

KARYOTYPE EVOLUTION IN CURIMATIDAE (TELEOSTEI, CHARACIFORMES) OF THE AMAZON REGION. I. STUDIES ON THE GENERA *Curimata*, *Psectrogaster*, *Steindachnerina* AND *Curimatella*

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ABSTRACT

Cytogenetic studies were carried out on nine species of fish belonging to four genera of the family Curimatidae (*Curimata ocellata*, *C. vittata*, *C. kneri*, *C. cyprinoides*, *C. inornata*, *Psectrogaster rutiloides*, *Steindachnerina leuciscus*, *Curimatella alburna* and *Curimatella meyeri*). All species were collected from the central Amazon basin. *C. ocellata* presented $2n=56$, whereas all other species presented $2n=54$ chromosomes. With respect to the NORs patterns, only one nucleolar chromosome pair was detected for each of the species, except for *C. vittata*, which presented only one silver-stained chromosome. There was obvious interspecific diversity with respect to NORs localization and position in the karyotype, suggesting the occurrence of rearrangements (translocations and/or transpositions).

INTRODUCTION

In vertebrates some groups present wide karyotypic diversity, as already observed by the analysis of chromosome number and shape in rodents (Matthey, 1973; Yonenaga *et al.*, 1976).

In other groups, however, such as some bats (Baker and Bickham, 1980), turtles (Bickham *et al.*, 1983), whales (Arnason, 1972) and felids (Matthey, 1973), the

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karyotypic structure has generally remained constant during the evolutionary process, even at the banding level.

There are other vertebrate groups in which karyotype conservation occurs only at the level of chromosome macrostructure (chromosome number and shape). However, when more accurate cytogenetic techniques are employed, the karyotypes are found to be not so conservative. Thus, it has been suggested that chromosome rearrangements of the non-Robertsonian type (inversions, duplications, deletions and translocations), may have played a highly significant evolutionary role in these groups, permitting the diploid number and often even the number of arms to remain constant, but with an almost constant occurrence of variation in the position of centromere, bands and nucleolar organizer region. This phenomenon also occurs in fish.

In fish there are families in which the diploid number is constant in many species, such as those of the family Cichlidae, in which a diploid number of 48 chromosomes, preferentially of the subtelocentric-acrocentric type (ST-A) has been detected in most of the neotropical species analyzed thus far, suggesting *a priori* a trend to chromosome evolution of the more conservative type (Kirpichnikov, 1973; Gold, 1979; Feldberg and Bertollo, 1985a).

The families Anostomidae, Prochilodontidae, Curimatidae, Chilodontidae, Parodontidae and Hemiodontidae present very similar chromosome numbers and morphology (Scheel, 1973; Galetti Jr. *et al.*, 1981, 1984; Pauls and Bertollo, 1983; Moreira-Filho, 1983; Pauls, 1985; Feldberg *et al.*, 1987; Porto and Feldberg, 1988; Venere and Galetti Jr., 1989; Cestari *et al.*, 1990). The diploid number detected for all the species analyzed thus far is $2n=54$ chromosomes, with a fundamental number close or equal to 108. However, a more detailed analysis shows the existence of sex chromosome differentiation, NOR transposition and species-specific heterochromatin patterns, clearly demonstrating that evolutionary divergences have occurred in several species, which were not necessarily accompanied by major changes in karyotype macrostructure.

Approximately 120 species currently make up the family Curimatidae which is found in Southern Central America and throughout South America. The greatest diversity of species is in the Amazon basin (Vari, 1989). This family was investigated in our study.

When young, the curimatid fish have conical teeth, but as adults they are toothless. They feed on slime, especially algae and detritus, and are known as either detritivorous or iliophagous fish. They play a very important role in the flow of energy and nutrient cycling within the ecosystem (Bowen, 1984; Araujo-Lima *et al.*, 1986; Vari, 1989).

At some sites within the Amazon region, these animals represent the main components of the fish fauna and are important in commercial and subsistence fishing (Lowe-McConnell, 1975; Géry, 1977; Vari, 1983a).

Few cytogenetic studies on species of the Curimatidae have been done. Scheel (1973) determined the haploid number of two species. Venere and Galetti Jr. (1989) described the karyotype and the nucleolar organizer regions (NORs) of 10 species from different hydrographic basins. The present study describes the karyotype structure and NORs of nine species of Amazonian curimatids, and includes a discussion of the possible chromosome evolution of the group.

