

Transposons

Most repeated sequences of the genome are derived from transposable elements. In humans, 45% of the genome belongs to this class of repeats (The Genome International Sequencing Consortium, 2001). Among vertebrates, two classes of transposon types can be recognized. The first class (i) includes three types that transpose through RNA intermediates: long interspersed elements (LINEs), short interspersed elements (SINEs), and long terminal repeat (LTR) retrotransposons; and the second class (ii) includes those sequences that transpose directly as DNA:DNA transposons. Fish genomes contain all types of known transposable elements (Volff *et al.*, 2003) and some of these elements were mapped onto the chromosomes (Table 4.4.2).

The small and compact genomes of the pufferfish *Tetraodon nigroviridis* and *Takifugu rubripes* are interesting for studying the repetitive sequences. The total content of transposons in the genome of *T. nigroviridis* is only 0.9%, a large fraction of which is constituted by LINE elements (0.4%) (Crollius *et al.*, 2000). The genomes of the two pufferfish contain a low repeat content (Aparicio *et al.*, 2002; Fischer *et al.*, 2004). On the other hand, *T. nigroviridis* contains a high diversity of transposable elements not observed in larger genomes such as those of the human and mouse (Aparicio *et al.*, 2002; Volff *et al.*, 2003). The transposable elements are compartmentalized in heterochromatins and are not randomly distributed in the genome of this pufferfish (DaSilva *et al.*, 2002; Bouneau *et al.*, 2003; Fischer *et al.*, 2004) (Table 4.4.2). Moreover, the distribution of repeats in the genome of *T. nigroviridis* is different from the one observed in humans, where repeat sequences comprise an important fraction of euchromatic DNA, and is more similar to the distribution observed in *Drosophila melanogaster* and *Arabidopsis thaliana* also having small genomes (Fischer *et al.*, 2004). Repetitive sequences such as minisatellites and transposable elements are clearly located in AT-rich chromosome regions in *T. nigroviridis* (Fischer *et al.*, 2004). Such compartmentalization of the pufferfish genome seems not to be a rule for fishes and might represent a characteristic of small and compact genomes.

Although cytogenetic studies of transposable elements in fishes are just starting, the preliminary results suggest that these elements can greatly contribute to the knowledge of fish genome evolution. For instance, a LINE element denominated CiLINE2, isolated from *O. niloticus* genome (Oliveira *et al.*, 1999) was detected by hybridization in

Table 4.4.2 Dispersed repetitive elements and their chromosomal distribution in fish species.

<i>Fish orders and species</i>	<i>Element type</i>	<i>Chromosome position</i>	<i>References</i>
Aulopiformes			
<i>Aulopus japonicus</i>		W chromosome	Ota <i>et al.</i> , 2003
Cypriniformes			
<i>Alburnus alburnus</i>	Gypse, Ty3	B chromosome	Ziegler <i>et al.</i> , 2003
Cyprinodontiformes			
<i>Xiphophorus maculatus</i>	XIR LTR-like	Y chromosome	Nanda <i>et al.</i> , 2000
Perciformes			
<i>Artedidraco shackletoni</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
<i>Bovichtus angustifrons</i>	Rex1, Rex3	Dispersed	
<i>Chionodraco hamatus</i>	Tc1-like	Pericentric, telomeric, interstitial	Capriglione <i>et al.</i> , 2002
<i>Chionodraco hamatus</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
<i>Dissostichus mawsoni</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
<i>Gobius niger</i>	Mariner-like	Overlapping NORs	Mandrioli <i>et al.</i> , 2001
<i>Gymnodraco acuticeps</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
<i>Gymnodraco victori</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
<i>Neopagetopsis ionah</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
<i>Notothenia coriiceps</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
<i>Oreochromis niloticus</i>	CiLINE2	Chromosome one and dispersed	Oliveira <i>et al.</i> , 1999
<i>Oreochromis niloticus</i>	Ron1	Chromosome one and dispersed	Bryden <i>et al.</i> , 1998; Oliveira <i>et al.</i> , 2003
<i>Oreochromis niloticus</i>	Ron2	Dispersed	Oliveira <i>et al.</i> , 2003
<i>Oreochromis niloticus</i>	On2318	Chromosome one and dispersed	Harvey <i>et al.</i> , 2003
<i>Oreochromis niloticus</i>	On239, Tc1-like	Centromeric, telomeric and dispersed	Harvey <i>et al.</i> , 2003
<i>Patagonotothen tessellata</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
<i>Trematomus hansonii</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
<i>Trematomus newnesi</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
<i>Trematomus bernacchii</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
<i>Trematomus pennellii</i>	Rex1, Rex3	Dispersed	Ozouf-Costaz <i>et al.</i> , 2004
Tetraodontiformes			
<i>Tetraodon fluviatilis</i>	Mariner-like	NOR-associated heterochromatins	Mandrioli and Manicardi, 2001
<i>Tetraodon nigroviridis</i>	Dm-Line	Heterochromatins	DaSilva <i>et al.</i> , 2002
<i>Tetraodon nigroviridis</i>	Tc1-like	Heterochromatins	DaSilva <i>et al.</i> , 2002
<i>Tetraodon nigroviridis</i>	Zebulon	Heterochromatins	Bouneau <i>et al.</i> , 2003
<i>Tetraodon nigroviridis</i>	Tol2	Heterochromatins	Fischer <i>et al.</i> , 2004
<i>Tetraodon nigroviridis</i>	Buffy1	4-5 chromosomes	Fischer <i>et al.</i> , 2004
<i>Tetraodon nigroviridis</i>	Rex3	Heterochromatins	Fischer <i>et al.</i> , 2004
<i>Tetraodon nigroviridis</i>	Babar	Heterochromatins	Fischer <i>et al.</i> , 2004

