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Cytotaxonomic and Evolutionary Considerations about Karyotipic Data of Fishes from the Iguaçu River Basin in South of Brazil

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ABSTRACT

The cytogenetic data available in the literature about the ichthyofauna of the Iguaçu River basin were analyzed in this review. The ichthyofauna was characterized by the high level of endemism and by the low diversity of species. Twenty-four of the eighty-one species were already karyotyped; six Characiformes, fourteen Siluriformes and four Perciformes. The chromosomal data showed the taxonomic and systematic complexity of the groups. Hypothesis related to the evolution of some Characiformes and Siluriformes groups from the Iguaçu River are proposed, as well as the utilization of karyotypic data for cytotaxonomy.

Key words: Neotropical region, fish cytogenetics, chromosome formulae

INTRODUCTION

The neotropical fauna is composed by near 8000 species and is considered as the most diverse epicontinental ichthyofauna in the world (Vari and Malabarba, 1998). Nearly 1000 species have been karyotyped so far, mostly by the Brazilian researchers (Brum and Galetti Jr., 1997; Almeida-Toledo, 1998). These studies permitted a better comprehension of some taxa with a not well-resolved taxonomy, besides establishing evolutionary relations in several groups. The ichthyofauna of the Iguaçu River basin was isolated from the Paraná River since the rise of the Iguaçu Falls 22 million years ago, that probably allowed the considerable endemism of this ichthyofauna (Sampaio, 1988; Lucinda, 1995; Garavello et al., 1997), which was estimated as 75% (Zawadski et al., 1999). Besides, the damming of some parts of the river as a result of tectonic reactivations (Bigarella et al., 1961) would have promoted alterations in the environments resulting in the low diversity of fish species in the Iguaçu River basin (Júlio Jr. et al., 1997). Nowadays, 81 species of Teleostei are known in the Iguaçu River basin (Ingenito et al., 2004), including three exotic species. This study aimed to present a review of all data about the

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cytogenetics of the fishes from the Iguaçu River and also on some taxonomic and evolutionary aspects of its ichthyofauna.

MATERIAL AND METHODS

Table 1 shows the information available about the karyotype of fishes from the Iguaçu River basin. The nomenclature and classification of the fishes followed basically Malabarba et al. (1998), Reis et al. (2003), Ingenito et al. (2004) and the current database in FishBase systematic (Froese and Pauly, 2007). The chromosomal anatomy and morphology permit to establish the karyotype of the species, mainly using: number of chromosomes of the diploid group (2N); fundamental number (FN), which represented the number of chromosomal arms of the complement; type of chromosomes, classified in metacentrics (m), submetacentrics (sm), subtelocentrics (st) and acrocentrics (a) according to the arms relation of Levan et al. (1964); karyotypic formula, represented by the quantity of each type of chromosome. Other diagnostic data were also observed here, such as the presence of sexual chromosomes; presence of B chromosome system; cases of natural triploidy (3N), besides a marker for the ribosomal gene activity by the use of the colloidal silver in the marking of the nucleolus organizing regions (NORs).

RESULTS AND DISCUSSION

The cytogenetic studies in the fishes from the Iguaçu River are still scarce. Most of the available data are found in the abstracts published in the materials of symposia and congresses. However, tendencies of karyotypic evolution might be seen as well as the use of karyotypic data for the taxonomy and systematic might be done. In neotropical fishes, pioneer data for the cytotaxonomy were presented by Bertollo et al. (1978) for *Hoplias malabaricus*. These data were also systematized in a checklist for the karyotypic diversity of neotropical fishes by Oliveira et al. (1988). Only twenty-four of the eighty-one species recognized at the moment for the Iguaçu River have been karyotyped (Table 1). Six of these species corresponded to Characiformes (25,00%), fourteen to Siluriformes (58,33%) and four to Perciformes (16,67%). However, this number was probably higher because in some other studies the individuals were not identified at the level of species.

Characiformes

For this order, most of the available studies are about species of the genus *Astyanax*. According to Sampaio (1988), Almiron et al. (2002), 0Azpelicueta et al. (2002) and Ingenito et al. (2004), the Iguaçu River contained at least ten species of *Astyanax*. *Astyanax altiparanae*, found all over the upper Paraná River basin, had its origin in the Iguaçu River mainly through introductions, as determined by Prioli et al. (2002) through molecular markers. The cytogenetic data showed that this might have occurred more than once through different stocks. The *Astyanax* of the Iguaçu River received the denominations *Astyanax* sp. B, *A.* sp. C, *A.* sp. D, *A.* sp. E and *A.* sp. F. Although these taxonomic entities were not nominal species yet, they were easily distinguished from each other and are clearly diagnosed in the reference literature (Severi and Cordeiro, 1994; Garavello et al., 1997; Ingenito et al., 2004; Kantek et al., 2007).