MATERIAL AND METHODS

The study was conducted on nine species of fish belonging to the family Curimatidae. They were collected in the Amazon basin in the region of the confluence of the Negro and Solimões rivers (lago Catalão), in the Solimões/Amazonas rivers (lago Camaleão and lago do Rei) and in two locations in the Uatumã river (a tributary of the left bank of the Amazonas river), at the confluence with the Jatapu river, and in the region of the Balbina hydroelectric dam (Figure 1).

The species studied were: *Curimata ocellata* Eigenmann and Eigenmann, *C. vittata* Kner, *C. kneri* Steindachner, *C. cyprinoides* Linnaeus, *C. inornata* Vari, *Psectrogaster rutiloides* Eigenmann and Eigenmann, *Steindachnerina leuciscus* Gunther, *Curimatella alburna* Eigenmann and Eigenmann and *C. meyeri* Steindachner.

Chromosome preparations were obtained from kidney cell suspensions using the air-drying technique of Bertollo *et al.* (1978), and the nucleolar organizer regions (NORs) were identified by the silver-staining method of Howell and Black (1980).

For a better visualization of the gradient of variation in chromosome size, morphometric analyses were performed: measurement of total length (TL) and relative length (RL%) of each chromosome pair in relation to the length of the haploid lot. The data were then grouped into relative size classes and the chromosome frequency for each class size was determined for each species. Chromosome types were divided into metacentrics (M), submetacentrics (SM) and subtelocentrics (ST), and all of them were considered to be biarmed chromosomes.

RESULTS

In Table I we present the karyotypic characteristics of the species analyzed. They all presented $2n=54$ chromosomes and $FN=108$, except for *C. ocellata* which presented $2n=56$ and $FN=112$. All karyotypes consisted of M-SM chromosomes, with only *C. kneri* presenting one ST pair (Figures 2 through 5).

No sex differences were detected in those species in which it was possible to perform this analysis.

