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Genomic organization and evolution of olfactory receptors and trace amine-associated receptors in channel catfish, *Ic*

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ABSTRACT

B : Channel catfish DA ed in the channel fish at genome, including 27 functional OR genes and 28 functional TAAR genes. Phylogenetic and orthogroup analyses were conducted to illustrate the evolutionary dynamics of the vertebrate ORs and TAARs. Collinear analysis revealed the presence of two conserved orthologous blocks that contain OR genes between the cat fish genome and zebrafish genome. The complete loss of a conserved motif in fish OR family H may contribute to the divergence of family H from other families. The dN/dS analysis indicated that the highest degree of selection pressure was imposed on TAAR subfamily 14 among all fish ORs and TAARs.

C : The present study provides understanding of the evolutionary dynamics of the two gene families (OR and TAAR) associated with olfaction in channel catfish.

G : This is the first systematic study of ORs and TAARs in catfish, which could provide valuable genomic resources for further investigation of olfactory mechanisms in teleost fish.

1. Introduction

Carnivorous fish use one of their chemosensory systems, the olfaction system, to detect and discriminate a broad spectrum of water-soluble substances. This system is mainly mediated by the olfactory receptors (ORs), a group of seven-transmembrane G protein-coupled receptors (GPCRs) in the class of rhodopsin. These receptors are expressed on the olfactory neurons, and can induce the signal transduction pathways that trigger behaviors [1–3]. When fish chase the preys in turbid waters, ORs are used as a compensation for limited visibility. Accordingly, preys have co-evolved to induce the OR-related aversion activities of predators. For instance, sea hares can release inks, which are composed of amino acids, to stimulate sea catfish to avoid predatory attacks [4]. In teleosts, ORs are used to mediate reproduction activities via sensation of odorants such as nucleotides, polyamines and bile salts [5,6]. ORs also have other roles, including self-expression regulation and auxiliary connection of sensory neurons [7].

In addition to ORs, trace amine-associated receptors (TAARs) are expressed on the olfactory epithelium. Although TAARs were initially considered as neurotransmitter receptors [8], several studies indicated that they have similar functions to ORs [9–16]. There are three clades in vertebrate TAARs: Clade I TAARs are found in both mammals and fish species, and they are expressed to detect primary amines through an aspartic acid on the third transmembrane domain ($Asp^{3.32}$; Ballesteros-Weinstein indexing); Clade II TAARs are found only in mammals, and they are expressed to detect tertiary amines; Clade III TAARs are found only in fish species, and they use $Asp^{5.42}$ instead of $Asp^{3.32}$ to detect amines [17,18]. However, some members of the fish TAAR subfamilies 13 and 14, which are not classified into any clades mentioned above, possess both $Asp^{3.32}$ and $Asp^{5.42}$ for detecting diamines [18].

The numbers of ORs and TAARs vary between mammals and fish species. Larger OR repertoires exist in mammalian species than in fish species. For instance, approximately 700 ORs have been identified in the human genome, and approximately 1200 ORs have been identified in the genomes of rodents [19,20]. The numbers of ORs in fish species are much smaller with zebrafish possessing the most ORs of 140 [21]. However, fish species possess more TAARs than mammals [22,23]. Moreover, the number of TAARs is far smaller than that of ORs in

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mammals, while the numbers of these two gene families are roughly equal in fish species. It is speculated that the number variation of OR/TAAR genes between mammals and fish species might mirror the evolutionary dynamics of this gene family.

In catfish, previous efforts were mainly focused on the physiological and neural studies of the ORs [24–28], while few studies have been conducted on TAARs. Here, upon the completion of the catfish reference genome assembly [29], this study first report the complete repertoires of ORs and TAARs and their organizations in the channel catfish genome, and provide insights into the evolutionary dynamics of these two gene families in vertebrates.

