypes by transposition of loci to one of the SDRs (D, e.g. [55]).

393 **Box 3. Transitions between monoicy and dioicy**

394 Transitions between dioicy and monoicy are common across all the eukaryotic groups that
395 have haploid sex determination. This type of transition has occurred several times in volvocine algae
396 [17], and, in mosses, transitions between dioicy and monoicy are very frequent and appear to have
397 occurred a few hundred times [40,48]. In the brown algae, separate haploid sexes (dioicy) is clearly
398 the ancestral state, with, again, several independent transitions to monoicy [53]. However, the
399 evolutionary forces and the proximate mechanisms driving these transitions are still poorly
400 understood. Monoicy is associated with polyploidy in mosses and liverworts [48] suggesting that
401 diploid bisexual gametophytes originated from unreduced spores of UV diploid sporophytes of

402 dioicous species and thus possessed all the genes necessary for both male and female sexual
403 functions. The male and female factors in some mosses are codominant, leading to monoicy when
404 both the male and female haplotypes are present in the same gametophyte [65]. However, in other
405 haploid systems the situation seems to be more complicated. Monoicous and dioicous hornworts
406 have similar chromosome numbers [48], arguing against polyploidy as a mechanism for transition to
407 monoicy. Also, dominance has been observed in some UV systems, for example the V or the U
408 chromosome are dominant in *Ectocarpus* [54] and *Marchantia* respectively [65]. In such systems, UV
409 polyploids (i.e., diploid gametophytes) are not hermaphroditic and transitions are unlikely to have
410 been driven by changes in ploidy suggesting the existence of alternative mechanisms. Epigenetic
411 silencing of a master dominant male sex-determining gene in certain tissues could lead to monoicy
412 by producing female organs if femaleness is the default state (as appears to be the case in *Ectocarpus*,
413 [54] and possibly *Volvox* [5]. Cases of monoicy have been reported in genetically male kelps [58].
414 Similarly, transitions from dioicy to monoicy in volvocine algae [17] may be related to epigenetic
415 control of expression for the dominant sex-determining gene *MID* [5,66]. In fungi, transitions from
416 heterothallism to homothallism have often evolved following gene capture. For instance, in many
417 ascomycetes homothallic strains are not heterozygous diploids but instead contain copies of both
418 mating types that can be alternatively expressed [67,68]. Additional studies of the evolution of
419 reproductive traits and correlation between life cycle and reproductive features will be needed to
420 understand the molecular mechanisms, ultimate causes, and evolutionary consequences of the
421 transitions between sex determination modes.

422 **Box 4. Volvocine algae and the evolution of sexes from mating types**

423 Among the different UV systems that have been characterized to date volvocine algae are unique in
424 having members that span the whole range from isogamy to anisogamy to oogamy, and these
425 organisms are therefore ideal models to study transitions between these states [22]. Despite their
426 history of MTL/SDR structural turnover, the volvocine algae have retained homologous regulatory
427 mechanisms for mating type specification by the RWP-RK family transcription factor gene *MID* (minus
428 dominance), which is found in either the *minus* mating type or the male SDR of all dioicous volvocine
429 species characterized to date [20,22,24,25]. In *Chlamydomonas* the presence/absence of a *MID* gene
430 whose expression is induced by nitrogen deprivation is the major determinant of minus/plus sexual
431 differentiation [24,69]. A test of *MID* function in *Volvox* showed that, like the case in *Chlamydomonas*,
432 presence/absence of the *Volvox MID* ortholog is the key determinant of spermatogenic/oogenic

