B microchromosomes in the family Curimatidae (Characiformes): mitotic and meiotic behavior

Tatiane Ramos Sampaio¹, Waleska Gravena², Juceli Gonzalez Gouveia¹, Lucia Giuliano-Caetano¹, Ana Lúcia Dias¹

¹ Laboratório de Citogenética Animal, Centro de Ciências Biológicas, Departamento de Biologia Geral, CCB, Universidade Estadual de Londrina, Rodovia Celso Garcia Cid, PR 445, Km 380, CEP 86051-970, P.O. Box 6001, Londrina, Paraná, Brasil. ² Laboratório de Evolução e Genética Animal, Instituto de Ciências Biológicas, Universidade Federal do Amazonas, Av. General Rodrigo Otávio, n.3000, Japiim II CEP 69070-000 Manaus, Amazonas, Brasil

Corresponding author: Ana Lúcia Dias (anadias@uel.br)

Academic editor: S. Grozeva | Received 2 June 2011 | Accepted 20 September 2011 | Published 9 November 2011

Citation: Sampaio TR, Gravena W, Gouveia JG, Giuliano-Caetano L, Dias AL (2011) B microchromosomes in the family Curimatidae (Characiformes): mitotic and meiotic behavior. Comparative Cytogenetics 5(4): 301–313. doi: 10.3897/CompCytogen.v5i4.1650

Abstract
In the present work, six curimatid species were analyzed: Cyphocharax voga (Hensel, 1870), C. spilotus (Vari, 1987), C. saladensis (Meinken, 1933), C. modestus (Fernández-Yépez, 1948), Steindachnerina biornata (Braga & Azepecueta, 1987) and S. insculpta (Fernández-Yépez, 1948) collected from two hydrographic basins. All samples presented 2n=54 meta-submetacentric (m-sm) chromosomes and FN equal to 108, and 1 or 2 B microchromosomes in the mitotic and meiotic cells of the six sampled populations showing inter-and intraindividual variation. The analysis of the meiotic cells in C. saladensis, C. spilotus, and C. voga showed a modal number of 54 chromosomes in the spermatogonial metaphases and 27 bivalents in the pachytene, diplotene, diakinesis and in metaphase I stages, and 27 chromosomes in metaphase II; in C. modestus, S. biornata, and S. insculpta spermatogonial metaphases with 54 chromosomes and pachytene and metaphase I with 27 bivalents were observed. The B microchromosome was observed as univalent in the spermatogonial metaphase of C. spilotus, in the pachytene stage in the other species, with the exception of C. saladensis, and S. biornata in metaphase I. New occurrences of the B microchromosome in C. voga, C. saladensis and S. biornata were observed, confirming that the presence of this type of chromosome is a striking characteristic of this group of fish.

Keywords
B microchromosome, meiosis, curimatids
Introduction

B chromosomes, also known as supernumerary or accessory chromosomes, are additional dispensable chromosomes present in some individuals of some populations in some species. They have probably originated from the A complement, but followed their own evolutionary paths, being found in different groups of both animals and plants (Camacho et al. 2000).

The irregular behavior of this chromosome type in mitosis and in meiosis causes it to accumulate selfishly in the germ line of many species, producing a non-Mendelian segregation with transmission rates higher than those yielded by the chromosomes of the A complement (Camacho et al. 2000). B chromosomes present in an individual can exhibit a parasitic, neutral or beneficial behavior (Jones and Rees 1982).

In freshwater Neotropical fish, the occurrence of B chromosomes has been reported in 61 species, distributed in 16 families of seven different orders and in distinct hydrographic basins, according with the revision accomplished by Carvalho et al. (2008). The order Characiformes possesses the majority of the species bearing B chromosomes, including 31 species of six different families: Anostomidae, Characidae, Crenuchidae, Curimatidae, Parodontidae and Prochilodontidae.

