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Divergence in the chromosomal distribution of repetitive sequences in Neotropical cichlid species of the genus *Lugubria*

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Abstract. Cytogenetic studies provide valuable insights into the evolutionary dynamics of fish genomes, particularly in groups with high species diversity and ecological relevance. Among Neotropical cichlids, chromosomal data have revealed both conservation patterns and significant structural variations, reflecting intense karyotypic diversification. In this context, mapping repetitive DNA sequences has proven useful in aiding understanding of genomic organization and chromosomal evolution. However, information remains scarce for several cichlid genera. The present study investigated the chromosomal distribution of repetitive sequences, such as 18S and 5S ribosomal genes, as well as telomeric sequences, in three Amazonian species of *Lugubria*: *L. cincta*, *L. strigata*, and *L. lugubris*. The results revealed a diploid number of 2n = 48, along with variations in the karyotypic formula among the species. Mapping of repetitive sequences revealed distinct patterns of 18S rDNA distribution, with clusters located on different chromosome pairs. Conversely, the 5S rDNA showed a conserved position on a subtelocentric/acrocentric pair in all three species. Furthermore, the presence of interstitial telomeric sequences in *L. cincta* and *L. strigata* indicates greater genomic plasticity in these species, suggesting more pronounced chromosome dynamics in the genus *Lugubria*. These data contribute to the understanding of chromosomal evolution and diversification in this diverse group of Neotropical cichlids and may aid in future cytotaxonomic studies.

Keywords: repetitive DNAs, neotropical cichlids, ribosomal genes.

INTRODUCTION

The Cichlidae family is one of the largest and most diverse families of freshwater fish in the world, and its geographic distribution spans most continents, including North, Central, and South America (Turner, 2007; Fricke et al. 2024). Neotropical cichlids constitute a prominent group within this family, comprising a wide variety of species adapted to different aquatic environments (Kullander, 2003; Kullander et al. 2010; Chakrabarty, 2004; Genner, 2023) and exhibiting a wide range of complex reproductive strategies, including territorial behavior and pronounced parental care (Balshine & Abate, 2021). Due to the rapid adaptive radiation of these species, cichlids have been considered important models for evolutionary studies (Matschiner et al. 2020; Singh et al. 2022). Neotropical cichlids, in particular, have been the subject of numerous scientific studies not only because of their diversity and intriguing behavior, but also because many species are threatened with extinction due to the degradation of their natural habitats and the introduction of exotic species into their ranges (ICMBio, 2018). The study of the genetic characteristics of this group has enabled a more comprehensive understanding of their evolutionary history, supporting insights into the kinship relationships among different species and genera, as well as contributing to taxonomic classification and understanding of their evolutionary trajectories (Arbour & López-Fernández, 2014; Torres-Dowdall et al. 2021).

The genus *Lugubria* comprises 16 large species distributed throughout the Amazon Basin, the Orinoco River, and Guiana. These species exhibit changes in body coloration related to sexual maturity throughout their life cycle (Varella et al., 2023). To date, chromosomal data are available for only four members of this genus, and these data remain largely limited to classical analyses. In general, *Lugubria* exhibits a diploid number of 2n = 48, the absence of heteromorphic sex chromosomes, and 18S rDNA and 5S rDNA sites typically located on a single chromosome pair. However, interpopulation variations in the karyotypic formula have been recorded for *Lugubria johanna*, *Lugubria cincta*, and *Lugubria lugubris*, suggesting a high rate of chromosomal rearrangements in this genus (Frade et al., 2019; Paiz et al., 2024).

Repetitive DNA refers to segments of DNA that occur in multiple copies within an organism's genome (Lower et al., 2019; Kejnovský & Jedlička, 2022). These sequences can be organized in tandem, forming highly repetitive regions—such as telomeric and centromeric sequences—which are involved in chromosome protection and proper segregation during cell division, or they may be dispersed throughout the genome, such as transposons and retrotransposons, which can influence genome evolution and are associated with chromosomal rearrangements and genetic diversification (Ayarpadikannan & Kim, 2014; Kejnovský & Jedlička, 2022; Šatović-Vukšić & Plohl, 2023). The function of repetitive DNA in the genome has been the subject of intense investigation because, although many of these elements do not encode proteins, they play essential roles in gene expression regulation, chromosomal structure, and genomic stability (Bernstein & Allis, 2005; Liao et al., 2023).

