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Karyotype reexamination of *Corydoras paleatus* (Siluriformes) and a review of the cytogenetics of genus with a focus on the ribosomal genes

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Abstract: The subfamily Corydoradinae is the second largest among the callictids, comprising three genera, with *Corydoras* Lacépède, 1803 being the largest in the number of species. The genus *Corydoras* has been divided into five groups of species based on differences in diploid number (2n), chromosomal morphology, and DNA content. Chromosome studies can provide crucial details on population differentiation. To better understand the chromosomal diversification that occurs in this fish group, the current study presents data from a population of *Corydoras paleatus* from the first plateau of Paraná, putting them in a comparative scenario. The specimens studied has 2n=44 chromosomes with a karyotypic formula of 18m+26sm. Although conserved, this karyotypic structure shows variation in other populations of *C. paleatus* already studied, a consequence of chromosomal rearrangements that modify the morphology of chromosomes without modifying the 2n, such as centromeric repositioning. C-banding revealed conspicuous pericentromeric markings in metacentric pairs 4 and 8 and in submetacentric pairs 10 and 13, whose bands have been considered a chromosomal marker not only for *C. paleatus* but also for the genus. Fluorescent in situ hybridization (FISH) showed the major rDNA (45S) in the terminal region of the long arm of metacentric pair 5. Such location has already been described in other populations of *C. paleatus*, as they have also been mapped in short arms, as well as at multiple *loci*. The present study also provides a review of the genus *Corydoras* regarding the 2n, karyotypic formula, and mainly regarding the number and location of the 45S and 5S rDNA, confirming a scenario in which chromosomal rearrangements have been modeling karyotypes of different populations and settling in the absence of gene flow, a consequence of vicariant events that occurred in the different hydrographic basins.
Keywords: Corydoradinae; chromosomes; evolution; rDNA.

Reexame do cariótipo de *Corydoras paleatus* (Siluriformes) e uma revisão citogenética do gênero com ênfase em genes ribossômicos

Resumo: A subfamília Corydoradinae é a segunda maior entre os calictídeos, composta por três gêneros, com *Corydoras* Lacépède, 1803 o maior em número de espécies. Diante de sua variabilidade cromossômica, o gênero *Corydoras* foi organizado em cinco grupos de espécies diferenciados quanto ao número diploide (2n), morfologia cromossômica e conteúdo de DNA. Estudos citogenéticos podem revelar informações importantes sobre a diferenciação de populações, e assim o presente trabalho baseado em marcadores cromossômicos, apresenta dados de uma população de *Corydoras paleatus* proveniente do primeiro planalto paranaense, os colocando em um contexto comparativo para melhor entender a diversificação que ocorre neste grupo de peixes. Os espécimes estudados apresentaram número diploide igual a 44 cromossomos com fórmula cariotípica de 18m+26sm. Embora conservada, tal estrutura cariotípica apresenta variação em

outras populações de *C. paleatus* já estudadas, reflexo de rearranjos cromossômicos que modificam a morfologia dos cromossomos sem modificar o 2n, como o reposicionamento centromérico. O bandamento C revelou marcações pericentroméricas conspícuas nos pares metacêntricos 4 e 8 e nos pares submetacêntricos 10 e 13, cujas bandas têm sido consideradas um marcador cromossômico não só para *C. paleatus* como para o gênero. A hibridização fluorescente in situ (FISH) evidenciou o maior DNAr (45S) na região terminal no braço longo do par metacêntrico 5. Tal localização já foi descrita em outras populações de *C. paleatus*, como também já foram mapeados em braços curtos e em múltiplos *loci*. O presente estudo também oferece uma revisão no gênero *Corydoras* quanto ao 2n, fórmula cariotípica e principalmente quanto ao número e localização do DNAr 45S e 5S, confirmando um cenário em que rearranjos cromossômicos vêm modelando cariótipos das diferentes populações e se fixando na ausência de fluxo gênico, consequência de eventos vicariantes ocorridos nas diferentes bacias hidrográficas.
Palavras-chave: Corydoradinae; cromossomos; evolução; rDNA.

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INTRODUCTION

The order Siluriformes is among the largest groups of fish with a wide distribution in tropical regions (TEUGELS, 1996). Catfish of the Callichthyidae family are easily recognized among other Siluriformes because they have two longitudinal series of bony plates along the side of the body and a pair of barbels at the junction of the lips (REIS, 2003). Approximately 90% of the species belong to the subfamily Corydoradinae, represented by the genera *Corydoras*, *Aspidoras*, and *Scleromystax*. The largest genus, *Corydoras* comprises 231 recognized species, distributed in the main river basins of South America (FRICKE et al., 2023).