the genomic DNA of all Tilapiini species tested from the genera *Oreochromis*, *Tilapia*, and *Sarotherodon*. It is interesting to note that DNA from *Oreochromis* and *Sarotherodon* species produced a hybridization pattern different from that of *Tilapia* species, thus suggesting the possibility that the CiLINE2 probe could be used to distinguish fishes of the genera *Tilapia* from those of *Oreochromis* and *Sarotherodon*. Fluorescence *in situ* hybridization with the CiLINE2 element evidenced in *O. niloticus* very small signals distributed more or less randomly over the chromatids of all chromosomes, but strikingly enriched along the terminal two-thirds of the long arm of chromosome pair one (Oliveira *et al.*, 1999) that corresponds to the putative XY sex chromosomes.

The distribution of two SINE sequences denominated ROn-1 and the ROn-2, on chromosomes of the Nile tilapia, investigated by fluorescence *in situ* hybridization by Oliveira *et al.* (2003), showed that both SINE sequences are organized in small clusters and dispersed in all the chromosomes. Moreover, the ROn-1 element is almost exclusively distributed in interstitial regions of chromosomes and copies of ROn-2 are localized near the telomeric region of several chromosomes. A large cluster of ROn-1 is found in the middle of the long arm of chromosome pair one. No similarity was observed in the distribution of SINEs and LINEs between the Nile tilapia chromosomes and mammalian chromosomes.

Whole chromosome probes obtained through microdissection and DOP-PCR-amplification from chromosome one of *O. niloticus*, hybridized more intensely in the long arm of chromosome one, suggesting the presence of large numbers of repetitive elements in this chromosome region (Harvey *et al.*, 2002). Cloning and sequencing of the microdissected DNA from the XY sex chromosomes (chromosome pair one) of the same species proved that these chromosomes are enriched with repetitive sequences, most of them transposable elements (Harvey *et al.*, 2003). Moreover, the distribution of repetitive elements in the sex chromosomes of *O. niloticus* suggests that there are significant differences between the X and Y chromosomes. Considering that the main differences detected between the X and Y chromosomes reside in the long arm (Foresti *et al.*, 1993), the development of new genetic markers capable of distinguishing the X and Y chromosomes will be of considerable value for aquaculture purposes.

The genome dynamics and chromosomal localization of two non-long terminal repeat retrotransposons (*Rex1* and *Rex3*) were studied in 13 species of notothenioid Antarctic fishes (Ozouf-Costaz *et al.*, 2004) (Table 4.4.2). Both *Rex1* and *Rex3* transposon elements were spread all over the chromosomes with accumulation in some particular regions, such as in the Y sex chromosome of *Chionodraco hamatus*. The presence of another transposon-like element (*Tc1*) (Capriglione *et al.*, 2002) was also identified in the Y chromosome of *C. hamatus*. Particularly, the *Tc1*-like element hybridizes interstitially to the long arm of the Y sex chromosome, which is supposed to originate in tandem or by Robertsonian fusion (Morescalchi *et al.*, 1996). This suggests that transposon elements might have been involved in notothenioid sex-chromosome differentiation.

