

Coleopterist's Corner



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Coleoptera Karyotypes: The evolution of sex chromosomes and chromosome number.



Coleoptera karyotypes have a long history of use by taxonomists and evolutionary biologists. In 1905, Nettie Stevens discovered the first empirical support for the role of chromosomes in sex determination through karyotype analysis of the yellow mealworm beetle, *Tenebrio molitor*. Stevens eventually identified what she called heterochromosomes in an additional 44 species of beetles. We now know that these heterochromosomes were the X and Y chromosome, and that as she inferred are indeed the key to sex determination.

Despite this early beginning, Coleoptera cytogenetics did not begin to flourish until the second half of the twentieth century. Beginning in the 1950s an increasing number of researchers such as Smith, Suomalainen, Takenouchi, Virkki, and Lanier turned their attention to the field of Coleoptera karyotype evolution and cytotaxonomy. By 1975, these and other workers had documented the karyotypes of thousands of species. It was at this time that the last synthesis of Coleoptera cytogenetics was completed, largely by Stanley G. Smith who was part of the Canadian Forestry Service. However, he passed away in 1976 and was unable to see its publication. His collaborator Nilo Virkki was responsible for the inclusion of much of Smith's previously unpublished work and its eventual publication in 1978 as a volume in the Animal Cytogenetics series. This synthesis contains a list of 2160 karyotypes documented in beetles prior to 1976.

Beetle karyotypes are typically produced through testes squashes, but the karyotype is reported in a way that is unique to the group. For example, a common karyotype is "9+X_y". This is called a meioformula and reveals that there are 9 autosomes, an XY sex determination system, and that a

small Y chromosome remains at a distance from the X during meiosis. In most organisms, the segregation of chromosomes into the gametes requires that matching paternal and maternal chromosomes pair with one another and recombine, exchanging genetic information between them. This process increases genetic diversity and holds the chromosomes in place until they can be pulled to the two daughter cells.

A large body of empirical and theoretical research predicts that Y chromosomes should degenerate and eventually be lost. Briefly, the presence of genes that have alleles that differ in their fitness in males and females will lead to a reduction and eventual cessation of recombination between most of the X and Y chromosome. Since most of the Y chromosome cannot recombine, that portion begins to degenerate due to forces like Muller's ratchet (the stochastic loss of high fitness chromosomes) and background selection (reduction in variation due to positive selection). Over time, this is expected to lead to the loss of genes on the portion of the Y chromosome that does not recombine and perhaps even the complete loss of the Y chromosome creating an XO sex determination system. However, in one suborder of beetles (Polyphaga) most species have sex chromosomes that pair at a distance and do not recombine. In table 1 the most common sex chromosome systems documented in beetles are described.

In addition to variation in sex chromosomes Coleoptera karyotypes also reveal variation in chromosome number. The lowest documented diploid chromosome number, 4, is found in the elaterid *Chalcolepidius zonatus*. The highest is found in the adaphagan *Dixus capito obscuroides*, which has

Table 1: Common Sex Chromosome Systems (SCS)

SCS	Explanation
XY	The X and Y have some region(s) that recombine during meiosis.
Xy	The X and Y have some region(s) that recombine during meiosis, and the Y is distinctly smaller than the X.
NeoXY	The X and Y have some region(s) that recombine during meiosis, and the sex chromosomes are much larger than closely related species. Authors use this annotation when they believe the sex chromosomes have fused with an autosomal chromosome.
X _{y_p} , X _{y_r} , X _{y_c}	Indicate that the X and Y chromosome do not recombine during meiosis, and instead are distinctly separated from one another. The subscript indicates the orientation of the sex chromosomes during meiosis.
XO	Indicate that the Y chromosome has been lost and males have an unpaired X.

a diploid complement of 70 chromosomes. However, the amount of variation in chromosome numbers among clades is highly heterogeneous. Some families such as Scarabaeidae exhibit remarkably little variation, the number of autosomes in this group ranges from 3 to 17 with a mode of 9; 73% of 430 species that have been examined exhibit this number. Meanwhile, other groups like Chrysomelidae exhibit far greater lability, with autosome numbers ranging from 3 to 31 with a mode of 11, but only 16% of the 886 species studied exhibit this mode.

Explanations for this variation among clades has focused on the relationship between the fitness effects of karyotype rearrangements and effective population sizes. Karyotypic rearrangements such as the fusion of chromosomes or translocations of portions of a chromosome are normally associated with a fitness cost. This means that they should be more common in species with smaller effective population sizes (natural selection will be weaker in small populations so they can fix through drift). Several papers beginning in the 1970s attempted to relate the variation in chromosome number to traits that might be important in determining effective population size. One study by Eduard Petitpierre focused on beetles, and showed a tentative relationship between variation in chromosome number and specialized feeding or winglessness.