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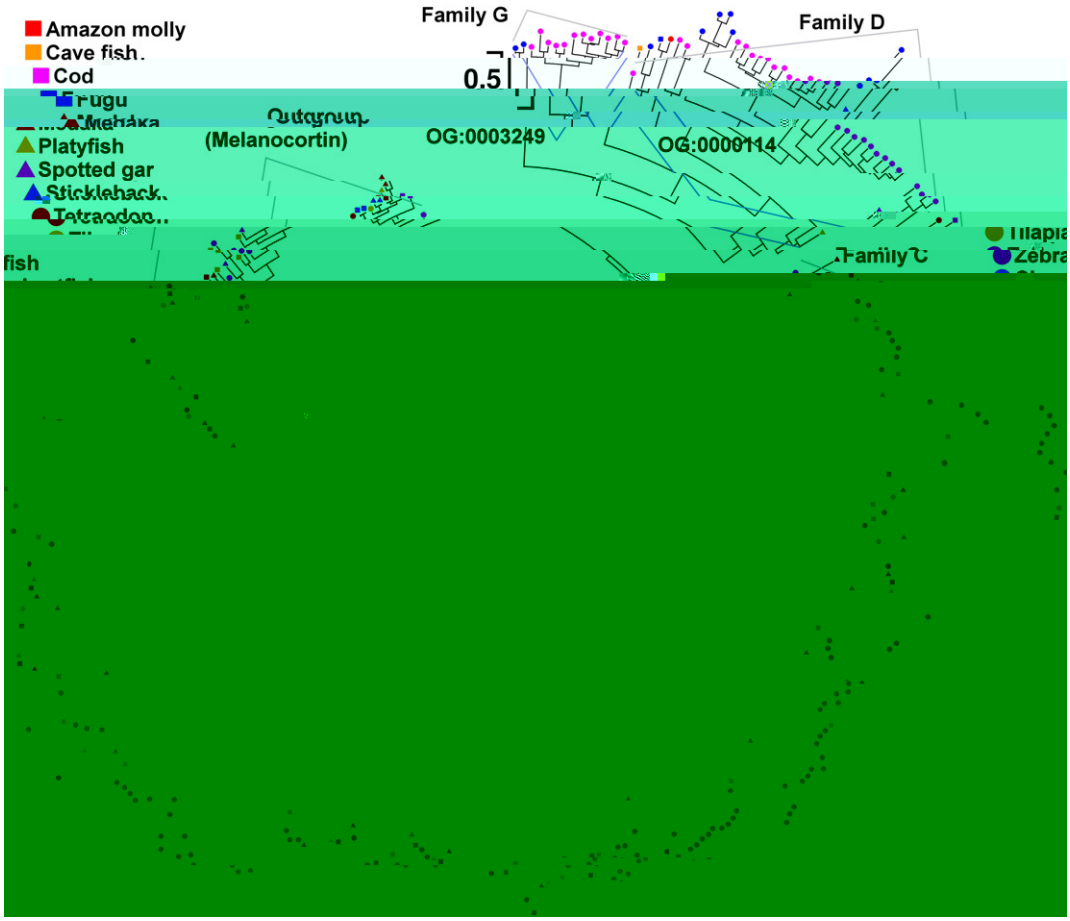

Fig. 1. A phylogenetic tree of ORs from 12 fish species (legends are indicated on the upper left side of the figure). Members from the same family are coverd with curves with their family names indicated outside of the curves in grey, while names of the orthogroups are indicated in the inside of the fi

support values were computed. Also, we used melanocortin and histamine receptor H2 as outgroups to root the phylogenetic trees for ORs and TAARs, respectively. MEGA6 was used for visualization [41]. We only used fish ORs to construct the phylogenetic tree, because the number of mammalian ORs is too large. Also, there are different nomenclature systems used among mammals, amphibians, birds and fish species.

Additionally, we conducted comparative genomic analysis using OrthoFinder [42], and orthogroups that contain ORs and TAARs were identified. Only clusters that consist of at least two orthologous or two paralogous were retained in our study [43].

2.4. C AA fi c fi

The genomic locations of the ORs and TAARs were compared between the catfish genome and zebrafish genome. Reciprocal blast (using catfish as query blast against zebrafish, and using zebrafish as query blast against catfish) and self-blast (self-blast of catfish, and self-blast of zebrafish) were conducted before running MCScanX for the detection of gene collinearity [44]. The results were visualized using Circos [45]. Tandem duplicated genes, which are defined as neighbors to each other while the distance between them is <10 kb, were also identified [46].

2.5. I fic c

Conserved motifs of ORs and TAARs were identified using MEME [47]. All amino acid sequences of ORs and TAARs were aligned using MUSCLE [38], and the gaps were removed using trimAl [48]. Only the top five conserved motifs were identified, with the motif length ranging from five to fifty.