The presence of transposon-derived elements are also common in the B chromosomes of diverse organisms from plants such as *Brachycone dichronosonidica* (Franks *et al.*, 1996) and *Rye* (Langdon *et al.*, 2000), and animals such as the insect *Nasonia vitripennis* (McAllister, 1995) and the fish *Astyanax scabripinnis* (Mestriner *et al.*, 2000). A specific retrotransposon-like element isolated in *Alburnus alburnus*, by AFLP, has been found abundant in B chromosomes and absent in the normal A chromosomes (Ziegler *et al.*, 2003).

Taken altogether, the results of studies on repetitive DNAs seem to have considerable value in clarifying several issues concerning the origin and evolution of sex and supernumerary chromosomes among the organisms and the genome evolution. The constant presence of repeated sequences in the sex and supernumerary chromosomes in fish species indicates that the repetitive DNAs have played an important role in the evolution of their genomes.

5S rDNA and 5S rDNA Variant Repeats

Chromosomal organization of 5S rDNA

Studies on ribosomal RNA genes have gained prominence in a broad range of animals and plants, especially in relation to species or population characterization, evolutionary relationships and genome structuring. In higher eukaryotes, ribosomal (rRNA) genes are organized as two distinct multigene families of tandemly arrayed repeats composed of hundreds to thousands of copies. One class is represented by the 45S rDNA, which consists of a transcriptional unit encoding for the 18S, 5.8S

and 28S rRNAs, and an intergenic non-transcribed spacer (IGS). Multiple copies of this array correspond to the nucleolar organizer regions (NORs). The other class (5SrDNA) consists of a highly conserved sequence of 120 base pairs (bp) coding for the 5S rRNA which is separated from each transcriptional unit by a variable non-transcribed spacer (NTS) (reviewed in Long and Dawid, 1980). While the rRNA genes are conserved even among non-related taxa, the non-transcribed spacers show extensive length and sequence variation, which can give an accentuated dynamism to the rRNA genes.

The chromosomal location of the 5S rRNA genes has been described for more than 60 fish species, representing distinct groups such as Acipenseriformes, Anguilliformes, Cypriniformes, Characiformes, Salmoniformes, Perciformes, and Tetraodontiformes and has been shown to be of great importance in the comprehension of the structure and organization of repeated sequences in their chromosomes (for review, see Martins and Wasko, 2004).

In most eukaryotes, the 5S rRNA genes are generally detected in distinct areas of the genome, organized as one or more tandemly repeated clusters, and the number of 5S rRNA genes ranges from 100 to 300,000 copies, which is usually higher than the number of 45S rRNA genes (Hadjiolov, 1985). In many vertebrates, 5S rRNA genes are located on a single chromosome pair, while 45S rDNA is often present on multiple chromosomes (Suzuki *et al.*, 1996; Makinem *et al.*, 1997). In amphibian (Schmid *et al.*, 1987; De Lucchini *et al.*, 1993) and fish species (Martins and Wasko, 2004; Mazzei *et al.*, 2004), the 5S rRNA genes can be found on several chromosomes. For most fish species, 5S rRNA genes have an interstitial position in the chromosomes, which suggests that such localization could represent some advantage related to the organization of these genes in the genome. Moreover, 45S and 5S rDNA loci may assume a syntenical organization in the chromosome (Pendás *et al.*, 1994; Mórán *et al.*, 1996; Mazzei *et al.*, 2004) or can be detected in different chromosome pairs (Martínez *et al.*, 1996; Martins and Galetti, 1999). However, the divergent locations of NORs and 5S rDNA loci seem to be the most common situation observed in fish and is by far the most frequent distribution pattern observed in vertebrates (De Lucchini *et al.*, 1993, Suzuki *et al.*, 1996). It was suggested that the distinct chromosome locations of 5S and 45S rDNA could represent some advantage compared to the linked condition (Martins and Galetti, 1999). Syntenic location of

5S and 45S clusters could facilitate translocations between the 45S and 5S arrays, causing disruptive interference in the structure and function of such genes. This could explain why most vertebrates have these 5S rDNA clusters on distinct chromosomes.

