



Cytogenetic analysis of five *Hypostomus* species (Siluriformes, Loricariidae)

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Abstract

In this work, we analyzed the karyotypes of five *Hypostomus* species. *Hypostomus* cf. *heraldoi*, from the Mogi-Guaçu River, had $2n = 72$ chromosomes, with a nucleolar organizer region (NOR) in one chromosomal pair. *Hypostomus regani*, from the Mogi-Guaçu River had $2n = 72$ chromosomes with NORs in two chromosomal pairs. *Hypostomus* sp., from the Mogi-Guaçu River basin, had $2n = 68$ chromosomes, with NORs in two chromosomal pairs. *Hypostomus* aff. *agna*, from Cavallo Stream, had $2n = 74$ chromosomes with NORs in two chromosomal pairs. *Hypostomus* cf. *topavae*, from Carrapato Stream, had $2n = 80$ chromosomes, with NORs in two chromosomal pairs. *Hypostomus* species showed marked diversity in the karyotypic formula, which suggested the occurrence of several Robertsonian rearrangements and pericentric inversions during the evolutionary history of this genus. This hypothesis was supported by the occurrence of a large number of uniarmed chromosomes and multiple NORs in a terminal position in most species and may be a derived condition in the Loricariidae.

Key words: chromosomes, evolution, Hypostominae, Neotropical fish, NOR.

Received: February 1, 2011; Accepted: June 15, 2011.

Introduction

Siluriformes is an extremely large fish order with a wide distribution throughout tropical regions (Ferraris, 2007). The number of known species in this region is about 3,100, but may be considerably higher (Reis *et al.*, 2003; Nelson, 2006; Ferraris, 2007). The largest family within the Siluriformes is the Loricariidae, with approximately 700 species distributed in eight subfamilies (Reis *et al.*, 2006; Ferraris, 2007; Chiachio *et al.*, 2008).

Loricariids occur in several habitats, from lagoons and swamps to rapids in sloping streams or rivers with rocky bottoms, at altitudes up to 3000 m. In large water channels, these fish are usually found on rocky bottoms facing into strong water currents (Garavello and Garavello, 2004) or along the margins where the current is moderate (Burgess, 1989). According to Suzuki *et al.* (2000), these fish exhibit a large diversity of adaptive strategies, with many species showing nest defense, parental care of eggs, brooder larvae behavior, and mouths adapted for feeding on algae and detritus.

Although the Loricariidae is one of the largest fish families in the world, the number of cytogenetically studied

species is still very low. There is marked inter-specific diversification in the diploid number, which ranges from $2n = 36$ chromosomes in *Rineloricaria latirostris* (Giuliano-Caetano L, Doctoral thesis, Universidade Federal de São Carlos, 1998) to $2n = 84$ in *Hypostomus* sp. (Cereali *et al.*, 2008). Cytogenetically, the Hypostominae is the best studied group within the Loricariidae, but it is also the most complex, with the diploid number varying from $2n = 38$ in *Ancistrus* sp. (Alves *et al.*, 2003) to $2n = 84$ in *Hypostomus* sp. (Cereali *et al.*, 2008). A very interesting feature in the Hypostominae (particularly within Hypostomini) is the inverse relationship between the diploid number and the number of chromosomes with two arms, which suggests the occurrence of several events of centric fusion/fission (Robertsonian rearrangements) during the evolution of this group (Artoni and Bertollo, 2001).

The Hypostomini consists of a single genus, *Hypostomus*, whose representatives have a relatively small, stout body, without a depressed caudal peduncle and adipose fin (Armbruster, 2004). This genus, which contains 125 valid species (Zawadzki *et al.*, 2008a; Carvalho *et al.*, 2010) and is distributed from Central America to southern South America (Ferraris, 2007), has the greatest karyotypic diversity within the family (Artoni and Bertollo, 1996, 2001; Artoni *et al.*, 1998). According to Artoni and Bertollo (1996), these fish exhibit non-conservative characteristics in diploid number, karyotypic macrostructure and chromo-