2.6.

The dN/dS analysis was conducted for each subfamily of ORs and TAARs using Datamonkey [49]. Only genes that were found in at least two species were included for the analysis.

3. Results and discussion

3.1. I fic AA c c fi

A total of 27 functional OR genes and 28 functional TAAR genes were identified in channel catfish. Furthermore, there were 20 OR pseudogenes and eight TAAR pseudogenes. The genomic locations of the ORs and TAARs were summarized in Table 1, and that of pseudogenes were summarized in Table S1. The identification of OR and TAAR pseudogenes in channel catfish was summarized in Table S2.

Mammals possess more ORs than TAARs, while fish species possess roughly equal ORs and TAARs. For instance, in humans, 339 functional ORs were identified while only 6 functional TAARs were identified [20,37]. In our study, the number of ORs was much closer to the number of TAARs. Similar results were also found in zebrafish after searching in ENSEMBL (159 ORs and 94 TAARs). One hypothesis for this phenomenon is that ligands or odorants detected by fish TAARs might be recognized by mammalian ORs, or vice versa [13,15,16,50]. Another hypothesis is that TAARs may play more important roles than ORs in the olfaction of fish species compared with mammals, owing to

different living environments. Generally, fish capture chemical compounds from water flux, while mammals capture odorant molecules from aspiratory flux [3].

3.2. G c AA c c fi

The ORs (both functional genes and pseudogenes) were located on five chromosomes, including chromosomes 11, 17, 18, 19, and 24. As in zebrafish, ORs in catfish were organized in clusters, and each cluster contained at least five members [21]. Detailed gene coordinates were listed in Table 1. For instance, two clusters were found on chromosome 17, one on chromosome 18 and one on chromosome 19. In addition, several smaller clusters and single genes were scattered on chromosomes 11, 17, 18 and 24. As a matter of fact, members of each subfamily resided together, while a broad genomic distance existed between the subfamilies, suggesting that members within each subfamily could be derived from lineage-specifi

OG:0000114, and family G belonged to orthogroup OG:0003249 (Fig. 1, and Table S3). For Family H, subfamilies 132, 133, 134, 135, 136, and 137 fell into orthogroup OG:0000252, subfamilies 130 and 131 fell into orthogroup OG:0001719, and subfamily 129 fell into orthogroup OG:0012694.

In this study, we used both the phylogenetic and orthogroup analyses to elucidate the evolutionary dynamics of ORs in fish species. The phylogenetic analysis was mainly based on pairwise comparison of ORs, while the orthogroup analysis was based on not only the self-comparison within each species genome but also the pairwise comparison among all species genomes used in the present study. Thus, the combination of these two analyses enables us to identify the catfish ORs properly.

Previous studies revealed that tandem duplication was a major type of duplication in teleosts [46], and might contribute to their evolution [44,51]. Furthermore, several tandem duplicated genes involved in sensory response pathways were enriched in zebrafish, and one olfaction-related GO term (olfactory receptor activity) was identified among these genes [46]. As in our results, most catfish ORs were originated from lineage-specific tandem duplication, while the remaining ORs were originated from the most recent common ancestor of all fish species.

A phylogenetic tree of TAARs was displayed in Fig. 2. Twenty-eight catfish TAARs were identified in the catfish genome, of which six belonged to Clade I, one belonged to Clade III, six belonged to subfamily 13, and 15 belonged to subfamily 14 (Fig. 2 and Fig. S3). It is apparent that fish TAARs possess a characteristic of species-specific gene expansion. For instance, in subfamily TAAR14, gene expansion led to the presence of 10 TAARs in zebrafish, and 15 TAARs in catfish (Fig. 2). Similar results were also found in Atlantic salmon [16]. TAAR gene expansion was also found in subfamily TAAR13 for both catfish and zebrafish (Fig. 2).