Ribosomal DNA (rDNA) is organized as tandem repeat arrays that encode crucial structural and functional components of the ribosome and is typically found as 45S and 5S clusters within eukaryotic genomes (Mishra et al., 2021). The process of rDNA evolution involves mutations, recombination, and concerted evolution, promoting both homogenization and diversity, and through these processes, enabling adaptation and stability within species over time (Wang et al., 2023). Telomeric DNA, in turn, plays essential roles in maintaining genomic stability, protecting against the loss of genetic information, and preventing cellular aging (Alanazi, Parkinson, & Haider, 2024). The study of telomeric regions is fundamental for understanding chromosome structure and behavior during cell division, as well as for identifying potential chromosomal rearrangements and anomalies. The evolution of these sequences involves recombination and mutation events, along with variations in telomeric length, which may be associated with mechanisms of adaptation and speciation (Belyayev et al., 2023).

This work presents the description of new cytotypes and the mapping of ribosomal DNA and telomeric sequences in three Amazonian species of *Lugubria*. Studying these repetitive DNA markers can help elucidate the processes that promote chromosomal diversification and genome organization through the construction of cytogenetic maps in *Lugubria*, as well as expand the available karyotypic data for the genus.

MATERIAL AND METHODS

The sample data used in this study are presented in Table 1, and the collection sites are shown in Figure 1. The specimens were cataloged in the collection of the Genetics and Cell Biology Laboratory at the Federal University of Pará. The taxonomic identification of *L. cincta*, *L. strigata*, and *L. lugubris* was performed based on the existing literature. Samples were collected under SISBIO license No. 89443, and the study was conducted

Table 1. General data of the samples analyzed in the present study.

Species	Sample size	Sex	Localization	Geographical coordinates
Lugubria cincta	4	Male	Bujarú River	1°45'28.4"S 47°58'14.5"W
Lugubria strigata	3	Male	Bujarú River	1°45'28.4"S 47°58'14.5"W
Lugubria lugubris	3	Male	Tapajós River	4°15'56.5"S 55°58'30.0"W