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somal banding (Artoni and Bertollo, 1996). Currently, most of the cytogenetic data on *Hypostomus* relate to the diploid number, karyotypic formulas and location of the NOR (Rubert *et al.*, 2008). The diploid number ranges from $2n = 52$ in *Hypostomus emarginatus* (Artoni and Bertollo, 2001) to $2n = 84$ in *Hypostomus* sp. (Cereali *et al.*, 2008) (Table 2). Some species have distinct karyotypic formulas and their chromosomal variation is accompanied by an increase in the number of subtelo/acrocentric chromosomes (Table 2). According to Artoni and Bertollo (1996), chromosomal rearrangements, such as centric fission and pericentric inversions, play an important role in the karyotype evolution of these fish. Sex chromosomes have been found in some Hypostominae, such as *Hypostomus* sp., with ZZ/ZW (Artoni *et al.*, 1998) and *Ancistrus* sp. 1, with XX/X0 (Alves *et al.*, 2006). *Hypostomus* has single or multiple NORs in the terminal portion of the chromosomes, as observed for other species of this genus (Table 2), with the number of silver-stained chromosomes varying from one (Artoni and Bertollo, 1996; Cereali *et al.*, 2008) to three (Artoni and Bertollo, 1996; Alves *et al.*, 2006) pairs.

Several *Hypostomus* species are morphologically very similar (Schubart, 1964; Schaefer, 1987; Reis *et al.*, 1990; Muller and Weber, 1992; Mazzoni *et al.*, 1994; Weber and Montoya-Burgos, 2002; Oyakawa *et al.*, 2005; Zawadzki *et al.*, 2008a,c), which makes their identification difficult. In addition, several new species await formal description. Cytogenetic studies have been very useful taxonomically since several fish groups identified only on the basis of morphological studies have been further characterized as a cluster of two or more isolated genetic units.

To improve our knowledge of the diversity and species relationships in *Hypostomus*, in this study we undertook a cytogenetic analysis of five species in this genus. We provide information on the karyotypic organization of these species and discuss some aspects of karyotypic evolution in this group of fish.

Material and Methods

Specimens of five species of *Hypostomus* were collected in streams and rivers from the upper Paraná River basin and Atlantic coastal Rivers (Figure 1, Table 1). The specimens were collected under a license from Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA). After the cytogenetic procedures, the fish were fixed in 10% formaldehyde and preserved in 70% ethanol for future taxonomic studies. Voucher specimens were deposited in the ichthyological collection of the Laboratório de Biologia e Genética de Peixes (LBP) of the Departamento de Morfologia do Instituto de Biociências, Universidade Estadual Paulista “Júlio de Mesquita Filho”, campus of Botucatu, São Paulo state.

Chromosomal preparations were obtained using the air drying technique (Foresti *et al.*, 1981) and nucleolar organizer regions (NORs) were detected by the silver impregnation technique of Howell and Black (1980). Chromosomal morphology was established based on the proportions of the arms, as proposed by Levan *et al.* (1964), and the chromosomal nomenclature commonly applied to fish (a - acrocentric, m - metacentric, sm - submetacentric and st - subtelocentric) was used.