Two orthologous groups were identified for vertebrate TAARs. Orthogroup OG:0000075 covered all genes in Clade I, Clade II and subfamily 13 (Fig. 2, and Table S3). Orthogroup OG:0000037 comprised all genes from Clade III and subfamily 14 (Fig. 2, and Table S3). In the phylogenetic analysis, Clade I and Clade II were also clustered together in a single clade, indicating that these two clades of TAARs might have

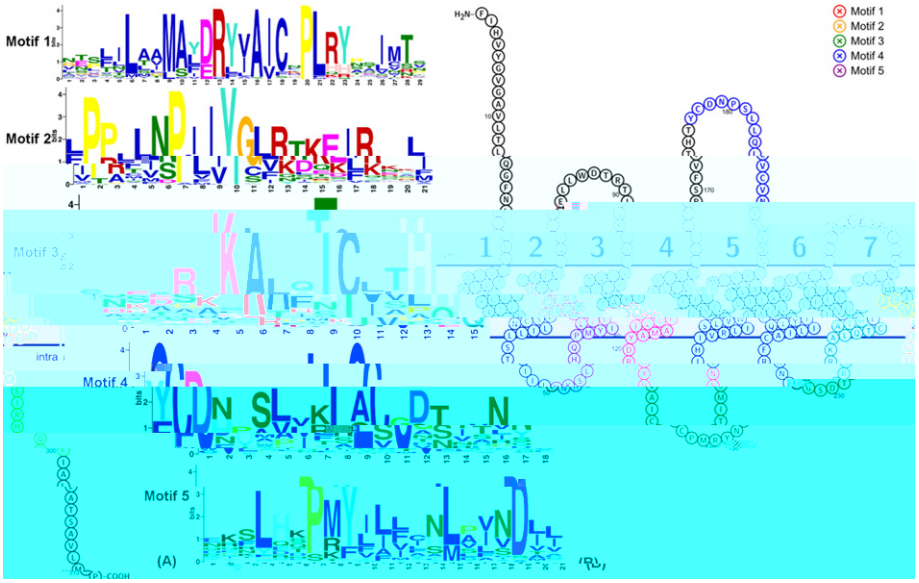

Fig. 4. Logo representation and distribution of the five best conserved motifs identified for teleost ORs. (A) Sequence logos of the conserved motifs, as the degree of conservation is indicated by the height of amino acid code. (B) The distribution of these motifs as displayed in the two-dimensional topology structure of ORs. The blue numbers represent the number of each trans-membrane domain.

while only one motif was spanned on an extracellular loop (Fig. 4B). Strikingly, the positions of these conserved motifs were overlapped with potential binding sites in the mammalian ORs [53], indicating that the binding sites of fish ORs might be similar to that of mammals.

Five best-conserved motifs were identified for fish TAARs. The logo presentations of these motifs, as well as their corresponding locations in the topology structure of TAARs (here, we used catfish taar14n as an example), were displayed in Fig. 5. Of these five motifs, motif 2 contained "NSXXNPXXYXXXYXWF" (where "X" represents any amino acid residue) (Fig. 5A), which is considered as the TAAR fingerprint motif [8]. Motif 3 possessed the sequence pattern of "DRY" (Fig. 5A), which can coordinate the conformational status of TAARs and then affect the binding affinity of TAAR [54]. The rest of the five motifs all contained conserved amino acid(s) identified in a previous study [8], most of which were located on trans-membrane domains (Fig. 5B). The distribution of all the conserved motifs was well consistent with the distribution of predicted ligand-binding sites [16], which are essential for the formation of ligand pocket vector [37]. We speculate that even though the sequence divergences are large among fish TAARs, the components and positions of ligand binding residues of fish TAARs remain highly conserved.

We observed that the conserved motifs' arrangement, in most cases (four pairs of conserved motifs), were generally identical between fish ORs and TAARs. For example, a conserved motif, which was spanned on the junction of the sixth trans-membrane region and the third intracellular loop, was identified in both ORs and TAARs. The sequence pattern of "DRY" was located on the same position of these two receptors, at the beginning of the second intracellular loop. Since both ORs and TAARs are involved in olfaction, they must initiate the same or similar intracellular signal cascades. Therefore, the similar distribution pattern of conserved motifs may indicate that ORs and TAARs have similar functions. We further explored this hypothesis through identifying conserved motifs for ORs and TAARs together. Three conserved motifs (data not shown) were overlapped with regions described above,