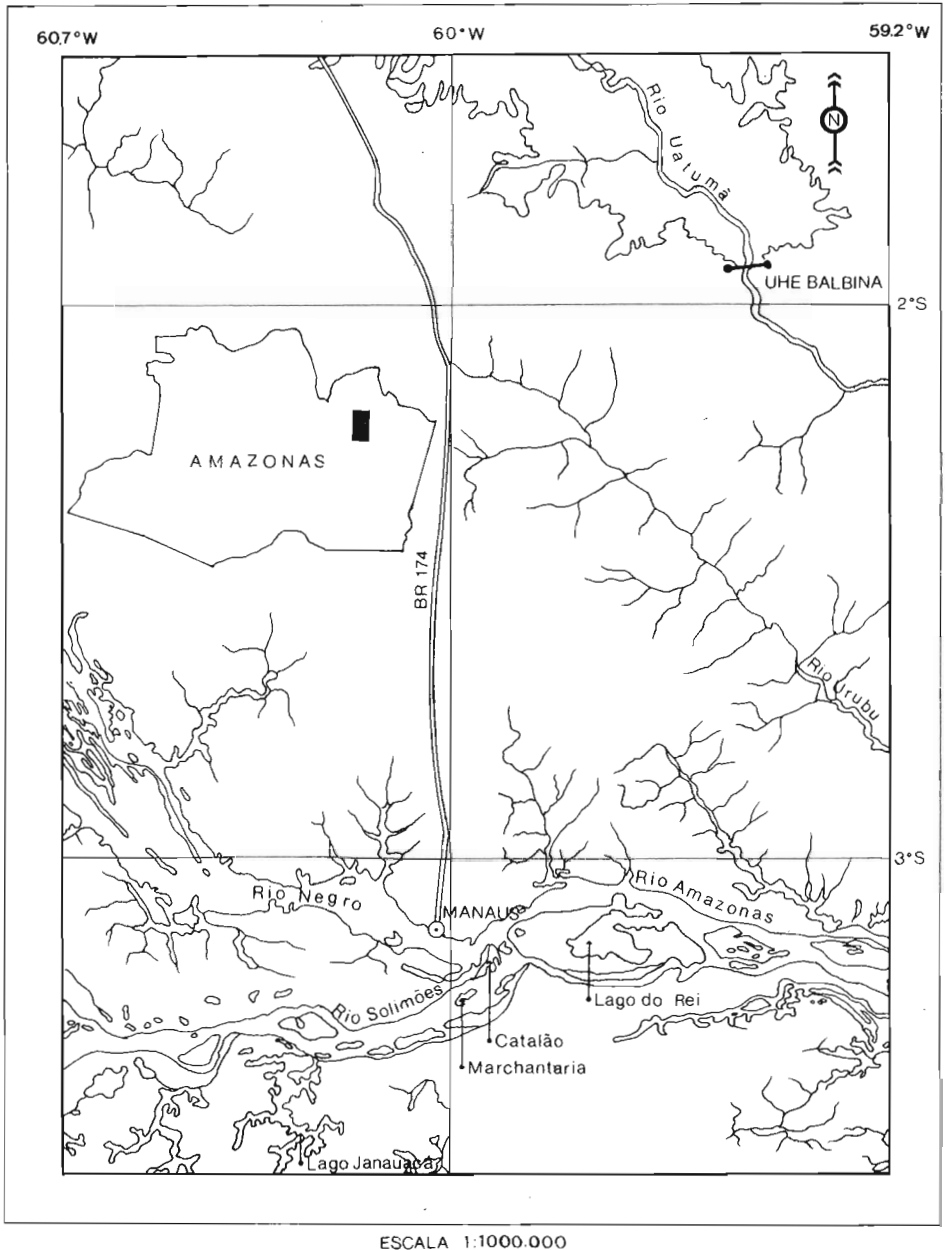


Figure 1 - Collection sites of the species studied in the Amazon basin.

Table I - Karyotypic characteristics of the species studied.

Species	No. of specimens		No. of cells		Chromosome types					NORs localization			
	Males	Females	Males	Females	2n	FN	M	SM	ST	A	Pair	Position	Arm
	<i>Curimata ocellata</i>	0	01	0	30	56	112	40	16	-	-	26° SM	Interst.
<i>C. vittata</i>	03	06	84	143	54	108	42	12	-	-	9° SM	Terminal	LA
<i>C. kneri</i>	05	05	154	131	54	108	40	12	02	-	27° ST	Terminal	SA
<i>C. cyprinoides</i>	01	01	66	106	54	108	44	10	-	-	3° M	Terminal	LA
<i>C. inornata</i>	01	07	04	136	54	108	40	14	-	-	21° SM	Interst.	SA
<i>Psectrogaster nutiloides</i>	06	12	148	569	54	108	42	12	-	-	9° M	Terminal	LA
<i>Steindachnerina leuciscus</i>	0	02	0	49	54	108	48	06	-	-	15° M	Terminal	SA
<i>Curimatella alburna</i>	01	0	55	0	54	108	46	08	-	-	14° M	Terminal	LA
<i>Curimatella meyeri</i>	01	08	11	193	54	108	46	08	-	-	9° M	Terminal	LA

(2n) diploid number; (FN) fundamental number; (M) metacentric; (SM) submetacentric; (ST) subtelocentric; (A) acrocentric; (SA) short arm; (LA) long arm.