Based on chromosomal and molecular data, the genus *Corydoras* is recognized as a paraphyletic group (NIJSSEN; ISBRUCKER, 1980; REIS, 1998; BRITTO, 2003; SHIMABUKURO-DIAS et al., 2004; ALEXANDROU et al., 2011). In addition, have been organized into five species groups that differ by diploid number, chromosome morphology, or DNA content (OLIVEIRA et al., 1992; SHIMABUKURO-DIAS et al., 2004). Cytogenetic studies commonly based on conventional analysis, revealed karyotypes ranging from 2n = 40 in *C. nattereri* to 2n = 134 in *C. aeneus* (TURNER et al., 1992). The chromosomal diversification found in this genus results from intense polyploidization events, chromosomal inversions, and centric fusion/fissions (OLIVEIRA et al., 1993; BARBOSA et al., 2017). A high variation is also observed in the heterochromatin distribution pattern, as well as in the location and number of the 45S rDNA (Nucleolar Organizer Regions) and the extranucleolar 5S rDNA (ARTONI et al., 2006; ROCHA et al., 2016; BARBOSA et al., 2017).

Detailed karyotypic analyses and descriptions of individuals provide important information regarding population differences since such variability is a reflection of phenotypic and adaptive effects (ARTONI et al., 2006). Therefore, in order to better understand the diversification process that occurs within the genus *Corydoras*, the current study presents the karyotype of a population of *Corydoras paleatus* from the first plateau of Paraná state, and puts them in an evolutionary context, through a comparative analysis based on a revision of the 2n, karyotypic formula, and rDNAs.

MATERIAL AND METHODS

Twelve specimens (5 males and 7 females) of *C. paleatus* were collected from the Parque Costa, Iguaçu river basin, Paraná, Brazil (25°36'23" S and 49°16'51" W). Fish capture was authorized by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio – license number 10538-1) and the processing was performed in accordance with the Ethical Committee on Animal Use (CEUA

29/2016) of the Universidade Estadual de Ponta Grossa and current Brazilian legislation.

Mitotic chromosomes were obtained from the anterior kidney using the method by Bertollo et al. (1978), and the slides were stained with 5% Giemsa diluted in phosphate buffer pH 6.8. C-banding was performed using barium hydroxide [5% $Ba(OH)_2$ at 25 °C for 3 min], subsequent incubation in salt solution (2×SSC at 60 °C for 25 min), and Giemsa 5% staining (SUMNER, 1972). Fluorescence *in situ* hybridization (FISH) technique was performed with an 18S rDNA probe from the fish *Prochilodus argenteus* (HATANAKA; GALETTI, 2004) according to Pinkel et al. (1986). The probe 18S was labeled with biotin-14-dATP by nick translation according to the instructions of the fabricant (BioNickTM Labeling System, Invitrogen). The detection and amplification of hybridization signals were carried out using streptavidin-FITC conjugated (Molecular Probes™, Invitrogen). The chromosome spreads were counterstained with propidium iodide and analyzed using ZEN digital image capture software coupled to a Carl Zeiss AxioLab A1 microscope. For karyotyping, the chromosomes were identified according to their arm ratio, as proposed by Levan et al. (1964). The review was founded on studies that provided some chromosomal information for the *Corydoras* species.

RESULTS AND DISCUSSION

Karyotype structure: diploid number and heterochromatin

Chromosomal studies have divided the species of the genus *Corydoras* into five groups according to differences in diploid number, chromosomal morphology, and DNA content (OLIVEIRA et al., 1992; SHIMABUKURO-DIAS et al., 2004). Our results showed that the population of *C. paleatus* from the upper Iguaçu River has a karyotype with 2n = 44 chromosomes, with a karyotype formula of 18m+26sm (Figure 1A). This karyotypic constitution is shared both by other populations of *C. paleatus*, as well as by *C. ehrhardti* and *C. nattereri* already described (Table 1). Such species, which occur in basins near the coast of southern and southeastern Brazil, are included in the same karyotypic group (Group 4): characterized by 2n = 40 to 52 with a high frequency of metacentric and submetacentric chromosomes (OLIVEIRA et al., 1992). On the other hand, there are also populations of *C. paleatus* with other karyotypic formulas (Table 1). This variation in karyotypes can be attributed to non-Robertsonian chromosomal rearrangements, although centromeric repositioning, which alters the chromosomal morphology without any chromosomal rearrangement (ROCCHI et al., 2012), may be an alternative pathway acting in the remodeling of karyotypes from the group.

Chromosomal rearrangements and variations in DNA content were very important in *Corydoras* evolutionary history. Karyotypes from Group 4, to which *C. paleatus* belongs, possibly originated from an ancestor belonging to Groups 2 or 3 by polyploidization followed by a reduction in the DNA content, as well as in the diploid number (as a result of end-to-end fusions). While Group 2 contains species with 2n = 74 to 102 and a prevalence of acrocentric chromosomes, Group 3 includes species with 2n = 56 to 60 and a high frequency of metacentric and submetacentric chromosomes. Species in Group 4 have approximately twice the DNA content of species belonging to Group 2 but with half the diploid number (OLIVEIRA et al., 1992).

