



Title	Achiasmy and sex chromosome evolution
Author(s)	Satomura, Kazuhiro; Osada, Naoki; Endo, Toshinori
Citation	Ecological Genetics and Genomics, 13 https://doi.org/10.1016/j.egg.2019.100046
Issue Date	2019-12
Doc URL	https://hdl.handle.net/2115/99532
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Rights(URL)	https://creativecommons.org/licenses/by-nc-nd/4.0/
Type	journal article
File Information	Ecol. Genet. Genom. 13_100046.pdf



1 Achiasmy and sex chromosome evolution

3 Kazuhiro Satomura¹, Naoki Osada^{1, 2}, and Toshinori Endo¹

5 1 Graduate School of Information Science and Technology, Hokkaido University, Hokkaido, Japan

6 2 Global Station for Big Data and Cybersecurity, GI-CoRE, Hokkaido University, Hokkaido,
7 Japan

9 address correspondence to Kazuhiro Satomura, k.satomura@ist.hokudai.ac.jp

11 Full postal address: Kita 14, Nishi 9, Kita-ku, Sapporo, Hokkaido, 060-0814, Japan,

12 Graduate School of Information Science and Technology, Hokkaido University

Abstract

Achiasmy is a phenomenon that the chiasma formation is absent during meiosis in one or both sexes. Achiasmy is one of the strategies for the cessation of recombination between sex chromosomes in various taxa. In sex chromosome evolution, the cessation of recombination is a crucial event for sex chromosome diversification. In the present review, we introduce the prevalence and mechanism of achiasmy and discuss the role of achiasmy in the sex chromosome evolution. Firstly, we review the research history of achiasmy in *Drosophila* species. In addition, we summarize the prevalence of achiasmy in a wide range of animal taxa and the rapid turnover of achiasmy. We also briefly describe the mechanism of achiasmatic meiosis in *Drosophila melanogaster* and the evolution of meiotic genes in *Drosophila* species. Secondly, we discuss sex chromosome evolution in achiasmatic species, wherein heterogametic sex chromosomes have no chance of meiotic recombination. In their evolutionary trajectory of sex chromosomes, the timing of recombination cessation and the level of genetic diversity are mostly dependent on how the Y (W) chromosome originated. We compare three different evolutionary trajectories of neo-Y chromosome in *Drosophila americana*, *Drosophila miranda*, and *D. albomicans*. Lastly, the hypothesis that achiasmatic meiosis facilitate the recruitment of B chromosome to Y (W) chromosome, proposed in three cases of insects, is discussed.

Keywords: Arthropoda, Genetic diversity, Haldane–Huxley rule, Male recombination, Meiotic recombination, Neo-sex chromosome

1. Introduction

Meiosis and sex determination are essential for sexual reproduction in eukaryotes.

Meiosis is a type of cell division that produces haploid gametes in germlines. During meiosis, the physical connections between homologous chromosomes (chiasmata) are formed via crossing over in order to segregate homologous chromosomes to opposite poles of the spindle, which results in the separation of homologous chromosomes into different daughter cells [1-3]. Among eukaryotic species, a large variation has been observed in the pairing and separation of homologous chromosomes during meiosis [3, 4].

Genetic sex determination systems have high diversity among eukaryotic species, such as the male heterogametic XY type, female heterogametic WZ type, and haploid sex-determining UV type [5,6]. The sex chromosome evolution in male XY and female WZ types share considerably high similarities; hereafter, we focus on only XY/WZ sex determination systems and use the term XY chromosomes as a representative. Sex chromosomes are established by acquiring master sex-determining genes and inherited through a sex-linked manner [7]. After the initiation of recombination suppression, the Y chromosome starts to degenerate and becomes heteromorphic. As a result, the X and Y chromosomes are easily distinguishable under the microscope, in many species [8].

A phenomenon of no chiasma formation during meiosis in one or both sexes is known as “achiasmy.” Both chiasmy and achiasmy have been observed in various eukaryotic taxa and the fate of sex chromosome evolution is drastically differentiated between chiasmatic and achiasmatic species (Fig. 1). In particular, achiasmy has an impact on sex chromosome evolution because it can stop recombination immediately, and the neo heterogametic sex chromosome loses preexisting genetic diversity via founder effect. However, rapid evolutionary turnover between chiasmy and achiasmy imply that achiasmy has some beneficial role and that a simple genetic mechanism controls

chiasmatic and achiasmatic meiosis.