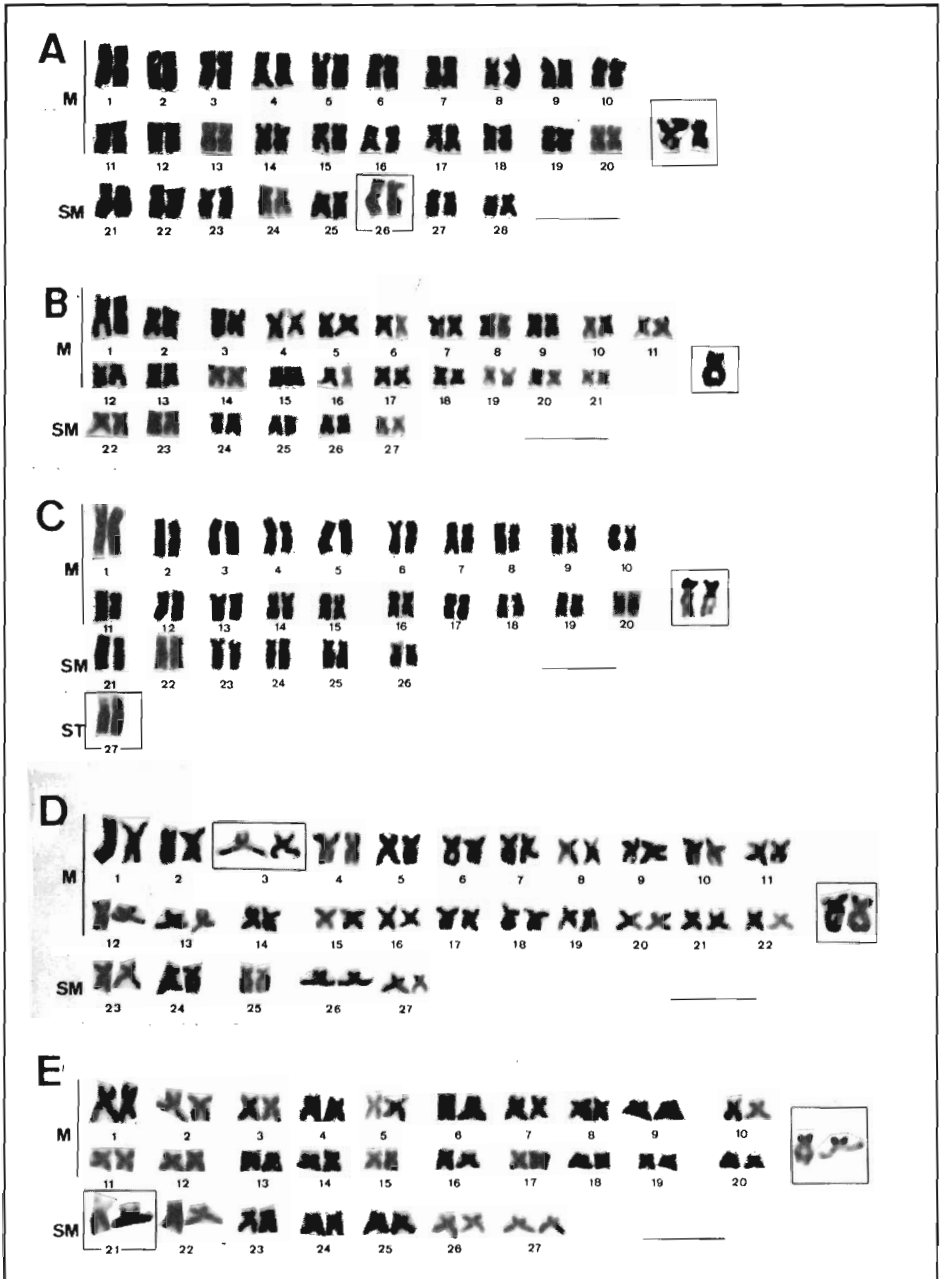


Figure 2 - Karyotype and nucleolar chromosomes of (A) *Curimata ocellata*, (B) *C. vittata*, (C) *C. kneri*, (D) *C. cyprinoides* and (E) *C. inornata*. (Bar = 10 μ m).