In the characiform *Leporinus*, two classes of 5S rDNA, one consisting of monomeric repeat units around 200 bp and another one with monomers of 920 bp were identified (Martins and Galetti, 2001). Each of these different-sized 5S rDNA classes was characterized by distinct NTS sequences and clustered in distinct chromosome pairs. Several studies of 5S rDNA sequences among fish species have identified variant types of the 5S rDNA tandem repeats characterized by remarkable differences in the NTSs. The presence of two types of tandem repeats of this ribosomal DNA has been observed in Characiformes (Martins and Galetti, 2001), Perciformes (Martins *et al.*, 2002) and Salmoniformes (Pendás *et al.*, 1994). In the tilapiine cichlid fish *O. niloticus*, two distinct 5S rDNA units were identified, each characterized by distinct NTSs that varied in nucleotide sequence and length between the loci. The first class has monomers of 1.405 bp (denominated 5S rDNA type I) and the second one has monomers of 475 bp (denominated 5S rDNA type II). An inverted 5S rRNA putative pseudogene and two putative 5S rRNA bona fide genes (one of them inverted) were also detected in the 5S rDNA type I (Martins *et al.*, 2002). Both classes were clustered in distinct chromosomes. While the 5S rDNA type I was detected in an interstitial position in the long arm of a subtelo-acrocentric chromosome pair (chromosome 3), the 5S rDNA type II was identified interstitially in the long arm of a different subtelo-acrocentric pair and at the terminal region of the short arm of another subtelo-acrocentric chromosome pair (chromosomes 9 and 13). The exhaustive investigation of NTS segments of 5S rDNA type I and type II allowed detection of the presence of only one type of NTS in the 5S rDNA type I and two subtypes of NTS in the 5S rDNA type II (Alves *et al.*, submitted). The subtypes detected in NTS of 5S rDNA type II are related to the presence of a 'TG' microsatellite expansion/deletion. Interestingly, the 5S rDNA type I is located in just one chromosome locus while the 5S rDNA type II is located in two different chromosome loci. Such data prove that the homogenization of the repeats in 5S rDNA can occur just within a specific locus, whereas different loci in the same genome can be highly differentiated in the nucleotide sequence and size of the repeat units. The assignment of different classes of 5S rDNA to distinct chromosome loci

reinforces the idea that distinct 5S rDNA classes occupy different chromosome positions and seem to evolve independently in individual nuclear environments.

Dynamic of 5S rDNA and variant-5S rDNA in the genome of *Hoplias malabaricus*

An interesting model to demonstrate the intense dynamism of the 5S rDNA repeats in the genome is the fish *Hoplias malabaricus*. Two tandem repetitive families denominated true-5S rDNA and variant-5S rDNA were isolated and characterized in the genome of this species (Martins *et al.*, submitted). The true-5S rDNA repeats contain entire coding regions for 5S rRNA while the variant-5S rDNA repeats contain a truncated coding region for the 5S rRNA (Fig. 4.4.2). Similarities were also observed in the NTS of both classes.

Chromosome hybridization was carried out using the true-5S rDNA and the variant-5S rDNA sequences as probes. Under low-stringent conditions, both probes hybridized in the centromeric region of 18 chromosomes and near the centromeres in the short arm of chromosome pairs 3 and 15. Under high-stringent conditions, the true-5S rDNA probe hybridized to the short arm of chromosome pairs 3 and 15 and the variant-5S rDNA probe to the centromeric region of 18 chromosomes (Figs. 4.4.1c, d).

