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Original article

Chromosomal distribution of the retroelements *Rex*1, *Rex*3 and *Rex*6 in species of the genus *Harttia* and *Hypostomus* (Siluriformes: Loricariidae)

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The transposable elements (TE) have been widely applied as physical chromosome markers. However, in Loricariidae there are few physical mapping analyses of these elements. Considering the importance of transposable elements for chromosomal evolution and genome organization, this study conducted the physical chromosome mapping of retroelements (RTEs) *Rex*1, *Rex*3 and *Rex*6 in seven species of the genus *Harttia* and four species of the genus *Hypostomus*, aiming to better understand the organization and dynamics of genomes of Loricariidae species. The results showed an intense accumulation of RTEs *Rex*1, *Rex*3 and *Rex*6 and dispersed distribution in heterochromatic and euchromatic regions in the genomes of the species studied here. The presence of retroelements in some chromosomal regions suggests their participation in various chromosomal rearrangements. In addition, the intense accumulation of three retroelements in all species of *Harttia* and *Hypostomus*, especially in euchromatic regions, can indicate the participation of these elements in the diversification and evolution of these species through the molecular domestication by genomes of hosts, with these sequences being a co-option for new functions.

Keywords: Armored catfish, Fluorescence *in situ* hybridization, Hypostominae, Loricariinae, Transposable elements.

Os elementos transponíveis (TE) têm sido amplamente aplicados como marcadores cromossômicos. Contudo, em Loricariidae, há poucas análises de mapeamento físico destes elementos. Considerando a importância de elementos transponíveis para a evolução cromossômica e organização genômica, este trabalho realizou o mapeamento físico cromossômico dos retroelementos (RTEs) *Rex*1, *Rex*3 e *Rex*6 em sete espécies do gênero *Harttia* e em quatro espécies do gênero *Hypostomus*, com o intuito de melhor compreender a organização e dinâmica dos genomas das espécies de Loricariidae. Os resultados evidenciaram um intenso acúmulo dos RTEs *Rex*1, *Rex*3 e *Rex*6 e distribuição dispersa em regiões heterocromáticas e eucromáticas no genoma das espécies estudadas. A presença de retroelementos em algumas regiões cromossômicas sugere sua participação em vários rearranjos cromossômicos. Além disso, o intenso acúmulo dos três retroelementos em todas as espécies de *Harttia* e *Hypostomus*, especialmente em regiões eucromáticas, pode indicar a participação destes elementos na diversificação e evolução destas espécies através da domesticação molecular pelo genoma dos hospedeiros, com estas sequências sendo co-optadas paras novas funções.

Palavras-chave: Cascudos, Elementos transponíveis, Hibridização *in situ* fluorescente, Hypostominae, Loricariinae.

Introduction

Repetitive elements have been widely applied as physical chromosome markers in comparative studies for localization of chromosomal rearrangements, identification and characterization of sex chromosomes, and chromosomal evolution analysis (Ferreira *et al*., 2011a). Among the various sequences used, the transposable elements (TEs) have been gaining space in studies on molecular cytogenetics.

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The TEs represent a significant portion of the genome of eukaryotes, being their main feature the mobility within the genome (Hartl *et al*., 1992). The insertion capacity of the TEs in different locations of the genome can change the function of the genes associated with them (Capy *et al*., 1998). This dynamic character causes TEs to have a major influence on the composition and evolution of the genome of animals and plants. According to their mechanism of transposition, the TEs are classified as retrotransposons (Class I – transposition occur via an RNA intermediate) or DNA transposons (Class II – transposition occur via DNA) (Biscotti *et al*., 2015; Carducci *et al*., 2018).

The class of retrotransposons includes long terminal repeat (LTR) retrotransposons and non-LTR retrotransposons (Biscotti *et al*., 2015; Carducci *et al*., 2018). According to Volff *et al*. (1999, 2001, 2002), the retroelements *Rex*1, *Rex*3 and *Rex*6 are abundant in the teleost genomes. This way, they have been the object of several studies on fish (Fischer *et al*., 2004; Teixeira *et al*., 2009; Schneider *et al*., 2013).

