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Retroduplication of rhodopsin gene 400 million years ago diversified the photoreception in fishes

Animals utilize light from the environment as important information sources. We can discriminate colors, brightness and shapes of objects by visual system. In addition, animals can detect daily and seasonal changes of the light environment to alter their activities. For these visual and non-visual photoreceptions, opsins function as universal photoreceptive proteins. Recent progress in whole genome sequencing has revealed that animals have various opsin genes. In general, mammals have less than 10 opsin genes (9 genes in the human genome), which contrasts with many opsin genes in non-mammalian vertebrates (about 20 genes in birds, reptiles and amphibians and 30~40 genes in teleosts). This is probably because of the nocturnal lifestyle in the early evolutionary process of mammals. These opsins are known to work not only in the retina but also in other tissues, such as brain. From the viewpoint of the genomic structure, most opsin genes have introns in their coding regions. However, a few opsin genes are characterized as single-exon genes. These intron-less genes are presumed to have been formed by the unique gene duplication mechanism, retroduplication (Fig.1(A)). Retroduplication is RNA-based gene duplication, which is quite different from DNA-based gene duplication, the copying and pasting of DNA sequence from one region to another in the genome. A gene is transcribed to produce mature spliced mRNA, which happens to be reverse transcribed and subsequently inserted into different genomic region. In most cases, these retrocopies are regarded as pseudogenes because of a lack of promoter sequences in intron-less cDNA. Thus, it is very interesting to reveal how the acquisition of functional retrocopies contributes to the gene diversification.

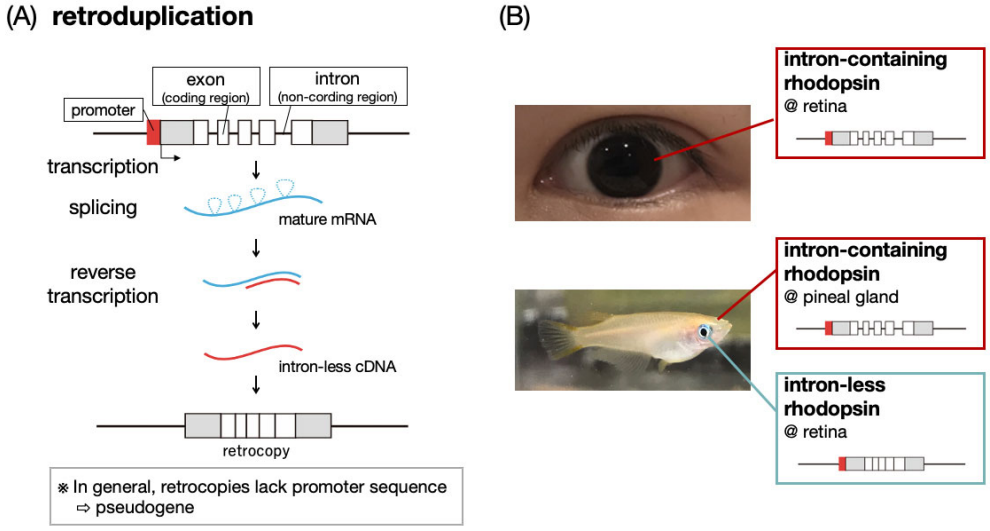

Fig. 1. (A) RNA-based gene duplication, retroduplication, produces an intron-less gene.
(B) Most vertebrates have a single intron-containing rhodopsin gene expressed in the retina, but teleosts have multiple rhodopsin genes, intron-less one expressed in the retina and intron-containing one expressed in the pineal gland.

In this study, we focused on an intron-less opsin gene, teleost rhodopsin gene. (Fig.1(B)) Rhodopsin is a visual photoreceptive protein in the rod photoreceptor cells of vertebrate retina. It has been known for a long time that teleost retinas express intron-less rhodopsin genes. Teleosts also have an intron-containing rhodopsin gene exclusively expressed in pineal gland which secretes melatonin to regulate circadian rhythm in the brain. The conservation of the genomic structures of intron-containing rhodopsin genes isolated from cartilaginous fishes and tetrapods suggests the possibility that, before the appearance of teleosts, the intron-less rhodopsin gene emerged by retroduplication and obtained the ability to express in the retina in place of parental intron-containing rhodopsin gene.