433 development for germ cell precursors that are formed in response to a pheromone called sex inducer
434 [5]. However, in the sex-reversed strains generated by ectopic *MID* expression in females or RNAi
435 knockdown in males the distinctly female or male patterns of germ cell precursor formation
436 (characterized by numbers, sizes and positions of germ cell precursors) were unaltered, indicating
437 that sex-related developmental functions other than *MID* are encoded in the SDRs of the *Volvox* UV
438 chromosomes. Moreover, while the germ cells that were formed in the sex-reversed strains of *Volvox*
439 were functional, they had a variety of defects that are evidence of gene content in the male and
440 female SDRs of *Volvox* becoming masculinized and feminized [5]. It was hypothesized that the high
441 degree of gametolog differentiation and expanded SDR size in *Volvox* might stem partly from sexual
442 antagonism operating in this oogamous mating system [20]. Charlesworth ((Charlesworth, 1978))
443 originally proposed a minimal two-locus model for the evolution of anisogamy where an allelically
444 dimorphic gamete size-control gene comes into tight linkage with a sex-determining region. A
445 prediction for this model is the presence of one or more dimorphic gamete size control genes being
446 present in the SDRs of oogamous/anisogamous volvocines but not isogamous ones. However, more
447 recent results have shown that anisogamy is compatible with a highly reduced SDR as is found in
448 *Eudorina* sp. where the male haplotype spans 7kb and contains just three genes, only one of which,
449 *MID*, is likely to be related to sex or mating (Hamaji et al., 2018). Thus, gametolog divergence as
450 observed in *Volvox* may arise secondarily after anisogamy has already been established (Ferris et al.,
451 2010; Hiraide et al., 2013). Even more unexpectedly, another recent study found that the *MID* gene
452 from an isogamous volvocine genus, *Gonium*, which is more closely related to *Volvox* than is
453 *Chlamydomonas*, could induce spermatogenesis in *Volvox* females (Geng et al., 2018). This finding
454 indicates that divergence of Mid function in volvocine algae was not the primary driver towards
455 anisogamy/oogamy, and suggests that changes in other parts of the Mid regulatory network
456 (interacting proteins and/or target genes) that are not encoded in the SDR were responsible for the
457 evolution of sexually dimorphic gametes. The elucidation of Mid binding sites and target genes in
458 selected volvocine species may shed light on how the Mid network expanded in multicellular
459 volvocine algae to drive the evolution of gamete dimorphism.

460 **Tables and Figures**

461 **Table 1** – Structural characteristics of UV SDRs across different organisms

462 **Figure 1** – Emergence of UV systems across the eukaryotic tree of life. Absolute time in million years
463 (Ma) is given based on [73]. Lineages where haploid sexual systems have been found are indicated

464 by red branches. Lineages where haploid sexual systems are suspected to have emerged are indicated
465 in orange. Simplified lineage phylogenies are based on [74] for Excavates, [75,76] for Opisthokonts,
466 [77] for Archaeplastida [78] for Haptophytes and Cryptophytes and [79] for the SAR supergroup.

467 **Figure I, Box 1** – Relationship between life cycle and sex determination system in diverse eukaryotes.

468 **Figure I, Box 2** – Schematic model for the evolution of UV systems compared with XY/ZW systems.

469 **Glossary**

470 **Dioecious:** describing diploid phase sex-determination with genetically distinct sporophytes
471 corresponding to each sex or mating type.

472 **Dioicous:** describing haploid phase sex or mating type determination with genetically distinct
473 gametophytes corresponding to each sex or mating type.

474 **Gametologs**: pairs of orthologous MTL/SDR genes that are derived from a single ancestral gene
475 located within the non-recombining region of opposite sex chromosomes (X and Y, Z and W or U and
476 V) or in the MT- and MT+ MTLs.

477 **Gonochoric:** used in metazoans with same meaning as dioecious (genetically determined sexes).
478 **Heterothallism:** mating incompatibility between genetically identical individuals, i.e. species with
479 genetically determined sexes or mating types. Usually used with microbial eukaryotes.

480 **Homothallism**: mating compatibility between genetically identical individuals, i.e., epigenetic sex
481 determination. Usually used with microbial eukaryotes.

482 **Mating type locus:** locus that determines mating type in isogamous heterothallic species.

483 **Monoicous**: Describing haploid phase sex determination or mating-type determination where both
484 gamete types are produced by the same gametophyte.

485 **Monoecious:** describing diploid phase sex determination or mating-type determination where both
486 male and female sporophytes are produced by the same individual i.e. epigenetic sex determination.
487 In angiosperms, the term 'hermaphrodite' is used specifically to denote the very common case where
488 separate male and female organs are present in the same flower ("perfect flowers"), while
489 monoecious refers to plants where the same individual produces distinct male and female flowers.

490 **Pseudoautosomal regions (PAR)**: recombining regions flanking the MTL/SDR on the sex or mating type
491 chromosomes.