Checking the data from Table 1, interpopulation differences could be identified in the nucleolus organizing region (NORs) of the species *Astyanax* sp. B, *Astyanax* sp. C and. *A. altiparanae*, suggesting an absence of gene flow between the samples from different places. Besides, in *Astyanax* sp. B and *A. altiparanae*, there were also differences in the fundamental number (FN) and in the karyotypic formula. Ribeiro (2004), using C-banding in *Astyanax* sp. B, observed high differences in the quantity of heterochromatins comparing samples from the middle and upper Iguaçu River. These information emphasized the taxonomic and systematic complexity of the group.

The samples of *Oligosarcus longirostris* also differed in the NORs as well as in the fundamental number (FN) and karyotypic formula significantly.

Hoplias malabaricus was an example of the complex species. Seven different karyotypic types (cytotypes A, B, C, D, E, F, G) were identified for this taxon all over its distribution (Bertollo et al., 2000). The cytotypes A and B were found in the Iguaçu River, and according to Vicari et al. (2006), one of these types could be found in the basin even before the geographic isolation 22 million years ago. However, Dergam et al. (1998), using RAPD

(Random Amplified Polymorphism DNA) molecular markers, considered that the samples from the Iguaçu River were originally from the Tibagi River. Sampaio (1988) suggested that the Characiformes were already very differentiated before the isolation of the Iguaçu River. The idea that the cytotype A of *H. malabaricus* could already be found in the basin before the isolation corroborates this hypothesis.

The diploid number varied from 2n = 42 (*H. malabaricus*) to 2n = 54 (*Glandulocauda melanopleura*), and the modal number was 2n = 50. According to Oliveira et al. (1988), Brum and Galetti Jr (1997), Fenocchio et al. (2003b) and Carvalho et al. (2002), the modal number for the order were 2n = 54. This discrepancy might be a result of the small number of taxa analyzed until now.

Table 1 - Karyologic data of the fishes from the Iguaçu River. Karyotypic variations are in parenthesis: *Astyanax sp.* B – two cytotypes; *Hoplias malabaricus* and *Steindachneridium sp.* – sexual system, males in parenthesis. X = presence, -- = absence. S = simple, M = multiple.

Taxa	Locality/River	2n	FN	Katyotype				B crom.	NOR system	3n	Ref.
Characiformes				m	sm	st	a				
Characidae											
Tetragonopterinae											
Astyanax altiparanae	Piraquara	50	94	6	30	8	6	--	S	--	1
Astyanax altiparanae	Nova Prata do Iguaçu	50	88	12	10	16	12	--	M	--	2
Astyanax altiparanae	--	50	90	10	26	4	10	--	M	--	3
Astyanax sp.	--	50	86	6	26	4	14	--	M	--	4
Astyanax sp.B	Nova Prata do Iguaçu	50	86	12	12	12	14	--	M	--	5
Astyanax sp.B	São Mateus do Sul	50	86	6	24	6	14	--	S	--	6
Astyanax sp.B	Salto Segredo reservoir	50	84	6	16	12	16	--	S	--	7
Astyanax sp.B	Guarani river	50	84(88)	6	28(32)		16(12)	--	M	--	6
Astyanax sp.B	Piraquara	50	88	4	22	12	12	--	M	--	8
Astyanax sp.B	Salto Caxias reservoir	50	86	6	24	6	14	X	--	--	9
Astyanax sp.C	Várzea river	50	84	6	28		16	--	M	--	10
Astyanax sp.C	Piraquara	50	84	4	22	8	16	--	S	--	11
Astyanax sp.C	São José dos Pinhais	50	84	4	22	8	16	--	M	--	11
Astyanax sp.D	Bicudo river	50	84	4	24	6	16	--	--	--	12
Astyanax sp.D	Upper Iguaçu river basin	50	84	4	24	6	16	--	--	--	12
Astyanax sp.D	Poço Claro river	50	84	4	24	6	16	--	--	--	12
Astyanax sp.D	Piraquara	50	84	4	24	6	16	--	M	X	13
Astyanax sp.E	Várzea river	50	84	6	28		16	--	M	--	10
Hyphessobrycon reticulatus	São Mateus do Sul	50	100					--	--	--	14
Acestrorhynchinae											
Oligosarcus longirostris	Quedas do Iguaçu	50	80	4	10	16	20	--	S, pair 21, a	--	15
Oligosarcus longirostris	Iguaçu National Park	50	84	6	16	12	16	--	S, pair 22, a	--	16
Oligosarcus longirostris	--	50	82	2	20	10	18	--	M	--	17
Oligosarcus longirostris	Guarani river	50	80	4	26		20	--	M	--	18
Glanduloclaudinae											
Glandulocauda melanopleura	Headwaters of Iguaçu river	54	94	8	18	14	14	--	--	--	19
Mimagoniates microlepis	Piraquara and Pequeno river	52	96	12	18	14	8	--	--	--	20
Erythrinidae											
Hoplias malabaricus	São José dos Pinhais	42	84	24	16(17)	02(01)	--	--	M	--	21
Hoplias malabaricus	Piraquara	42	84	10	22	--	--	--	M	--	21
Hoplias malabaricus	Palmeira	42	84	24	18	--	--	--	M	--	22