The first work to record the presence of the B chromosome in the family Curimatidae was carried out by Venere and Galetti (1985) in an individual of *Cyphocharax modestus* (Fernández-Yépez, 1948) collected from the Tiete River, municipality of Águas de São Pedro/SP, which proved to be entirely heterochromatic. Since then, other populations of *Cyphocharax modestus* and other species, such as *Cyphocharax spilotus* (Vari, 1987), *Cyphocharax gouldingi* Vari, 1992 and *Steindachnerina insculpta* (Fernández-Yépez, 1948) have shown the presence of this extra chromosome (Gravena et al. 2007; Venere et al. 2008).

The current study examines the frequency, behavior and distribution of B microchromosomes in mitotic and meiotic cells in six fish species of the family Curimatidae from two hydrographic basins.

Material and methods

Six species of the family Curimatidae were analysed: *Cyphocharax voga* (Hensel, 1870), *C. spilotus* (Vari, 1987), *C. saladensis* (Meinken, 1933), *C. modestus* (Fernández-Yépez, 1948), *Steindachnerina biornata* (Braga & Azpelicueta, 1987) and *S. insculpta* (Fernández-Yépez, 1948), collected from the Laguna dos Patos Hydrographic System/RS and Paranapanema River basin/SP/PR (Fig. 1, Table 1). Voucher specimens are catalogued in the Zoology Museum of the Universidade Estadual de Londrina, Paraná state, under catalog numbers: MZUEL 5105 – *Cyphocharax voga*; MZUEL 5106 – *C. spilotus*; MZUEL 5058 – *C. saladensis*; MZUEL 1374 – *C. modestus*; MZUEL 5059 – *Steindachnerina biornata* and MZUEL 1042 – *S. insculpta*. 
Mitotic chromosomes were obtained by direct preparation removing the anterior kidney, according to Bertollo et al. (1978) and meiotic chromosomes were obtained using gonadal cells by technique developed by Kligerman and Bloom (1977), with modifications. Chromosomes were characterized as metacentric (m) and submetacentric (sm), according to Levan et al. (1964).

**Results and discussion**

All samples analyzed showed a diploid number of 54 meta-submetacentric chromosomes (m-sm) and a fundamental number (FN) equal to 108 (Fig. 2). This karyotype structure is often found in this fish group, and are conservative among the species of the family Curimatidae, as already observed by Brassesco et al. (2004) and Venere et al. (2008). Among the populations studied, *Cyphocharax voga* and *C. spilotus* collected in Capivara stream/RS and *C. modestus* and *Steindachnerina insculpta* collected in Três Bocas stream/PR are living in sympatry.

*Figure 1.* a Map of Brazil  b Collection sites of Paranapanema River basin: Água dos Patos River in the São Paulo state, Pavão stream, Jacutinga River and Tres Bocas stream in the Parana state c Collection sites of Laguna dos Patos Hydrographic System: Forquetinha River, Saco da Alemoa River, Agronomic Experiment Station of UFRGS’s Dam and Capivara stream in the Rio Grande do Sul state.
One B microchromosome was observed in all populations studied, with variation in the number and frequency among them (Fig. 2). In the species *Cyphocharax voga*, *C. spilotus*, *C. saladensis* and *Steindachnerina biornata* belonging to the Laguna dos Patos Hydrographic System, there was an inter-and intraindividual variation from 0 to 1 B microchromosome in the somatic cells (Table 2). In *Cyphocharax modestus* and *Steindachnerina insculpta*, from the Paranapanema River basin, up to two B microchromosomes, also exhibiting inter-and intraindividual variation, were detected in the somatic cells (Table 3). As proposed by Jones and Rees (1982), these variations among species represent a mitotic instability of this chromosome, probably due to its non-Mendelian behavior during cell division.

Of the total number of somatic cells with B microchromosomes analyzed in six species of Curimatids, there was a variation from 3.3% in *Cyphocharax saladensis* to 15.4% in *Steindachnerina insculpta*. Among the species belonging to the Laguna dos Patos Hydrographic System, *C. voga* showed the highest percentage of B cells (11.1%), followed by *S. biornata* with 8%, *C. spilotus* with 4.8%, and *C. saladensis* with 3.3% (Table 2).