Despite *Rex*1, *Rex*3 and *Rex*6 are usually analyzed together, they have differences in structural organization (Carducci *et al*., 2018). *Rex*1 comprises apurinic/apyrimidinic endonuclease sequences located upstream (or downstream) of the reverse transcriptase domain, a conserved 3'-untranslated region followed by an oligonucleotide sequence (Volff *et al*., 2000; Carducci *et al*., 2018). *Rex*3 is characterized by domains of reverse transcriptase, absence of LTR flanking regions, a 3'-end that comprises two repeats of GAA and tandem repeats of GATC, and the stop codon that are located at 3 nucleotides upstream of the first GAA repeat. *Rex*6 consists of a reverse transcriptase and a putative restriction enzyme-like endonuclease (Carducci *et al*., 2018).

Loricariidae is composed of 983 valid species (Fricke *et al*., 2019). Within this family, Hypostominae and Loricariinae are among the subfamilies with the highest number of species and chromosomal diversity. *Harttia* is a genus of the subfamily Loricariinae that has 26 valid species (Fricke *et al*., 2019). Of these, only eight species present cytogenetic data (Alves *et al*., 2003; Kavalco *et al*., 2005; Centofante *et al*., 2006; Rodrigues, 2010; Blanco *et al*., 2012a, 2013, 2014, 2017). The genus *Harttia* has conspicuous karyotype diversity, with diploid numbers (2n) ranging from 52 chromosomes in *Harttia carvalhoi* Miranda Ribeiro, 1939 females (Centofante *et al*., 2006) to 62 chromosomes in *Harttia absaberi* Oyakawa, Fichberg & Langeani, 2013 (cited as *Harttia* sp. n) (Rodrigues, 2010). The genus *Hypostomus* belongs to the subfamily Hypostominae. More than 120 species are described for this genus (Zawadzki *et al*., 2010), of which only a small number presents cytogenetic studies (Bitencourt *et al*., 2012; Traldi *et al*., 2012, 2013a, 2013b). This genus is little conserved from the chromosomal standpoint, with 2n ranging from 54 chromosomes for *Hypostomus plecostomus* (Linnaeus, 1758) (Muramoto *et al*., 1968) to 84 chromosomes for *Hypostomus* sp. 2 (Cereali *et al*., 2008).

This study conducted the chromosome mapping of retroelements *Rex*1, *Rex*3 and *Rex*6 in species of the genus *Harttia* and *Hypostomus*, aiming to better understand the organization of the genomes and chromosomal evolution of species of the Loricariidae family.

Material and Methods

Species analyzed and chromosome preparations. Seven species of the genus *Harttia* and four species of the genus *Hypostomus* from different Brazilian river basins were analyzed (Tab. 1). The procedures were performed according to the Ethics Committee on Animal Experimentation (process: 13/2014) of the Universidade Estadual de Ponta Grossa (UEPG), Brazil. The animals were identified and deposited at the Museu de Zoologia da Universidade de São Paulo (MZUSP), Brazil (Tab. 1). The metaphase chromosomes were obtained from portions of the anterior kidney, following the protocols described (Foresti *et al*., 1993; Blanco *et al*., 2012b).

DNA extraction and isolation of retroelement. Genomic DNA extraction was performed using 0,05g of liver from a sample of *Harttia kronei* Miranda Ribeiro, 1908 and *Hypostomus nigromaculatus* (Schubart, 1964), stored in absolute alcohol, according to the phenol-chloroform method (Sambrook *et al*., 2001). Retroelements *Rex*1, *Rex*3 and *Rex*6 were amplified by PCR using the primers described (Volff *et al*., 1999, 2000, 2001). The reactions were carried out for a final volume of 25 µl, containing 100-200 ng of genomic DNA, 0.2 µM of each primer, 0.16 mM of dNTPs, 0.5 U of *Taq* DNA polymerase (Invitrogen®), 1.5 mM of magnesium chloride, 10x Buffer (without chloride), and distilled water. PCR cycle conditions were: 95°C for 5 minutes, 35 cycles at 95°C for 40 seconds, 55°C for 40 seconds and 72°C for 2 minutes, with subsequent final extension cycle at 72°C for 5 minutes. The amplified fragments were analyzed in agarose gel 1%, measured in spectrophotometry device (BioPhotometer - Eppendorf). PCR reactions with the same conditions described above were performed with Biotin-11-dUTP (Roche Applied Science) for use of these products as probes for fluorescence *in situ* hybridization (FISH).

Sequencing and analysis of sequences. PCR products were purified using the GFX PCR DNA and Gel Purification kit of Amersham-Pharmacia Biotech. Sequencing reactions were carried out using the DYEnamic ET Dye Terminator kit (with Thermo Sequenase™ II DNA polymerase) according to the protocol for the MegaBACE 1000. The edition of sequences *Rex*1, *Rex*3 and *Rex*6 of *H. kronei* and *H. nigromaculatus* was performed with the software BioEdit Sequence Alignment Editor, version 7.0.5.3 (Hall *et al*., 1999). Subsequently, these sequences were deposited in the GenBank database (http://www.ncbi.nih.gov).