(Cont. ...)

(Cont. Table 1)

Taxa	Locality/River	2n	FN	Katyotype				B crom.	NOR system	3n	Ref.
Hoplias malabaricus	Nova Prata do Iguaçu	42	84	24	18	--	--	--	M	--	23
Siluriformes											
Auchenipteridae											
Glanidium ribeiroi	Salto Caxias reservoir	58	112	28	16	10	4	--	S, pair 17, sm	--	24
Glanidium ribeiroi	Quedas do Iguaçu	58	108	24	14	12	8	--	S, pair 1, m	--	25
Callichthyidae											
Callichthys callichthys	Upper Iguaçu river basin	58	--	--	--	--	--	X	M	--	26
Corydoras paleatus	Quedas do Iguaçu	44	88	44		--	--	--	M	--	27
Corydoras paleatus	Salto Caxias Reservoir	44	86		18	24	2	--	M	--	28
Corydoras paleatus	Upper Iguaçu river basin	44	88	20	24	--	--	--	M	--	29
Pimelodidae											
Heptapterus hollandi	Quedas do Iguaçu	42	78	22	10	4	6	--	S, pair 13, sm	--	30
Pimelodus ortmanni	Palmeira	56	--	--	--	--	--	--	S, sm	--	31
Pimelodus ortmanni	Quedas do Iguaçu	56	102	20	12	14	10	--	S, pair 18, st	--	32
Pimelodus ortmanni	Salto Caxias reservoir	56	106	24	18	8	6	X	S, pair 4, st	--	33
Pimelodus sp.	Salto Caxias reservoir	56	110	24	26	4	2	--	S, st	--	34
Pimelodus sp.	Salto Caxias reservoir	56	108	30	14	8	4	X	S, pair 4, st	--	33
Rhamdia branneri	Quedas do Iguaçu	58	112	30	10	14	4	X	S	X	35
Rhamdia quelen	Guarapuava	58	112	36	14	4	4	X	S	--	36
Rhamdia quelen	Upper Iguaçu river basin	58	116	32	16	6	4	X	S, st	--	37
Rhamdia sp.	Guarapuava	58	112	36	14	4	4	X	M	--	36
Rhamdia voulezi	Guarapuava	58	112	36	14	4	4	X	S, pair 29, a	--	36
Rhamdia voulezi	Quedas do Iguaçu	58	112	30	10	14	4	--	S, pair 28, m	--	38
Steindachneridion sp.	Foz do Jordão	56	102	20(21)	24(23)	2	10		S, pair 24, a	--	39
Trichomyteridae											
Trichomycterus davisi	Três Barras	54	108	40	12	2	--	--	S, pair 2, m	X	40/41
Trichomycterus davisi	Lapa	54	108	42	10	2	--	--	S, pair 2, m	--	42
Trichomycterus stawiarski	Três Barras	54	108	42	8	4	--	--	S, pair 2, m	--	40
Trichomycterus sp.	Três Barras	54	108	42	10	2	--	--	S, pair 2, m	--	40
Loricariidae											
Ancistrus sp.	Salto Segredo reservoir	48	92	18	14	12	4	--	S, st	--	43
					eight cytotypes *						
Ancistrus sp.	Salto Caxias reservoir	50	--					--	S, st	--	43
Ancistrus sp.	Alto Alegre river	50	88	12	14	12	12	--	S, pair 21, a	--	44
Hypostomus albopuntactus	São João river	74	114	8	18	14	34	--	S	--	45
Hypostomus commersoni	Quedas do Iguaçu	68	104	10	18	8	32	--	M	--	45
Hypostomus derby	Quedas do Iguaçu	68	102	10	8	16	34	--	M	--	45
Hypostomus myersi	Quedas do Iguaçu	74	118	12	14	18	30	--	S	--	45
Perciformes											
Cichlidae											
Cichlasoma facetum	São Mateus do Sul	48	58			10	38	--	S, a	--	46
Crenicichla iguassuensis	Quedas do Iguaçu	48	66	2	4	12	30	--	S, pair 2, sm	--	47
Crenicichla iguassuensis	Iguaçu National Park	48	66	2	4	12	30	--	S, pair 2, sm	--	47
Crenicichla iguassuensis	Salto Caxias reservoir	48	74		8	40		--	S, pair 1, m	--	48
Geophagus brasiliensis	São Mateus do Sul	48	54	--	6	42		--	S, a	--	46
Geophagus brasiliensis	Salto Caxias reservoir	48	52		4	44		--	S, a	--	49

