GENOMICS

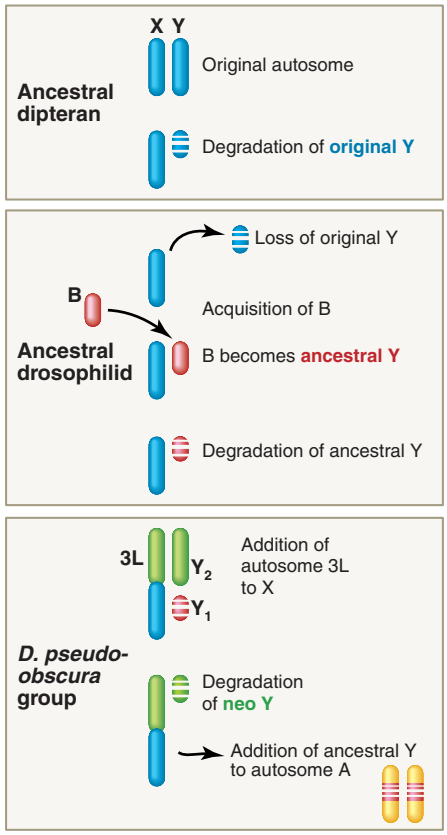
Recycling the Y Chromosome

Jennifer A. Marshall Graves

The Y chromosome must be the strangest element of any genome. In mammals and insects where the mode of chromosomal sex determination is an XX female and XY male, the male-specific Y chromosome is usually small and, unlike ordinary chromosomes, contains numerous repetitive DNA sequences. The Y bears only a few active genes, many of which encode proteins that determine male sex or are involved in reproduction. Comparisons between different species indicate that Y chromosomes degrade rapidly and can even disappear. What happens then?

Fruit flies are model insects that have proved valuable for studying evolutionary changes in sex chromosomes. The original Y chromosome of *Drosophila* species apparently disappeared more than 60 million years ago, and was replaced by a usurper—a blob of repetitive DNA that learned how to pair with the X, and scrounged useful genes from other chromosomes. This "ancestral" Y is shared by species in both major *Drosophila* subgroups. But that is far from the end of the story. Now it appears that in one group of drosophilids, this ancestral Y has itself been retired, and has been recycled by hitching a ride on a non–sex chromosome (autosome). On page 108 of this issue, Carvalho and Clark (*1*) reveal that the Y chromosome of *D. pseudoobscura*—the second of many *Drosophila* species to have its genome sequenced—is unrelated to the ancestral Y. Taking advantage of the outpouring of *D. pseudoobscura* genome data, these investigators tracked down the genes from the ancestral Y of this drosophilid species, and found them leading a blameless existence in ordinary chromosome pairs. Meanwhile, *D. pseudoobscura* sports a new Y, created from an autosome that at some point became fused to the X in this group of flies (see the figure).

Studies of the Y chromosome in many taxa have implied that Y degradation is a one-way street. X and Y chromosomes are thought to have evolved from an ordinary pair of autosomes when one member of the pair acquired a male-determining locus (*2*). Other male-advantage alleles accumulated at this site on the proto-Y, and the male-specific package was preserved by preventing recombination between the X and Y during meiosis. All sorts of dreadful genetic accidents—mutations, deletions, invasion by repetitive elements—occurred in this region of low recombination, progressively degrading the Y into a wasteland of discarded and defunct sequences, and sparing only those genes that acquired a selectable male-specific function. In addition, the Y appropriated some handy genes from autosomes that already had, or later acquired, a male-specific function.



The rise and fall of drosophilid Y chromosomes. The ancestral Y chromosome in most drosophilids, and the neo-Y in the *D. pseudoobscura* subgroup, are completely unrelated. Neither is related to the original Y or to the X, both of which evolved from an autosome pair (blue). The original Y was degraded and ultimately lost. In a drosophilid ancestor 63 million years ago, a B chromosome (red) became paired with the X. This ancestral Y acquired male-specific genes from elsewhere in the genome. In an ancestor of the *D. pseudoobscura* subgroup 18 million years ago, the X fused with an autosome arm (3L, green) to generate an XY_1Y_2 system. The Y_1 chromosome (ancestral Y) fused to an autosome (A, yellow). The Y_2 chromosome underwent partial degradation, retaining only male-specific genes, and now acts as a neo-Y in this group of flies.

