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Transmission rate variation among three B chromosome variants in the fish *Prochilodus lineatus* (Characiformes, Prochilodontidae)

MANOLO PENITENTE[1], TATIANA A. VOLTOLIN[1], JOSÉ A. SENHORINI[2], JEHUD BORTOLOZZI[1], FAUSTO FORESTI[3] and FÁBIO PORTO-FORESTI[1]

[1]Laboratório de Genética de Peixes, Universidade Estadual Paulista,
Av. Eng. Luiz Edmundo Carrijo Coube, 1401, Vargem Limpa, 17033-360 Bauru, SP, Brasil
[2]Laboratório de Genética e Reprodução de Peixes, Instituto Chico Mendes de Conservação da Biodiversidade/ICMBio,
Centro Nacional de Pesquisa e Conservação de Peixes Continentais/CEPTA,
Rodovia SP 201, Km 6,5, 13630-970 Pirassununga, SP, Brasil
[3]Laboratório de Biologia e Genética de Peixes, Universidade Estadual Paulista,
Distrito de Rubião Júnior, s/n, 18618-970 Botucatu, SP, Brasil

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ABSTRACT

Cytogenetic studies were developed in Prochilodus lineatus (Valenciennes 1836), describing an interesting system of small supernumerary chromosomes. The purpose of this work is to study the frequency and morphology of B chromosomes in individuals from the parental line and the inheritance patterns of these elements in individuals obtained from controlled crosses in the species *P. lineatus*. The transmission rate of B chromosomes revealed a k_B=0.388 for the acrocentric type, a kB=0.507 for the metacentric type and a k_B=0.526 for the submetacentric type. The obtained results raise hypothesis that B-acrocentric chromosomes are involved in an extinction process in this species, while the metacentric and submetacentric supernumerary elements comprises a neutral mechanism and follows a Mendelian transmission rate.

Key words: supernumerary chromosomes, controlled crosses, curimbatá, cytogenetic, inheritance.

INTRODUCTION

B chromosomes are widely distributed among eukaryotes and their occurrence has been reported in ten species of fungi, nearly 1,300 plants, and over 500 animals (Camacho 2005). In addition, B chromosomes have been described to date in 38 species of Neotropical fish (Oliveira et al. 2009). These structural elements have been identified in diverse karyotypes, but intriguing questions still persist about their structure, function or behavior.

The first evidence of B chromosomes in Neotropical fishes was identified in *Prochilodus lineatus* (Pauls and Bertollo 1983). This species presents a diploid number of 54 chromosomes of the metacentric and submetacentric types, with a fundamental number of 108 (Pauls and Bertollo 1983, 1990, Oliveira et al. 1997, Cavallaro et al. 2000, Jesus and Moreira-Filho 2003, Artoni et al. 2006, Voltolin et al. 2009). Cytogenetic studies of individuals of *P. lineatus* captured at different locations revealed a numerical variation of supernumerary chromosomes in all populations analyzed, and the number of extra-chromosomes

Correspondence to: Fabio Porto-Foresti
E-mail: fpforesti@fc.unesp.br

always ranged from zero to seven (Pauls and Bertollo 1983, Oliveira et al. 1997, Cavallaro et al. 2000, Jesus et al. 2003). However, Voltolin et al. (2011) recently detected the presence of eight and nine supernumerary chromosomes in individuals of this species resulting from induced crossings.

Supernumerary chromosomes exhibit a remarkable variation in size and morphology among fish, i.e., the occurrence of large genomic elements as macrochromosomes was described in species of the genus *Astyanax* (Maistro et al. 1992, Salvador and Moreira-Filho 1992, Vicente et al. 1996, Moreira-Filho et al. 2001, Ferro et al. 2003, Hashimoto et al. 2008); of medium size in *Rhamdia* (Fenocchio and Bertollo 1990, Fenocchio et al. 2000); and also as small elements identified as microchromosomes in *Prochilodus* (Pauls and Bertollo 1983, 1990, Venere et al. 1999, Cavallaro et al. 2000, Oliveira et al. 2003, Voltolin et al. 2009). Artoni et al. (2006), studying specimens of *P. lineatus* from the Mogi-Guaçu River, observed the presence of three types of supernumerary microchromosomes in this species, which were classified as B-acrocentric, B-metacentric, and B-submetacentric.

