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Transposable elements as a potential source for understanding the fish genome

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Abbreviations: TE, transposable element; LINE, long interspersed element; SINE, short interspersed element; NOR, nucleolus organizer region; MLEs, element mariner-like

Transposable elements are repetitive sequences with the capacity to move inside of the genome. They constitute the majority of the eukaryotic genomes, and are extensively present in the human genome, representing more than 45% of the genome sequences. The knowledge of the origin and function of these elements in the fish genome is still reduced and fragmented, mainly with regard to its structure and organization in the chromosomes of the representatives of this biological group, with data currently available for very few species that represent the great variety of forms and existing diversity. Comparative analyses ascertain differences in the organization of such elements in the species studied up to the present. They can be part of the heterochromatic regions in some species or be spread throughout the genome in others. The main objective of the present revision is to discuss the aspects of the organization of transposable elements in the fish genome.

Introduction

Transposable elements (TEs) are repetitive DNA sequences, comprising a group of segments with the capacity to move throughout the chromosomes or transpose between non-homologous sites within the genome. In a first approach, this transposition capacity gives origin to structural alterations, such as duplications or deletions in the insertion sites, promoting the emergence of polymorphisms that may result in the variability of the number of copies inside and among species and, as consequence, lead to changes in the gene structure and expression.[1]

TEs are characterized by their variability and can be classified into two main classes, according to their structural organization and transposition mechanism within the genome. Retrotransposons belong to class I type of mobile elements, which move within the genome utilizing reverse transcriptase, an enzyme that can promote the synthesis of a DNA filament from a RNA template. This class includes the retrotransposons that are characterized by flanking long terminal repeats (LTRs) and the retroposons called non-LTR retrotransposons that lack terminal repeats, as well as the SINEs (short interspersed elements) and LINEs (long interspersed elements) that stand out for the length of the segments and for their molecular structure.[2-6] Based on the phylogeny of their reverse transcriptase, retrotransposons include four distinct lineages: *Ty1/copia, BEL, DIRS* and *Ty3/gypsy*.[7] Two of these lineages, *Ty1/copia* and *Ty3/gypsy,* are abundant in animals and plants and have been extensively characterized. The *BEL* and *DIRS* lineages are less abundant and have only recently been described in reference 8. Class II is constituted by the transposons, which represent sequences that spread as DNA fragments.[5,9]

The elements identified either in class I or class II are found in the genome of all organisms[10] in different amounts, representing a relatively large fraction of the eukaryotic genome. In mammals, TEs constitute more than 45% of the genome, while in other organisms they represent just a small fraction, as in the pufferfish *Fugu rubripes*, in which these elements represent 2.7% of the sequences.[11]

The evolutionary dynamics of TEs in several groups, such as insects, fish, birds and mammals are drastically different. The genomes of mammals contain few, very abundant, but relatively inactive types of transposable element lineages, while species of Drosophila and fish shelter several lineages of these genomic elements, which are typically less abundant, but apparently more harmful.[10] In numerous species of insects and fish, families of different transposable element lineages with a relatively low number of copies have remained active for an extremely long period of time.[10,12] Abrusán and Krambeck[13] suggest that the variation of diversity and activity of TEs among several animal genomes is caused by the difference in the host defense mechanisms in opposition to the TEs activity.

Until recently, TEs have been labeled junk-DNA or parasites because they do not perform a clear function inside of the genome.[14] However, recent studies on these elements are modifying this view. Today, it is already known that those elements have a significant influence on the evolution of the genomes as part of chromosome rearrangements,[15] acting in the regulation and repair of some genes,[16,17] as well as in the differentiation of sex chromosomes.[18,19] Then, it can be established that the transposable elements participate and possibly even interfere in the genome evolutionary processes, either for their transposable

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activity, causing structural mutations within the chromosomes, or for their repetitive nature, which is related to the increase in chromosome rearrangement rates. Koga et al.[20] considered that the impact of the transposable elements on the genome of vertebrates can be higher than usually supposed.

Transposable Elements in Fish Genomes

Studies involving comparative genomics have revealed that most vertebrate lineages contain different populations of retrotransposable elements and DNA transposons with significant differences being frequently observed among species of the same lineage.[9] All types of transposable elements can be found within the fish genome, where a diversity level not found in mammals and birds is observed.[10] Regarding chromosome organization, TEs can be organized in clusters or dispersed throughout the genome.