In the Paranapanema River basin, the population of the *Steindachnerina insculpta* from the Pavão stream/PR showed 15.4% of their somatic cells with B microchromosomes, followed by the populations of the Jacutinga River/PR with 10% and Água dos Patos River/SP with 8.6%. The species *Cyphocharax modestus* from the Tres Bocas stream/PR presented 5% of their cells with B microchromosomes (Table 3). The data

### Table 1. Species analysed, collection sites and hydrographic basins.

| Species                  | Number of individuals | Collection sites                                                                 | Basins               |
|--------------------------|-----------------------|----------------------------------------------------------------------------------|----------------------|
| *Cyphocharax voga*       | 1♀, 1♂                | Saco da Alemoa River, Eldorado do Sul, RS, Brazil                               | Laguna dos Patos     |
|                          |                       | S 29°59’15.6", W 51°14’24.1"                                                    | Hydrographic System  |
|                          | 2♀, 9♂                | Capivara stream, Barra do Ribeiro, RS, Brazil                                   |                      |
|                          |                       | S 30°17’33.3", W 51°19’23.6"                                                    |                      |
| *Cyphocharax spilotus*   | 2♀, 3♂                | Capivara stream, Barra do Ribeiro, RS, Brazil                                   |                      |
|                          |                       | S 30°17’33.3", W 51°19’23.6"                                                    |                      |
| *Cyphocharax saladensis* | 1♀, 10♂               | Agronomic Experiment Station of UFRGS’s Dam, Eldorado do Sul, RS, Brazil        |                      |
|                          |                       | S 30°05’36.2", W 51°40’41.8"                                                    |                      |
| *Steindachnerina biornata* | 1♀, 1♂            | Forquetinha River, Canudos do Vale, RS, Brazil                                 |                      |
|                          |                       | S 29°19’20.9", W 50°14’3.6"                                                    |                      |
| *Cyphocharax modestus*   | 2♀, 5♂                | Tres Bocas stream, Londrina, PR, Brazil                                         | Paranapanema River   |
|                          |                       | S 23°17’12.9", W 51°13’58.2"                                                    |                      |
| *Steindachnerina insculpta* | 3♂                  | Tres Bocas stream, Londrina, PR, Brazil                                         |                      |
|                          |                       | S 23°17’12.9", W 51°13’58.2"                                                    |                      |
|                          |                       | Pavão stream, Sertanópolis, PR, Brazil                                          |                      |
|                          | 4♀, 8♂                | Jacutinga River, Londrina, PR, Brazil                                           |                      |
|                          |                       | S 23°23’6.6", W 51°04’35.8"                                                    |                      |
|                          | 1♀, 5♂                | Água dos Patos River, Iepê, SP, Brazil                                          |                      |
|                          |                       | S 22°41’17.7", W 51°05’23.9"                                                   |                      |
collected from both basins corroborate the constant presence of this type of chromosome in the Curimatidae family, constituting a striking characteristic of the group, even when its incidence is low.

Specimens of *Cyphocharax voga* collected at two localities in the Laguna dos Patos Hydrographic System (Saco da Alemoa River and Capivara stream) not presented interpopulation differences in the number and frequency of the Bs. Likewise were not observed significant differences between the four populations of *Steindachnerina insculpta*, belonging to Paranapanema River basin.

The B microchromosome was observed in four species of curimatids collected from different populations: *Cyphocharax gouldingi* (Venere et al. 2008), *C. modestus* (Gravena et al. 2007), *C. spilotus* (Brassesco et al. 2004), *Steindachnerina insculpta* (Gravena et al. 2007), and three new species assessed in this study: *Cyphocharax saladensis, C. voga* and *Steindachnerina biornata*, representing 18.42% of all species studied, always small in size with inter and intra individual variation (Table 4). Among these, *Cyphocharax modestus* and *Steindachnerina insculpta* are the species that possess B microchromosomes in all populations studied, besides being the species that have the widest range of cytogenetic studies to date.
Camacho et al. (2000), reported that differences in the incidence of B chromosomes among populations depend on selection factors (such as relationship between the Bs and the environmental conditions, including temperature and altitude), historical factors (such as number of generations since the origin of Bs in the population or even in the species), transmission factors (in relation to the mechanisms of accumulation), and random factors. These four types of factors, which are likely to act simultaneously,
B microchromosomes in the family...