A mechanism of genetic control in the transmission patterns of these extra elements has been demonstrated in some animals, including the grasshopper *Myrmeleotettix maculatus* (Shaw and Hewitt 1985, Shaw et al. 1985), the mealy bug *Pseudococus affinis* (Nur and Brett 1987, 1988), the grasshopper *Eyprepocnemis plorans* (Herrera et al. 1996) and also in some plants including *Hypochoeris maculata* (Parker et al. 1982), *Aegilops speltoides* (Cebriá et al. 1994), and *Allium schoenoprassum* (Bougourd and Plowman 1996).

The knowledge about the inheritance of supernumerary chromosomes in fish carriers is still scarce in the literature. The process was identified in fish for the first time in *Poecilia formosa* (Schartl et al. 1995). Later, Oliveira et al. (1997) and Voltolin et al. (2010) conducted studies on the inheritance of B chromosomes in *P. lineatus* and found that the transmission pattern of these chromosomes follows a regular expected meiotic behavior in individuals of both sexes, showing a Mendelian rate. Different models are proposed to explain the presence, accumulation and possible effects of B chromosomes in the organisms (White 1973), as well as the parasitic model (Östergren 1945, Nur 1966a, b, 1977), or the selfish model (Jones 1985, Shaw and Hewitt 1990).

The present study performed a thorough analysis of the transmission pattern of three different types of B chromosomes found in *P. lineatus*, through controlled crosses, establishing relations on the dynamics, maintenance and transmission of the microchromosomes found in this species, in order to better understanding the processes involved in the inheritance of these genomic elements.

MATERIALS AND METHODS

Two groups of *Prochilodus lineatus* were cytogenetically analyzed. The first was composed of 50 samples from the natural population of the Mogi-Guaçu River, Pirassununga, São Paulo, Brazil, used as parental generation. The second group involved in controlled crossings, so that six males and six females of the parental generation were selected to form eight couples through the combination of gametes (Fig. 1). The controlled crosses were performed at the Centro de Pesquisa e Gestão dos Recursos Pesqueiros Continentais/ Instituto Chico Mendes de Conservação da Biodiversidade, CEPTA/ICMBio, Pirassununga, São Paulo, Brazil. The second group was composed of 113 individuals obtained from eight crosses representing the filial generation.

The chromosome preparations of the parental generation were obtained from a lymphocyte culture following the method used by Fenocchio and Bertollo (1988). The chromosome preparations of individuals in the filial generation were obtained from kidney fragments according to the protocol

COUPLE 1	COUPLE 2
Male 1 X Female 1 2B (1m/1sm) 2B (1a/1m)	Male 2 X Female 2 3B (1a/2sm) 3B (1a/2m)
COUPLE 3	**COUPLE 4**
Male 3 X Female 3 4B (1a/1m/2sm) 3B (1m/2sm)	Male 4 X Female 4 5B (3m/2sm) 5B (4m/1sm)
COUPLE 5	**COUPLE 6**
Male 4 X Female 3 5B (3m/2sm) 3B (1m/2sm)	Male 5 X Female 5 6B (3m/3sm) 5B (4m/1sm)
COUPLE 7	**COUPLE 8**
Male 6 X Female 6 1B (1m) 3B (2m/1sm)	Male 5 X Female 3 6B (3m/3sm) 3B (1m/2sm)

Fig. 1 - Controlled crosses involving *Prochilodus lineatus* individuals with different numbers of supernumerary chromosomes indicated in association of sex in individuals of parental lines. m: B-metacentric, sm: B-submetacentric, a: B-acrocentric.

followed by Foresti et al. (1981). All representatives of the parental generation were marked with magnetic tags and cytogenetically identified according to the number and type of supernumerary chromosomes to enable the achievement of controlled crossings.