Fluorescence *in situ* hybridization. All hybridization processes followed the protocol described (Pinkel *et al*., 1986), about high stringency condition of 77% (200 ng of each probe, 50% formamide, 10% dextran sulfate, 2xSSC, pH 7.0 - 7.2, at 37ºC overnight). After hybridization, the slides were washed twice in 15% formamide/0.2xSSC at 42°C for 10 minutes each, and then two washes of five minutes each were performed in 4xSSC/0.05% Tween at room temperature. The metaphases were analyzed in an epifluorescence microscope (Olympus BX51), and the images were captured by the camera system (Olympus DP72).

Results

Isolation of elements *Rex*1, *Rex*3 and *Rex*6. The partial sequences of retrotransposons *Rex*1, *Rex*3 and *Rex*6 isolated from *H. kronei* and *H. nigromaculatus* presented between 430 and 555 base pairs and were deposited in the GenBank database (Tab. 2).

Tab. 1. Information of the species collected.

Species	Locality	Hidrographic Basin	GPS	Voucher numbers	Specimens analyzed
		Harttia			
H. gracilis	Machadinho Stream, Santo Antônio do Pinhal - SP, Brazil	Sapucaí-Mirin	S: 22º48'31" W: 45º41'21"	MZUSP 111384	7 ♂ 6 ♀
H. carvalhoi	Grande Stream, Pindamonhangaba - SP, Brazil	Paraíba do Sul	S: 22º47'08" W: 45º 27'19"	MZUSP 109782	8 ♂ 6 ♀
H. kronei	Açungui River, Campo Largo - PR, Brazil	Ribeira	S: 25º22'44" W: 49º39'08"	MZUSP 109783	8 ♂ 9 ♀
H. longipinna	São Francisco River, Pirapora - MG, Brazil	São Francisco	S: 17º21'22,8" W: 44º56'59,5"	MZUSP 106767	5 ♂ 7 ♀
H. loricariformis	Paraitinga River, Cunha - SP, Brazil	Paraíba do Sul	S: 22º52'22" W: 44º51'0,2"	MZUSP 111386	6 ♂ 8 ♀
H. punctata	Itiquira River, Formosa - GO, Brazil	Tocantins	S: 15º19'25" W: 47º25 26"	MZUSP 111385	8 ♂ 10 ♀
H. torrenticola	Araras Stream, Doresópolis - MG, Brazil	São Francisco	S: 20º16'15" W: 45º55'39"	MZUSP 109784	6 ♂ 7 ♀
		Hypostomus			
H. ancistroides	Lapa Stream, Ipeúna - SP, Brazil	Corumbataí	S: 22º23'10,1" W: 47º47'0,01"	MZUSP 110802	10 ♂ 8 ♀
H. iheringii	Lapa Stream, Ipeúna - SP, Brazil	Corumbataí	S: 22º23'10,1" W: 47º47'0,01"	MZUSP 106769	5 ♂ 6 ♀
H. nigromaculatus	Lapa Stream, Ipeúna - SP, Brazil	Corumbataí	S: 22º23'10,1" W: 47º47'0,01"	MZUSP 110801	7 ♂ 5 ♀
H. tapijara	Ribeira de Iguape River, Registro - SP, Brazil	Ribeira	S: 24º29'25,35" W: 9º49'4910"	MZUSP 109785	9 ♂ 10 ♀

Tab. 2. Retroelements obtained in the present work.

Species	Retroelements	Size	GenBank number	Similarity values with sequences of GenBank
Harttia kronei	*Rex*1	548pb	MH595484	66.73% - *Otocinclus flexilis* Cope, 1894 (GQ505951.1)
Hypostomus nigromaculatus	*Rex*1	553pb	MH595485	83.81% - *Hisonotus leucofrenatus* (Miranda Ribeiro, 1908) (GQ505952.1) 72.64% - *Pseudotocinclus tietensis* (Ihering, 1907) (GQ505953.1)
Harttia kronei	*Rex*3	433pb	MH595486	91.63% - *Characidium gomesi* Travassos, 1956 (MG028000.1) 89.65% - *Pseudotocinclus tietensis* (GQ505954.1)
Hypostomus nigromaculatus	*Rex*3	436pb	MH595487	91.41% - *Characidium gomesi* (MG028000.1) 90.38% - *Pseudotocinclus tietensis* (GQ505954.1)
Harttia kronei	*Rex*6	535pb	MH595488	76.45% - *Cichla kelberi* Kullander & Ferreira, 2006 (FJ687589.1)
Hypostomus nigromaculatus	*Rex*6	549pb	MH595480	82.60% - *Cichla kelberi* (FJ687589.1) 81.28% - *Astronotus ocellatus* (Agassiz, 1831) (HM535309.1)