492 **Sex chromosome:** chromosome in an organism with male and female gametes (anisogamy or

493 oogamy) that carries the sex-determining region.

494 **Sex-determining region:** region of a sex chromosome containing the locus that determines sex, often
495 an extensive, non-recombining region spanning many kilobases.

496 **Sexual antagonism:** pertains to genes or alleles that increase reproductive fitness when expressed in
497 one sex or mating type but decrease reproductive fitness when expressed in the opposite sex or
498 mating type.

499 **Strata:** chromosomal regions that have become part of the non-recombining MTL/SDR at different
500 evolutionary times.

501 **U and V chromosomes**: female (U) and male (V) chromosomes that determine sex during the haploid
502 phase of the life cycle.

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666

667

Table 1 – Structural characteristics of UV SDRs across different organisms

	Total sequence (Mbp)			Number of genes			Gene density (genes/Mbp)			Average gene length (bp)			Average intron length			GC (%)			Repeats (%)		
	VSR	USR	Genome	VSR*	USR*	Genome	VSR	USR	Genome	VSR	USR	Genome	VSR	USR	Genome	VSR	USR	Genome	VSR	USR	Genome
Ectocarpus sp.	0.92	0.93	205	20 (11)	22 (11)	15779	22.82	23.7	76.9	25710	18836	6974	3605	3691	702	51.29	44.74	54.02	n.d.	n.d.	23.00
U. partita	1.0	1.5	n.d.	46 (23)	67 (23)	n.d.	46	44.6	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
C. reinhardtii	0.20	0.40	111	25 (22)	35 (22)	17732	118 (122)	109 (111)	159.6	3489	3482	3895	358	354	420	61	60	64.1	n.d.	n.d.	n.d.
G. pectorale	0.5[b]	0.37[b]	149	24(21)	24(21)	17990	46	58	121	4726	3981	3993	279	176	350	61	59.7	64.5	n.d.	n.d.	n.d.
Y. unicocca	0.17[b]	0.27[b]	134[a]	18 (17)	18 (17)	n.d.	109	67.2	n.d.	4811	5052	n.d.	n.d.	n.d.	n.d.	60.3	60.1	61.1	n.d.	n.d.	n.d.
Eudorina sp.	0.007	0.09	184[a]	3 (2)	3 (2)	n.d.	428	33.3	n.d.	1437	5112	n.d.	n.d.	n.d.	n.d.	51.4	53.9	61.0	n.d.	n.d.	n.d.
V. carteri	1.13	1.51	131	60 (50)	55 (50)	14958	54	39	114	6062	7198	5300	584	618	400	53	52	56.1	70.00	72	21
M. polymorpha	6	4.37	220	105 (19)	74 (20)	19470	17.6	17.4	88.5	n.d.	n.d.	n.d.	n.d.	n.d.	392	n.d.	n.d.	n.d.	74.7	70.8	22.2

Abreviations:
n.d.: not determined
USR: U-specific region
VSR: V-specific region
*Number of gametologs indicated in brackets.
[a]Genome size shown for *MT+* or female strain of *Yamagishiella* and *Eudorina*, respectively.
[b]Minimum size estimates for VSR and USR regions
References for *Ectocarpus* sp.: [54,55], *U. partita*: [52]; *C. reinhardtii*: [20,21,32]; *G. pectoral*: [21]; *Y. unicocca* and *Eudorina* sp.: T. Hamaji and H. Nosaki, personal communication; *V. carteri*: [20,21]; *M. polymorpha*: [43,44]

