

Two papers unraveled the mystery of sex determination and benthic adaptation of the flatfish

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Half-smooth tongue sole. Female (top) Male (bottom) Credit: SL Chen

Researchers from Yellow Sea Fisheries Research Institute, Chinese Academy of Fisheries Sciences, BGI-Shenzhen and other institutes have successfully decoded the first genome of a flatfish - half-smooth tongue sole (*Cynoglossus semilaevis*), providing insights into ZW sex chromosome evolution and adaptation to a benthic lifestyle. The data generated in this project also lay foundation on the genetic breeding of

tongue sole. The latest study has been published online today in *Nature Genetics*. In another study published in *Genome Research* at the same time, the researchers also uncovered the epigenetic mechanism underlying the temperature-dependent sexual reversal as well as the trans-generational inheritance of such sexual reversal phenomena in tongue sole.

The genetic mechanisms underlying sex determination as well as the origin and evolution of [sex chromosomes](#) have fascinated biologists for decades. Half-smooth tongue sole is an important cultured marine flatfish along China coast, whose sex is primarily determined by the inheritance of sex chromosomes (genetic sex determination, GSD) but also affected by environmental temperature ([environmental sex determination](#), ESD). In normal condition, the sex of tongue sole is determined by the ZW/ZZ sex determination system with female containing a heteromorphic W chromosome. However, if juvenile fish are reared in high temperature, the genetic females (ZW) can develop into phenotypic males (so-called pseudo-males). Interestingly, these sex-reversed pseudo-males are fertile and can mate with normal females to produce viable offspring. Astonishingly, most of their genetic female offspring (ZW) develop into pseudo-males, but without temperature induction. Thus, with its complex sex determination system governed by the interaction between genetic determination and environmental factors, tongue sole is an excellent model to understand the molecular mechanism of sex determination in fishes and the interplay of genome and environment.

In this study, the researchers sequenced and assembled the genomes of one male (ZZ) and one female (ZW) tongue sole, respectively. Based on the difference of sequencing depth of Z/W linked-scaffolds between female and male, together with the high-resolution genetic map constructed by SSR and SNP, they assembled the Z and W chromosome of tongue sole at high quality. Using the Z-W homologous genes, they

estimated that the age of the tongue sole sex chromosome pair is relatively young (about 30 million years), which contrasts with the age of hundreds of millions of years for the mammalian and avian sex chromosomes. Interestingly, researchers found that the sex chromosomes of tongue sole are derived from the same ancestral vertebrate protochromosome as the avian W and Z chromosomes. Furthermore, the same gene on the Z chromosome, *dmrt1*, which is the male-determining gene in birds, showed convergent evolution of features that are compatible with a similar function in tongue sole.

To understanding the regulatory mechanisms involved in the temperature-dependent [sex reversal](#) as well as the inheritance of sex reversal in tongue sole, researchers then analyzed the gonadal DNA methylomes and transcriptomes of normal males (ZZ), pseudo-males (ZW), normal females (ZW), and the offspring of a pseudo-male crossed with a female. They found that, after phenotypic sexual reversal, the genome-wide methylation patterns of genetic females have been accurately shaped to the patterns of normal males. Furthermore, the methylation changes after sex reversal were enriched in genes in the sex determination pathway. By comparing parental and offspring samples, researchers also found that the methylation changes between parental pseudo-males and females were inherited by offspring pseudo-males, probably explaining why the offspring genetic females of pseudo-males can undergo sexual reversal without temperature induction. For organisms with sex chromosomes, a challenge for the sex-reversed individuals is the unequal gene dosage on sex chromosomes when compared with normal individuals. For example, pseudo-males (ZW) of tongue sole lack one Z chromosome compared with normal males (ZZ), and contain one extra W chromosome with female-specific genes. Thus, how to revolve gene dosage inequality on sex chromosomes is a fundamental question for sex reversal. Researchers found that, dosage compensation only occurs in a restricted, methylated cytosine enriched Z chromosomal region in pseudo-male testes, achieving equal expression

level in normal male testes. Some spermatogenesis-related genes were found in this region. For the W chromosome, they observed that many W-linked genes are still actively expressed in pseudo-males. The researchers speculate that the expression of these W-linked genes may compensate the dosage of their counterparts on the Z chromosomes. However, female-specific genes, such as *figla*, were suppressed in pseudo-males by methylation regulation. In conclusion, the researchers propose that epigenetic regulation plays multiple crucial roles in sexual reversal of tongue sole fish.

Flatfish are characterized by a transition from pelagic to benthic habitats when they metamorphose from free swimming larvae to bottom-dwelling fish, accompanied by a series of biological and phenotypic changes, such as eye migration, displacement of internal organs, the difference of pigmentation and the sensitivity of light. By comparing the transcriptomes of pelagic and benthic fish, the researchers revealed that the differentially expressed genes between these two developmental stages are enriched in genes potentially involved in adaptation to a benthic lifestyle. They also identified 15 positively selected genes, which have putative roles in metamorphosis. In addition, they found that the expression levels of rod pigment (*rh1*) and cone pigment (*lws1*) genes, which are responsible for scotopic vision and long-wavelength-sensitivity, respectively, were significantly up-regulated in benthic stages, whereas the expression of the middle-wavelength-sensitive pigment gene (*rh2*) was significantly up-regulated in pelagic stages. Moreover, they also found that several crystallin genes were lost or became pseudogenes. They speculate that these changes reveal the adaptation of the tongue sole visual system after shifting to the benthic environment with weak light conditions. As compensation, tongue sole have developed a strong lateral –line sense organ and especially, the papillae-a specific mechanoreceptorsense organ during evolution.

Dr. Guojie Zhang, who is the leading author of both papers from China

National Genebank of BGI, said: "The evolution of sex is one of the major transitions in evolution, that has significantly enhanced the adaptation ability of the species. However, our knowledge of sex determination mechanisms is still very limited. Vertebrates have various sex-determination mechanisms. The [sex determination](#) process of many vertebrate species is regulated by environmental cues, like temperature. Investigation of the molecular mechanisms underlying this process will shed new lights on the understanding of the interaction between functional gene networks and their regulations by environmental factors, and increase our knowledge on how genome evolution drives species diversification and diversity."

More information: Paper 1: [dx.doi.org/10.1038/ng.2890](https://doi.org/10.1038/ng.2890)
Paper 2: www.genome.org/cgi/content/abstract/gr.162172.113

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