Physical mapping of the elements *Rex*1, *Rex*3 and *Rex*6 by FISH. In all species analyzed in this study, the elements *Rex*1, *Rex*3 and *Rex*6 were present in most chromosomes, both in euchromatic and heterochromatic regions, occurring variations in quantities of the three retroelements in the species (Figs. 1, 2 and 3).

In *Harttia longipinna* Langeani, Oyakawa, Montoya-Burgos, 2001, it is notable the absence of hybridization signal of *Rex* elements in a conspicuous heterochromatic block of the pair 23 and in supernumerary chromosomes (Fig. 1). In *Harttia torrenticola* Oyakawa, 1993, *Rex* elements were not found in the prominent block located in the centromeric heterochromatin of the largest metacentric pair (pair 1) and in the allocated block in terminal position of the long arm of the largest acrocentric pair (pair 22) (Fig. 2). In *H. carvalhoi*, it is notable that in the first metacentric pair (X chromosome), in contrast to that found in *H. torrenticola*, all *Rex* elements were highlighted (Fig. 2). For *Hypostomus iheringii* (Regan, 1908), no hybridization signal of *Rex* elements was identified in the heterochromatic block of the chromosome pair 5 (Fig. 3).

Discussion

Comparative analysis of the elements *Rex* of *H. kronei* and *H. nigromaculatus* with sequences deposited in the GenBank database revealed a greater similarity of these sequences with species belonging to Loricariidae and other fish families (Tab. 2). The *Rex*1 sequence presents similarities between phylogenetically distant species (Volff *et al*., 2000), as verified for *Rex*1, *Rex*3 and *Rex*6 (Mazzuchelli *et al*., 2009; Borba *et al*., 2013). In this way, we observed that the three retroelements analyzed are present in several groups of fish and maintain high similarity in their sequences.

In most cases described, the *Rex* retroelements are preferentially accumulated in heterochromatic portions (Fischer *et al*., 2004; Da Silva *et al*., 2002; Bouneau *et al*., 2003; Ozouf-Costaz *et al*., 2004). However, just as it were found for other species of Loricariidae (Ferreira *et al*., 2011b; Pansonato-Alves *et al*., 2013; Silva *et al*., 2014; Favarato *et al*., 2016), the data of this study highlight the location of these elements in both heterochromatic and euchromatic regions of the genome. This feature appears to be a common characteristic of the species belonging to this family.

In *H. longipinna*, there is a conspicuous heterochromatic block allocated in the acrocentric pair 23 (Blanco *et al*., 2012a), in which it was not detected the presence of any of the retroelements tested, as well as in the supernumerary chromosomes of this species. The absence of the elements *Rex* in the B chromosomes of *H. longipinna* discards the role of these retrotransposons in the origin of these accessory chromosomes. Still, it is possible to infer the probable origin of these B chromosomes from this acrocentric pair. This hypothesis is based on two facts: (i) these RTEs are shared by all Loricariidae previously analyzed (Ferreira *et al*., 2011b; Pansonato-Alves *et al*., 2013; Silva *et al*., 2014; Favarato *et al*., 2016) and *Hypostomus* (analyzed in this study), therefore, the invasion in the genome of *Harttia* is prior to the emergence of the clade and; (ii) the pair 23 is the only chromosome pair free from invasion of the *Rex* elements in this species. In *H. torrenticola*, was not detected the presence of *Rex* elements tested in the heterochromatic block in the terminal position of the long arm of the largest acrocentric pair 22 (Blanco *et al*., 2013).

The absence of *Rex* elements in specific heterochromatic regions is not exclusivity of *Harttia*. In *H. iheringii*, there is a conspicuous heterochromatic block allocated in the long arm of the submetacentric pair 5, block involved in a possible process of heterochromatinization and evidenced under the polymorphic condition (Traldi *et al*., 2012). In the individual analyzed (heterozygous for the heterochromatic block), the presence of the retroelements tested was not detected in the heterochromatic region of the chromosome carrying the block.