The chromosome morphology was determined according to the ratio of arms established by Levan et al. (1964), and the chromosomes were classified as metacentric (m), submetacentric (sm) and acrocentric (a) and arranged in descending order of size.

For the determination of B chromosome modal numbers, 30 well spread metaphase cells per individual were analyzed. The transmission rate of B chromosomes (kB) was calculated from the mean number of B chromosomes in the progeny, divided by the total number of parental Bs, according to López-León et al. (1992).

RESULTS

The basic sample analyzed comprised 50 specimens of *Prochilodus lineatus* collected from the natural population of the Mogi-Guaçu River, having up to six B chromosomes in their somatic cells. There was no intraindividual variation in natural population and in the whole filial generation. The frequency of supernumerary chromosomes found on this natural population was 6.34% of B-acrocentric, 53.18% of B-metacentric, and 40.48 % of B-submetacentric (Fig. 2). These data show a predominance of B-metacentric and B-submetacentric types in the natural population of curimbatá from the Mogi-Guaçu River. In addition, we analyzed 113 individuals from the filial generation (F1), obtained from eight controlled crosses. The B-acrocentric type was present in the parental generation in individuals of only three crossings, confirming the low frequency found in the natural population of the Mogi-Guaçu River, whilst B-metacentric and B-submetacentric were involved in all crosses.

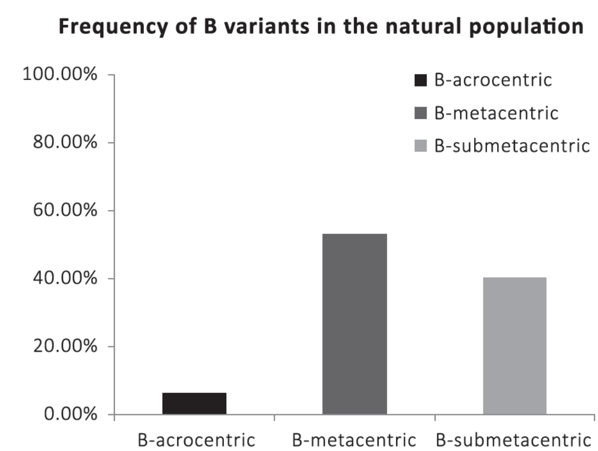

Fig. 2 - Frequency of different types of B chromosomes found in specimens of *Prochilodus lineatus* in the natural population of Mogi-Guaçu River. The B-acrocentric showed the lowest incidence (6.34%) while the B-metacentric presented 53.18% and the B-submetacentric presented 40.48%.

The analysis of the filial generation showed that B-acrocentric type was less frequent than B-metacentric and B-submetacentric types in the whole F1 generation in controlled crosses (Table I). Furthermore, it was possible to calculate the average of transmission rate (k_B) of each morphological type of B chromosome to investigate the transmission pattern of the three variants of supernumeraries,

TABLE I
Frequency of each supernumerary chromosome variant on filial generation in controlled crosses.

Couples	♂	♀	n	f_a	f_m	f_{sm}
Couple 1	2B(1m/1sm)	2B(1a/1m)	14	5 (16.6%)	17 (56.7%)	8 (26.7%)
Couple 2	3B(1a/2sm)	3B(1a/2m)	14	10 (25.0%)	15 (37.5%)	15 (37.5%)
Couple 3	4B(1a/1m/2sm)	3B(1m/2sm)	20	9 (14.5%)	23 (37.0%)	30 (48.5%)
Couple 4	5B(3m/2sm)	5B(4m/1sm)	12	------	35 (59.3%)	24 (40.7%)
Couple 5	5B(3m/2sm)	3B(1m/2sm)	15	------	27 (47.3%)	30 (52.7%)
Couple 6	6B(3m/3sm)	5B(4m/1sm)	17	------	59 (63.4%)	34 (36.6%)
Couple 7	1B(1m)	3B(2m/1sm)	10	------	16 (76.2%)	5 (23.8%)
Couple 8	6B(3m/3sm)	3B(1/2sm)	11	------	17 (38.6%)	27 (61.4%)