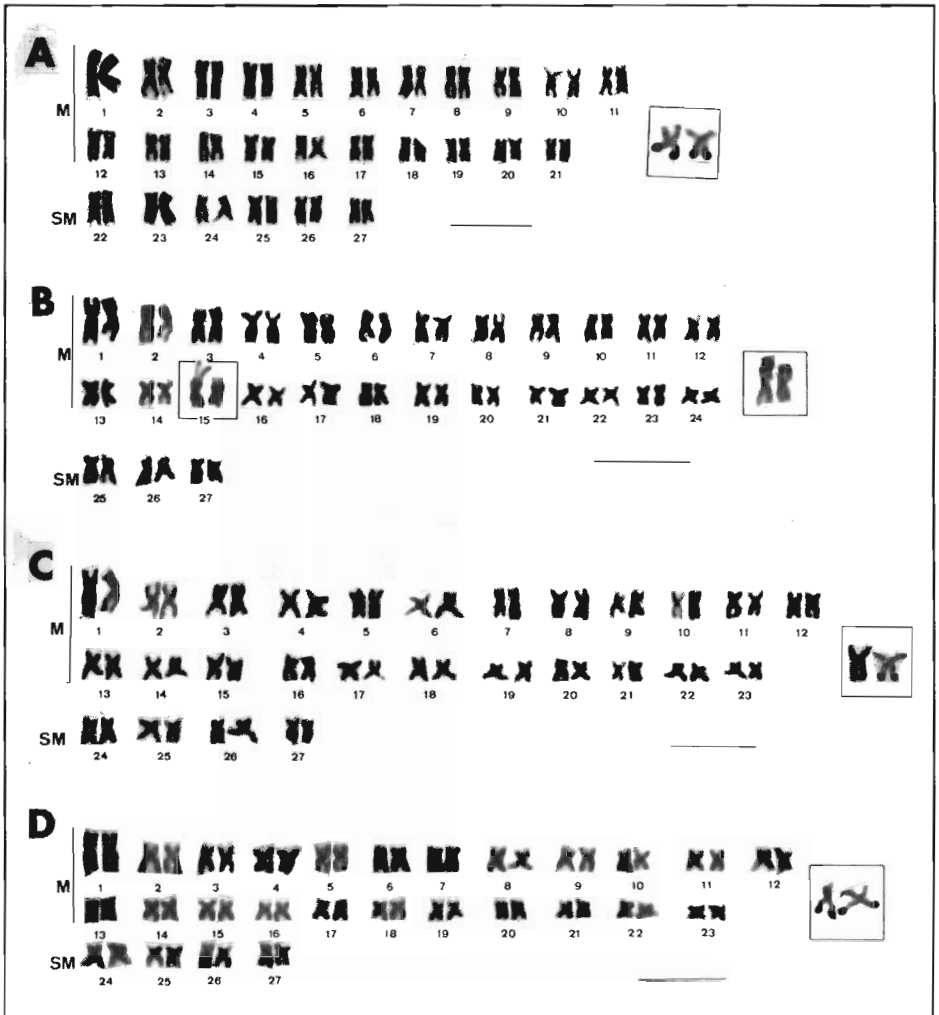


Figure 3 - Karyotype and nucleolar chromosomes of (A) *Psectrogaster rutiloides*, (B) *Steindachnerina leuciscus*, (C) *Curimatella alburna* and (D) *C. meyeri*. (Bar = 10 μ m).

All species had only one NOR-bearing pair per complement, except for *C. vittata* which presented only one NOR-bearing chromosome. However, the NORs were located on different chromosomes and at different positions (Figure 6). Secondary constrictions, visible by standard staining, coincided with silver-stained regions, as observed in Figures 2 and 3.