It makes it difficult to evaluate the action of each one separately, even when a more detailed study of each species occurs.

The analysis of meiotic cells in *Cyphocharax saladensis*, *C. spilotus* and *C. voga* showed a modal number of 54 chromosomes in spermatogonial metaphases and 27 bivalents in the stages of pachytene, diplotene, diakinesis and metaphase I, and 27 chromosomes in metaphase II (Fig. 3). In *Cyphocharax modestus*, *Steindachnerina biornata* and *S. insculpta*, spermatogonial metaphases with 54 chromosomes and pachytene and

| Species                     | Locality            | Specimens | Sex | Number of B chromosome | Total number of cells |
|-----------------------------|---------------------|-----------|-----|------------------------|----------------------|
| *Cyphocharax modestus*      | Tres Bocas stream   | 2656      | ♂   | 5 0 0                  | 5                    |
|                             |                     | 3815      | ♂   | 18 0 0                 | 18                   |
|                             |                     | 3909      | ♀   | 8 0 0                  | 8                    |
|                             |                     | 3992      | ♀   | 46 3 1                 | 50                   |
|                             | Total               |           |     | 77 3 1                 | 81                   |
|                             | %                   |           |     | 95 3,75 1,25           |                      |
| *Steindachnerina insculpta* | Pavão stream        | 3277      | ♂   | 3 2 0                  | 5                    |
|                             |                     | 3278      | ♂   | 8 0 0                  | 8                    |
|                             | Total               |           |     | 11 2 0                 | 13                   |
|                             | %                   |           |     | 84,6 15,4 0            |                      |
|                             | Água dos Patos River| 3393      | ♀   | 40 8 0                 | 48                   |
|                             |                     | 3407      | ♂   | 18 0 0                 | 18                   |
|                             |                     | 3408      | ♂   | 11 2 1                 | 14                   |
|                             |                     | 3409      | ♂   | 21 0 0                 | 21                   |
|                             |                     | 3411      | ♂   | 22 0 0                 | 22                   |
|                             |                     | 3745      | ♂   | 5 0 0                  | 5                    |
|                             | Total               |           |     | 117 10 1               | 128                  |
|                             | %                   |           |     | 91,4 7,8 0,8           |                      |
|                             | Jacutinga River     | 3453      | ♀   | 15 2 1                 | 18                   |
|                             |                     | 3454      | ♀   | 22 0 0                 | 22                   |
|                             |                     | 3461      | ♂   | 14 0 0                 | 14                   |
|                             |                     | 3462      | ♂   | 20 0 0                 | 20                   |
|                             |                     | 3465      | ♂   | 23 1 0                 | 24                   |
|                             |                     | 3862      | ♀   | 6 0 0                  | 6                    |
|                             |                     | 3986      | ♂   | 2 0 0                  | 2                    |
|                             |                     | 3987      | ♀   | 5 0 0                  | 5                    |
|                             |                     | 3991      | ♂   | 4 0 0                  | 4                    |
|                             |                     | 3993      | ♀   | 3 0 0                  | 3                    |
|                             |                     | 4046      | ♂   | 8 0 0                  | 8                    |
|                             |                     | 4049      | ♂   | 4 10 0                 | 14                   |
|                             | Total               |           |     | 126 13 1              | 140                  |
|                             | %                   |           |     | 90 9,3 0,7            |                      |
Table 4. Cytogenetic data of different species of curimatids (2n: diploid number; FN: number fundamental; Bs: supernumerary chromosomes).