The C-banding revealed, in addition to centromeric bands, conspicuous pericentromeric heterochromatic blocks on metacentric pairs 4 and 8 and submetacentric pairs 10 and 13 (Figure 1B). This pattern, in which constitutive heterochromatin in some pairs is amplified from pericentromeric regions to proximal regions in short or long arms, also represents a peculiarity of *Corydoras* karyotype Group 4 (OLIVEIRA et al., 1992). Differences in the amount and location of these heterochromatic blocks in karyotypes have been considered a population marker for *C. paleatus* (OLIVEIRA et al., 1993; SHIMABUKURO-DIAS et al., 2004; ARTONI et al., 2006; BARBOSA et al., 2017), highlighting the role of heterochromatin in karyotype differentiation, and its potential contribution as a component in the chromosomal evolution of the group. Heterochromatin, normally rich in repetitive sequences, can through deletion and amplification events, not only promote

differences in genome size (BOSCO et al., 2007; NOLETO et al., 2009), but can also play an important role in speciation and/or adaptation. As genomic changes are likely to be under selective pressures, if an optimal karyotypic organization confers an adaptive advantage to its carriers in a given environment, it may spread and eventually become established in a population (KIRKPATRICK; BARTON, 2006; HOOPER; PRICE, 2015; MARTINEZ et al., 2015), especially in *Corydoras* given its wide geographic distribution (all of South America).

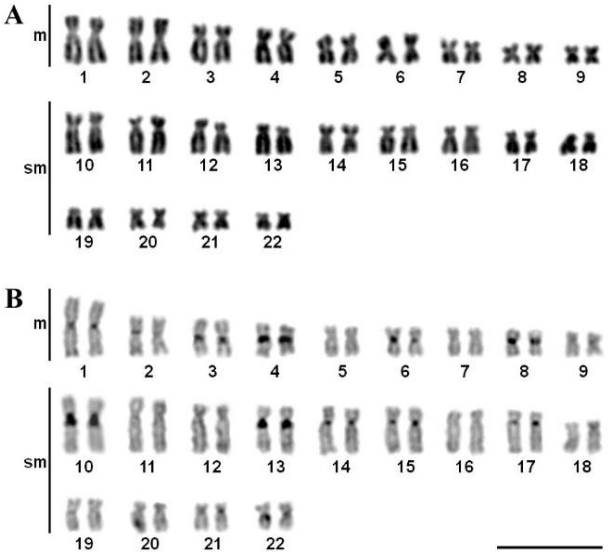

Figure 1. Karyotypes of *C. paleatus* arranged from (A) Giemsa stained and (B) C-banding, respectively. Bar = 10 μm.

Ribosomal DNA sequences in Corydoras

FISH with rDNA probes can detect the true number of rDNA 45S *loci*, regardless of their gene expression. This technique showed the 45S rDNA sites in the terminal region of the long arm of metacentric pair 5 (Figure 2). The simple pattern (a single pair of 45S rDNA-bearing chromosomes) in the terminal location is considered the ancestral condition for the Siluriformes (OLIVEIRA; GOSZTONYI, 2000). Such location is found in 100% of the species/populations of *Corydoras* already karyotypically studied, and may also be in short arms and at multiple *loci* (see Table 1). The variation in the number and location of rDNA sites is due to their organization into long repetitive sequences in tandem and their high transcription activity, which makes them hot spots for chromosomal rearrangements (POTAPOVA; GERTON, 2019; WARMERDAM; WOLTHUIS, 2019). Additionally, rDNA dynamics have also been correlated with transposable element activity and polyploidization followed by loss of DNA sequences (MONDIN; AGUIAR-PERECIN, 2011; BARROS et al. 2017; WARMERDAM; WOLTHUIS, 2019). In fact, the polyploidy characteristic of *Corydoras* species of Group 4, increased the number of 45S rDNA sites, however, in some species, there were losses of sites after polyploidization.

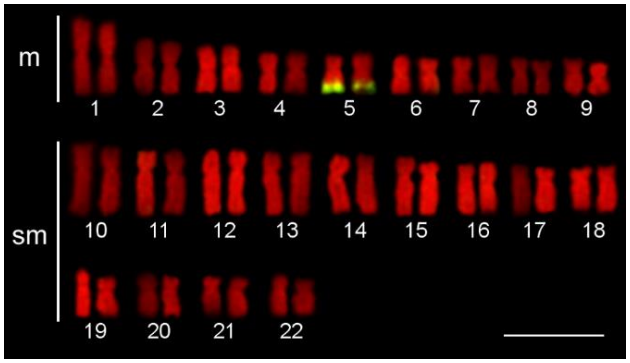

Figure 2. Karyotype of the *C. paleatus* subjected to FISH with 18S rDNA probes (yellow). Bar = 10 μm.