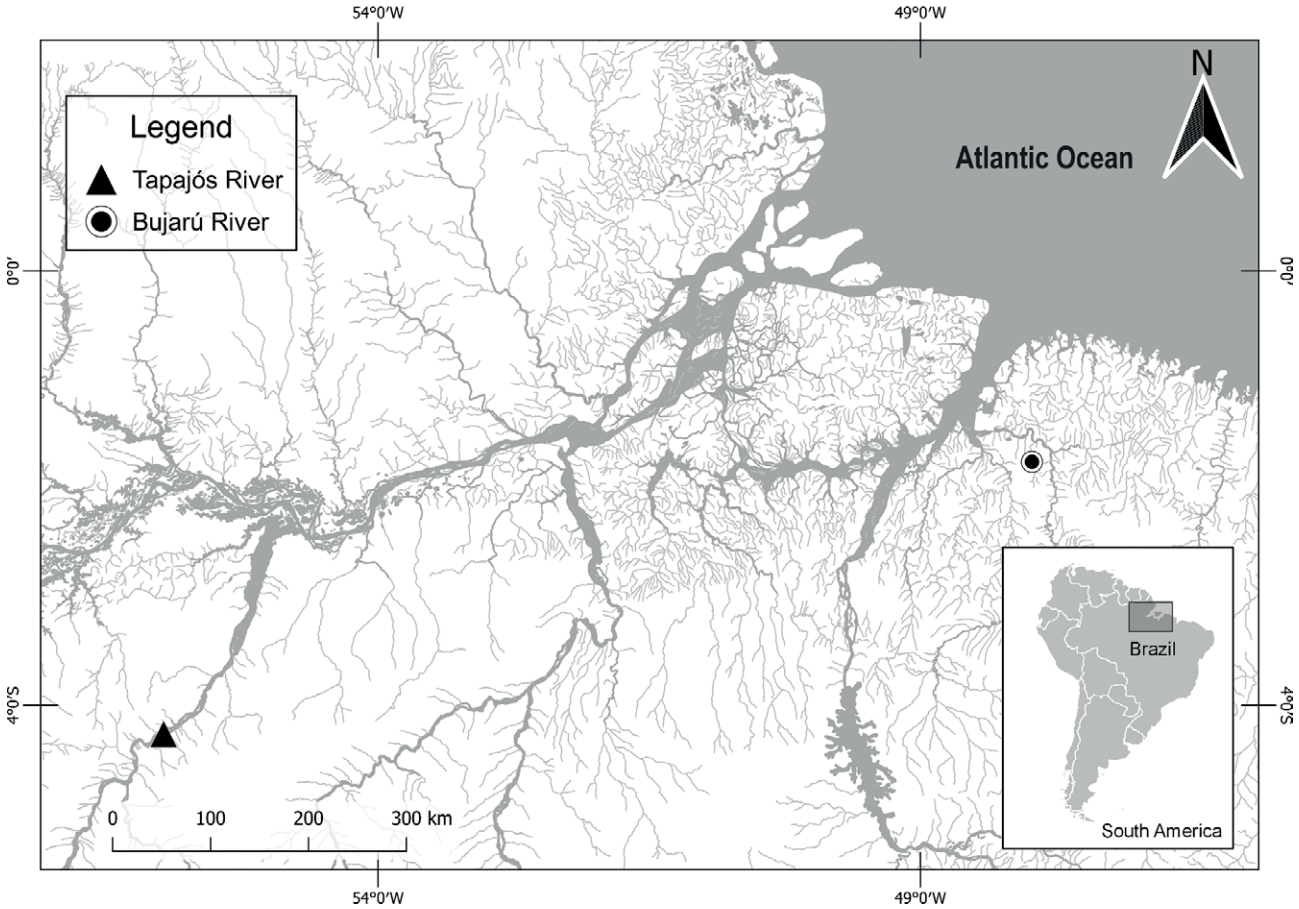

Figure 1. Map indicating the collection sites of the *Lugubria* samples analyzed in this study.

with approval from the Ethics Committee on the Use of Animals of the Federal University of Pará (CEUA 8803211223).

Chromosome preparations were obtained according to Bertollo et al. (2015). Chromosomes were classified according to Levan et al. (1964).

The total genomic DNA of *Lugubria* was extracted using the GenElute Mammalian Genomic DNA Miniprep kit (Sigma-Aldrich, St. Louis, MO, USA). 18S and 5S rDNA sequences for Fluorescent *in situ* Hybridization (FISH) were amplified by Polymerase Chain Reaction (PCR) following the protocol of Martins & Vicari (2012), using the genomic DNA of *Lugubria*, with the following set of primers: 18S rDNA: 18SF (5'-CCG CTT TGG TGA CTC TTG AT-3') and 18SR (5'-CCG AGG ACC TCA CTA AAC CA-3') (Gross et al. 2010); 5S rDNA: 5SF (5'-GCC ACA CCA CCC CTG AAC AC-3') and 5SR (5'-GCC TAC GAC ACC TGG TAT TC-3') (Suarez et al. 2017), and labeled with biotin using the BioNick kit (Invitrogen) following the manufacturer's protocol. Telomeric sequences were amplified and labeled by PCR using digoxigenin-11-dUTP with complementary primers (TTAGGG)n and (CCCTAA)n, without using template DNA, according to Ijdo et al. (1991).

FISH was performed according to Pinkel et al. (1986). The hybridization solution composed of 2 μL of probe, 50% formamide, 2xSSC, and dextran sulfate was denatured together with chromosomal DNA in a thermoblock at 90°C for 10 min. Hybridization occurred overnight at 37°C. Probes were detected with avidin-CY3 or antidigoxigenin-FITC. Chromosomes were counterstained with 4',6-diamidino-2-phenylindole (DAPI) containing Vectashield antifading.

The slides were analyzed using an Olympus BX41 microscope and photographed with a Canon Powershot A95 digital camera. FISH images were captured with an AxioCam camera coupled to a Zeiss D2 epifluorescence microscope using Zen2 software (Zeiss). Image editing, including brightness and contrast adjustments and karyotype assembly, was performed using Adobe Photoshop CS6.