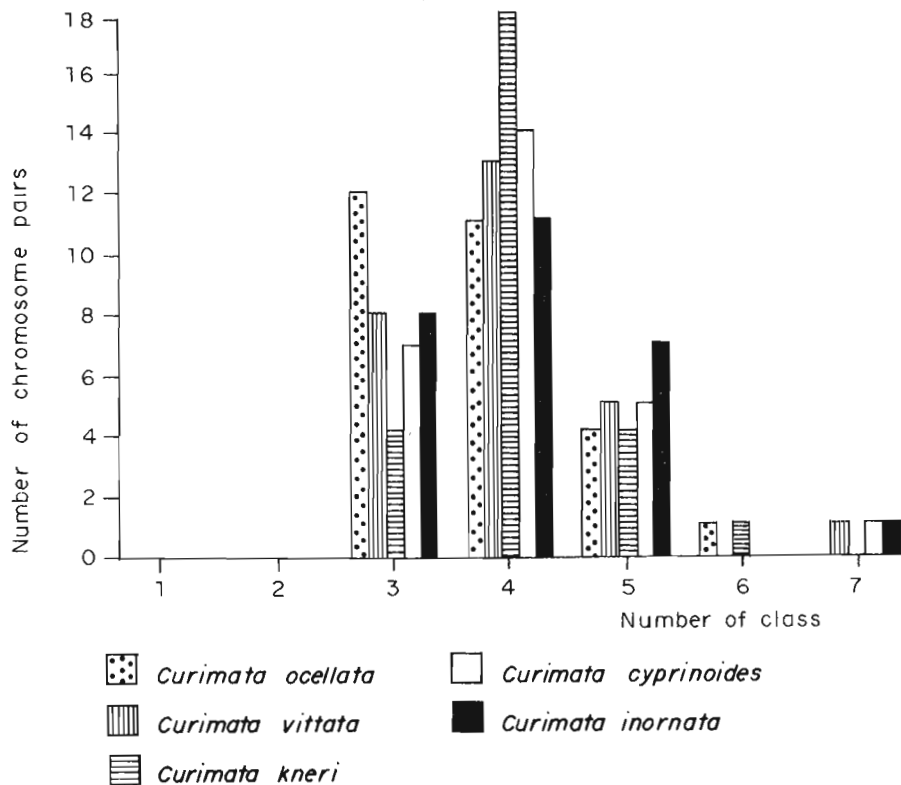


Figure 4 - Chromosome frequency for the species of the genus *Curimata* analyzed. The chromosomes are distributed by relative size class (% of the haploid set).

DISCUSSION

Evolution of chromosome macrostructure in Curimatidae

According to the phylogenetic analysis proposed by Vari (1983b), Prochilodontidae, Curimatidae, Anostomidae and Chilodontidae can be regarded as closely related monophyletic units because of the synapomorphic characters that they share.

Karyotypically, almost all of the species analyzed thus far in these families present $2n=54$ chromosomes and $FN=108$ (Hinegardner and Rosen, 1972; Scheel, 1973;

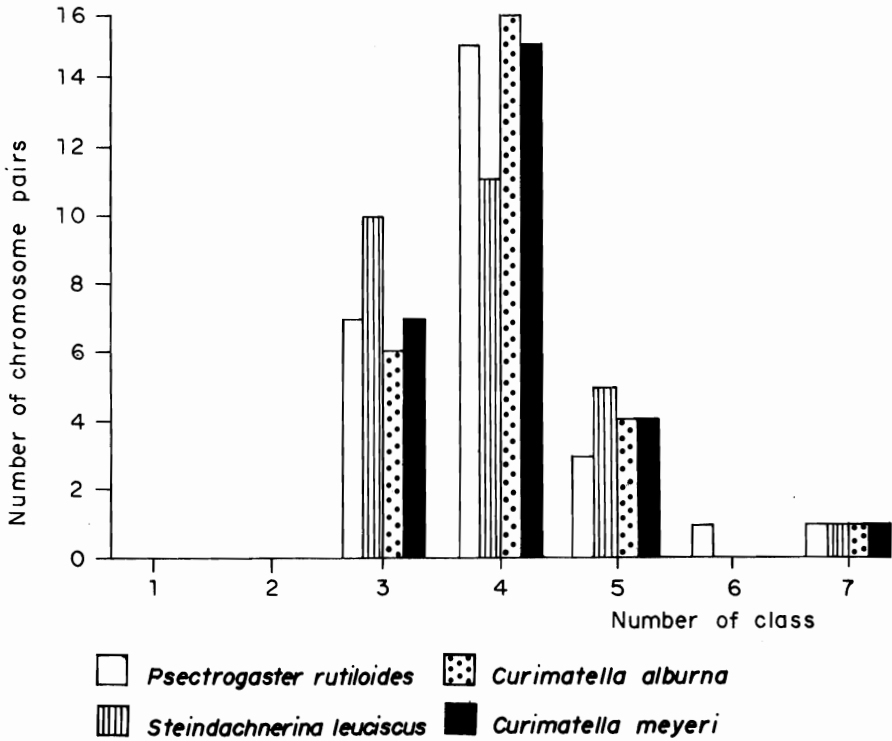


Figure 5 - Chromosome frequency of the species of the genera *Psectrogaster*, *Steindachnerina* and *Curimatella*. The chromosomes are distributed by relative size class (% of the haploid set).

Ojima *et al.*, 1976; Bertollo *et al.*, 1980; Galetti Jr. *et al.*, 1984; Venere and Galetti Jr., 1989; Cestari *et al.*, 1990), which strengthens the hypothesis proposed by Vari (1983b).

On the basis of data from the literature and the present results, we suggest that the $2n=54$ chromosomes of the M-SM type are the ancestral karyotype of the family Curimatidae, and variations from this condition represent derived characters.