Since Smith and Virkki's 1978 compilation cytogenetic data for beetles has continued to accumulate, but these records are largely scattered in papers

with either narrow taxonomic or geographic focus. This has hampered any attempt to understand large-scale patterns of sex chromosome and chromosome number evolution across Coleoptera. To eliminate this barrier my advisor, Jeffery Demuth, and I created the Coleoptera karyotype database (<http://www.uta.edu/karyodb/>). This resource now contains 4,797 beetle karyotypes, and we envision it as a long-term repository allowing immediate access to information that was previously scattered among hundreds of journal articles in several languages. Our database allows users to 1) quickly create and download karyotype datasets for analysis with comparative methods, 2) identify organisms that may be interesting targets for future sequencing projects, 3) discover what lineages have been neglected and may be fruitful targets for future cytogenetic and cytotaxonomic research. We have begun using this database to explore the evolution of sex chromosomes and chromosome number in Coleoptera.

Sex Chromosome Evolution:

The variation in sex chromosomes and meiotic behavior that beetles exhibit offer an opportunity to explore the evolution of sex chromosomes across unprecedented time and taxonomic scales. In particular, sex chromosome systems where the X and Y do not recombine offer an opportunity to test the hypothesis that Y chromosomes are lost more frequently in clades that lack recombining sex chromosomes than in clades where the sex chromosomes do recombine. In the first published use of

the karyodb database, we test this hypothesis. We first built a molecular phylogeny for over 1,000 taxa in the karyotype database, and then used comparative methods to model the evolution of sex chromosomes. Our results showed that this widely accepted explanation for the source of XO species did not fit the pattern we observe in beetles. In fact, we observed quite the opposite. Transitions where the Y is lost occur much more frequently from recombining sex chromosomes (XY to XO transitions) than do transitions from non-recombining sex chromosomes (Xyp to XO; figure 1).

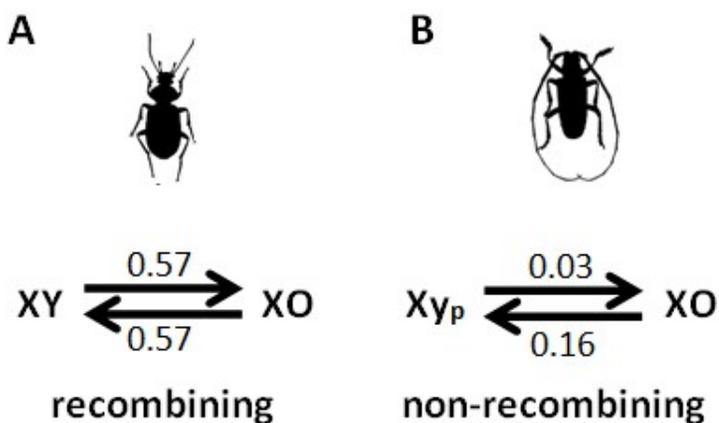


Figure 1: Rates of transition between sex chromosome systems. Rates are probabilities of a transition per 100 MY, in clades with recombining sex chromosomes (A) and those without recombination (B).

This finding led us to reexamine the literature of not only beetle sex chromosome behavior but also behavior of sex chromosomes during meiosis in mammals. Our conclusion from this research is that Y chromosomes that require recombination are fragile. More specifically, our “Fragile Y” hypothesis states that as selection leads to Y chromosomes with a very small recombining region, it increases the opportunity for generation of XO offspring through aneuploidy events. The full description of this research is available in the June 2014 issue of *Genetics*.

Chromosome Number Evolution:

We built on previous efforts to understand chromo-

some number evolution by modeling the evolution of chromosome number across beetles using time calibrated molecular phylogenies. This approach is producing the first robust estimates of the rate of karyotype evolution in beetles. We have combined these estimates with natural history data to better understand the driving forces in karyotype evolution in beetles. Preliminary results indicate that the variation in rates of karyotype evolution observed in beetles is strongly correlated with a number of traits that we expect to have large impacts on effective population size. For example, in genera where many species likely have very small effective population size, the rate of karyotype evolution is faster than closely related genera where the effective population size is expected to be larger.

Conclusions:

Despite our ability to now sequence whole genomes karyotypes remain valuable sources of data. Karyotypes are a highly variable and complex trait that offers an opportunity to detect changes in genome organization, uncover phylogenetic history, and distinguish cryptic species. Our initial analyses show that karyotype evolution can be successfully modeled and reveal important insights into the evolution of beetles. Additionally, the variation that we are uncovering in the rates of karyotype evolution may have important implications for understanding the forces responsible for the astounding diversity of some beetle groups. Finally, even in cases where whole genome sequencing is being done, karyotypes offer a quick and inexpensive form of preliminary data. This information can provide important guidance in choosing species that will be most informative in answering specific biological questions. While we continue to make every effort to include all published beetle karyotypes in our database, we also welcome contributions and corrections. You may contact us or submit data at coleochromosomes@gmail.com.

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