| Species                     | 2n | FN  | Bs  | B Size | References* |
|-----------------------------|----|-----|-----|--------|-------------|
| Curimata cyprinoides        | 54 | 108 | -   | -      | 3, 15       |
| Curimata inornata           | 54 | 108 | -   | -      | 3, 15       |
| Curimata kneri              | 54 | 108 | -   | -      | 3           |
| Curimata ocellata           | 56 | 112 | -   | -      | 3           |
| Curimata vittata            | 54 | 108 | -   | -      | 3           |
| Curimatella albina          | 54 | 108 | -   | -      | 3           |
| Curimatella dorsalis        | 54 | 108 | -   | -      | 8, 12       |
| Curimatella imaculata       | 54 | 108 | -   | -      | 15          |
| Curimatella lepidura        | 54 | 108 | -   | -      | 2           |
| Curimatella meyeri          | 54 | 108 | -   | -      | 3           |
| Curimatopsis myersi         | 46 | 46  | -   | -      | 8           |
| Cyphocharax gilbert         | 54 | 108 | -   | -      | 6, 15       |
| Cyphocharax cf. gillii      | 54 | 108 | -   | -      | 2           |
| Cyphocharax gouldingi       | 54 | 108 | 0 - | 1 Micro| 15          |
| Cyphocharax modestus        | 54 | 108 | 0 - | 4 Micro| 1, 2, 7, 9, 13, 14, 16, 17, 18 |
| Cyphocharax nagelli         | 54 | 108 | -   | -      | 2, 15       |
| Cyphocharax cf. spilurus    | 54 | 108 | -   | -      | 2           |
| Cyphocharax splotus         | 54 | 108 | 0 - | 1 Micro| 11, 12, 18  |
| Cyphocharax vanderi         | 54 | 108 | -   | -      | 2           |
| Cyphocharax roxa            | 54 | 108 | 0 - | 1 Micro| 2, 12, 18   |
| Cyphocharax platanus        | 58 | 116 | -   | -      | 12, 15      |
| Cyphocharax saladensis      | 54 | 108 | 0 - | 1 Micro| 18          |
| Potamorhina altamazonica    | 102| 106 | -   | -      | 4           |
| Potamorhina latior          | 56 | 112 | -   | -      | 4           |
| Potamorhina pristigaster    | 54 | 108 | -   | -      | 4           |
| Potamorhina squamALEVIS     | 102| 106 | -   | -      | 12          |
| Pectrogaster amazonica      | 54 | 108 | -   | -      | 15          |
| Pectrogaster curviventeris  | 54 | 108 | -   | -      | 8, 12       |
| Pectrogaster rutiloides     | 54 | 108 | -   | -      | 3           |
| Steindacherina amazonica    | 54 | 108 | -   | -      | 15          |
| Steindacherina bipartata    | 54 | 108 | 0 - | 1 Micro| 18          |
| Steindacherina brevipina    | 54 | 108 | -   | -      | 8, 12       |
| Steindacherina conspersa    | 54 | 108 | -   | -      | 2, 12       |
| Steindacherina elegans      | 54 | 108 | -   | -      | 2           |
| Steindacherina gracilis     | 54 | 108 | -   | -      | 15          |
| Steindacherina cf. guentheri| 54 | 108 | -   | -      | 10          |
| Steindacherina insculpta    | 54 | 108 | 0 - | 2 Micro| 2, 5, 13, 14, 15, 17, 18 |
| Steindacherina leucisca     | 54 | 108 | -   | -      | 3           |

References: 1 Venere, Galetti (1985)  2 Venere, Galetti (1989)  3 Feldberg et al. (1992)  4 Feldberg et al. (1993)  5 Oliveira, Foresti (1993)  6 Venere, Galetti-Jr (1995)  7 Martins et al. (1996)  8 Navarrete, Julio-Jr. (1997)  9 Venere et al. (1999)  10 Carvalho et al. (2001)  11 Fenocchio et al. (2003)  12 Brassesco et al. (2004)  13 Gravena et al. (2007)  14 Teribebe et al. (2008);  15 Venere et al. (2008)  16 De Rosa et al. (2007)  17 De Rosa-Santos et al. (2008)  18 present study.
metaphase I with 27 bivalents were observed (Fig. 4). It was possible to observe the B microchromosome as univalent in the spermatogonial metaphase in *Cyphocharax spilotus*; in the pachytene stage in *C. spilotus, C. voga, C. modestus, Steindachnerina biornata* and *S. insculpta*; and in metaphase I in *S. biornata* (Figs 3, 4).