On the other hand, while the 45S rDNA sites show numerical variation and positional conservation, the 5S rDNA sites are conserved in number, but the location varies between terminal and proximal regions of the chromosomes (Table 1). This contrasting scenario is thought to be caused by the functional differences between the 45S and 5S rDNAs, which are a result of their location in different chromosomal compartments, leading them to undergo different evolutionary processes (MANTOVANI et al., 2005).

The location of 45S and 5S rDNA sites on distinct chromosomes is the most common condition in vertebrates (GORNUNG, 2013), indicating independent evolution of these multigene families. In *Corydoras*, although this is the most frequent pattern, the location on the same chromosome of the two multigene rDNA families was observed in *C. ehrhardti* (in different positions) and in *C. carlae* (in co-location) (see Table 1).

Table 1. Summary of the chromosome findings for *Corydoras* species: (2n) diploid number, (m) metacentric, (sm) submetacentric, (st) subtelocentric, (a) acrocentric, 45S = number and location of 45S rDNA sites, 5S = number and location 5S rDNA sites.

Species	Locality	2n	Karyotypic Formula				rDNA locus		Reference
			m	sm	st	a	45S	5S	
C. britskii	Corumbá, Mato Grosso do Sul	90	4	14	22	54	? ?	?	Takagui et al. (2014)
C. carlae	Pinhal de São Bento, Paraná	46	22	22	2		6	6	Rocha et al. (2016)
C. ehrhardti	Jaraguá do Sul, Santa Catarina	44	18	26			4 7	-	Oliveira et al. (1993)
C. ehrhardti	Ponta Grossa, Paraná	44	18	26			?	-	Artoni et al. (2006)
C. ehrhardti	Ponta Grossa, Paraná	44	18	26			3	3	Barbosa et al. (2017)
C. lacrimostigmata	Prudentópolis, Paraná	58	22	36			20 25	4	Barbosa et al. (2017)
C. nattereri	Morretes, Paraná	44	18	26			7	-	Oliveira et al. (1993)
C. paleatus	Rio Grande, Rio Grande do Sul	44	22	22			5 9	-	Oliveira et al. (1993)
C. paleatus	São Leopoldo, Rio Grande do Sul	44	20	24			8 11	-	Oliveira et al. (1993)
C. paleatus	Curitiba, Paraná	44	20	24			4 8 11	-	Oliveira et al. (1993)

Table 1 (cont.). Summary of the chromosome findings for *Corydoras* species: (2n) diploid number, (m) metacentric, (sm) submetacentric, (st) subtelocentric, (a) acrocentric, 45S = number and location of 45S rDNA sites, 5S = number and location 5S rDNA sites.

C. paleatus	Ponta Grossa, Paraná	44	18	26			? ?	-	Artoni et al. (2006)
C. paleatus	Ponta Grossa, Paraná	44	18	26			5	12	Barbosa et al. (2017)
C. paleatus	São Mateus, Paraná	44	18	26			5 11	20	Barbosa et al. (2017)
C. paleatus	Curitiba, Paraná	44	18	26			5	-	Present study
C. sodalis	Aquário	74	16	18	10	30	27	-	Shimabukuro-Dias et al. (2004)

In the latter, since the hybridization signals apparently overlap, the two rDNA classes can exhibit adjacent or intercalated arrangements. In terms of functional activity, the association of the two gene families on the same chromosomal segment is possible, since they are transcribed by different machinery and possibly from different DNA strands: the 5S rRNA gene is transcribed by RNA polymerase III in the opposite direction to the synthesis of the pré-45S rRNA by RNA polymerase I (DROUIN, 1999; DAVIDIAN et al., 2022; DYOMIN et al., 2023).

FINAL REMARKS

The data from the current study, when compared to those of other *Corydoras* species and populations, support a scenario of karyotypic diversification, in which rearrangements shaped and became fixed in karyotypes of different species and/or populations, as a result of vicariant events that occurred in the different hydrographic basins, which disrupted gene flow (WEITZMAN et al., 1988). The genus *Corydoras* is shown as a group in which many questions have not yet been clarified. New cytogenetic patterns tend to emerge, mainly involving different populations, and provide evidence for novel interpretations regarding the chromosomal evolution of the group. Complementary approaches, mainly the mapping of some classes of repetitive DNAs, will allow access to the molecular composition of the heterochromatic portion of the genomes, and thus clarify dynamic processes related to the karyotypic diversification of this group of fish.

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