Fish represent the most diversified group of vertebrates,[21] with an estimated number 27,977 valid species. However, studies related to the identification of transposable elements in the genome of these organisms are still scarce, with genomes sequenced for only four species,[11,22-24] compared to the great diversity of species described until now, since the physical mapping data, indispensable for their characterization, have been accomplished in 32 species to date (**Table 1**).

Until the 1990s, works with TEs were restricted to few species which mostly simply described TEs structure and composition inside of the genome. With the progress in molecular and cytogenetics techniques, the interest in this genomic area has grown, as much as the descriptive point of view in relation to the physical mapping of such elements. Besides the accomplishment of genome sequencing projects in teleost fish species, such as the pufferfish *Takifugu rubripes*[11] and *Tetraodon nigroviridis*,[23] as well as in the zebrafish *Danio rerio*[22] and in the medaka *Oryzias latipes*,[24] the knowledge of the structure and function of TEs has grown, helping mainly with the characterization of different families of these repetitive elements in the genome of these organisms.

Mapping of Retrotransposons and Transposons in Fish Genome

Within the fish group, various transposable elements have been studied so far and 15 transposable elements in the genome of 32 species of different orders have been physically mapped. The different results of these researches were compiled and are shown in **Table 1**, and will be further discussed.

The transposable elements of the retrotransposon class are among the best studied within fish species, and may be fairly closely related to retrotransposon Ty3/Gypsy, Ty1/copia, DIRS1 and to BEL retrotransposon.[10,25-28] Among the described retrotransposable elements, ten of them exhibit data on their localization on fish chromosomes. Among these are elements of the Rex group (retrotransposable elements characterized for the first time in the genome of the Xiphophorus fish). The element Rex1, 3 and 6 are non-long terminal repeat having been active during the evolution of different fish lineages.[28-31] Besides a reverse transcriptase, Rex1 and Rex3 also encode an apurinic/apyrimidinic endonuclease, while Rex6 was the first retrotransposon identified in vertebrates and has a restriction enzyme-like (REL) endonuclease. Theses elements appear as the most studied with regard to their mapping in fish chromosomes, as shown in the **Table 1**.

Rex elements are present in the genome of different species of teleost fishes and have undergone some retrotranspositions during their dispersion process, some of which identified as relatively recent events.[28-33] According to the data presented in **Table 1**, Rex elements show a differentiated organization among the studied species, and such elements have been physically mapped in 28 fish species. In 11 of those species, Rex are organized in heterochromatin regions, and in the other 17 they are dispersed throughout the genome.

In the order Perciformes, the Rex element seems to be organized in clusters within the genome of the majority of the species of the family Cichlidae. The analysis of different Rex elements revealed that they are compartimentalized in pericentromeric heterochromatic regions, suggesting that these elements are part of the structure and organization of heterochromatic areas.[34,35] Similar data on the organization of Rex elements was observed in Perciformes, representatives of the Antartic fish as in the species *Notothenia coriiceps*.[33]

In the family Cichlidae, more specifically in the genome of the Nile Tilapia *Oreochromis niloticus*, besides the Rex elements[35] several other TEs, such as the LINE CiLINE2,[36] non-LTR On2318 and Tc1-like On239,[37] SINE ROn-1,[38,39] and ROn-2 [39] have been encountered. In *O. niloticus,* these TEs are found generally dispersed in the genome and may also be related to sex differentiation within this species.[37,40] Another interesting fact is that besides being present in the heterochromatic regions, Rex elements are generally concentrated on the first chromosome pair, which appears entirely marked with such elements.[35] In this species, the first chromosome pair seems to correspond to the sex chromosomes,[41,42] which possibly originated from fusion processes.[43] The determined localization of Rex elements in this chromosome pair could indicate that these TEs might be involved in such chromosome rearrangements.[35] A similar case has also been reported to have occurred with other elements, such as TEs CiLINE2,[36] On2318,[37] and ROn-1,[38,39] which are preferentially situated on the long arm of the largest chromosome pair.

Another interesting case of TEs of the Rex type and Tc1-like presenting association with the process of sex differentiation occurs in the species *Chionodraco hamatus*.[33] In this species, retrotransposon Rex3 and transposon Tc1-like, besides being part of heterochromatic regions, are located in a pericentromeric region on the long arm of chromosome Y. The band observed on the long arm of chromosome Y could correspond to the short arm of one of the autosomes involved in the fusion that gave origin to this chromosome.[33] The authors suggest that accumulation of transposable elements have already existed in autosomes before the occurrence of fusion, which would indicate that transposons might be influencing the process of molecular differentiation of the sex chromosomes of this species of fish and, therefore, in the structuring of the sex chromosomes.