This theory accounts well for the peculiarities of the human Y chromosome (*3*). Its ~50-Mb male-specific region retains only 45 active protein-coding genes, many with male-specific functions in sex determination (*SRY*) and spermatogenesis. A few were recruited from other parts of the genome, but most (including those with essential functions in male reproduction) have partners on the X, from which they diverged more than 300 million years ago. These genes are all that remain of the 1400 or so that were on the ancient autosome, now represented by the X. Therefore, we can calculate the rate at which genes have been lost, and predict that the entire human Y will disappear in about 10 million years (*4*). The Y already has been lost in two groups of rodents: the mole voles of Eastern Europe and the spinous country rats of Japan (*5*, *6*). The sex-determination gene *SRY* has evidently been replaced by a new sex-determining trigger elsewhere in the genome. This theory, however, does not account for the Y chromosome of our favorite model insect, *D. melanogaster*, whose Y chromosome is unrelated to the X. Perhaps it was degraded beyond recognition. Or, as with the mole voles, maybe it was completely lost and replaced.

One radical suggestion was that the drosophilid Y evolved, not from the X, but from one of the enigmatic supernumary B chromosomes that sometimes parasitize the genomes of plants and insects and even those of a few mammals. Derived, apparently at random, from all manner of repetitive sequences, B chromosomes live a lonely life, unable to pair with each other or the normal A chromosomes at meiosis. Yet there seems to be some strange affinity between unpartnered nonhomologous chromosomes, prompting the suggestion (*7*) that a B chromosome may have presented itself to the X as a possible partner. Although nonhomologous, this match was the best that either of the unpartnered elements could make. It would confer advantages to both chromosomes at meiosis, where singles are not welcome. Once it began to squire the X during meiosis in male germ cells, this new Y chromosome acquired genes that were moved or copied from autosomes, and these in turn became male-specific. This must have happened at least 60 million years ago, because the ancestral Y is shared by most *Drosophila* species. But not all.

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The new analysis by Carvalho and Clark (*1*) shows that *D. pseudoobscura* and its close relatives have a completely different Y. This cannot be the original Y that evolved by degradation of the original autosome pair, because the *D. pseudoobscura* subgroup of species diverged only 18 million years ago from the other drosophilid groups and lies nested within species that share the ancestral Y. So this substitution of Y chromosomes must represent a subsequent step and may teach us much about Y chromosome evolution. Was the ancestral Y completely degraded and, in turn, replaced? What happened to useful genes on the ancestral Y? Where did the new Y come from? Carvalho and Clark looked in the genome of *D. pseudoobscura* for homologs of genes on the ancestral Y, and found several of them alive and well and living in clusters on other chromosomes. This suggests that the ancestral Y was not utterly degraded, but was just shifted to the autosomes. Such an event is not unprecedented; at least two genes on the missing Y of the XO spinous country rat have moved to the X (*6*)

Thus, genes that were present in a single copy on the ancestral Y are now present in double-dose copies on an autosome pair. They have retained the testis-specific expression that they evolved during their spell on the ancestral Y. Most strikingly, the genes of the ancestral Y, bloated by millions of years of retroelement insertion, have shrunk back to a normal size in their new location. The ancestral Y has been recycled. There is life after death for the Y chromosome after all.

Where did the new *D. pseudoobscura* Y come from? Carvalho and Clark suggest that it is the relic of yet another autosome. We know that the large X in the *D. pseudoobscura* group was put together by fusion of the X with the arm of an autosome, 3L (see the figure). This leaves not only the original Y (Y_1) unpaired in males, but also one copy of the original autosome (now called Y_2). After recycling of Y_1, the Y_2 chromosome must have taken over, and is now going through the familiar degradation process. Sure enough, Carvalho and Clark found that most of the 15 genes on this neo-Y are homologous to genes on the *D. melangaster* 3L. It will be interesting to see whether these genes have already acquired male-specific functions.

Over the last 100 million years, *Drosophila* species have stuck to the same X, but experimented with at least three quite different Y chromosomes (see the figure). Vertebrate taxa may exhibit a similar phenomenon. For instance, the 5X and 5Y chromosomes of the platypus—which link the mammalian XY and bird ZW sex chromosome systems—exhibit a chain of chromosomes that underwent serial exchanges (translocations) (*8*). Meanwhile, the multiple sex chromosome–autosome translocations found in pygmy mice (*9*) and frogs (*10*) show us how one vertebrate sex chromosome system can evolve into another.