RESULTS

Lugubria cincta, *L. strigata* and *L. lugubris* presented a diploid number 2n=48 (Figure 2). *L. cincta* and *L. lugubris* presented a fundamental number FN=56, while *L. strigata* showed FN=54. The karyotypes observed in the three species demonstrated the following karyotypic formulas: *L. cincta* (8m/sm+40st/a), *L. strigata* (6m/sm+42st/a) and *L. lugubris* (8m/sm+40st/a). Sex chromosomes with morphological differentiation were not observed in the analyzed males.

FISH with the 18S rDNA probe revealed clusters in a single chromosome pair in each species. In *L. cincta*, 18S rDNA was observed in the terminal region of the short arm of metacentric pair 1 (Figure 2a). In *L. strigata*, this sequence showed a large cluster extending from the interstitial to the terminal region of the long arm of submetacentric pair 2 (Figure 2b). In *L. lugubris*, this sequence was observed in the terminal region of the long arm of subtelocentric pair 12 (Figure 2c).

The 5S rDNA was detected in the karyotypes of *L. cincta*, *L. strigata* and *L. lugubris* in the interstitial region of the long arm of pair 15 (Figure 2).

FISH with a telomeric probe demonstrated, in all species, the presence of these sequences at the ends of all chromosome arms, in addition to interstitial telomeric sequences (ITSs) in *L. cincta*, in pairs 1, 2, 3, 6, 8, 10, 14, 16 and 17 and in *L. strigata*, in pairs 1 and 6 (Figure 2).

Figure 3 presents an idiogram showed the locations of the repetitive sequences analyzed in this study.

DISCUSSION

The karyotypes observed in *L. cincta*, *L. strigata*, and *L. lugubris* in this study corroborate those previously described by other authors. Interestingly, the previous populations of these species analyzed cytogenetically are located in regions distant from the sampling sites of the present study. Benzaquem et al. (2008), for example, described the karyotypes of *L. cincta* and *L. lugubris* from specimens from Lake Catalão, in Amazonas State (1,300 km away); Poletto et al. (2010) and Valente et al. (2012) used specimens of *L. strigata* from the Araguaia-Tocantins River (Mato Grosso State- more than 1,600 km away) to characterize the karyotype of this species. Thus, our results promote an increase in the geographic distribution of these cytotypes and reveal a great conservation of the karyotypic macrostructure in the members of *Lugubria*. Similar findings were described between two distinct populations of *Lugubria johanna* (Frade et al. 2019). Despite the karyotypic stability observed in Cichlidae (Majtánová et al., 2019), Paiz et al. (2024) recorded in specimens from Lake Catalão (Amazonas State) karyotypic formulas of *L. cincta* (2m + 4sm + 32st + 10a) and *L. lugubris* (6sm + 22st + 20a) divergent from the findings of the present study and Benzaquem et al. (2008); considering that fish from lake environments present a high rate of chromosomal alterations (MacGuigan et al., 2023), this may be a case of intraspecific polymorphism in the Catalão Lake region, originated by inversion-type rearrangements (considering the conservation of 2n = 48), maintained by intrinsic factors of this population.

The distribution of rDNA sequences, specifically the 18S and 5S ribosomal RNA genes, in cichlid chromosomes has been the subject of extensive research. Regarding 5S rDNA, Nakajima et al. (2012) observed that, in 48 cichlid genomes analyzed, more than 52% presented clusters of these sequences located in the interstitial region of the long arm of subtelocentric/acrocentric chromosomes, as observed in the findings of the present study, confirming the conserved behavior of these sequences, especially among Neotropical cichlids, which presented this pattern in 82% of cases. On the other hand, in Amazonian peacock bass species, Quadros et al. (2020) showed distinct distribution patterns of 5S rDNA located in interstitial and distal positions in different chromosome pairs. These findings collectively demonstrate conserved and variable distribution patterns of 5S rDNA sequences in cichlids, reflecting the complex evolutionary dynamics of these genomic elements (Schneider et al., 2013). The position of the 5S rDNA sites in *Lugubria* shows that this sequence is