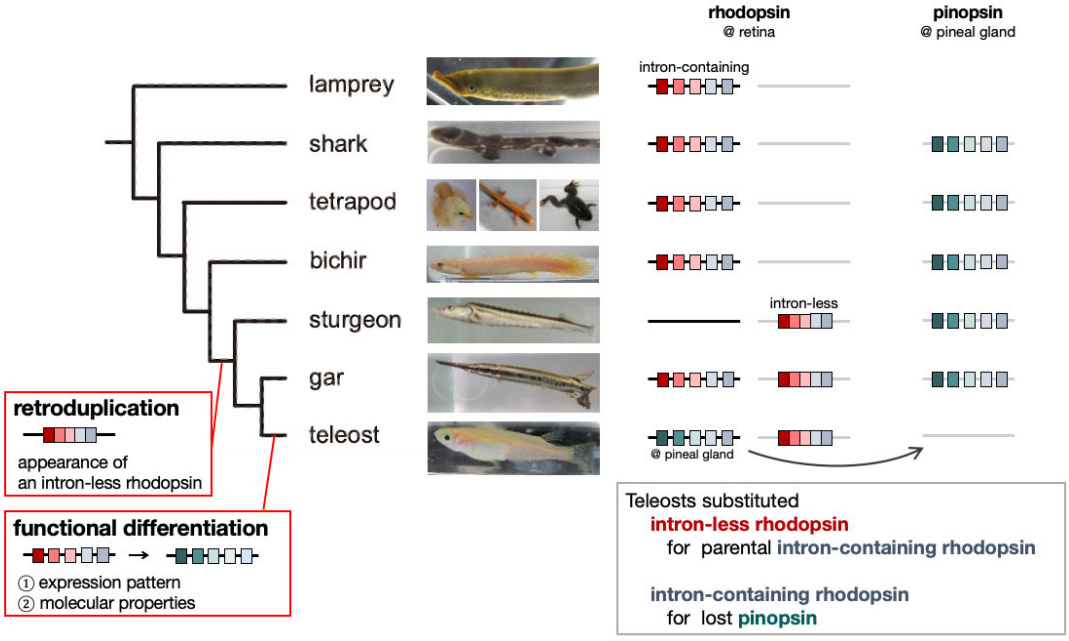

Fig. 2. Stepwise evolutionary model of fish intron-containing and intron-less rhodopsin genes. Bichir maintains a single intron-containing rhodopsin gene for retinal photoreception and pinopsin gene for pineal photoreception like tetrapods. After branching of the bichir lineage, retroduplication resulted in the formation of an intron-less rhodopsin gene. Subsequently after branching of the gar lineage, the intron-containing rhodopsin gene changed its expression pattern and molecular properties to function exclusively in pineal gland, accompanied with the loss of pinopsin gene.

In order to unravel the evolutionary origin of teleost intron-less and intron-containing rhodopsin genes, we analyzed the rhodopsin genes of non-teleost fishes, bichir, sturgeon and gar, which are often regarded as “living fossils”. We isolated the rhodopsin genes to reveal their phylogenetic relationship, their expression patterns in the retina and brain and the molecular properties of the proteins they encode. Our analysis suggests that retroduplication of the rhodopsin gene occurred after branching of the bichir lineage to produce an intron-less rhodopsin gene and, after branching of the gar lineage, the parental intron-containing rhodopsin gene changed its expression pattern and molecular properties to function exclusively in the pineal gland. Abundant expression of intron-containing rhodopsin gene in the pineal gland may have caused the loss of the pinopsin gene, an

original pineal opsin, in the teleost lineage. Pinopsin is characterized as a pineal opsin in a wide range of vertebrates except for mammals and teleosts. We speculate that teleosts utilized intron-containing rhodopsin gene for pineal photoreception instead of pinopsin. Therefore, we concluded that retroduplication of the rhodopsin genes 400 million years ago changed the roles of opsin genes for visual and pineal photoreceptions in fishes (Fig.2). The flexible RNA-based and DNA-based gene duplications expanded the opsin genes in fishes to adapt to various aquatic light environment, which may have led to the biodiversity of fishes on earth.

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