n: total of individuals analyzed in the filial generation, a: number of B-acrocentric found on parents, m: number of B-metacentric, sm: number of B-submetacentric, f_a: frequency of the B-acrocentric in offspring, f_m: frequency of the B-metacentric, f_{sm}: frequency of the B-submetacentric.

where the types B-acrocentric, B-metacentric, and B-submetacentric presented respectively the following mean values: k_{Ba}=0.388, k_{Bm}=0.507 and k_{Bsm}=0.526 (Fig. 3). B-acrocentric type presented the lowest average transmission rate.

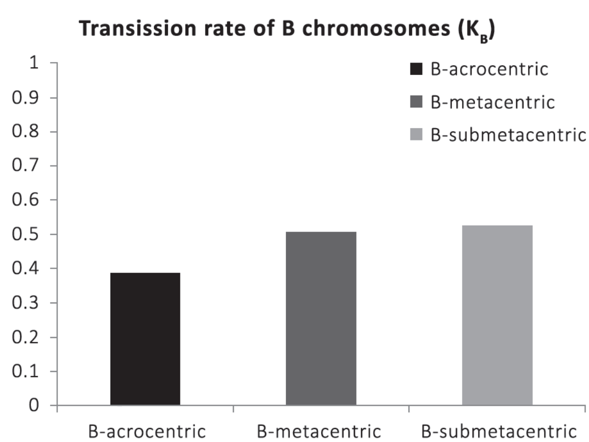

Fig. 3 - Average transmission rate (k_B) of B chromosome types in offspring of *Prochilodus lineatus* resulting from controlled crosses. The value of k_B was 0.388 for the B-acrocentric, 0.507 for the B-metacentric, and 0.526 for the B-submetacentric.

DISCUSSION

Studies performed on the inheritance patterns of supernumerary chromosomes in the specie *P. lineatus* by Oliveira et al. (1997) and Voltolin et al. (2010) reported that the transmission of microchromosomes was consistent with the Mendelian rate (k_B=0.500). These data describe only the numerical frequency variation of microchromosomes B in Prochilodus. However, Artoni et al. (2006), studying specimens of *P. lineatus* from the Mogi-Guaçu River, revealed the presence of three morphological variants of supernumerary microchromosomes in this species that were classified as B-acrocentric, B-metacentric and B-submetacentric, but no information about the frequency of the different types was included in the results.

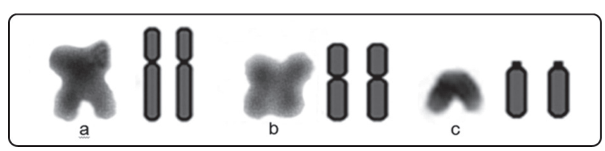

Fig. 4 - Types and relative size of supernumerary chromosomes found in *Prochilodus lineatus*. (**a**) submetacentric; (**b**) metacentric; and (**c**) acrocentric.

Cytogenetic analysis performed in the present study confirmed that there is no intraindividual variation of B chromosomes in natural population and in the F1 generation, these results are consistent with those by Oliveira et al. (1997), Cavallaro et al. (2000) and Voltolin et al. (2010). Furthermore, we found the three types of B microchromosomes in individuals of the parental line, collected directly in the natural population, in a similar result as described by Artoni et al. (2006) (Fig. 4), but it was observed that B-metacentric and B-submetacentric types were more frequent than B-acrocentric type (Fig. 2). The low frequency of B-acrocentric chromosomes was observed both in individuals from the natural population of the Mogi-Guaçu River and in individuals produced by induced crossings involving the parental line sample. So it may be noted that similar frequency patterns for the three types of extra chromosomes can be found in nature and in captive conditions, and the data points to the fact that B-acrocentric chromosome may have a lower transmission rate when compared to the other two types of B in this species.