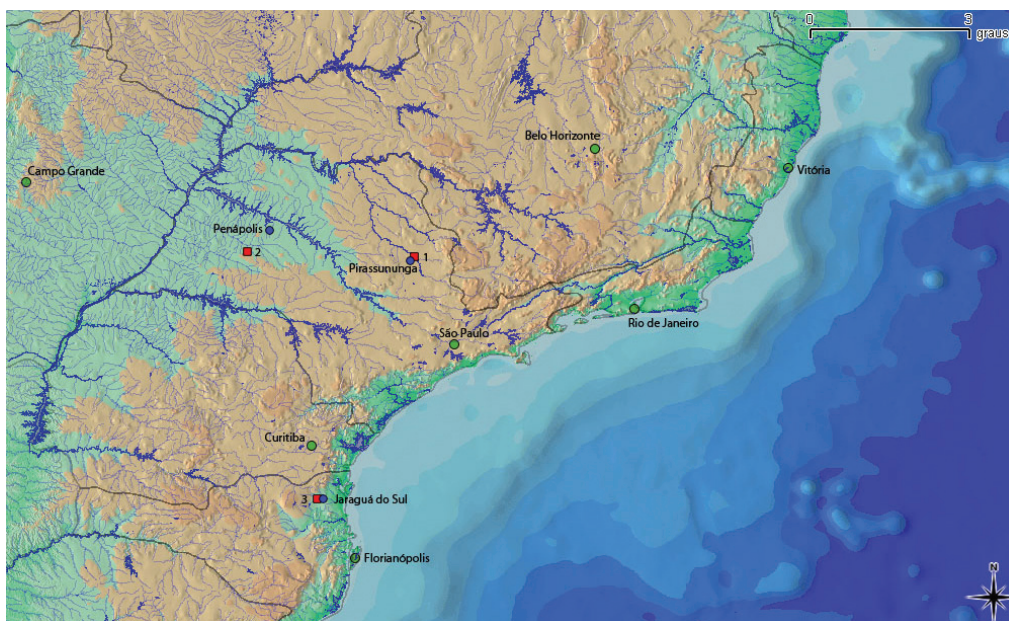


Figure 1 - Partial hydrographic map of Brazil showing the collection sites for the species of *Hypostomus* found in the upper Paraná River basin and Atlantic coastal rivers. The collection sites marked by red squares are: 1 - Mogi-Guaçu River (GPS: 21°55'37.6" S and 47°22'04.4" W), 2 - Carrapato River (GPS: 21°50' S and 50°30' W); and 3 - Cavalo Stream (GPS: 26°28'15" S and 49°10'57" W). Blue circles indicate the cities closest to the collection sites and green circles indicate the corresponding state capitals.

Table 1 - *Hypostomus* species analyzed in this study. The fish were deposited in the ichthyological collection of the Laboratório de Biologia e Genética de Peixes (LBP), UNESP Botucatu, São Paulo, Brazil.

Species	Collection site	LBP no.	Specimens analyzed
<i>Hypostomus</i> aff. <i>agna</i>	Cavalo Stream, Jaraguá do Sul, SC (southern Brazilian coastal River basin)	2360	2 males and 2 females
<i>Hypostomus</i> cf. <i>heraldoi</i>	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	4208	2 males and 2 females
<i>Hypostomus regani</i>	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	3943	8 males and 2 females
<i>Hypostomus</i> cf. <i>topavae</i>	Carrapato Stream, Penápolis, SP (Paraná River basin)	3249	2 males and 2 females
<i>Hypostomus</i> sp.	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	3943	2 males and 2 females

Results and Discussion

The five species analyzed (Table 2) showed diploid numbers ranging from $2n = 68$ chromosomes in *Hypostomus* sp. to $2n = 80$ in *Hypostomus* cf. *topavae*. All of the species, except for *Hypostomus regani*, were analyzed karyotypically for the first time. There were no sex-linked chromosomal differences in any of the species.

Specimens of *Hypostomus* cf. *heraldoi*, from the Mogi-Guaçu River, had a diploid number of $2n = 72$ chromosomes composed of 6 m, 6 sm, 26 st and 34 a (Figure 2A, Table 2). This diploid number was the same as in *H. goyazensis* (Alves *et al.*, 2006), *H. regani* (Artoni and Bertollo, 1996; Alves *et al.*, 2006) and *Hypostomus* sp. B, *Hypostomus* sp. C, *Hypostomus* sp. D1 and *Hypostomus* sp. D2 (Artoni and Bertollo, 1996) (Table 2), although all of these species can be differentiated by their karyotypic organization.

Hypostomus regani, from the Mogi-Guaçu River, had $2n = 72$ chromosomes, with a karyotypic formula of 6 m, 6 sm, 32 st and 28 a (Figure 2B, Table 2), which partially confirmed the results of Artoni and Bertollo (1996) and Alves *et al.* (2006), who observed the same diploid number as found here but different karyotypic formulas (Table 2). *Hypostomus regani* is one of the most widely-distributed species throughout the Paraná-Paraguay River basin. Based on alloenzymatic data, Zawadzki *et al.* (2008b) identified genetically-structured populations of *H. regani* from the Manso Reservoir (Paraguay River basin), Itaipu Reservoir (lower portion of the upper Paraná River basin) and Corumbá Reservoir (upper portion of the upper Paraná River basin). These findings indicate that differences in the karyotypic formulas of *H. regani* populations are not uncommon.

Hypostomus sp., from the Mogi-Guaçu River, had $2n = 68$ chromosomes that consisted of 6 m, 6 sm, 32 st and 24 a (Figure 2C, Table 2). This diploid number was also found in *H. ancistroides* (Michele *et al.*, 1977; Artoni and Bertollo, 1996; Alves *et al.*, 2006). However, *Hypostomus* sp. differs from *H. ancistroides* in its karyotypic structure (Table 2).