So Y chromosomes can be created and destroyed, re-created and recycled. The Y is dead. Long live the Y.

References

1. A. B. Carvalho, A. G., Clark, *Science* **307**, 108 (2005).
2. B. Charlesworth, D. Charlesworth, *Philos. Trans. R. Soc. London B Biol. Sci.* **355**, 1563 (2000).
3. H. Skaletsky *et al.*, *Nature* **423**, 825 (2003).
4. J. A. M. Graves, *Trends Genet.* **18**, 259 (2002).
5. W. Just *et al.*, *Nature Genet.* **11**, 17 (1995).
6. Y. Arakawa *et al.*, *Cytogenet. Genome Res.* **99**, 303 (2002).
7. J. H. P. Hackstein *et al.*, *BioEssays* **19**, 317 (1996).
8. F. Grützner *et al.*, *Nature* **432**, 913 (2004).
9. F. Veyrunes *et al.*, *Chromosome Res.* **12**, 369 (2004).
10. M. Ogata *et al.*, *Genetics* **164**, 613 (2003).

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ASTRONOMY

How Is the Solar Corona Heated?

Robert W. Walsh

The Sun's outer atmosphere (the corona) contains highly ionized atoms that can only form at a temperature of millions of degrees. Such high temperatures are thermodynamically inexplicable, given that the underlying photosphere and chromosphere (see the first figure) are much cooler (6000 K and at least 4300 K, respectively). Some extra source must deposit energy into the corona to create the steep temperature gradient. This source must also balance energy losses through radiation emitted into space, heat loss from the corona through thermal conduction and mass loss through the solar wind and eruptions such as solar flares. The energy budget needed to power the corona is quite small (about 0.01%) relative to the global solar energy output, but the specific coronal heating mechanism(s) that operate in the corona have been difficult to identify.

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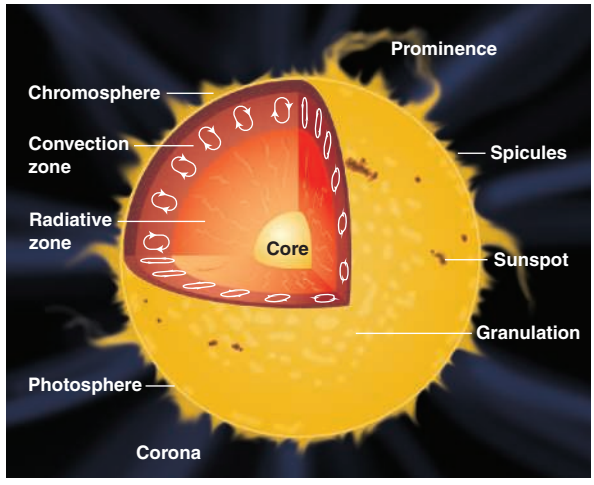
Recently, our understanding of coronal physics has been revolutionized by the space-based Solar and Heliospheric Observatory (SOHO). Residing 1.5 million km sunward from Earth, SOHO's unique vantage point enables continuous monitoring of solar activity. Together with the Transition Region and Coronal Explorer (TRACE) satellite, SOHO can probe the corona at optical, ultraviolet, and extreme ultraviolet wavelengths. The two spacecraft have provided unparalleled observational data, revealing a corona that is dominated by the Sun's magnetic field. Extreme ultraviolet observations show that this field channels the coronal material along the field lines to form a range of loop-like plasma strands (see the second figure).

Because the corona is a hot, magnetized plasma, one should calculate all the forces that act on each charged particle, including the effect of the magnetic field itself. This task is enormous because of the huge number of ions and electrons that make up the plasma. However, the spatial scales considered are often much larger than the dis-



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The structure of the Sun. The solar interior is composed of the core, the radiative zone, and the convection zone; the solar atmosphere consists of the photosphere, the chromosphere, and the corona. Continually streaming out from the Sun into interplanetary space is the solar wind. This sketch is adapted from an educational resource provided by the Space Weather Center (www.spaceweathercenter.org/resources/05/solarscapes/fig1.pdf).

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