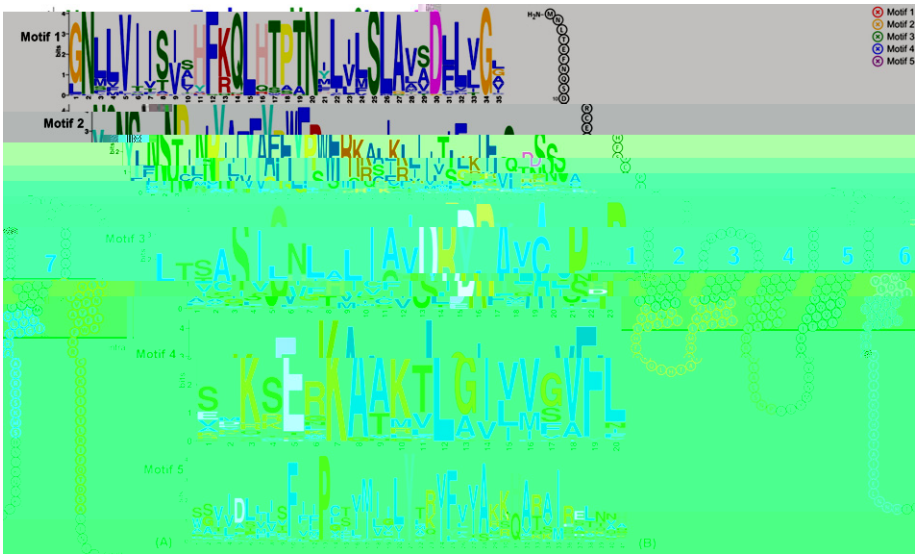

Fig. 5. Logo representation and distribution of the five best conserved motifs identified for teleost TAARs. (A) Sequence logos of the conserved motifs, as the degree of conservation is indicated by the height of amino acid code. (B) The distribution of these motifs as displayed in the two-dimensional topology structure of TAARs. The blue numbers represent the number of each trans-membrane domain.

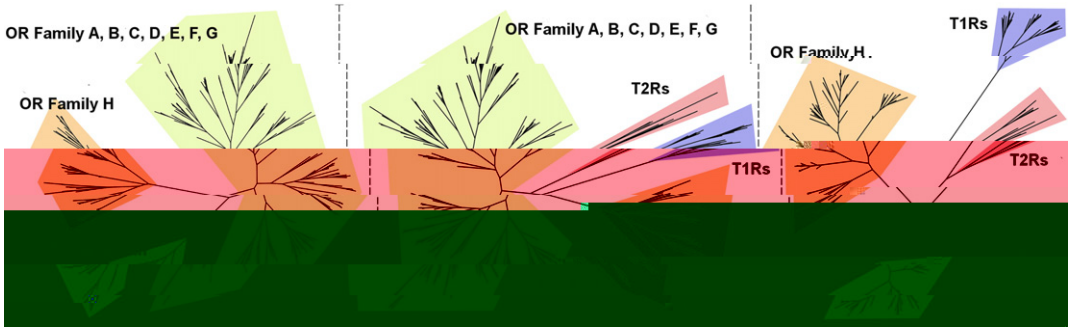

Fig. 6. Divergence of family H from other ORs. (A) A phylogenetic tree of all OR families with melanocortin. (B) A phylogenetic tree of all OR families with taste receptors. (C) A phylogenetic tree of family H with melanocortin and taste receptors.

indicating that fish ORs and TAARs share similar sequence patterns at certain locations. Taken together, we inferred that fish TAARs might share the same function with fish ORs based on the motif analysis, but functional studies for validation are still needed in the future.

3.6. D c H

Family H is considered as a group of fish ORs that were originated from an ancient duplication event [21]. This was also found in our phylogenetic analysis, with the first event being the divergence of family H from other families (Fig. 5). Family H was not clustered with other families (Fig. 6A) even using more evolutionary distant gene families as outgroups (Fig. 6B). However, family H was clustered into a single clade that was clearly separated from these outgroups (Fig. 6C). Here, the conserved motif analysis for all the fish OR families allowed us to unveil a new mechanism underlying this phenomenon. Motif 4 was not found in family H, suggesting that the loss of motif 4 may contribute to the divergence of family H from other families (Fig. 4B). Interestingly, this motif, spanning entirely on the second extracellular loop, contains the cysteine residue that is essential for the formation of ligand binding pocket [53]. Thus, we inferred that the fish ORs from family H might lose their sensing ability completely, or that they may possess weaker ligand-receptor affinities compared with fish ORs in other OR families.