The prevalence of B-metacentric over the B-acrocentric type in the transmission inheritance patterns was also identified by Araújo et al. (2002) in populations of the wasp *Trypoxylon albitarse*. The authors affirmed that the B-metacentric chromosome showed a higher efficiency of transmission in relation to the acrocentric type. However, the few studies involving the inheritance of morphological types of supernumerary in fish permitted only to correlate the low frequency of B-acrocentric found both in natural and captive populations of *P. lineatus* to transmission efficiency.

TABLE II
Relationship between the k_B with frequency of the supernumerary chromosomes variants.

B variant	F	F%	K_B
acrocentric	8	6.34%	0.388
metacentric	67	53.18%	0.507
submetacentric	51	40.48%	0.526

k_B: transmission rate of B chromosomes, f: numeric frequency, f%: percentage frequency.

The results obtained in the present work demonstrate the emergence of an intrinsic relationship between the frequency of each type of extra chromosome with its respective supernumerary transmission rate (k_B), where the B-acrocentric type showed a transmission rate lower than the number existing in the parental generation (k_B=0.388), leading automatically to a lower incidence of the filial generation (Table I), and in a similarly way to the low frequency observed in the natural population (Fig. 2). The B-metacentric (k_B=0.507) and B-submetacentric (k_B=0.526) types show a Mendelian rate (k_B=0.500), which exhibits neutralization stage, and are more frequent in the natural population (53.18% and 40.48%, respectively). However, the transmission rate of the B-acrocentric type indicates the occurrence of an imminent decline process that may result in the extinction of this morphological type in the population of the Mogi-Guaçu River, if no structural modification occurs in their chromosome structure, as proposed by Camacho et al. (2000).

The hypothesis proposed by Araújo et al. (2002) that B-acrocentric chromosomes have by themselves a lower transmission rate when compared to the two other supernumeraries cannot be discarded. Concerning the Mendelian rate the B-meta and submetacentric types are in a neutral stage and can mutate along the evolutionary process to remain in the genome of this species. Based on these two hypotheses, which can guarantee the maintenance of different types of B in the genome of *P. lineatus*, it is possible to propose that the metacentric and submetacentric B chromosomes types have a higher transmission rate.

Therefore, new population surveys on the frequency of the different types of B chromosomes found in the natural population of the Mogi-Guaçu River, as well as a greater number of controlled crosses involving also individuals non-carriers of supernumeraries, associated with further studies about the meiotic behavior of these genomic elements in this species are necessary for a better understanding of the dynamics and inheritance of B chromosomes in *P. lineatus* from the Mogi-Guaçu River.

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RESUMO

Estudos citogenéticos foram desenvolvidos em *Prochilodus lineatus* (Valenciennes 1836), os quais descrevem um interessante sistema de pequenos cromossomos supranumerários. O objetivo deste trabalho foi estudar a frequência e morfologia dos cromossomos B em indivíduos a partir da linhagem parental e os padrões de herança destes elementos em indivíduos obtidos a partir de cruzamentos controlados na espécie *P. lineatus*. A taxa de transmissão dos cromossomos B revelaram um k_B=0,388 para o tipo acrocêntrico, k_B=0,507 para o tipo metacêntrico e k_B=0,526 submetacêntrico. Os resultados obtidos levantam hipóteses de que os cromossomos B do tipo acrocêntrico se encontram em fase de extinção, enquanto que os supranumerários do tipo metacêntrico e submetacêntrico encontram-se em fase de neutralização, seguindo uma taxa de transmissão Mendeliana.

Palavras-chave: cromossomos supranumerários, cruzamentos controlados, curimbatá, citogenética, herança.

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