In this review, we summarize previous and ongoing research on achiasmy and sex chromosome evolution. In the second section, we present (2.1) the research history of achiasmy, (2.2) the prevalence of achiasmy in animal taxa, and (2.3) the molecular mechanism of male achiasmy in *D. melanogaster*. Afterward, in the third section, we summarize sex chromosome evolution in (3.1) chiasmatic species and (3.2) achiasmatic species using the evolution of neo-sex chromosome in *Drosophila* species as the examples. In addition, we introduce (3.3) the hypotheses regarding the origin of Y chromosomes.

2. Achiasmy in animal taxa

2.1 The history of achiasmy in *Drosophila* species

In the early 1900s, the absence of recombination in a heterogametic sex, that is achiasmy, was reported for a male fruit fly *Drosophila melanogaster* by Morgan [9, 10] and a female silkworm *Bombyx mori* by Tanaka [11]. More recently, the difference in recombination rate between males and females has been reported in a wide range of eukaryotic species, which is known as “heterochiasmy” [12]. In heterochiasmatic species, lower recombination rates have been mostly observed in the heterogametic sex rather than the homogametic sex [12]. The prevalence of achiasmy and heterochiasmy implies that the impediment of genetic exchange between X and Y chromosomes is beneficial for sexual organisms, as proposed is Haldane-Huxley rule [13, 14].

Following the report of male achiasmy in *D. melanogaster* [9, 10], several studies have discovered spontaneous male recombination through cross experiments in *Drosophila virilis* [15], *Drosophila simulans* [16], and *Drosophila bipectinata* [17], and by cytological observation in *Drosophila subobscura* [18] and *Drosophila willistoni* [19].

Spontaneous male recombination in *D. melanogaster* was also reported by Hiraizumi [20]. However, the observed recombination events were quite rare, amounting to less than 0.1% in the case of *Drosophila*. Such rare recombination can occur during mitosis, which has been universally observed in Diptera taxa [21]. Moreover, the mechanism of male recombination induced by *P*-element has gradually been understood over the past 20 years [22]. Therefore, rare recombination events in male *Drosophila* have been interpreted as accidental events such as mitotic recombination. Ironically, this research history provides paradoxical proof regarding the universality of male achiasmy in *Drosophila* species (Fig. 2). So far, most of the knowledge regarding achiasmy remains limited to *Drosophila* species; only a few studies showed female achiasmy through cross experiments in Lepidoptera species: *B. mori* [13, 23], *Heliconius* species [24], and *Ephestia kuehniella* [25].

2.2 The prevalence and evolution of achiasmy

Not only in Diptera taxa, achiasmy has been reported in a wide variety of species of protostomes [26-30], especially in Arthropoda. For example, achiasmy in male germline of species some Diptera [31-39], Hemiptera [40-49], Mantodea [50-54], Acarina [55], Scorpiones [56-59], Orthoptera [60], Mecoptera [61-64], Coleoptera [65], Araenae [66], and Pseudoscorpionida [67], and achiasmy in female germline of Lepidoptera [25,68], Copepoda [69-71], and Trichoptera [72] have been reported. Bisexual achiasmy was also reported in Annelida [26], Platyhelminthes [27, 28] and Mollusca [29, 30]. The achiasmatic species observed so far were summarized in Table 1. In contrast to the prevalence of achiasmy in vertebrates, achiasmy has not been reported in vertebrates. In most cases, achiasmy was observed in heterogametic sex alike heterochiasmatic species.

111 In addition, the absence of chiasma formation during meiosis in the above-mentioned
112 examples were found only via microscopic observations [25-72]; except for *Drosophila*
113 and Lepidoptera species, genetic verification for achiasmy has a few examples such as
114 *Myzus persicae* of the Hemiptera species [73]. Therefore, it is still uncertain whether the
115 absent of chiasmata strictly coincides with the absent of meiotic recombination.