In both types of cell division, the number of cells without B microchromosomes was greater than number of cells with B microchromosomes in the species of Curimatidae. Camacho et al. (2000) suggest that the small number of chromosomes in diploid cells represents the maximum that a species is able to tolerate as adults.

In others groups of fishes with B-chromosomes meiotic analysis has been performed in order to understand the behavior of this chromosome, as in *Prochilodus lineatus* (Valenciennes, 1836) from the Mogi Guaçu River (Pirassununga/SP), whose studies of the synaptonemal complex showed that no B chromosome paired with autosomal chromosomes. In the late pachytene stage, 27 paired bivalents and small bivalent, trivalent and quadrivalent B chromosomes were observed. The pairing of B chromosomes was interpreted as a result of homology between these chromosomes (Dias et al. 1998).

Borin and Martins-Santos (2004) analyzed *Pimelodus sp.* and *P. ortmanni* Hasselmann, 1911 from the Iguacu River, in the Parana state, which had 2n=56 and intraindividual variations from 0 to 4 B chromosomes in the somatic cells. The meiotic analysis confirmed the presence of these chromosomes, with a variation ranging from 0 to 2 B chromosomes in metaphase I, but could not confirm whether these Bs were univalent or bivalent. The species *Rineloricaria pentamaculata* Langeani & Araujo, 1994 from the Tauá stream, Parana River basin, studied by Porto et al. (2010), also

---

**Figure 3.** Meiotic cells: *Cyphocharax saladensis* a–f *Cyphocharax spilotus* g–l and *Cyphocharax voga* m–r belonging to Laguna dos Patos Hydrographic System. The arrows indicate the B microchromosome univalent in g, h and n.
showed a variation in the diploid number from 56 to 59 chromosomes, attributed to the presence of B chromosomes, which ranged from 0 to 3 in the somatic cells, and confirmed by the meiotic analysis that showed 28 bivalents in metaphases I and II and small univalents. These data support the classification of such elements as supernumerary or B chromosomes, indicating meiotic instability in the transmission to the offspring (Porto et al. 2010).

The meiotic data presented in this study are the first for Curimatidae, and also indicate the instability of the B microchromosome during meiosis, demonstrating that this chromosome has no homology with any normal chromosome complement in these species. Analyses of the synaptonemal complex in the analyzed species would be

---

**Figure 4.** Meiotic cells: *Cyphocharax modestus a–c*, *Steindachnerina biornata d–f* and *Steindachnerina insculpta g–i*. The arrows indicate the B microchromosome univalent in b, e, f and h.
interesting to complement the study of the meiotic behavior of B microchromosome in the species Curimatidae.

According Camacho et al. (2000), these chromosomes could be originated from the A chromosomes (intraspecific origin) or as result of mating between species (interspecific origin). Some authors discuss the origin of the B chromosomes in different species of fish as in *Astyanax scabripinnis* (Jenyns 1842) (Moreira-Filho et al. 2004), Amazon species cichlids (Feldberg et al. 2004) and *Rhamdia quelen* (Quoy & Gaimard, 1824) (Moraes et al. 2009).

There are two hypotheses that could explain the origin of B chromosomes in *C. modestus* and *S. insculpta*, according Martins et al. (1996). The first one suggests that these chromosomes arose in some ancestor of the family and were eliminated in species where they are not found today. The second one suggests that B chromosomes have a more recent and independent origin in the species that bear it.