(Cont. ...)

(Cont. Table 1)

Taxa	Locality/River	2n	FN	Katyotype	B crom.	NOR system	3n	Ref.
Tilapia rendalli	Salto Caxias reservoir	44	54	10 34	--	S, sm	--	49
Tilapia rendalli	--	44	62	-- 10 8 26	--	M	--	49

References: 1 = Domingues (2006); 2 = Cenci and Margarido (1999); 3 = Porto and Martins-Santos (2001); 4 = Fauaz et al. (1990); 5 = Barros and Margarido (1999); 6 = Robaina and Cestari (1998a); 7 = Dias and Júlio Jr (1996); 8 = Ribeiro (2004); 9 = Fazoli et al. (2003); 10 = Dalabona and Cestari (1995); 11 = Kantek et al. (2003); 12 = Kantek (2005); 13 = Kantek et al. (2007); 14 = Robaina and Cestari (1998b); 15 = Rubert and Margarido (2007); 16 = Cunha et al. (2001); 17 = Martinez and Júlio Jr. (2000); 18 = Cestari (1996); 19 = Sass et al. (2003); 20 = Nardino et al. (2004); 21 = Lemos et al. (2002); 22 = Vicari et al. (2003); 23 = Vicari et al. (2006), 24 = Ravedutti and Júlio Jr. (2001); 25 = Roman and Margarido (2000); 26 = Maurutto et al. (2006); 27 = Kavalco and Margarido (2000); 28 = Santi and Martins Santos (2001) 29 = Oliveira et al. (1993); 30 = Roman and Margarido (2002); 31 = Terencio et al. (2001); 32 = Margarido and Gavasso (2000); 33 = Borin and Martins-Santos (2004); 34 = Souza (2003); 35 = Roman and Moreira-Filho (2002); 36 = Abucarma and Martins-Santos (2001); 37 = Fenocchio et al. (2003a); 38 = Margarido and Roman (2000); 39 = Swarça (2003); 40 = Borin and Martins-Santos (1999); 41 = Borin and Martins-Santos (2002); 42 = Sato et al. (2004); 43 = Lara (1998); 44 = Tchaicka and Margarido (2000); 45 = Casale et al. (2002); 46 = Quijada and Cestari (1999); 47 = Margarido et al. (2001); 48 = Mizoguchi and Martins-Santos (1999); 49 = Mizoguchi (2005). * cyt. 1 = 18m+8sm+10st+14a; cyt. 2 = 18m+9sm+6st+17a; cyt. 3 = 18m+8sm+11st+13a; cyt. 4 = 18m+10sm+10st+12a; cyt. 5 = 15m+8sm+15st+12a; cyt. 6 = 19m+8sm+11st+12a; cyt. 7 = 16m+8sm+10st+16a; cyt. 8 = 18m+10sm+12st+10a.