116 Because achiasmy has been reported in a wide range of Arthropoda [9-11, 15-19, 23-
117 76], thus it remains unclear whether the ancestral trait was chiasmatic or achiasmatic. In
118 addition, these traits were not always consistent even within a taxonomic group. For
119 example, although almost all *Drosophila* species are achiasmatic, male recombination
120 was exceptionally observed in *Drosophila ananassae* [77, 78]. Likewise, an exceptional
121 chiasma formation in germlines of both sexes was observed in Bittacidae [63], which
122 belongs to the achiasmatic taxa Mecoptera. Conversely, male achiasmy was found in two
123 species of Thericleinae [60], while the species in Orthoptera [79] are generally chiasmatic.
124 Furthermore, the switch from chiasmy to achiasmy in only 0.55 million years evolution
125 is also reported in *Drosophila albomicans* (see the detail in the subsection 3.2; Fig. 2)
126 [80]. These examples suggest that chiasma formation during meiosis easily switches
127 through evolution.

128 129 2.3 Molecular basis of achiasmatic meiosis in male *D. melanogaster*

130 How can achiasmatic species accomplish meiosis without the physical lock between
131 homologous chromosomes? We briefly introduce the mechanism employed in male *D.*
132 *melanogaster* as an example (for details, see McKee et al. [81]). The distinctive keys for
133 accomplishing the achiasmatic meiosis of *D. melanogaster* were the homologous pairing
134 site and physical sequestration [82]. In early meiosis I, homologous autosomal pairs,

except for dot chromosomes, do not form chiasmata, but are aggregated with unstable meiotic pairing and are equally dispensed not with forming chiasmata but only with unstable meiotic pairing [83, 84]. The meiotic pairing between homologous autosomes is accomplished using many specific pairing sites [84], whereas the meiotic pairing between X–Y chromosomes is mediated by the ~12 kb length tandem repeat cluster of ribosomal RNA genes including intergenic spacer sequence [85], called *bobbed* loci [86, 87]. The paired homologous chromosomes are partitioned by nuclear envelope until they segregated to opposite poles [88].

Meiotic genes in *Drosophila* species are also unique compared with sibling chiasmatic taxa. A essential meiotic gene *mei-W68*, a *spo11* homolog in *Drosophila* species, which initiates recombination by double-strand break, requires synaptonemal complex formation in most cases. In *Drosophila* species, however, *mei-W68* induces double-strand break without synaptonemal complex formation in female germline [89, 90]. Another essential meiotic gene *spn-A*, a *rad51* homolog in *Drosophila* species, which has a crucial role of meiotic pairing and double-strand break repair, is dispensable for male meiotic pairing in *Drosophila* [91]. Moreover, *Drosophila* species often lack orthologs of meiotic genes; about 40% of orthologs involved in recombination shared among Arthropoda have not been found in *Drosophila* species [92]. The rapid evolution of meiotic genes is also observed among *Drosophila* species. Meiotic genes in *Drosophila* tend to be highly duplicated and many species-specific genes have been identified [93].

In this subsection, we introduced the molecular mechanism of achiasmatic meiosis in *Drosophila* species. However, even in chiasmatic meiosis in mammals, achiasmatic meiosis restricted in heteromorphic sex chromosomes has been observed [94-96]. During meiosis, such sex chromosomes are physically separated by the sex body (XY body) [97].

In this respect, the difference of meiosis between achiasmatic and chiasmatic species is whether chiasmata formation is ceased between all chromosomes or only between heteromorphic sex chromosomes. Achiasmy seemed to have important roles for sex chromosome meiosis.

3. Sex chromosome evolution under chiasmy/achiasmy

3.1 Sex chromosome evolution in chiasmatic species

Sex chromosomes in eukaryotic taxa have various origins and different levels of heteromorphy between X and Y chromosomes [98]. In theory, the conflict of natural selection on sexually antagonistic genes contribute to establish of recombination suppression between sex chromosomes (Fig. 1) [99]. The cessation of recombination is a definitive event for XY divergence; this has been a topic of interest for a century [100].

The recombination suppression of sex chromosomes spreads from a small sex-determining region [101, 102] to almost the entire Y chromosome [103]. Because recombination suppression is often established by the inversion or translocation of large chromosome segment, recombination suppression progress in a stepwise rather than a continuous manner [104-106]. Such stepwise recombination suppression would create a segmental sex chromosome structures with different level of differentiation between X and Y chromosomes, which is referred to as evolutionary strata [107-110].