Considering the genomic invasion by *Rex* elements prior to the division of the clades within Loricariidae, the association between heterochromatic blocks and the absence of *Rex* elements in some heterochromatic portions of *Harttia* and *Hypostomus* species allows us to assume that the compartmentalized heterochromatin of these blocks prevented the dispersion of retroelements in these chromosomal regions. However, the possible existence of a small amount of retroelements in these regions cannot be disregarded, making it impossible to detect by FISH, as it is proposed for a heterochromatic block allocated in pair 2 of *Hypancistrus* cf. *debilittera* (Silva *et al*., 2014), which does not display the sequence of retrotransposon *Rex*3.

The analyses with nuclear and mitochondrial molecular markers, showed a close proximity between *H. carvalhoi* and *H. torrenticola*, to the point that these species represent a monophyletic clade (Costa-Silva, 2009). Posteriorly, this proximity between the two species was confirmed through chromosomal markers (Blanco *et al*., 2013). These authors attribute to the centric fission of the largest metacentric pair, which was shared only between these two species, as the event responsible for the origin of the system of sex chromosomes XX/XY_1Y_2 present in *H. carvalhoi*. The FISHs revealed an accumulation of elements *Rex*1, *Rex*3 and *Rex*6 in the heterochromatic and pericentromeric region of the largest metacentric pair in *H. carvalhoi* (X chromosome) and the absence of these elements in the largest metacentric pair of *H. torrenticola* (pair 1). Considering the fact that TEs can be considered hot spots for rearrangements (Valente *et al*., 2011), the presence of such retroelements in the pericentromeric region of the X chromosome of *H. carvalhoi* may have aided in the fission that culminated in the formation of chromosomes Y_1 and Y_2; however, it cannot be ruled out the invasion of these RTEs after the emergence of the multiple sex chromosomes system.