The true-5S rDNA repeats of *H. malabaricus* were nearly identical with a low value for the mean genetic distance (0.001) between the repeats, suggesting that such sequences are governed by strong selective pressure. On the other hand, the high (0.045) mean genetic distance between the repeats of the variant-5S rDNA suggests that these sequences are free of selection pressure. One evidence of the intense

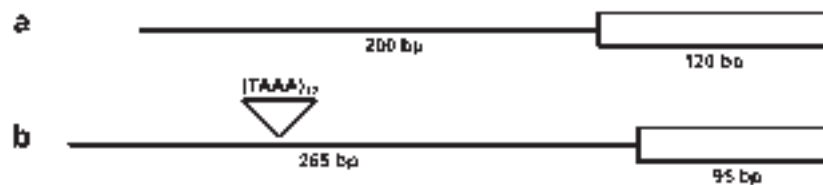


Fig. 4.4.2 Schematic representation of the true-5S rDNA (a) and the variant-5S rDNA (b) repeats isolated in *Hoplias malabaricus*. The boxes indicate segments with similarity to the coding region and the horizontal lines the NTS. The size of the NTS and the 5S rRNA coding region, and the TAAA microsatellite are indicated.

dynamism of the variant-5S rDNA sequences is the presence of the expanded TAAA microsatellite. To explain the difference between the genetic distance of the true-5S rDNA and the variant-5S rDNA satellite sequence, it is possible to hypothesize that a transfer of true-5S rDNA units to the centromeric position changed the status of the selective pressure under the 5S rRNA genes, making them free to multiply and spread over the centromeres of several chromosome pairs, as has been demonstrated for other centromeric satellite sequences.

The organization and evolution of tandem repetitive DNAs is governed by particular patterns of evolution such as unequal exchange, transposition, RNA-mediated transposition and gene conversion (Dover, 1986). Drouin and Moniz de Sá (1995) suggested the hypothesis that RNA-mediated transposition is the mechanism responsible for the unusual linkage of 5S rRNA genes to other tandemly repeated multigene families. According to the authors, the RNA-mediated transposition could be responsible for the dispersion of single copies of 5S rDNA repeats, whereas covalently closed circular DNA (cccDNA) molecules containing 5S rRNA genes would be expected to sometimes lead to the insertion of several 5S RNA gene copies within other sequences in the genome. Such cccDNA molecules have been found in many eukaryotes species, including mammals, chicken, *Drosophila*, and plants (reviewed in Renault *et al.*, 1993). Several classes of cccDNAs have been found in *D. melanogaster* embryos, one of whom contains a variable number of sequences homologous to 5S rRNA genes (Pont *et al.*, 1987). Therefore, in *H. malabaricus*, the first copies of the variant-5S rDNA could have transferred to centromeric position throughout cccDNAs. Alternatively, the variant-5S rDNA satellite sequence could have originated in the centromeric region of chromosomes 3 or 15 by duplication or chromosome inversion involving some adjacent 5S rDNA copies present in these chromosomes. The first variant-5S rDNA copies could have associated with other repetitive sequences in the centromeric heterochromatin that facilitated its dispersion to the other chromosomes due to concerted evolutionary mechanisms.

It cannot yet be addressed whether these repeats may confer some structural or functional advantage to the chromosomes as a component of the centromeric DNA in *H. malabaricus*. Centromeres have been recognized as evolutionary dynamic regions of the genome (Eichler and Sankoff, 2003); but although they have been well investigated in cases

from animals to fungi, important tasks remain to be understood (Henikoff *et al.*, 2001). The centromere is vital to the correct sorting of chromosomes during cell division, being essential for the appropriate maintenance and segregation of the genetic material. Although this role is conserved throughout evolution, the DNA sequences found in centromeric regions are often variable (Henikoff *et al.*, 2001). Disturbances in the structural and functional organization of the centromeres are critical in terms of leading to problems such as developmental defects and cancer. The centromeric regions are rich in repetitive DNAs, which is a common trait in humans (Willard and Wayne, 1987), mice (Kipling *et al.*, 1991; Narayanswami *et al.*, 1992), maize (Kaszás and Birchler, 1996), *Drosophila* (Murphy and Karpen, 1995), *Neurospora* (Centola and Carbon, 1994), and yeast (Clark, 1990). One interesting finding is that the expanded TAAA motif in the variant-5S rDNA is similar to the short A-rich motifs identified in the centromeric satellite DNAs of different fish species, as previously reported in this chapter. These short sequences are quite similar, showing considerable homology to other centromeric motifs found in humans (Vissel *et al.*, 1992), mice (Wong and Rattner, 1988), and reptiles (Cremisi *et al.*, 1988), a fact which suggests that such sequences play an important role in the structure and function of the *H. malabaricus* centromere.