Once recombination suppression is established, the non-recombining Y chromosomal region (NRY) is drastically degenerated by various evolutionary forces, such as natural selection and genetic drift. Along with the degeneration, the effective population size of NRY is also drastically reduced, which is theoretically one-fourth of the effective population size of an autosome [111].

183 If the degeneration of Y chromosomal gene has deleterious effects in males, its
184 gametologous gene on X chromosome could compensate the amounts of transcripts in
185 males; this phenomenon is called as dosage compensation [5, 112, 113]. The dosage
186 compensation has been observed in wide range of taxa, but not found in some organisms
187 such as birds [114, 115]. The dosage compensation has two types; *Drosophila* and
188 nematode upregulate X chromosomal gene expression in males whereas mammals
189 upregulate X chromosomal gene expression in both sexes and one X is inactivated in
190 female [115].

191 The drastic changes of NRY would not only be deleterious but also be adaptive. Gene
192 loss of on NRY is slower in the genes predominantly expressed in males than that in the
193 other genes [116, 117]. Moreover, parallel gene gain and loss on NRY have been observed
194 in many different taxa [118-120]. These lines of evidence suggest that strong natural
195 selection promoted such masculinization and feminization processes of sex chromosomes.
196 Because recurrent gene gain and loss on NRY have been frequently observed in many
197 different taxa, the gene gain and loss must be directly driven by strong natural selection,
198 or indirectly driven by other evolutionary processes such as hitchhiking effect [121]
199 and/or by background selection [122]. Such recurrent selective processes would lead the
200 lack of genetic diversity on NRY [123, 124].

201 On the contrary, the partly recombining regions on Y chromosomes, that is,
202 pseudoautosomal region (PAR) [125], is preserved on Y chromosomes in many
203 chiasmatic species [126], because the identical sequences between X and Y chromosomes
204 are essential for meiotic pairing in male germline [127, 128]. Since meiotic recombination
205 occurs on PAR, PAR genes inherit via the Mendelian inheritance pattern and have larger
206 genetic diversity than NRY genes [129]. In some chiasmatic species, the Y chromosome

has no PAR; such sex chromosomes show achiasmatic meiosis [94-96]. If sex chromosomal pairs cannot form chiasmata during meiosis, Y chromosome shows achiasmatic evolutionary pattern even in chiasmatic species.

Sex chromosome evolution is an irreversible process, but chromosomal inversion and fusion will join an autosomal chromosomal region to a sex chromosomal region [101, 110, 130, 131]. The chromosomal fusion sometimes generates “neo-sex chromosome.”

3.2 Sex chromosome evolution in achiasmatic species

The sex chromosome evolution in achiasmatic species has been well studied in the neo-sex chromosome evolution of *Drosophila* taxa. In achiasmatic species, neo-Y chromosome can be generated in two different ways of chromosome fusion: the Y-autosome fusion and X-autosome fusion (Fig. 3). If the neo-Y chromosome originated from the Y-autosome fusion, the neo-Y chromosome is of single origin and has no chance of obtaining preexisting genetic diversity through recombination. Thus, cessation of recombination is achieved at the time of the neo-Y chromosome origination, and the neo-Y chromosome can obtain genetic diversity only through the accumulation of mutation. In contrast, the neo-Y chromosome generated by the X-autosome fusion has genetic diversity like the neo-X chromosome. The neo-Y chromosome can obtain genetic diversity through recombination as autosomes in female germline and the recombination rate gradually reduces as the neo-X chromosome becomes fixed in the population. The major feature of sex chromosome evolution in achiasmatic species is that the timing of recombination cessation and genetic diversity decrease depend on the mode of sex chromosome origination (Fig. 1, Fig. 3).

Here, three different examples of sex chromosome evolutions in *Drosophila* are

introduced. First, the neo-Y chromosome of *D. americana* results from the X-autosome fusion, but the neo-X chromosome has not become fixed in the populations (Fig. 4). The age of the neo-sex chromosome is younger than 0.47 million years ago (MYA), which is the divergence time from the sibling species *Drosophila texana* [132]. The neo-Y chromosome still has high genetic diversity because it can recombine with the neo-X chromosomes in the females without the neo-X chromosome [133]. However, the recombination on the neo-X chromosome started to be suppressed near chromosomal inversion breakpoints and genetic diversity around the regions has been reduced [134, 135]. In the future, under neutral expectation, the neo-Y chromosome's genetic diversity would decrease to one-fourth of autosomal genetic diversity.