Siluriformes

Until 1995, only one species of the genus *Pimelodus* was known in the Iguaçu River (*Pimelodus ortmanni*). Garavello and Shibatta (1995) registered a new species using morphological features (*Pimelodus* sp.). Isoenzyme (Renesto et al., 2000) and chromosomal (Borin and Martins-Santos, 2004) data corroborated that it was really a new species. According to Borin and Martins-Santos (2004), *Pimelodus* sp. was more similar to *P. maculatus* (collected in the Paraná River basin) than to *P. ortmanni* and, in this way, like in the Characiformes, these two species could exist before the rise of the Iguaçu Falls.

Silfvergrip (1998) suggested that *Rhamdia voulezi* and *R. branneri* of the Iguaçu River were synonymous of *Rhamdia quelen*. The similarity in the karyotypic formula supported this hypothesis (Table 1). However, there were karyotypes with simple and multiple NORs, which might be indicating that these taxa were really different species. Abucarma and Martins-Santos (2001), based on the differences in the B chromosomes, considered that *R. branneri*, *R. voulezi* and *Rhamdia* sp. were distinct taxonomic entities. Thus further studies would be necessary and would help to solve the taxonomy of this group.

Sato et al. (2004), based on chromosomal data, suggested that there were at least two groups of *Trichomycterus* cis-Andean species. The species of the Iguaçu River fit in the second group, which had two relevant features: (1) the two largest metacentric (m) pairs of chromosomes were similar in size and also were significantly bigger than the other metacentric chromosomes; and (2) the NORs were interstitial and located in a big pair of metacentric chromosomes. These features were also found in species like *T. paolence* (Torres et al., 1998), *T. diabolus* (Torres et al., 2004) and *Trichomycterus* aff. *itatiayae* (Sato et al., 2004).

The last one was collected in the Tibagi River basin, whereas the other two were originally from the Paranapanema River basin, both relatively close to the Iguaçu River basin. Chromosomal similarities and the proximity in the geographic distribution might be the evidence of a possible common origin for these species.

The *Hypostomus* species of the Iguaçu River could be grouped into two cladograms; one composed by species with 68 chromosomes and other by the species with 74 chromosomes. Casale et al. (2002) related these two groups to body coloration and isoenzyme patterns. Other hydrographic basins also have species with 2n = 68 and 2n = 74 chromosomes (Artoni and Bertollo, 2001), showing that the origin of these two groups was earlier than 22 million years, when there was no geographic barrier between the Iguaçu River and other basins. However, Montoya-Burgos (2003) proposed that the main geological/cladogenetic episode in the evolutionary history of the genus *Hypostomus* occurred between 12 and 4 million years ago. In this way, the occurrence of this genus in the Iguaçu River due to upper river captures from other basins after the formation of the Iguaçu Falls was a hypothesis that must be considered. Weitzman et al. (1988) and Ingenito et al. (2004) suggested a historical relationship (upper river captures) between the Iguaçu River and adjoining basins.

The diploid number in the order varied from 2n = 42 (*Pariolius hollandi*) to 2n = 74 (*Hypostomus myersi* and *H. albopuntactus*) and the modal

number was 2n = 58, same data observed by Oliveira et al. (1988).

Perciformes

The data of this study agreed with the ones in the literature (Fenocchio et al., 2003b), which registered a highly conservative tendency with karyotypes composed by 2n = 48 chromosomes and simple NORs. The karyotypic formulas of the Perciforme species analyzed in the present study indicated a predominance of acrocentric chromosomes, while two armed chromosomes were more often found in Characiformes and Siluriformes. These data agreed with the chromosomal evolutionary tendencies reported by Oliveira *et al.* (1988) and Fenocchio et al. (2003b). Thus, karyotypic data should be real for the cytotaxonomy of fishes from the Iguaçu River basin. These is need for the majority of the fish species already described from this region, as in *Astyanax*, *Hoplias* and *Rhamdia*, and the enlargement of the access to the karyotype of species not studied yet over this aspect.

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RESUMO

Nesta revisão são analisados os dados citogenéticos disponíveis na literatura relativos à ictiofauna da bacia do Rio Iguaçu, a qual é caracterizada pelo alto grau de endemismo e pela baixa diversidade de espécies. Das oitenta e uma espécies conhecidas, vinte e quatro já foram cariotipadas sendo 6 Characiformes, 14 Siluriformes e 4 Perciformes. Os dados cromossômicos evidenciam a complexidade taxonômica e sistemática dos grupos. São propostas hipóteses relacionadas à evolução de alguns grupos de Characiformes e Siluriformes do Rio Iguaçu, assim como o aproveitamento de dados cariotípicos para a citotaxonomia.

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