Several previous studies have found evidence of 45S rDNA-related sequence elements either dispersed or clustered throughout eukaryotic genomes. These elements have been characterized mainly as non-coding, small-unit tandem repeats of variable copy number and have been identified in various eukaryotic species, including yeast (Childs *et al.*, 1981), animals (Arnheim *et al.*, 1980; Kominami and Muramatsu, 1987; De Lucchini *et al.*, 1988; Lohe and Roberts, 1990), and plants (Unfried *et al.*, 1991; Falquet *et al.*, 1997). The results presented here for the fish *H. malabaricus* show that similar elements also may have originated from 5S rDNA. Dispersed 5S rDNA variants and pseudogenes seem to be common in mammals (Emerson and Roeder, 1984; Doran *et al.*, 1987; Leah *et al.*, 1990). On the other hand, certain interesting features of the variant-5S rDNA repeats of *H. malabaricus* include high copy number, the tandem array, and their centromeric positioning.

Repetitive DNA sequences are subject to the action of several molecular mechanisms and are thought to be the most rapidly evolving components of eukaryotic genomes. The results discussed for

H. malabaricus also represent an apt example of the fluidity of repetitive sequences in providing novelties to the genomic organization of the centromeric region of vertebrates. The satellite variant-5S rDNA family has propagated within the centromeric region of several chromosomes and has been favored during the evolution due to a possible role in the centromere structure and function. Once again, it seems clear that studies on the repetitive sequences can provide interesting insights for the comprehension of the genome structuring and evolution.

Chromosomal Dynamics of Repetitive Sequences

Repetitive sequences, which correspond to a large fraction of the genomes, are governed by particular patterns of evolution such as unequal exchange, transposition, RNA mediated transposition and gene conversion that lead to a non-Mendelian segregation of repeats. It has been believed that multigene families evolve according to homogenization processes governed by molecular drive and concerted evolution (Dover, 1986; Elder and Turner, 1995), resulting in a sequence similarity of the repeat units that is greater within rather than between species. According to the results observed for the 5S rDNA repeat organization in the *Leporinus* (Martins and Galetti, 2001) and *Oreochromis niloticus* (Martins *et al.*, 2002; Alves *et al.*, submitted) genome, the homogenization in the repeat units is greater within a specific cluster. Repeats of different clusters, located at distinct chromosomes for example, can differ considerably. Although several mechanisms have been proposed as driving homogeneity among repetitive families, gene conversion and unequal exchange are the major drivers, since they occur in meiosis as well as mitosis (Crease and Lynch, 1991). Unequal exchange occurs when there is incomplete alignment between two chromosomes. One chromosome will gain extra genetic material while the other will lose DNA. When a mutation occurs in one member of a multigene family, the variant can be lost or maintained. If the variant is not lost, unequal exchange can increase the copy number of this variant in the multigene family. This new member of the repetitive family can spread across a population by several evolutionary ways such as natural selection, genetic drift, migration and bottleneck effect.

Ohno *et al.* (1968) postulated that gene duplication was the main driving force of vertebrate evolution. Once a gene was duplicated, one copy was no longer constrained by selection and any mutation that

occurred in the duplicated copy could potentially lead to new expression patterns or altered functions, leaving the original copy to provide its required function. Over recent years genetic studies, including the sequencing of the human genome, have verified that duplications of the genome have led to the complexity of human genes when compared to flies and worms (Horvath *et al.*, 2001). With the knowledge of the entire sequence of several genomes from bacteria to humans, it has become clear that the increase in the genome size is correlated with the gain of duplicated non-coding sequences. In fact, whereas bacteria have small genomes with the presence or not of few duplicated DNA segments, the higher eukaryotes, like humans and other vertebrates have large genomes with the presence of large amounts of repetitive sequences. Thereby, the evolution and differentiation of the genomes seem to have occurred by acquisition of duplicated segments. These sequences can play a role in the chromosome structure, segregation, and evolution, nuclear architecture, species evolution, and repression/activation of gene transcription. The presence of large amounts of repetitive sequences seem to act as a buffer by acting in the compartmentalization of genes, linkage groups and chromosomes, contributing to the necessary conditions that make the genome a perfect functional unit.

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