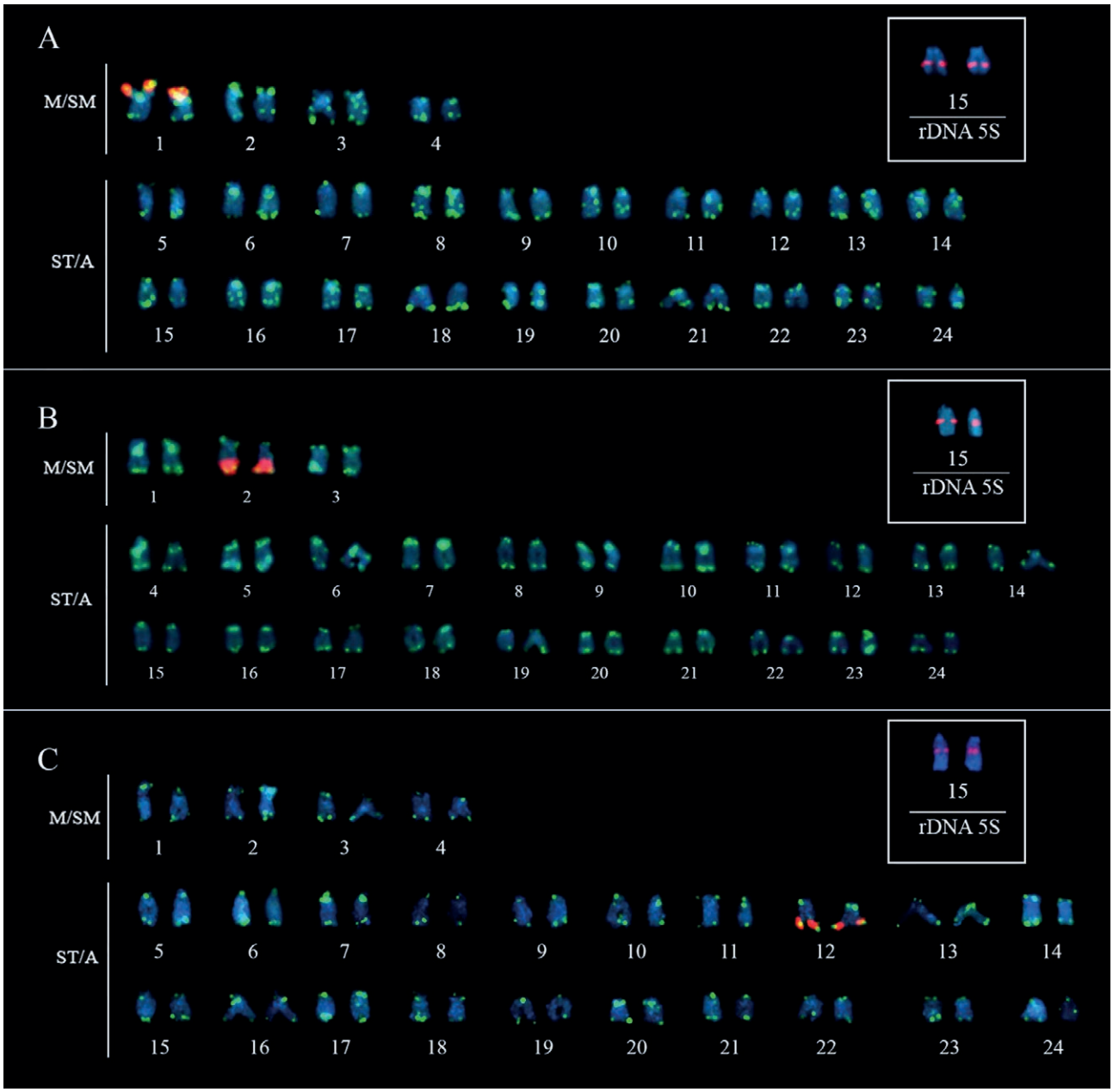

Figure 2. Double FISH with telomeric sequence probes (green signal) and 18S rDNA sequence probes (red signal) in the karyotype of (A) *L. cincta*, (B) *L. strigata*, and (C) *L. lugubris*. Yellow signals represent syntenic regions. The highlighted boxes show FISH with 5S rDNA sequence probes (red signal). All chromosomes were counterstained with DAPI.

highly conserved in this group. This is because, in addition to having an invariable diploid number (2n=48), the location of this sequence in the interstitial region of the long arm of an st/a pair remains constant in all studies carried out to date, including the present work (Frade et al. 2019, Paiz et al. 2024) (Table 2).