The physical mapping of transposable elements carried through in *Tetraodon nigroviridis* chromosomes disclosed that

Table 1. Data compilation of transposable element and its chromosome localization in fish species

Order, family and species	Transposable element	Chromosome localization	Reference
Characiformes			
Erythrinidae			
Erythrinus erythrinus	Rex3	Dispersed	Cioffi et al.[47]
Cypriniformes			
Cyprinidae			
Alburnus alburnus	Gypsy, Ty3	B chromosome	Ziegler et al.[50]
Cyprinodontiformes			
Poeciliidae			
Xiphophorus maculatus	XIR LTR-like	Y chromosome	Nanda et al.[60]
Perciformes			
Artedidraconidae			
Artedidraco shackletoni	Rex1, Rex3	Dispersed	Ozouf-Costaz et al.[33]
Bathydraconidae			
Gymnodraco acuticeps	Rex1, Rex3	Dispersed	Ozouf-Costaz et al.[33]
Gymnodraco victori	Rex1, Rex3	Dispersed	Ozouf-Costaz et al.[33]
Bovichtidae			
Bovichtus angustifrons	Rex1, Rex3	Dispersed	Ozouf-Costaz et al.[33]
Cichlidae			
Astronotus ocellatus	Rex1, Rex3, Rex6	Heterochromatins	Mazzuchelli and Martins[61]
Cichla kelberi	Rex1, Rex3, Rex6	Heterochromatins and dispersed	Teixeira et al.[62]
Chaetobranchus flavescens	Rex1, Rex3, Rex6	Heterochromatins	Valente et al.[35]
Haplochromis obliquidens	Rex1, Rex3, Rex6	Dispersed	Valente et al.[35]
Hemichromis bimaculatus	Rex1, Rex3, Rex6	Heterochromatins	Valente et al.[35]
Heros efasciatus	Rex1, Rex3, Rex6	Heterochromatins	Valente et al.[35]
Melanochromis auratus	Rex1, Rex3, Rex6	Heterochromatins	Valente et al.[35]
Oreochromis niloticus	Rex1, Rex3, Rex6	Dispersed and chromosome one	Valente et al.[35]
Oreochromis niloticus	CiLINE2	Dispersed and chromosome one	Oliveira et al.[36]
Oreochromis niloticus	On2318	Dispersed and chromosome one	Harvey et al.[37]
Oreochromis niloticus	On239, Tc1-like	Dispersed, centromeric and telomeric	Harvey et al.[37]
Oreochromis niloticus	ROn-1	Dispersed and chromosome one	Bryden et al.,[38] Oliveira et al.[39]
Oreochromis niloticus	ROn-2	Dispersed and chromosome one	Oliveira et al.[39]
Satanoperca jurupari	Rex1, Rex3, Rex6	Heterochromatins and dispersed	Valente et al.[35]
Symphysodon aequifascistus	Rex3	Heterochromatins	Gross et al.[34]
Symphysodon discus	Rex3	Heterochromatins	Gross et al. [34]
Symphysodon haraldi	Rex3	Heterochromatins	Gross et al. [34]
Gobiidae			
Gobius níger	Mariner-like	Overlapping NORs	Mandrioli et al.[51]
Nototheniidae			
Dissostichus mawsoni	Rex1, Rex3	Dispersed	Ozouf-Costaz et al.[33]
Notothenia coriiceps	Rex1, Rex3	Heterocromatins	Ozouf-Costaz et al.[33]
Patagonotothen tessellata	Rex1, Rex3	Dispersed	Ozouf-Costaz et al.[33]
Trematomus newnesi	Rex1, Rex3	Dispersed	Ozouf-Costaz et al.[33]
Trematomus hansoni	Rex1, Rex3	Dispersed	Ozouf-Costaz et al.[33]
Trematomus bernacchii	Rex1, Rex3	Dispersed	Ozouf-Costaz et al.[33]
Trematomus pennellii	Rex1, Rex3	Dispersed	Ozouf-Costaz et al.[33]
Siluriformes			
Loricariidae			

Table 1. Data compilation of transposable element and its chromosome localization in fish species (continued)

