



# Genomic origins of insect sex chromosomes

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Recent efforts to catalog the diversity of sex chromosome systems coupled with genome sequencing projects are adding a new level of resolution to our understanding of insect sex chromosome origins. Y-chromosome degeneration makes sequencing difficult and may erase homology so rapidly that their origins will often remain enigmatic. X-chromosome origins are better understood, but thus far prove to be remarkably labile, often lacking homology even among close relatives. Furthermore, evidence now suggests that differentiated X or Y-chromosomes may both revert to autosomal inheritance. Data for ZW systems is scarcer, but W and Y-chromosomes seem to share many characteristics. Limited evidence suggests that Z-chromosome homology is more conserved than X counterparts, but broader sampling of both sex chromosome systems is needed.

## Addresses

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Insects have evolved myriad ways of producing males and females, but chromosomal sex determination is the most common (Box 1). Sex chromosomes are thought to originate from a pair of ancestral autosomes that evolve a sex determining locus [1]. The sex-limited allele defines a proto Y or W chromosome in male or female heterogametic respectively. As sexually antagonistic mutations (i.e. those that benefit one sex at the expense of the other) arise, selection will favor decreased recombination between the male or female sex determining allele and the matching male or female beneficial allele. Once recombination becomes suppressed, the sex-limited region of the proto Y or W chromosome is subject to a variety of population genetic forces that are expected to result in mutational decay and gene loss [2]. The phylogenetically widespread observation of XO (ZO) species [3] indicates that decay of the Y(W) often results in its complete loss [4••]. However, decay is not inevitable.

Some lineages retain homomorphic sex chromosomes over long evolutionary time scales (e.g. Isoptera). Additionally, Y and W chromosomes often reemerge in clades that are ancestrally XO or ZO (e.g. Lepidoptera), a strong indication - even in the absence of sequence data - that not all sex-limited chromosomes are homologous [5•,6]. Following we review the genomic origins and turnover of differentiated sex chromosome in insects with particular emphasis on recent genome sequencing and comparative phylogenetic efforts (for more comprehensive reviews of sex chromosomes and their evolution see [7,8]).

## Y-chromosome evolution

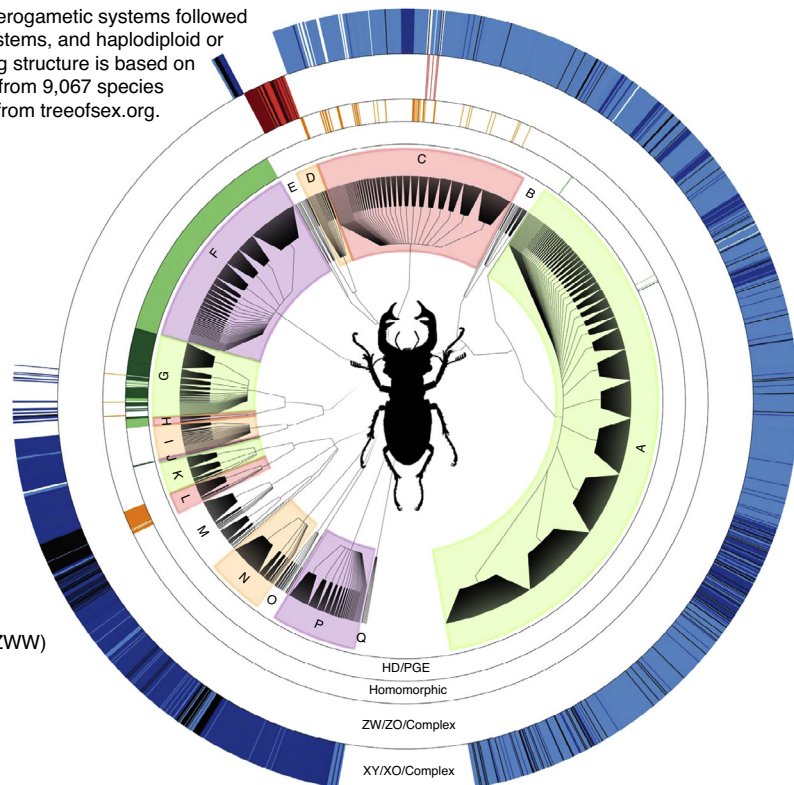
Male heterogamety (XY, XO) is the most abundant form of sex determination in insects (Box 1), having been documented in 24 of 28 orders encompassing 77% of sexually reproducing species investigated. However, the sex specific portions of Y-chromosomes are some of the least well-understood regions of all genomes. Since they do not recombine, they cannot be studied with traditional genetic methods and the decay process leaves them highly repetitive and heterochromatic, making them very difficult to sequence and assemble (but see [9]). Indeed, the most universal observation about sex specific chromosomes (Y or W) is that they rapidly accumulate transposable elements and become heterochromatic. While genomes from both sexes have been included in many whole-genome sequencing projects, efforts to systematically mine this potential source of Y chromosome information are relatively recent (e.g. [10,11]) and in most species Y-chromosome reads remain relegated to the large bin of small, unmapped scaffolds. Consequently, the most detailed information we have about Y-chromosome origins, structure, and gene content is based on concerted efforts to sequence a few species of mammals [9,12,13,14,15•,16,17] and *Drosophila* [18–23].