3.7. /

To measure the natural selection pressure that was imposed on fish ORs and TAARs, the global synonymous (dS) and non-synonymous (dN) rates were calculated for selected subfamilies. The global ratios of dN/dS were well below 1.0 for all subfamilies, a theoretical boundary for positive and negative selection (Fig. 7A). The fish TAAR14s exhibited the highest dN/dS ratio, followed by the TAAR13s. We speculated that these two subfamilies were inclined to increase the frequency of some certain alleles under selective pressure. To explore this hypothesis, we conducted site-by-site (or codon-by-codon) analysis for each subfamily. As expected, positive selection sites (<0.1) were found in subfamily 14 (Fig. 7B). Previous study reported that two zebrafish TAAR14s contain both $Asp^{3.32}$ and $Asp^{5.42}$, indicating that a transformation occurred in fish TAARs [18]. In our results, nine catfish TAAR14s contained both $Asp^{3.32}$ and $Asp^{5.42}$, including TAAR14c, TAAR14f, TAAR14g, TAAR14k, TAAR14m, TAAR14n, TAAR14q, TAAR14r and TAAR 14s, and they could be candidate diamine receptors. Therefore, we conclude that fish TAAR subfamily 14 was imposed with the highest degree of natural selection pressure among all fish ORs and TAARs.

4. Conclusions

In the present study, we report the complete repertoires of ORs and TAARs in channel catfish. Two conserved orthologous blocks that contain ORs as anchor genes were identified between the catfish genome and zebrafish genome. The arrangements of conserved motifs were generally identical between fish ORs and TAARs. The complete loss of a conserved motif in OR family H might contribute to its divergence from other families. The highest level of selection pressure was imposed on fish TAAR subfamily 14 among all fish OR and TAAR subfamilies.

Supplementary data to this article can be found online at doi:10.1016/j.bbagen.2016.10.017.

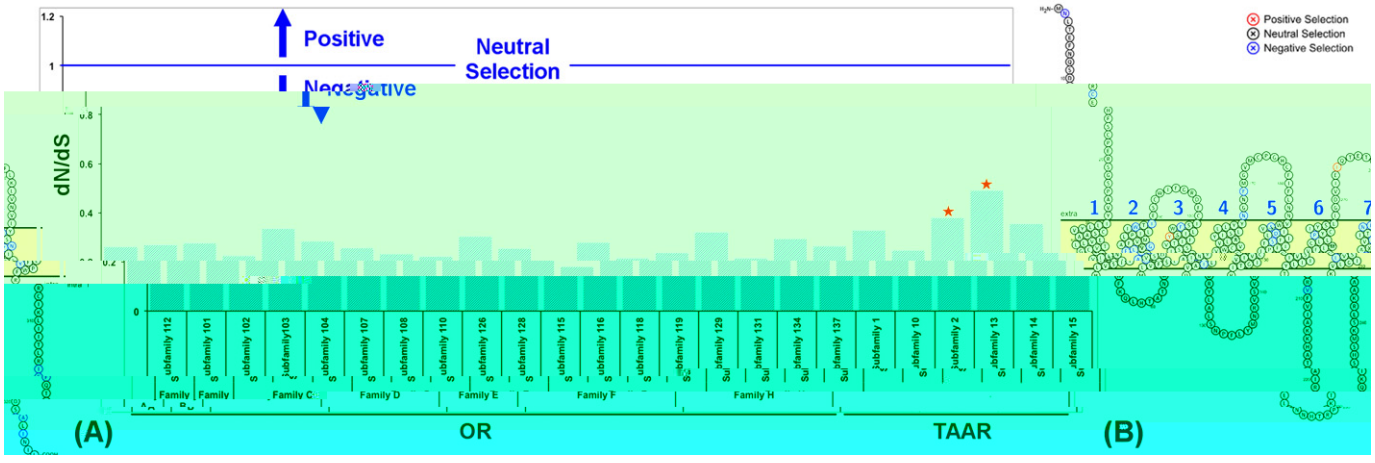

Fig. 7. Selection pressure imposed on both ORs and TAARs. (A) dN/dS ratios of each subfamily for both OR and TAAR. (B) The distribution of positive, neutral and negative sites for teleost Class III TAAR as displayed in two-dimensional topology structure.

Transparency Document

The Transparency document associated with this article can be found in the online version.

Acknowledgements

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