The results obtained in this study provides more information about the occurrence of B microchromosomes in the curimatids, confirming its presence in *Cyphocharax spilotus*, *C. modestus* and *Steindachnerina insculpta*, previously described in other populations, and showing new events in *Cyphocharax voga*, *C. saladensis* and *Steindachnerina biornata*. These data confirm the outstanding characteristic of this type of chromosome in this group of fish and its mitotic and meiotic instability and allow a further discussion about the origin of Bs in the family Curimatidae.

**Acknowledgements**

The authors are grateful to CNPq for fellowships, to Dr. Luiz R. Malabarba for the identification of the studied species from the Laguna dos Patos Hydrographic System/RS and MSc Larissa Bettin Pires and Fábio H. Takagui for assistance in the construction of maps.

**References**

Bertollo LAC, Takahashi CS, Moreira-Filho O (1978) Cytotaxonomic considerations on *Hoplias lacerdae* (Pisces, Erythrinidae). Brazilian Journal of Genetics 1 (2): 103–120.

Borin LA, Martins-Santos IC (2004) Study on karyotype and occurrence of B chromosomes in two endemic species of the genus *Pimelodus* (Siluriformes, Pimelodidae) from the River Iguaçu. Hereditas 140: 201–209. doi: 10.1111/j.1601-5223.2004.01812.x

Brassesco MS, Pastori MC, Roncati HA, Fenocchio AS (2004) Comparative cytogenetics studies of Curimatidae (Pisces, Characiformes) from the middle Paraná River (Argentina). Genetics and Molecular Research 3(2): 293–301.

Camacho JPM, Sharbel TF, Beukeboom LW (2000) B-chromosome evolution. Philosophical Transactions of the Royal Society of London B: Biological Sciences 355(1394): 163–178. doi: 10.1098/rstb.2000.0556
Carvalho ML, Oliveira C, Foresti F (2001) Cytogenetic analysis of three species of the families Characidae and Curimatidae (Teleostei, Characiformes) from the Acre River. Chromosome Science 5: 91–96.

Carvalho RA, Martins-Santos IC, Dias AL (2008) B chromosomes: an update about their occurrence in freshwater Neotropical fishes (Teleostei). Journal of Fish Biology 72: 1907–1932. doi: 10.1111/j.1095-8649.2008.01835.x

De Rosa LV, Foresti F, Martins C, Oliveira C, Sobrinho PE, Wasko AP (2007) Cytogenetic analyses of two Curimatidae species (Pisces; Characiformes) from the Paranapanema and Tietê Rivers. Brazilian Journal of Biology 67(2): 333–338. doi: 10.1590/S1519-69842007000200020

De Rosa-Santos LV, Foresti F, Martins C, Oliveira C, Wasko AP (2008) Identification and description of distinct B chromosomes in *Cyphocharax modestus* (Characiformes, Curimatidae). Genetics and Molecular Biology 31 (1): 265–269. doi: 10.1590/S1415-47572008000200019

Dias AL, Foresti F, Oliveira C (1998) Synapsis in supernumerary chromosomes of *Prochilodus lineatus* (Teleostei: Prochilodontidae). Cytology 51(2): 105–113.

Feldberg E, Porto JIR, Bertollo LAC (1992) Karyotype evolution in Curimatidae (Teleostei, Characiformes) of the Amazon region. I. Studies on the genera *Curimata*, *Psectrogaster*, *Steindacherina* and *Curimatella*. Brazilian Journal of Genetics 15(2): 369–383.

Feldberg E, Porto JIR, Nakayama CM, Bertollo LAC (1993) Karyotype evolution in Curimatidae (teleostei, Characiformes) from the Amazon region. II. Centric fissions in the genus *Potamorhina*. Genome 36: 372–376. doi: 10.1139/g93-051

Feldberg E, Porto JIR, Alves-Brinn MN, Mendonça MNC, Benzaquem DC (2004) B chromosomes in Amazon cichlid species. Cytogenetics and Genome Research 106: 195–198. doi: 10.1159/000079287

Fenocchio AS, Pastori MC, Roncati HA, Moreira-Filho O, Bertollo LAC (2003) A cytogenetic survey of the fish fauna from Argentina. Caryologia 2: 197–204.