Figure 1

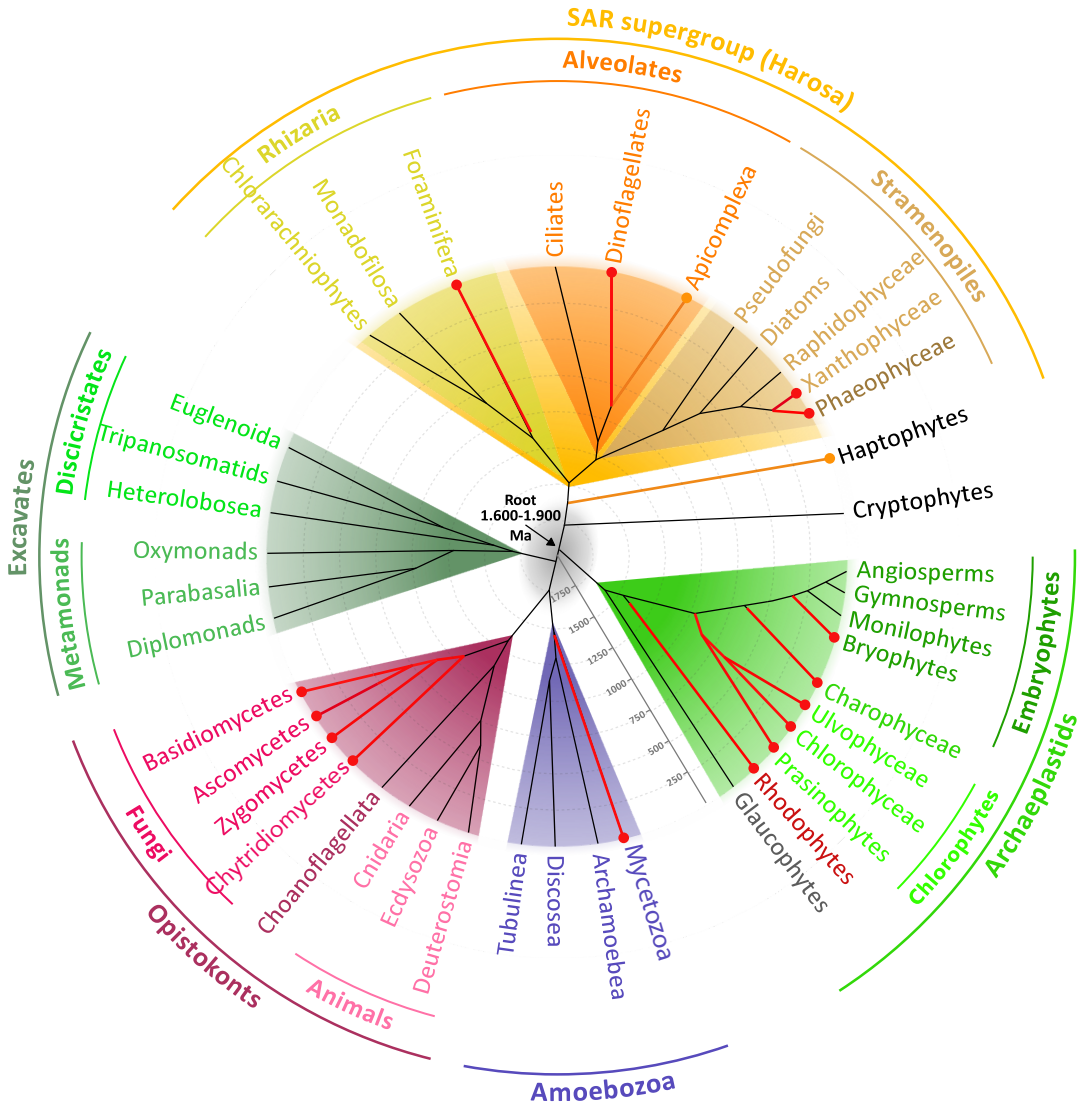

SAR supergroup (Harosa)
Alveolates
Rhizaria
Stramenopiles
Chlorarachniophytes
Monadofilosa
Foraminifera
Ciliates
Dinoflagellates
Apicomplexa
Pseudofungi
Diatoms
Raphidophyceae
Xanthophyceae
Phaeophyceae
Haptophytes
Cryptophytes
Excavates
Discicristates
Metamonads
Euglenoida
Tripanosomatids
Heterolobosea
Oxymonads
Parabasalia
Diplomonads
Root
1.600-1.900
Ma
750
1500
1250
1000
750
500
250
Angiosperms
Gymnosperms
Monilophytes
Bryophytes
Embryophytes
Charophyceae
Ulvophyceae
Chlorophyceae
Prasinophytes
Chlorophytes
Rhodophytes
Glaucophytes
Archaeplastids
Basidiomycetes
Ascomycetes
Zygomycetes
Chytridiomycetes
Fungi
Choanoflagellata
Cnidaria
Ecdysozoa
Deuterostomia
Animals
Opistokonts
Tubulinea
Discosea
Archamoebea
Mycetozoa
Amoebozoa

