The story of X -- evolution of a sex chromosome

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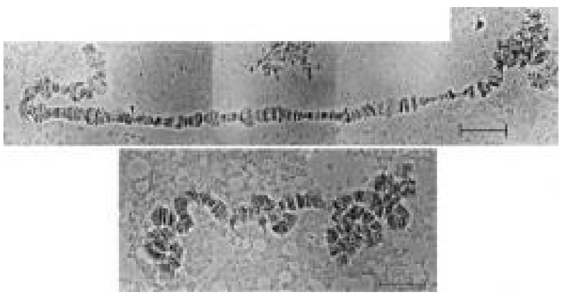

The neo-X (top) and neo-Yof the fruit fly Drosophila miranda, showing how the Y has shrunken slightly through loss of genes. The X has remained about the same size as the fly's other chromosomes, though its genes are in the process of adapting to the Y's degeneration. (Doris Bachtrog/UC Berkeley)

(PhysOrg.com) -- Move over, Y chromosome - it's time X got some attention. In the first evolutionary study of the chromosome associated with being female, University of California, Berkeley, biologist Doris Bachtrog and her colleagues show that the history of the X chromosome is every bit as interesting as the much-studied, male-determining Y chromosome, and offers important clues to the origins and benefits of sexual reproduction.

"Contrary to the traditional view of being a passive player, the X chromosome has a very active role in the evolutionary process of sex chromosome differentiation," said Bachtrog, an assistant professor of integrative biology and a member of UC Berkeley's Center for

Theoretical Evolutionary Genomics.

Bachtrog, UC Berkeley post-doctoral fellow Jeffrey D. Jensen and former UC San Diego post-doc Zhi Zhang, now at the University of Munich, detail their findings in this week's edition of the open-access journal PLoS Biology.

"In our manuscript, we demonstrate for the first time the flip side of the sex chromosome evolution puzzle: The X chromosome undergoes periods of intense adaptation in the evolutionary process of creating new sections of the genome that govern sexual differentiation in many species, including our own," she said.

Not all animals and plants employ genes to determine if an embryo becomes male or female. Many reptiles, for example, rely on environmental cues such as temperature to specify male or female.

But in life forms that do set aside a pair of chromosomes to specify sex - from fruit flies to mammals and some plants - the two X chromosomes inherited by females look nearly identical to the other non-sex chromosomes, so-called autosomes, Bachtrog said. The Y chromosome, however, which is inherited by males in concert with one X chromosome, is a withered version of the X, having lost many genes since it stopped recombining with the X chromosome.

In mammals, that probably took place about 150 million years ago, while in the fruit fly Drosophila melanogaster, a laboratory favorite, the sex chromosomes arose independently about 100 million years ago. In both humans and fruit flies, the Y chromosome has dwindled from a few thousand genes to a few dozen.

Hence the intense interest in why and how the Y chromosome lost genes once it stopped interacting with the X. Scientists have found that, as the only chromosome pair that doesn't break and recombine every time a cell divides, the XY pair in males is unable to take advantage of the main way deleterious genetic mutations are eliminated. The XX pair in females does recombine, but for the Y, the only way to get rid of a bad mutation in a gene is to inactivate or delete the entire gene. Over millions of years, inactive genes are lost, and the Y shrinks.

"If you have no recombination, natural selection is less effective at removing detrimental genes," said Bachtrog. "Y is an asexual chromosome, and it pays a price for that: It keeps losing genes."

Bachtrog, whose career has revolved mostly around the study of the degeneration of the Y chromosome, decided to focus on the X chromosome several years ago and went about searching for sex chromosome pairs that have arisen more recently - and thus might be in the process of adapting to their new role. Her paper centers around study of the three sex chromosomes in a rare western fruit fly, Drosophila miranda, a darker-colored cousin of D. melanogaster. (Many creatures have more than one pair of sex chromosomes; the platypus, for example, has five pairs, all inherited together.)

While one of D. miranda's sex chromosomes is descended from the original sex chromosome that appeared in Drosophila nearly 100 million years ago, a second originated perhaps 10 million years ago, and the third about a million years ago. The older two look much alike, Bachtrog said: The Y chromosome in each pair has lost genes to become a shadow of its former self, while the two X chromosomes are indistinguishable from each other.

The third and youngest sex chromosome is different. The Y is not yet shriveled, though it contains many non-functional genes - about half the total - that will eventually be lost. The X, which is dubbed neo-X, is undergoing rapid change, however, with about 10 times the normal amount of adaptation seen in the autosomes, according to the researchers.

By adaptation, Bachtrog means that the gene sequences in the X chromosome are becoming fixed as random mutations have finally settled on a few beneficial changes that accommodate the increasingly irrelevant Y chromosome. Between 10 and 15 percent of neo-X genes show adaptation, compared to only 1-3 percent of autosome genes.

"In hindsight, that is not surprising," Bachtrog said. "Neo-X is facing a much more challenging situation than the autosomes because its pair, the Y chromosome, is degenerating. Its genes are no longer producing proteins, so neo-X has to compensate by up-regulating its genes. We find a lot of genes on the X chromosome are involved in dosage compensation."

In humans, for example, all genes on the X chromosome are twice as active to account for the lack of genes on the Y. Women accommodate this by inactivating one entire X chromosome so as not to produce too much protein, Bachtrog said.

Another change in neo-X that Bachtrog suspects is taking place is the elimination of genes that are harmful to females. Biologists have realized recently that some genes have opposite effects in males and females, and evolution is a tug of war between males jettisoning genes that they find detrimental only to have females put them back, and vice versa.

"A good place to put sexually antagonistic genes that are beneficial to one sex but detrimental to the other is on the sex chromosomes," she said. The Y always ends up in the male, she said, so genes on the Y chromosome won't affect females.

"Conversely, the X chromosome becomes feminized with genes that are good for the female but detrimental to the male," said Bachtrog, adding that the X also becomes demasculinized, losing genes that are of use only in the male.

In search of more insights into the evolution of the X chromosome, Bachtrog said she is looking for fruit fly species with older and younger sex chromosomes "to study sex chromosome evolution in action." She said evidence suggests that adaptation to being a sex chromosome is most intense between 1 and 10 million years after it starts. Bachtrog also is completing assembly of the genome sequence for D. miranda, which is not among the 12 species of Drosophila currently targeted by the genome sequencing community. She hopes that the fly will become a model system like D. melanogaster.

"Now, finally, we are within reach of studying model systems like D. miranda that we couldn't think of several years ago," she said, predicting that "whole genome comparisons will revolutionize evolutionary biology, ecology and many other fields."

Source: University of California - Berkeley (news : web)

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