Hypostomus aff. *agna*, from Cavalo Stream, had $2n = 74$ chromosomes, with 8 m, 10 sm, 32 st and 24 a (Figure 3A, Table 2). This diploid number was also observed in *H. paulinus*, *H. strigaticeps* (Michele *et al.*, 1977) and *H. albopunctatus* (Artoni and Bertollo, 1996) (Table 2), but all

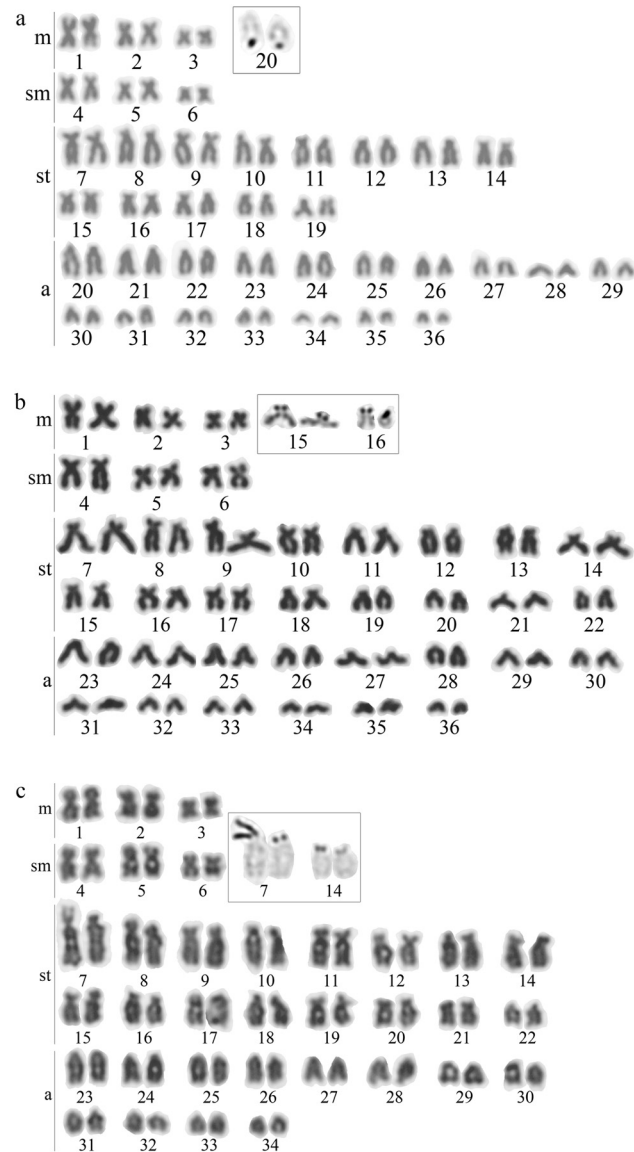


Figure 2 - Karyotypes and NOR-bearing chromosomes (insets) of: a) *Hypostomus* cf. *heraldoi*, b) *Hypostomus regani* and c) *Hypostomus* sp., all from the Mogi-Guaçu River.

of these species can also be differentiated by their karyotypic structure.

Hypostomus cf. *topavae*, from Carrapato Stream, had $2n = 80$ chromosomes, consisting of 6 m, 8 sm, 42 st and 24

Table 2 - Summary of the available cytogenetic data for *Hypostomus*.