The second example is a case of the neo-Y chromosomes of *Drosophila miranda* which is generated from the Y-autosome fusion (Fig. 4). The neo-Y chromosome has not experienced meiotic recombination during 1 million years after the divergence between the neo-X and the neo-Y chromosomes [136]. Because the duration of 1 million years was sufficiently longer than the intraspecific coalescent time, the ratio of the neo-Y to neo-X chromosome genetic diversity should be one-fourth. Nevertheless, the present neo-Y genetic diversity of *D. miranda* was approximately 100 times lower than the neo-X genetic diversity which would be attribute to the natural selection on genes under complete linkage [137]. The neo-Y chromosome has retained male-biased expression genes [138] whereas many other genes were degenerated [121, 139]. A key of the evolution after the Y-autosome fusion is the lack of recombination since the origination,. The sex chromosome evolution under both X-autosome and Y-autosome fusion, which was observed in *Drosophila busckii* [140], therefore, should follow trajectory similar to *D. miranda*.

The third example is an exceptional case in *D. albomicans*. The neo-X and neo-Y chromosomes were both created by both X-autosome and Y-autosome fusion as *D. buskii*, 0.24 MYA (Fig. 4). Male recombination is absent in *D. albomicans*, but present in its sister species *Drosophila nasuta* and the ancestral polymorphisms are shared between the neo-X and neo-Y chromosomes in *D. albomicans*. The observed pattern indicated the switch from chiasmy to achiasmy in the ancestors of *D. albomicans* within 0.55 million years [80]. The rapid switch from chiasmy to achiasmy could be explained by the model of positive selection on recombination suppression between the newly formed sex chromosomes in *D. albomicans*. However, the mechanism of the change has not been uncovered yet.

Interestingly, although the observation in *D. albomicans*, suggested a switch from chiasmy to achiasmy, a case in the opposite direction has not been found in the other species. Hence, sex chromosomes may favor the absence of recombination in heterogametic sex and would utilize achiasmy to cease recombination.

3.3 Origin of Y (W) chromosome under achiasmy and the B chromosome origin hypothesis

The Y chromosome in *Drosophila* taxa is believed to have a common ancestor, except for the *pseudoobscura* subgroup [141]. *Drosophila* Y chromosome would have never experienced recombination because many species of sibling taxa in Diptera and almost all *Drosophila* species are achiasmatic [9, 10, 15-19, 31-39, 75]. Although *Drosophila* Y chromosomes have enough time to acquire genetic diversity since the origination (60~80 MYA, Fig. 2) [142-145], the genetic diversity on NEY observed in *D. melanogaster* was lower than the expected level under the neutrality (one-fourth of that of autosome) owing

to their demographic history [146] and/or recurrent hitchhiking [118]. As a result, *Drosophila* Y chromosome has been degenerated and lost homology to the X chromosome except for the *bobbed* loci (Fig. 5) [147].

On the other hand, B chromosome origin of *Drosophila* Y chromosome was proposed [148]. B chromosomes are extra chromosomes that are believed to have been derived from autosome or sex chromosomes [149] and do not show the Mendelian inheritance pattern [150]. The B chromosomal sequence is mostly degenerated like Y chromosome sequence [149] and some Y chromosome, as of mealworm beetle, is difficult to distinguish from B chromosome [151]. The B chromosome origin model was also proposed for the Y chromosome in an achiasmatic Homoptera species whose sibling species were X0 type [152], and for the W chromosome in Lepidoptera species whose ancestral types were thought as Z0 [153].

For B chromosome to be Y chromosome, the B chromosome should be inherited with the X chromosome in the sex-linked manner. Although it seems much difficult, achiasmy would facilitate the recruitment of B chromosome to Y chromosome as discussed by Nokkala et al. [154]. In X0 sex-determining insects, B chromosomes show meiotic pairing with X chromosomes in some Orthoptera [155-158] and Homoptera [154] species. The same B chromosome recruitment mechanism can be applied to the origination of *Drosophila* Y chromosome, because the sex of *Drosophila* is determined by X:A ratio controlled by *sxl* gene and the Y chromosome is not involved in the sex-determination process [159, 160]. Moreover, distinctive behaviors of pairing chromatids have been reported in Hexapoda, such as the ring configuration [161], distance-segregating [71, 162] and multivalent association [163, 164]. The multivalent association was also observed in *D. ananassae* subgroup [165, 166]. In the meiosis of Heteroptera, holocentric sex

chromosomes showed the multiple binding patterns of spindle fibers [167].