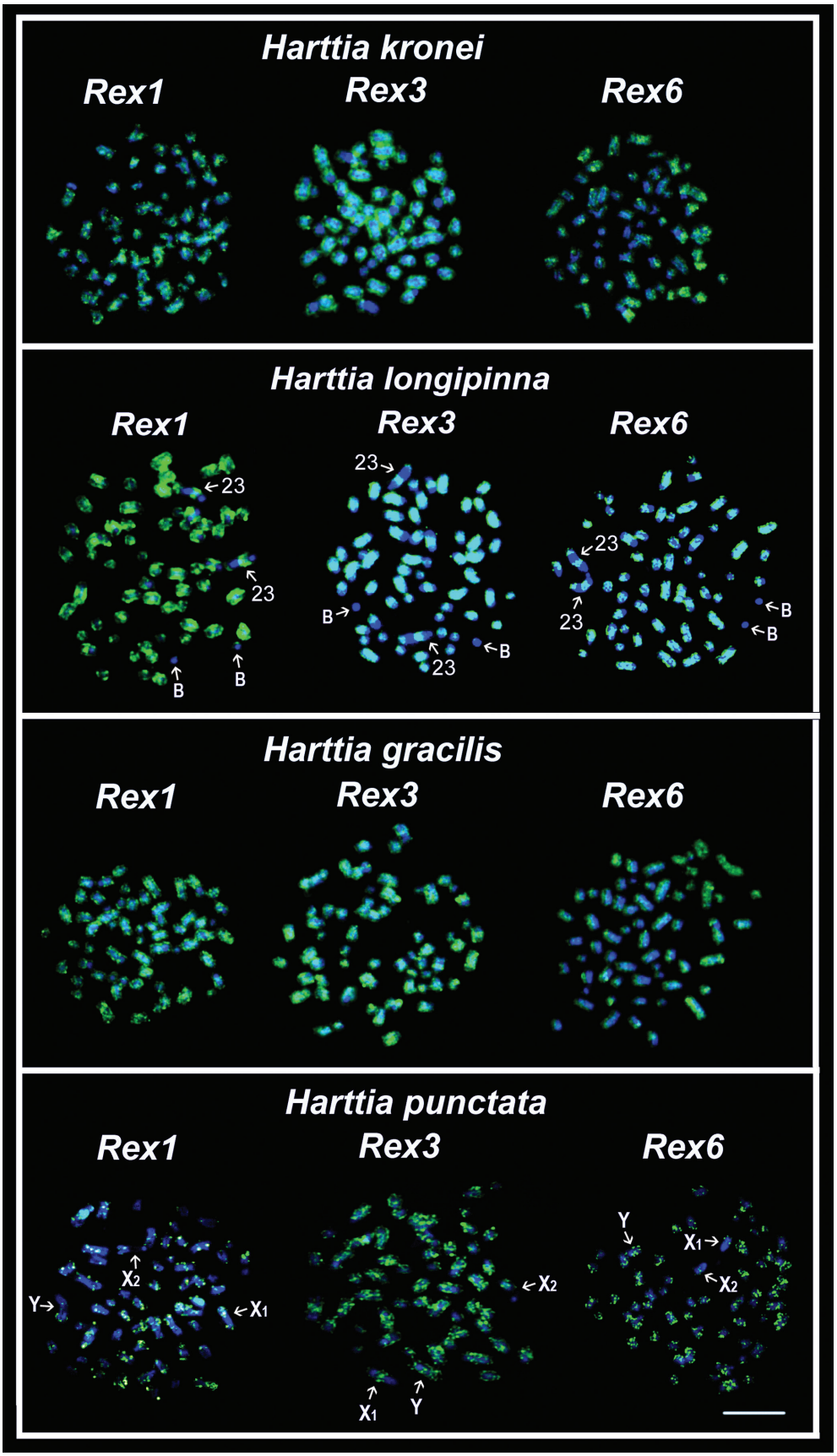

Fig. 1. Metaphases of the *Harttia* species submitted to FISH with probes of the *Rex* elements. The numbers indicate chromosomal pairs in highlighted. Bar = 10 µm.