Thus, in the genus *Curimata* we find one species (*C. ocellata* with $2n=56$ chromosomes) which we believe to have undergone karyotype evolution by centric fission in a given chromosome pair. Also, pericentric inversions or even another rearrangement probably occurred in this species, which maintained the karyotypic structure consisting only of M-SM chromosomes and a larger number of arms. The remaining species in this genus maintained $2n=54$ and $FN=108$, although with different

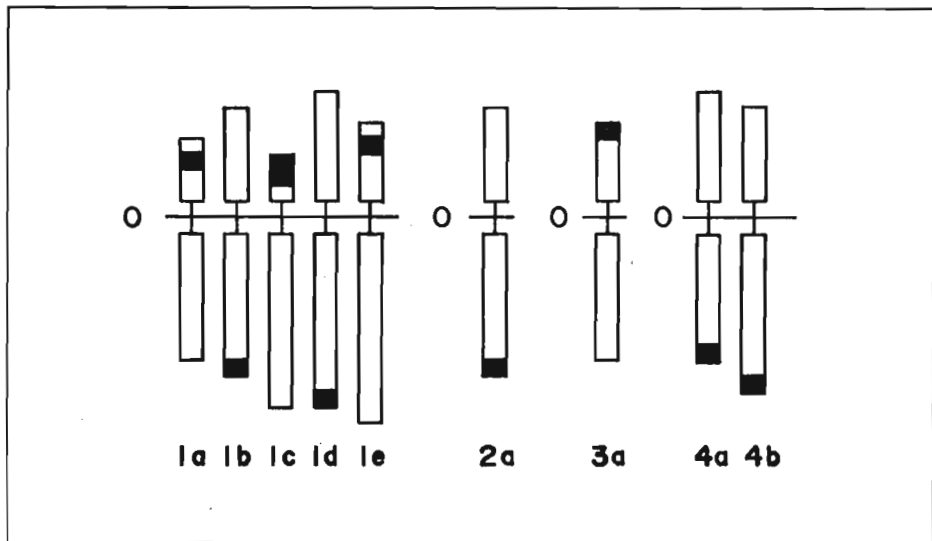


Figure 6 - Chromosome phenotypes of the NORs of the species analyzed: (1a) *Curimata ocellata*, (1b) *C. vittata*, (1c) *C. kneri*, (1d) *C. cyprinoideas*, (1e) *C. inornata*, (2a) *Psectrogaster rutiloides*, (3a) *Steindachnerina leuciscus*, (4a) *Curimatella alburna*, and (4b) *C. meyeri*. Idiogram based on the relative length of the nucleolar organizer pair.

karyotype formulae and different distributions of chromosome pairs by size class (Figures 2 and 4).

In the genus *Curimata* we also noted that the karyotype formulae of *C. vittata* (42M+12SM) and *C. cyprinoideas* (44M+10SM), and the 1st and 2nd chromosome pairs in the complement, showed great karyotype similarity. In turn, *C. kneri* (40M+12SM+2ST) and *C. inornata* (40M+14SM) also show karyotypic affinity. These observations are somewhat in contrast to the phylogenetic hypothesis proposed by Vari (1989) for the genus *Curimata*, in which *C. kneri* is closely related to *C. cyprinoideas*. However, our results only indicate interspecific karyotype similarities and they are not being used to polarize the characters in order to establish phylogenies.

The other curimatid species analyzed in the present study, presented $2n=54/FN=108$, although karyotype formulae were different: *Psectrogaster rutiloides* (42M+12SM), *Steindachnerina leuciscus* (48M+6SM), *Curimatella alburna* (46M+8SM) and *Curimatella meyeri* (46M+8SM) (Figure 3). The chromosome distribution by size class is species-specific (Figure 5). For these species, we suggest a karyotype evolution based on non-Robertsonian rearrangements, possibly inversions or

even translocations, which did not modify the chromosome number but modified chromosome morphology.

In a study of 10 other curimatid species, Venere and Galetti Jr. (1989), detected the maintenance of a karyotype structure with $2n=54$ chromosomes of the M-SM type, suggesting a low evolutionary rate in the chromosome macrostructure of this group.

These data, taken together with those presented here show a tendency for maintenance of the karyotype macrostructure in Curimatidae. However, more pronounced karyotype rearrangements have also occurred during the evolutionary history of this group as observed in the genera *Potamorhina* (Feldberg *et al.*, in preparation), *Curimatopsis* (Scheel, 1973) and *Steindachnerina* (Rocha and Giuliano-Caetano, 1990).