Figure I, Box 1

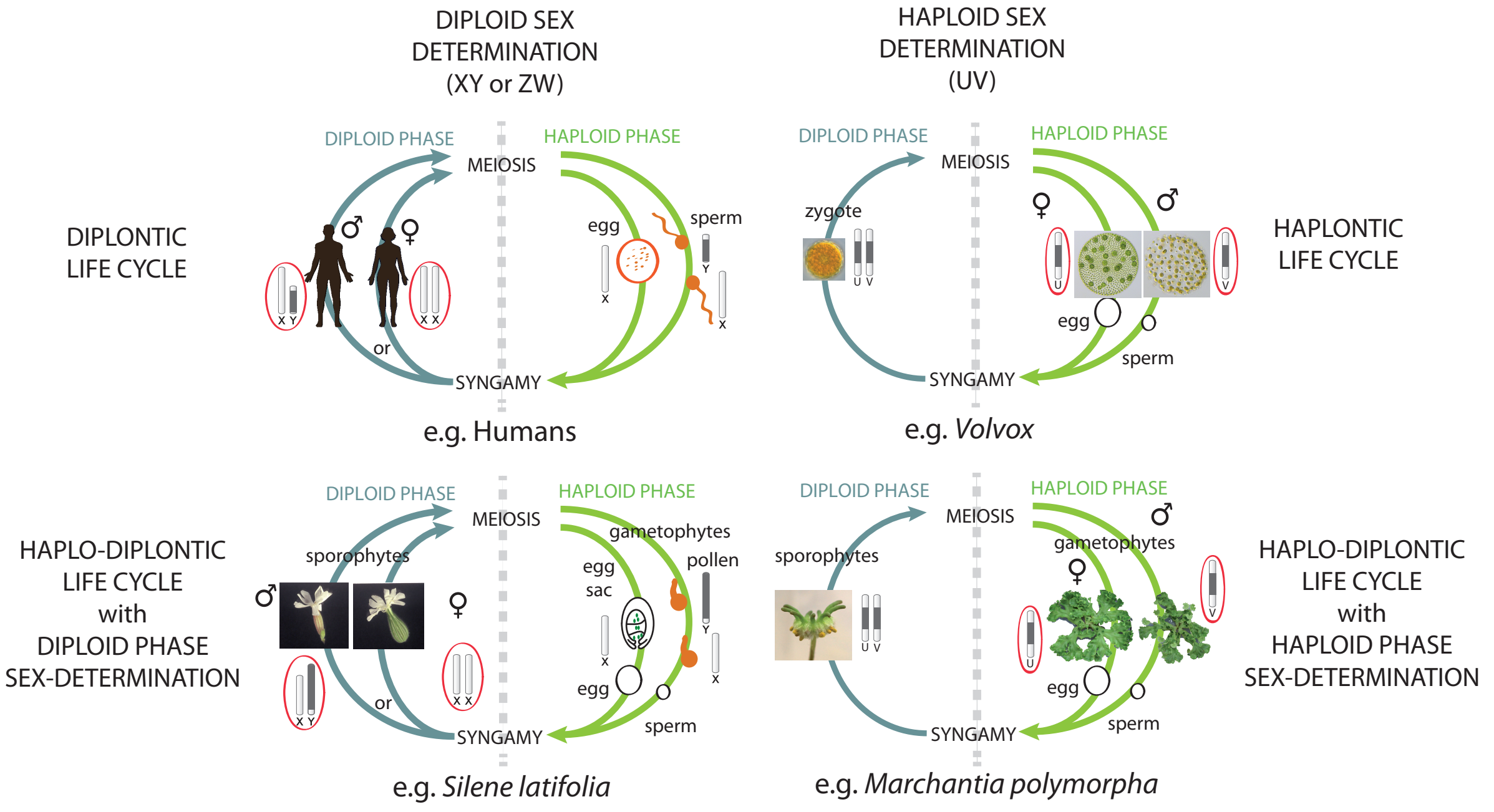
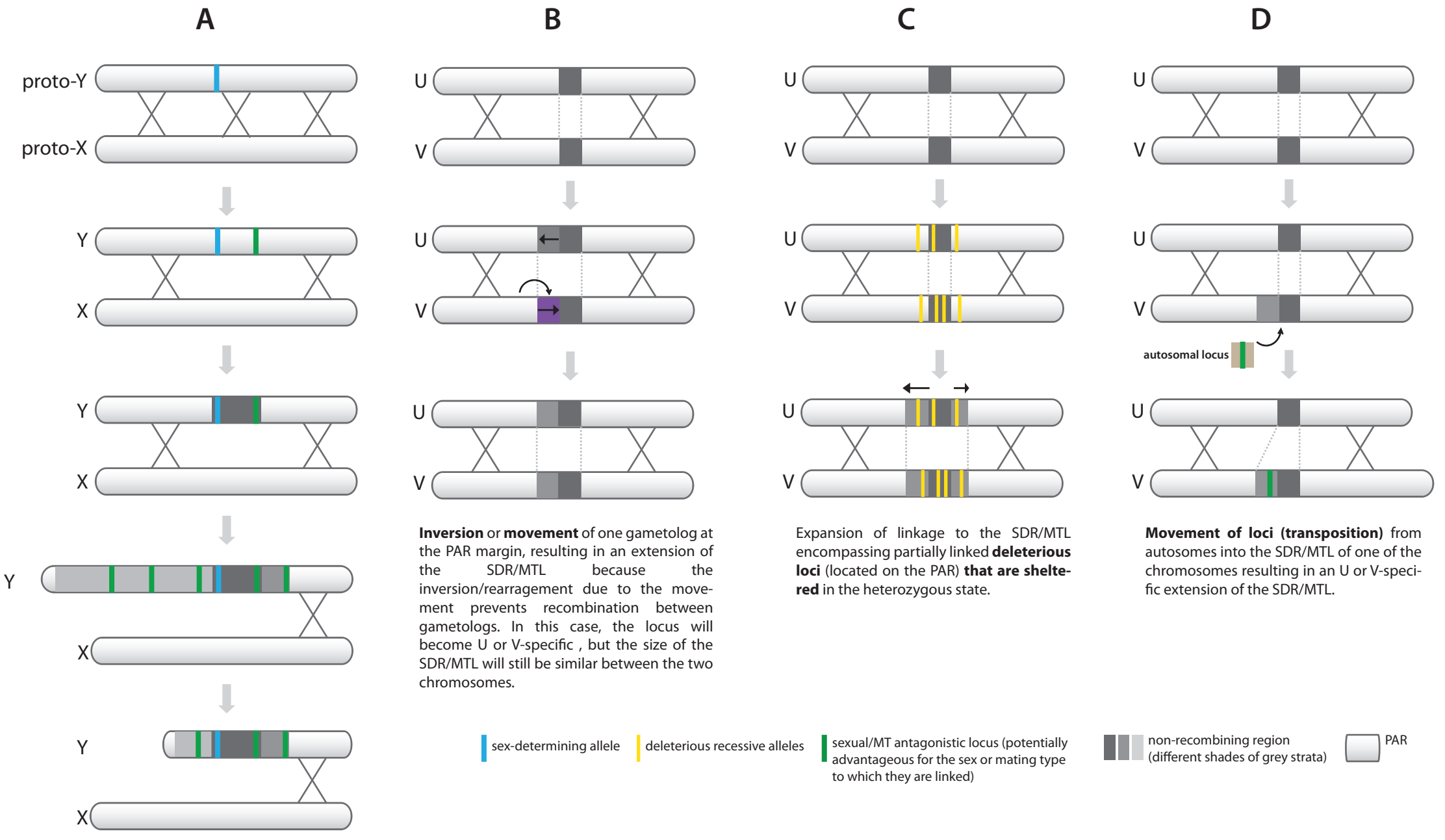


Figure I, Box 2



Inversion or **movement** of one gametolog at the PAR margin, resulting in an extension of the SDR/MTL because the inversion/rearragement due to the movement prevents recombination between gametologs. In this case, the locus will become U or V-specific , but the size of the SDR/MTL will still be similar between the two chromosomes.

Expansion of linkage to the SDR/MTL encompassing partially linked **deleterious loci** (located on the PAR) **that are sheltered** in the heterozygous state.

Movement of loci (transposition) from autosomes into the SDR/MTL of one of the chromosomes resulting in an U or V-specific extension of the SDR/MTL.