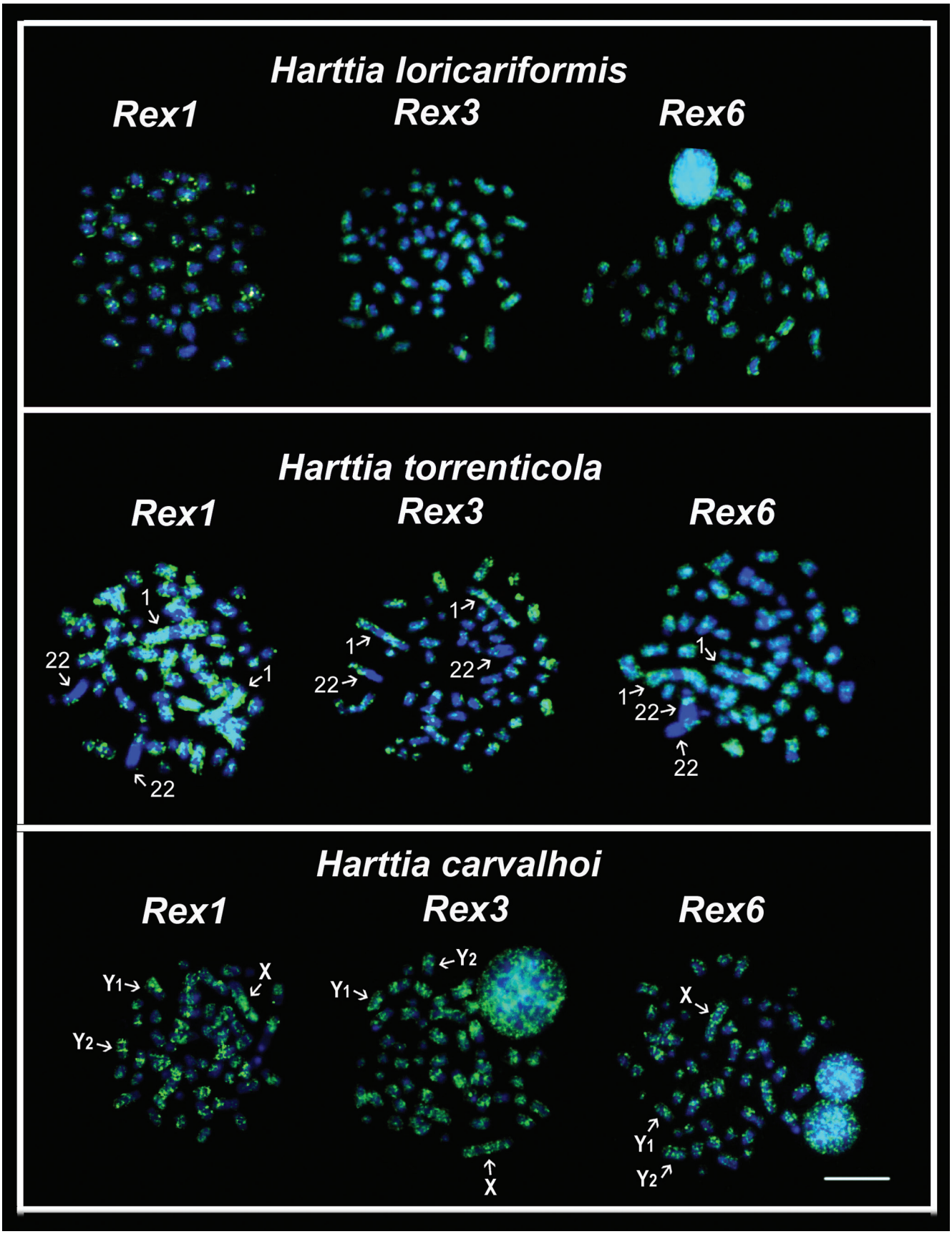

Fig. 2. Metaphases of the *Harttia* species submitted to FISH with probes of the *Rex* elements. The numbers indicate chromosomal pairs in highlighted. Bar = 10 μm.