Achiasmatic meiosis has large variation and the formation of meiotic pairing seems flexible. To become Y chromosome, the B chromosome may only require sequences such as spindle binding or sites for meiotic pairing with the X chromosome.

4. Conclusions and perspectives

Discussion of achiasmy requires both cytological and genetic views, but the knowledge is limited to a few model species. The present review summarized the currently available information of achiasmy, although the amount of information is limited. Achiasmy has been reported in various animal taxa, suggesting rapid turnover between chiasmatic and achiasmatic traits. The repeated establishment of achiasmy would be a result of natural selection to cease recombination between the heterogametic sex chromosomes. The achiasmy has a huge impact on early sex chromosome evolution and origination. Meiosis, sex determination, and meiotic recombination are representative biological processes in eukaryotes, and they are not independent of each other. The variation of meiotic process implies that meiosis is flexible, and achiasmy occurs more easily than thought. To elucidate the many enigmas of achiasmy, revealing the mechanism underlying switching the trait and the variation of meiosis including achiasmy are crucial. Cytological observations and comparative genomics in a wide range of taxa will eventually clarify the evolutionary history and genetic consequences of achiasmy.

Acknowledgments

The study is partly supported by the Japan Society for the Promotion of Science KAKENHI Grant number 18H05511.

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Figure Legends

Fig. 1. The schematic models of evolutionary process for recombination suppression in chiasmatic and achiasmatic sex chromosome evolution. The dark and shaded areas on chromosomes represent nonrecombining regions. The asterisks represent the master sex determining genes. (upper lane) When an autosome obtained the master sex determining gene, the pair of homologous autosomes turn into sex chromosomes. In the case of chiasmatic species, the recombination at neighboring of the Y specific region is suppressed gradually. (lower lane) On the other hand, in the case of achiasmatic species, Y chromosome has no chance to recombine with X chromosomes.

Fig. 2. Schematic tree of *Drosophila* species presented in this review and the origin of their sex chromosomes. The white branches of tree indicate chiasmy and black branches indicate achiasmy. “X origin” indicates the X chromosome origination in *Drosophila* [147, 148]. “Y transition” indicates the Y chromosome translocation to an autosome in the *D. pseudoobscura* lineage [143]. “X fusion”s indicate the X-autosome fusion events and “Y fusion”s indicate the Y-autosome fusion events.

Fig. 3. The schematic models of evolutionary steps for recombination suppression in different modes of neo-sex chromosome origination. The dark and shaded areas on chromosomes represent nonrecombining regions. The asterisks represent the master sex determining genes. (upper lane) If a neo-Y chromosome originates from X-autosome

fusion, the neo-Y chromosome is chiasmatic in female germline (lower lane). In contrast, if a neo-Y chromosome originates from Y-autosome fusion, the neo-Y chromosome is achiasmatic because it is transmitted through male.

Fig. 4. Neo-sex chromosomes in four *Drosophila* species (see text for details). In *D. americana*, the neo-X chromosome has not been fixed in the population, and, there are several patterns of karyotypes. In *D. albomicans* and *D. busckii*, both sex chromosomes fused with a pair of autosomes, but the autosomes are not the same between the two species. In *D. miranda* the neo-Y chromosome was generated by Y-autosome fusion, but X-autosome fusion did not occur.

Fig. 5. The schematic models of recombination suppression progression in different scenarios of Y chromosome origin. The dark and shaded areas on chromosomes represent nonrecombining regions. The asterisks represent the master sex determining genes. The mode of recombination suppression in the Y chromosome of autosome origin is the same as Fig. 1 chiasmatic type (upper lane). In contrast, if the Y chromosome originates from a B chromosome, it had only a few genes and the X and Y chromosomes should have no homology. Therefore, recombination between the Y and X chromosomes do not occur (lower lane).