Gravena W, Teribele R, Giuliano-Caetano L, Dias AL (2007) Occurrence of B chromosomes in *Cyphocharax modestus* (Fernández-Yépez., 1948) and *Steindacherina insculpta* (Fernández-Yépez, 1948) (Characiformes, Curimatidae) from the Tibagi River basin (Paraná State, Brazil). Brazilian Journal of Biology 67(4 Suppl): 905–908. doi: 10.1590/S1519-69842007000500014

Jones RN, Rees H (1982) B chromosomes. Academic Press, London, Great Britain, 266pp.

Kligerman AD, Bloom SE (1977) Rapid chromosome preparations from solid tissues of fishes. Journal of the Fisheries Research Board of Canada 34: 266–269. doi: 10.1139/f77-039

Levan A, Fredga K, Sandberg AA (1964) Nomenclature for centromeric position on chromosomes. Hereditas 52: 201–220. doi: 10.1111/j.1601-5223.1964.tb01953.x

Martins C, Giuliano-Caetano L, Dias AL (1996) Occurrence of a B chromosome in *Cyphocharax modesta* (Pisces, Curimatidae). Cytobios 85: 247–253.

Moraes VPO, Carneiro JS, Dias AL (2009) B Chromosomes in Four Different Populations of *Rhamdia quelen* (Siluriformes, Heptapteridae): A Comparative Study of Frequency and Distribution. Folia Biologica (Kraków) 57: 3–4: 165–169. doi: 10.3409/fb57_3-4.165-169
Moreira-Filho O, Galetti Junior PM, Bertollo LAC (2004) B chromosomes in the fish Astyanax scabripinnis (Characidae, Tetragonopterinae): overview in natural populations. Cytogenetics and Genome Research 106(2–4): 230–234. doi: 10.1159/000079292

Navarrete MC, Júlio Junior HF (1997) Cytogenetic analysis of four curimatids from the Paraguay Basin, Brasil (Pisces: Characiformes, Curimatidae). Cytologia 62: 241–247. doi: 10.1508/cytologia.62.241

Oliveira C, Foresti F (1993) Occurrence of supernumerary microchromosomes in Steindachnerina insculpta (Pisces, Characiformes, Curimatidae). Cytobios 76: 183–186.

Porto FE, Portela-Castro ALB, Martins-Santos IC (2010) Possible origins of B chromosomes in Rinelocaria pentamaculata (Loricariidae, Siluriformes) from the Paraná River basin. Genetics and Molecular Research 9(3): 1654–1659. doi: 10.4238/vol9-3gmr859

Teribele R, Gravena W, Carvalho K, Giuliano-Caetano L, Dias AL (2008) Karyotypic analysis in two species of fishes of the family Curimatidae: AgNO₃, CMA₃ and FISH with 18S probe. Caryologia 61(3): 211–215.

Venere PC, Galetti PM (1985) Natural triploidy and chromosome B in the fish Curimata modesta (Characiformes, Characidae). Brazilian Journal of Genetics 8: 681–687.

Venere PC, Galetti PM (1989) Chromosome evolution and phylogenetic relationships of some neotropical Characiformes of the family Curimatidae. Brazilian Journal of Genetics 12: 17–25.

Venere PC, Galetti Junior PM (1995) Multiple longitudinal bands in fish chromosomes: comparison of structural G-banding and replication R bands among curimatids. Cytobios 84: 71–78.

Venere PC, Miyazawa CS, Galetti Junior PM (1999) New cases of supernumerary chromosomes in Characiform fishes. Genetics and Molecular Biology 22(3): 345–349. doi: 10.1590/S1415-47571999000300010

Venere PC, Souza IL, Silva LK, Dos Anjos MB, De Oliveira RR, Galetti Junior PM (2008) Recent chromosome diversification in the evolutionary radiation of the freshwater fish family Curimatidae (Characiformes). Journal of Fish Biology 72: 1976–1989. doi: 10.1111/j.1095-8649.2008.01814.x