The presence of multiple 18S rDNA sites in cichlid genomes, with varying numbers in different species, indicates a dynamic evolutionary process shaping the chromosomal distribution of these sequences (Gross et al. 2009; Nakajima et al., 2012; Frade et al. 2019; Nirchio et al., 2020). The present study is the first to generate data on the physical mapping of 18S rDNA in *L. strigata*, locating it in pair 2 of this species. The pattern found for *L. cincta* is similar to that described for the specimens studied by Paiz et al. (2024). In both cases, our FISH

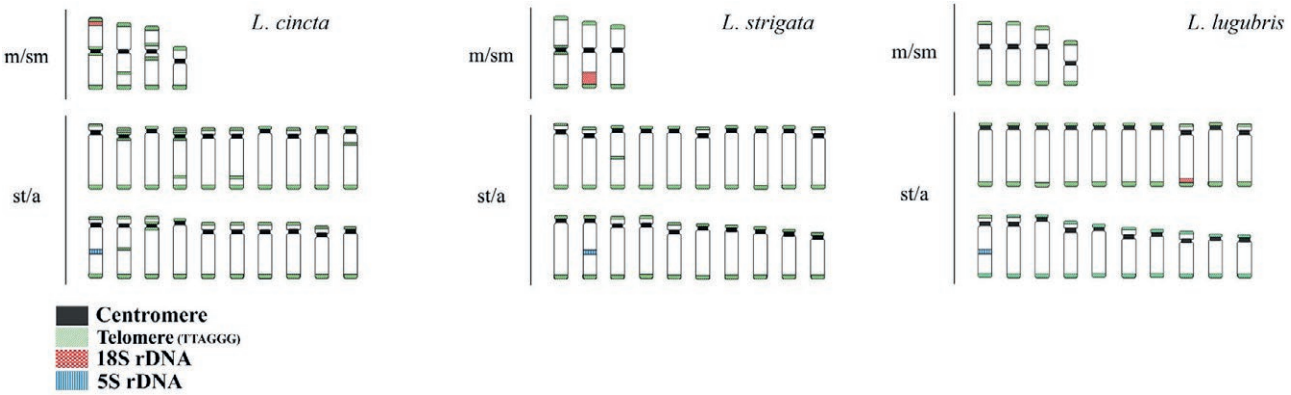

Figure 3. Idiogram of the metaphases of *L. cincta*, *L. strigata*, and *L. lugubris* indicating the proposed positioning for the telomeric sequences (green / diagonal lines), 18S rDNA sequences (red / grid of squares) and 5S rDNA sequences (blue / vertical lines). Centromeres are shown in solid gray.

data corroborate the number of Ag-NOR bands observed by Benzaquem et al. (2008) and Valente et al. (2012) for *L. cincta* and *L. strigata*, respectively. Our results revealed only one ribosomal site located in pair 12 for *L. lugubris*, which disagrees with the findings of Paiz et al. (2024), who showed ribosomal cistrons in several pairs of the karyotype of this species. This result highlights the occurrence of pericentric inversions during the chromosomal evolution of the genus *Lugubria*, ratifying the evolutionary trend influenced by pericentric inversions, generating chromosomes with two arms, proposed by Feldberg et al. (2003) for Neotropical cichlids. In contrast, a large number of 18S rDNA sites were evidenced in *L. johanna* (Frade et al., 2019). Unlike other members of *Lugubria*, the colocalization of 18S rDNA and interstitial telomeric sequences (ITSs) may have contributed to greater plasticity of this ribosomal DNA in *L. johanna*, since this association can generate unstable sites in the chromosomes (Frade et al., 2019). The different distribution patterns of 18S rDNA in the chromosomes of the four *Lugubria* species karyotypes, as demonstrated in this study and by Frade et al. (2019), allow us to differentiate them, contributing to their cytotaxonomy, which highlights the relevance of these markers in understanding the evolution and phylogeny of these species.