The NORs patterns of Curimatidae

For a long time the study of fish NORs was limited to a few isolated and not systematically related species, which prevented the evaluation of the potential of the technique as a tool for the analysis of related groups.

In many fish groups, such as Parodontidae (Moreira-Filho *et al.*, 1984), Hemiodontidae (Porto and Feldberg, 1988), Prochilodontidae (Pauls and Bertollo, 1983; Pauls, 1985; Feldberg *et al.*, 1987), Cichlidae (Feldberg and Bertollo, 1985b) and Salmininae (Marco, 1986), this technique has not provided much clarification in cytotaxonomic studies, because in the species thus far analyzed, the NORs are located on corresponding chromosomes.

However, this is not the case for other groups of fish such as the Cyprinidae (Gold, 1984; Amemiya and Gold, 1986, 1988), Anostomidae (Galetti Jr. *et al.*, 1984), Tetragonopterinae (Portela *et al.*, 1988) and Triportheinae (Falcão, 1988), in which NOR studies have been used as an excellent additional tool for the characterization of species.

In this study, all the species presented only one pair of homologues responsible for nucleolar organization, as detected in species of the Prochilodontidae, Curimatidae, Anostomidae and Chilodontidae. However, there was interspecific diversity in NOR position and localization in the karyotypes (Table I and Figures 2, 3 and 6). In addition to this diversity, *C. vittata* presented only one of the homologues with a NOR, whereas in most interphase nuclei two silver-stained nucleoli were visible. This may be a case of variation in the transcriptional activity of rDNA cistrons, which is determined by the protein needs of the cell, when one homologue or the other may be active. This has been detected in *Leporinus reinhardti* (Galetti Jr., 1984) and in *Chaetobranchopsis australe* (Feldberg and Bertollo, 1985b).

Using NORs as characters for interspecific relationships in the genus *Curimata*, we noted that *C. ocellata*, *C. kneri* and *C. inornata* presented the NOR on the short arm, with small differences in localization, probably as a result of chromosome

rearrangements. The other two species, *C. vittata* and *C. cyprinoides*, also showed similarities with respect to this character, with a terminal NOR on the long arm of a large metacentric. These phenotypes must have become established in *Curimata* through rearrangements involving the NOR and the changing of its position, possibly by translocation or even transposition.

The NOR patterns of *P. rutiloides*, *Curimatella alburna* and *C. meyeri* are also similar, with the NORs occurring in the terminal portion of the long arm of a medium-sized pair of metacentric chromosomes. In contrast, *Steindachnerina leuciscus* presents a phenotype different from these, but similar to that of species of the same genus, *S. insculpta* and *S. elegans* (Venere and Galetti Jr., 1989).

The data available thus far permit us to infer that, although most Curimatidae species present $2n=54$ M-SM chromosomes, Robertsonian and non-Robertsonian rearrangements have occurred in their karyotype evolution. This leads to different karyotype formulae and to distinct chromosome distributions by size class and to different positions. However, despite the tendency for conservation of a similar chromosome macrostructure ($2n=54/M-SM$) in most species, variation in this chromosome number can occur, as is the case for *C. ocellata* (present paper), *Curimatopsis* sp (Scheel, 1973), *Steindachnerina* sp. (Rocha and Giuliano-Caetano, 1990), *Potamorhina altamazonica* and *P. latior* (Feldberg *et al.*, in preparation).

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RESUMO

Foram realizados estudos citogenéticos em 9 espécies pertencentes a 4 gêneros da família Curimatidae (*Curimata ocellata*, *C. vittata*, *C. kneri*, *C. cyprinoides*, *C. inornata*, *Psectrogaster rutiloides*, *Steindachnerina leuciscus*, *Curimatella alburna* e *Curimatella meyeri*). Todas as espécies estudadas foram coletadas na bacia amazônica central. *Curimata ocellata* apresentou $2n=56$ sendo que as demais apresentaram $2n=54$ cromossomos a exemplo de outras famílias de Characiformes. Quanto ao padrão de NORs, apenas um par cromossômico nucleolar foi detectado para todas as espécies, com exceção de *C. vittata* que apresentou só um cromossomo marcado pela prata. Diversidade interespecífica quanto à localização e posição da NOR no cariótipo foi evidente, sugerindo que rearranjos (translocação e/ou transposição) ocorreram.

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