Hisonotus leucofrenatus	Rex1, Rex3	Dispersed	Ferreira et al.[46]
Paratocinclus maculicauda	Rex1, Rex3	Dispersed	Ferreira et al.[46]
Pseudotocinclus tientensis	Rex1, Rex3	Dispersed	Ferreira et al.[46]
Tetraodontiformes			
Tetraodontidae			
Tetraodon fluviatilis	Mariner-like	NOR-associated heterochromatins	Mandrioli and Manicardi[52]
Tetraodon nigroviridis	Rex1, Rex3	Heterochromatins	Da Silva et al.,[44] Bouneau et al.,[45] Fisher et al.[45]
Tetraodon nigroviridis	Dm-Line	Heterochromatins	Da Silva et al.[44]
Tetraodon nigroviridis	Tc1-like	Heterochromatins	Da Silva et al.[44]
Tetraodon nigroviridis	Zebulon	Heterochromatins	Bouneau et al.[45]
Tetraodon nigroviridis	Tol2	Heterochromatins	Fischer et al.[32]
Tetraodon nigroviridis	Buffy	4–5 chromossomes	Fischer et al. [32]
Tetraodon nigroviridis	Babar	Heterochromatins	Fischer et al. [32]

Rex1 and Rex3 and Tc1-like transposons,[44] and Tol2 and *Buffy1,*[32] are accumulated in preferential regions of the chromosome heterochromatin, in a way similar to that observed for some species of cichlids. Rex1 and Rex3 elements can also be associated with other retrotransposable elements as in the case of the Zebulon, which is present in the genome of pufferfish, concomitant with Rex3.[45] Fischer et al.[32] showed that the transposable elements are frequently associated with minisatellites and normally accumulated in heterochromatin regions. Using the FISH technique, the authors demonstrated that Tc1, Dm-Line and Rex3 are located in the great majority of the centromeres and in some telomeres, suggesting that heterochromatin present in these chromosomic regions serves as a possible reservoir of these transposable elements. These results disclose a high degree of compartmentalization for the genome of the pufferfish, *T. nigroviridis*, showing a clear separation between the heterochromatin regions, which are poor in genes and euchromatin regions, where the active genetic segments are generally situated.

With regards to TEs genome structuring, the different organization of these chromosome sites between the components of the order Siluriformes draws researchers' attention. Studies carried with the retrotransposons Rex1 and Rex3 in three species of the subfamily Hypoptopomatinae by Ferreira et al.[46] disclosed a genomic organization sufficiently differentiated from that found among the representatives of other orders of fish already studied. Such elements are spread throughout the genome of the species and are more intensely present in the euchromatic regions of the chromosomes. However, some blocks of TEs are coincident with the heterochromatic regions, suggesting that the standard of distribution of these retroelements can be distinct in the different orders of fish.[46] However, the authors also admit there are factors, such as the stringency in the application of the FISH technique, which may justify the differences found, since the perfect visualization of the markings provided by this technique depends on the number of TEs copies in the genome and on the degree of stringency applied in the technical experiments.

The chromosome mapping of the same retroelements carried through representatives of the order Perciformes from the Antartic[33] revealed a similar organization in the genome of the species of this order. On the other hand, Cioffi et al.[47] describes a more complex structuring of TEs in *Erythrinus erythrinus*. This species, pertaining to the order Characiformes, presents an expressive intrapopulational chromosome diversity, with four cytotypes differentiated by the number, chromosome morphology and presence of heteromorphic systems of sex chromosomes.[48] The analysis of two cytotypes, i.e., cytotype A with 2n = 54 with a chromosome homomorphic system and cytotype D, with a diploid number = 52 chromosomes in females and 51 in males, using 5S rDNA probes and Rex3 shows that the Rex3 element is dispersed throughout all chromosomes and that the 5S DNAr is collocated with Rex3 in specific chromosomes. The synteny of these repetitive regions strengthens a possible structural and functional association of such sites in the genome, allowing inference into its role in the establishment of chromosome systems related to the sex. The authors point out that the origin of metacentric chromosome Y in cytotype D has possibly occurred by centric fusion, which is evidenced by the presence of one telomeric site in interstitial position and by the association of DNAr with Rex3 in this chromosome.[47]

Besides being part of heterochromatin regions of chromosomes of some species and spread throughout the genome in others, TEs can also be associated with supranumerary or B chromosomes in teleosts. B chromosomes, additional genomic elements found in organisms, are usually heterochromatic, and do not generally present homology to the elements of the A complement.[49] The species *Alburnus alburnus* is characterized by the presence of a great supranumerary chromosome, of a size comparable to the biggest sized complement of the species, which can be present in different frequencies depending on the sampled population. Analyses with FISH showed that Gypsy/Ty3 retrotransposon is exclusively located on chromosome B of this species,[50] and is absent on a B chromosome of a related species, *Rutilus rutilus*. The authors suggest the occurrence of a specific dispersion process of this retrotransposable element during the evolution of the supranumerary chromosomes in this group of fish.