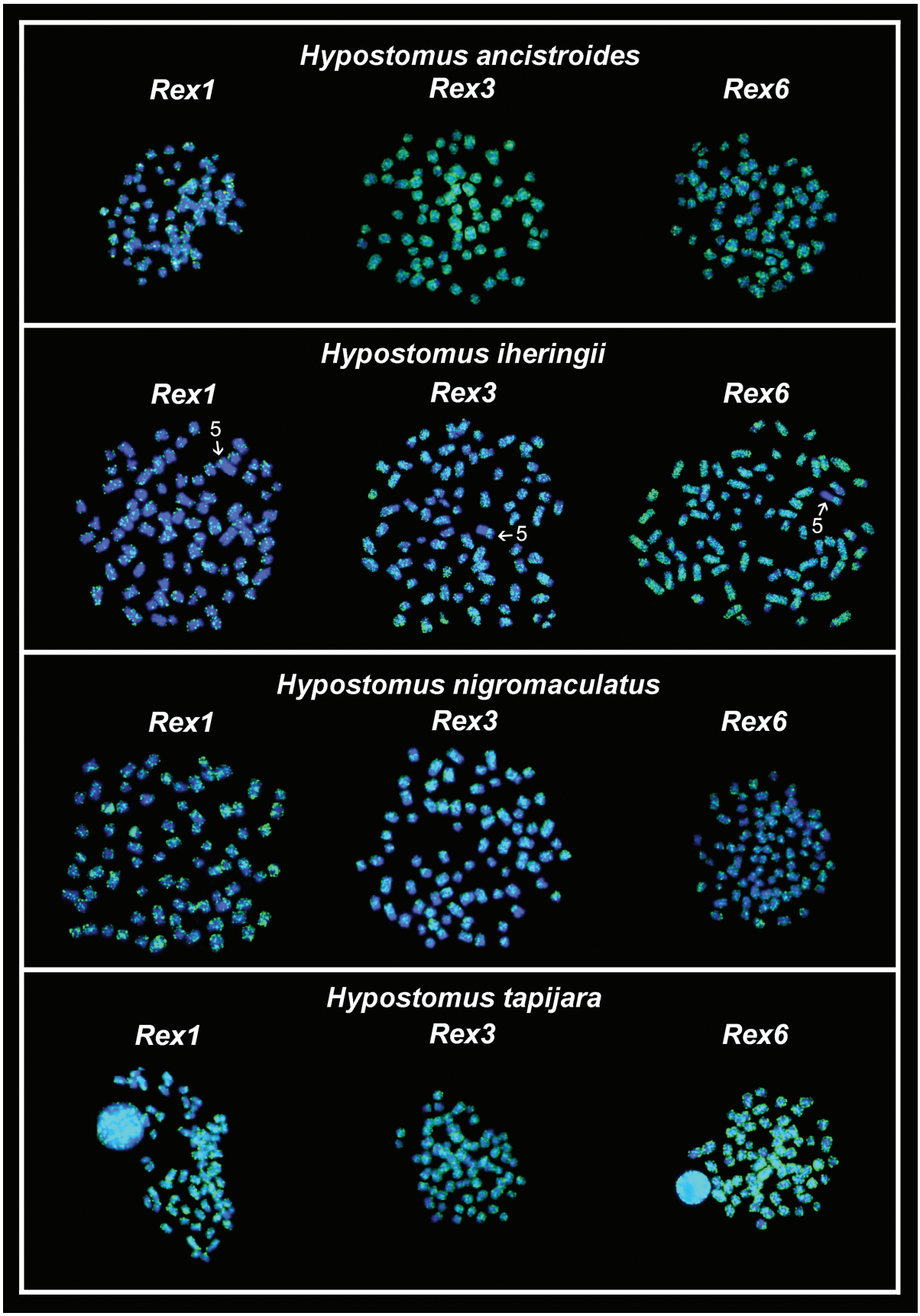

Fig. 3. Metaphases of the *Hypostomus* species submitted to FISH with probes of the *Rex* elements. The numbers indicate chromosomal pairs in highlighted. Bar = 10 µm.

The retroelement *Rex*1 revealed the largest accumulation in pair 15 of *H. ancistroides* and in pairs 2 and 30 of *H. nigromaculatus* (Pansonato-Alves *et al*., 2013). However, for these species, in this study, the accumulation was not directed only to these pairs. In addition, the results observed indicate a greater accumulation of this sequence in these species. Thus, we observed the occurrence of population variations of this marker for these species.

Rex elements have been undergoing some rearrangement processes, some of which identified as recent events (Ferreira *et al*., 2011a). The dispersed pattern of elements *Rex*1, *Rex*3 and *Rex*6 found for the species analyzed in this study was also found in groups that present a wide chromosomal variety such as in *Erythrinus erythrinus* (Bloch, Schneider, 1801) (Cioffi *et al*., 2010) and species of the Hypoptopomatinae family (Ferreira *et al*., 2011b). On the other hand, in groups that present a sharper conservation on the karyotypic macrotexture, such as cichlids, these retroelements are allocated preferentially in the centromeric and telomeric region of most chromosomes (Valente *et al*., 2011). This difference in the distribution of TEs, here represented by *Rex* elements, is possibly related to a number of copies of these sequences in the genome of different species. Whereas the retroelements present a significant influence on chromosomal evolution for being often associated with chromosomal rearrangements (Raskina *et al*., 2008), the dispersed distribution of *Rex* retroelements combined with their abundances in the genome of the species studied here can possibly be related with the karyotypic diversity found in Loricariidae.

Studies with repetitive elements dispersed in genomes already demonstrated that they, after the invasion, tend to be silenced and undergo molecular deterioration until they are incorporated into the host genome (Fernández-Medina *et al*., 2012). In the molecular deterioration phase, the element becomes inactivated and progressively accumulates mutations, insertions and deletions in neutral rates up to completely lose its identity or be lost from the host genome (Fernández-Medina *et al*., 2012). We verified that the deterioration of the elements dispersed transforms these copies in neutral sequences in the genome, and they may serve as raw material to the domestication by the host genome (Miller *et al*., 1997). The concept of molecular domestication was used to describe the process where a TE sequence has a co-option to perform a function different from the original for which it was selected and bring benefits to the host genome (Miller *et al*., 1997). In fact, copies of truncated TE elements can modulate the gene expression in the host genome by providing new regulatory sites, alternatives to "splice" sites, signs of polyadenylation, new binding sites of transcription factors as well as post-transcriptional regulation and the translation regulation (Marino-Ramirez *et al*., 2005; Muotri *et al*., 2007; Polavarapu *et al*., 2008). In addition, it has been shown that numerous genes for microRNAs derive from TEs (Piriyapongsa *et al*., 2007). Thus, the intense invasion of the elements of the *Rex* family in *Hartti*a and *Hypostomus*, demonstrated by the physical location of these elements with the accumulation in euchromatic regions, can represent new genomic and evolutionary alternatives, acting in the adaptation and differentiation of these species.

The transposable elements due to their mobility in the genome have a significant influence on chromosomal evolution because they are often associated with chromosomal rearrangements. In this context the presence of retroelements in some chromosomal regions suggest their participation in various chromosomal rearrangements. In addition, after the invasion on a host, the transposable elements can undergo the molecular domestication process, having a co-option to perform a function different from the original for which it was selected, generating benefits for the host genome. Thus, the intense accumulation of *Rex*1, *Rex*3 and *Rex*6 in all species of *Harttia* and *Hypostomus* especially in euchromatic regions can be indicative of the participation of these elements in the diversification and evolution of these species by the acquisition of new functions.

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Where read: *Hypostomus nigromaculatus*	*Rex*6	549pb	MH595480
Should read: *Hypostomus nigromaculatus*	*Rex*6	549pb	MH595489