The *D. melanogaster* Y, which is thought to represent the ancestral Y of the genus, has only 13 protein-coding genes, all of which derive from autosomal duplications. One of them, *Suppressor of Stellate*, is multicopy and has convergently acquired and amplified the number of X-linked copies. Intriguingly, Soh and colleagues [9] recently discovered a similar convergent amplification of genes on the mouse X and Y. In both mouse and *D. melanogaster* the dually acquired X and Y amplicons may be the relic of a co-evolved meiotic driver/suppressor system [24–26]. The lack of orthologous genes between the ancestral *Drosophila* X and Y has caused some to speculate that the Y arose from a supernumerary B chromosome [20,21,27,28]. However, it is also possible that homology has been erased by gene losses in the ancestor of

## Box 1

Genus level distribution of sex determination characteristics in insects. The colored bars indicate the presence of a character in a genus. The exterior ring indicates male heterogametic systems followed by female heterogametic, homomorphic systems, and haplodiploid or paternal genome elimination. The branching structure is based on taxonomy and the figure incorporates data from 9,067 species representing 2725 genera. Data available from treeofsex.org.

- |                |                 |
|----------------|-----------------|
| A Coleoptera   | J Phthiraptera  |
| B Megaloptera  | K Blattodea     |
| Neuroptera     | L Isoptera      |
| Raphidioptera  | M Embiidina     |
| Strepsiptera   | Grylloblata     |
| C Diptera      | Mantodea        |
| D Lepidoptera  | Phasmatodea     |
| E Mecoptera    | N Orthoptera    |
| Siphonaptera   | O Dermaptera    |
| Trichoptera    | Plecoptera      |
| F Hymenoptera  | Zoraptera       |
| G Hemiptera    | P Odonata       |
| H Thysanoptera | Q Ephemeroptera |
| I Psocoptera   | Zygentoma       |
- 
- |  |
|--|
| ■ XY   |
| ■ XO   |
| ■ ZW   |
| ■ ZO   |
| ■ Multiple XY; Multiple ZW (e.g. XXXY, ZWWW) |
| ■ Haplodiploidy                              |
| ■ Paternal Genome Elimination                |



Drosophilid flies. The latter explanation finds indirect support from three lines of evidence in concert. First, there is considerable turnover of Y linked genes across the genus. Only 3 of the 12 single copy Y-linked autosomal protein-coding genes are conserved across all members of the genus studied so far, except for the *D. pseudoobscura* lineage, which shares none [21]. Second, the *D. pseudoobscura* neo-Y is highly degenerated and heterochromatic, like the *D. melanogaster* Y, yet is not homologous. In the *D. pseudoobscura* lineage, the ancestral *Drosophila* X fused to Muller element D (Figure 1) and the ancestral Y reverted to autosomal inheritance by fusing to the dot chromosome [29,30]. Despite being only 13–15 million years old (compared to >60 for the ancestral Y) the neo-Y of *D. pseudoobscura* retains only ~15 genes (or pseudo-genes) [18], suggesting that the ancestral Y of *D. melanogaster* has had ample time to lose all of its X-linked homologs. Finally, investigations of the neo-sex chromosomes in *D. miranda* and *D. albomicans* suggest that Y-chromosomes begin the decay process very early by down regulating gene expression of Y-linked copies, and then rapidly begin to lose genes [22,31,32]. In *D. miranda* the neo-Y, which formed by a Y to autosome fusion approximately 1–2 million years ago,

has already accumulated a large number of transposable elements and 40% of the ancestral autosomal genes have been pseudogenized or lost [23]. The data from *Drosophila* are consistent with theoretical expectations and from Y-chromosome observations in therian mammals where the Y rapidly lost genes early in its evolution but has remained stable and gained several genes that are exclusively expressed in the male germline [15].

Unlike evolutionary theory and observations surrounding the decay of the Y, we have a relatively limited understanding of the factors that govern rates of Y chromosome gain and loss (i.e. XO->XY or XY->XO transitions). However, the mechanics of meiosis might play a role [5]. Analysis of all available Coleoptera sex chromosome karyotype data (4724 karyotypes analyzed over a phylogeny with 1126 operational taxonomic units) shows that species requiring chiasmatic meiosis gain and lose Y-chromosomes much faster than species that evolve alternative segregation mechanisms (e.g. achiasmatic meiosis or asynaptic sex chromosomes). Based on this observation Blackmon and Demuth proposed the fragile Y hypothesis, suggesting that as recurrent selection to

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