The Nucleolar Organizer Regions (NOR) are described as highly repetitive genome sites related to the rRNA synthesis. These repetitive regions present small, active transcription sites and non-transcribed spacing segments with their own structural dynamics, in which the presence of transposons located close to the genome regions has been identified. This is the case of the element mariner-like (MLEs), which is associated with NOR in *Gobius niger*[51] and *Tetraodon fluviatilis* species.[52] In *T. fluviatilis,* the MLEs are located on chromosome pairs 5 and 12, strictly next to the NOR-associated heterochromatin, without exhibiting a random distribution across the genome of the species.[52] On the other hand, in *Gobius niger* the association of MLEs with the NOR regions can be attributed to the presence of NOR heteromorphism observed in those regions.[51]

Southern Blot experiments carried with transposons Tol1 and Tol2 isolated from the medaka genome (*Oryzias latipes*) by Koga et al.[53] allowed verification that the *Tol1* element is present in seven of the nine species of *Oryzias* studied, suggesting that this element might be present in the common ancestry shared by these species. The presence of the *Tol2* element was evidenced in only two closely related species, i.e., *O. curvinotus* and *O. latipes*.[53] The authors postulate that the Tol2 transposable element might be contributing to genetic variation, acting as a natural mutant in its host organism. Thence, the development and performance of the transposable elements in the vertebrate genome evolution seems to be more significant than it has usually been postulated.[20]

Other transposable elements have also had their composition evidenced in fish species other than those participating in chromosome mapping studies. This is the case of the elements of the families HE1 and HER1 in elasmobranchs,[54] CORE-SINE isolated elements in salmonids,[55] Mermaid,[56] Zfl2-1 and Zfl2-2 isolated in zebrafish,[57] and tdr1 isolated in *Danio rerio*,[58] among others. It is considered that the marking of these elements and their respective mapping in the genome of the species could substantially increase knowledge of the structure and function of these genomic components in fish, and consequently in vertebrates.

Final Considerations

Studies involving physical mapping of transposable elements in fish are still scarce compared to the number of existing species in this biological group. The data presented in the current revision show that the knowledge of TEs is still incipient in regard to their composition, localization and possible functions in the genome. However, the data described in the literature to date indicate a clearly differentiated organization standard of TEs in the genome of the fish species. In those fishes belonging to basal lineages with genomes as large as Characiformes (for example *Erythrinus erythrinus*) and Siluriformes (for example Hypoptopomatinae species), and fishes belonging more derived groups like Perciformes, but also with large genomes [as *Oreochromis niloticus* and suborder Notothenioidei (Artedidraconidae, Bathydraconidae, Bovichtidae, Nototheniidae)], the TEs present a sufficiently distinct organization, and are dispersed throughout the genome, usually occupying euchromatic regions, in the same way observed for TEs in human and insects.[10] On the other hand, fishes belonging to derived groups such as the Tetraodontiformes *T. nigroviridis*, whose genome is extremely compact, the separation between the region rich in gene segments and the regions poor in genes is evident,[32,44] and apparently TEs use heterochromatin as shelters, since their presence can only be tolerated in regions poor in genes where there is less selection pressure.[59]

The evidence of such diversity in TEs chromosome organization could lead to the hypothesis that the fact that these elements present a differentiated number of copies in the species would justify the diversified standard identified in the species studied up to the present, since the FISH technique usually applied detects copies that are highly repetitive within the genome.

In view of the presented panorama, it is manifest that all transposable elements mapped and described show a differentiated organization in the genome species. However, within the same species, all isolated TEs present the same behavior within the respective genome. This can be seen especially in studies accomplished in *O. niloticus* and *T. nigriviridis*, whose genomes bearing such elements have been more intensively analyzed. Although the currently available information on the structural organization, evolution and functional behavior of TEs in the fish genome are still very fragmented and restricted to few species, the data seem to evidence their participation in the mechanisms of formation of sex chromosomes, supranumerary chromosomes, and in the evolution of the genome of teleosts.

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