Additionally, the presence of several ITSs in the karyotypes of *Lugubria cincta* and *Lugubria strigata* raises several questions and possible interpretations. First, the presence of these ITSs suggests additional genomic complexity in these organisms, as these sequences may play important roles in chromosome stability and gene regulation (Lee et al. 2021; Lu & Liu, 2024). The observed pattern of telomeric sequence distribution corroborates the high variability in the distribution pattern of these repetitive sequences observed in Cichlinae species (Frade et al. 2019; Nirchio et al., 2020; Quadros et al. 2020). ITSs can arise during DNA break repair; however, when considering the evolutionary lines proposed for the karyotype of Neotropical cichlids (Feldberg et al. 2003), it can be concluded that many of the observed ITSs are artifacts of recent chromosomal rearrangements.

The identification and characterization of ITSs in *Lugubria* can provide valuable insights into genome evolution in the Crenicichlina, as well the possible mechanisms of adaptation and genetic diversification. Furthermore, such information contributes to a better understanding of the dynamics of chromosomal rearrangements, genomic plasticity, and the evolutionary processes that have shaped the genome of these fishes over time (Ocalewicz, 2013; Lafuente & Beldade, 2019; Vicari et al. 2022).

In summary, the data presented in this work reveals a duality in the distribution of rDNA sequences in Neotropical cichlids, highlighting both conserved patterns, such as the position of 5S rDNA, and variable patterns such as the distribution of 18S rDNA and the great diversity of ITSs. Taking into account that rDNA sequences cluster during interphase to form one or more nucleoli (Cazaux et al. 2011), the location of 5S and 18S rDNA clusters in different chromosomal regions enables complex evolutionary dynamics within the Crenicichlina, since these sequences can directly or indirectly influence chromosome structure and composition, as suggested by Molina & Galetti-Jr. (2002) for species of the genus *Cromis*, by Cazaux et al. (2011) for rodents of the genus *Mus*, and by Marajó et al. (2022) for species of the genus *Rineloricaria*. The observation of multiple 18S rDNA sites and telomeric sequences in different *Lugubria* species not only reflects genomic plasticity within cichlids but also suggests a fundamental role for these sequences in the genome evolution of these organisms (Ocalewicz,

Table 2. Repetitive sequence mapping data in *Lugubria*. The acronyms represent (st/a) subtelocentric/acrocentric chromosome, (t) terminal region, (i) interstitial region, (UN) unidentified pair, (*) signal observed in only one of the homologues, (All) signal observed in all chromosomes, (pc) pericentromeric region.

Species	2n	Repetitive sequences			Reference	Group
		18S rDNA	5S rDNA	Telomeric		
Lugubria johanna AB	48	$1p^{*t}$, $5q^{t}$, $6q^{*t}$, $17q^{*t}$, $22p^{*t}$	$st/aUNq^{i}$	All^{t}, $1p^{*t}$, $5q^{t}$, $6q^{*t}$, $17q^{*t}$, $22p^{*t}$	Frade et al. (2019)	*Lugubris*
Lugubria johanna CA	48	2p - all over the arm, $16q^{*t}$	$st/aUNq^{i}$	All^{t}, 2p - all over the arm, $16q^{*t}$	Frade et al. (2019)	*Lugubris*
Lugubria cincta	48	$1p^{t}$	$18q^{i}$	All^{t}, $2q^{i}$, 3^{pc}, 6^{pc}, $8q^{i}$, $10q^{i}$, $14q^{i}$, $16q^{i}$, $17q^{i}$	Present study	*Lugubris*
Lugubria strigata	48	$2q^{t}$	$17q^{i}$	All^{t}, 1^{pc}, $6q^{i}$	Present study	*Lugubris*
Lugubria lugubris	48	$12q^{t}$	$15q^{i}$	All^{t}	Present study	*Lugubris*

2013; Bolzán, 2017). Understanding the distribution of repetitive DNAs in cichlids not only contributes to our understanding of their evolutionary biology but also provides insights into the mechanisms underlying cichlid diversification and adaptation.

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