Species	Location	2n	Karyotype	NOR	Reference
<i>Hypostomus</i> aff. <i>agna</i>	Cavalo Stream, Jaraguá do Sul, SC (southern Brazilian coastal River basin)	74	8m+10sm+32st+24a	2	This study
<i>Hypostomus affinis</i>	Jacuí Stream, SP (Paraíba do Sul River basin)	66	14m+14sm+12st+26a	3	Kavalco <i>et al.</i> (2004)
<i>H. aff. auroguttatus</i>	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	76	8m+30sm+38st/a	1	Artoni and Bertollo (1996)
<i>H. albopunctatus</i>	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River Basin)	74	10m+20sm+44st/a	3	Artoni and Bertollo (1996)
<i>H. ancistroides</i>	Monjolinho Stream, São Carlos, SP (Piracicaba River basin)	68	16m+18sm+34st/a	3	Artoni and Bertollo (1996)
<i>H. ancistroides</i>	-	68	10m+28sm+30st/a	-	Michele <i>et al.</i> (1977)
<i>H. ancistroides</i>	Araquá River, Botucatu, SP (Tietê River basin)	68	18m+10sm+12st+28a	3	Alves <i>et al.</i> (2006)
<i>H. emarginatus</i>	Araguaia River, Barra do Garças, MT (Araguaia River basin)	52	16m+30sm+6st	1	Artoni and Bertollo (2001)
<i>H. goyazensis</i>	Vermelho River, Goiás Velho, GO (Araguaia River basin)	72	10m+16sm+10st+36a	1	Alves <i>et al.</i> (2006)
<i>Hypostomus</i> cf. <i>heraldoi</i>	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	72	6m+6sm+26st+34a	1	This study
<i>H. macrops</i>	-	68	10m+14sm+44st/a	-	Michele <i>et al.</i> (1977)
<i>H. nigromaculatus</i>	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	76	8m+20sm+48st/a	1	Rubert <i>et al.</i> (2008)
<i>H. nigromaculatus</i>	Três Bocas Stream, Londrina, PR (Tibagi River basin)	76	6m+20sm+50st/a	2	Rubert <i>et al.</i> (2008)
<i>H. nigromaculatus</i>	Ribeirão dos Apertados, Londrina, PR (Tibagi River basin)	76	8m+20sm+48st/a	2	Rubert <i>et al.</i> (2008)
<i>H. paulinus</i>	-	74	10m+ 20sm+44st/a	-	Michele <i>et al.</i> (1977)
<i>H. regani</i>	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	72	6m+6sm+32st+28a	2	This study
<i>H. regani</i>	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	72	10m+20sm+42st/a	-	Artoni and Bertollo (1996)
<i>H. regani</i>	Araquá River, Botucatu, SP (Tietê River basin)	72	12m+18sm+26st+16a	1	Alves <i>et al.</i> (2006)
<i>H. strigaticeps</i>	-	74	8m+4sm+62st/a	-	Michele <i>et al.</i> (1977)
<i>Hypostomus</i> cf. <i>topavae</i>	Carrapato Stream, Penápolis, SP (Paraná River basin)	80	6m+8sm+42st+24a	2	This study
<i>Hypostomus</i> sp.	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	68	6m+6sm+32st+24a	2	This study
<i>Hypostomus</i> sp. 2	Perdido River, Planalto da Bodoquena, MS (Paraguai River basin)	84	6m+16sm+62st/a	1	Cereali <i>et al.</i> (2008)
<i>Hypostomus</i> sp. 3	Salobrinha Stream, Planalto da Bodoquena MS (Paraguai River basin)	82	6m+12sm+64st/a	1	Cereali <i>et al.</i> (2008)
<i>Hypostomus</i> sp. 3	Salobrinha Stream, Planalto da Bodoquena, MS (Paraguai River basin)	84	6m+12sm+66st/a	1	Cereali <i>et al.</i> (2008)
<i>Hypostomus</i> sp. A	Rincão River, Rincão, SP (Piracicaba River basin)	70	18m+14sm+38st/a	2	Artoni and Bertollo (1996)
<i>Hypostomus</i> sp. B	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	72	12m+18sm+42st/a	1	Artoni and Bertollo (1996)
<i>Hypostomus</i> sp. C	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	72	10m+18sm+44st/a	2	Artoni and Bertollo (1996)
<i>Hypostomus</i> sp. D1	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	72	10m+26sm+36st/a	2	Artoni and Bertollo (1996)
<i>Hypostomus</i> sp. D2	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	72	14m+20sm+38st/a	2	Artoni and Bertollo (1996)
<i>Hypostomus</i> sp. E	Mogi-Guaçu River, Pirassununga, SP (Mogi-Guaçu River basin)	80	8m+16sm+56st/a	2	Artoni and Bertollo (1996)

2n = diploid number; a = acrocentric; m = metacentric; sm = submetacentric; st = subtelocentric. NOR = number of chromosomal pairs with nucleolar organizer regions.



Figure 3 - Karyotypes and NOR-bearing chromosomes (insets) of: a) *Hypostomus* aff. *agna* from Cavalo Stream and b) *Hypostomus* cf. *topavae* from Carrapato Stream.

a (Figure 3B, Table 2). This diploid number was also found in *Hypostomus* sp. E (Artoni and Bertollo, 1996) (Table 2), although *H. cf. topavae* can be differentiated from its congeners by its karyotypic organization.

Based on cytogenetic studies, Artoni and Bertollo (2001) found that in the Hypostominae higher chromosomal numbers are associated with a greater number of unarmed chromosomes, whereas low diploid numbers are associated with a higher number of biarmed chromosomes. Similarly, the high diploid numbers in *Hypostomus* are associated with a high number of unarmed chromosomes (Table 2). Alves *et al.* (2003, 2005, 2006) suggested that the diploid number $2n = 54$ and the presence of many biarmed chromosomes are primitive characteristics of the Loricariidae. Their conclusion was based mainly on the wide occurrence of this diploid number and karyotypic formulas in basal loricariid taxa, such as members of the subfamilies Neoplecostominae and Hypoptopomatinae. The available data (Table 2) therefore corroborate and reinforce the hypothesis of Artoni and Bertollo (1996) that centric fissions and pericentric inversions have had an important role in the evolution of this fish group.

Our results showed that *Hypostomus* species have single or multiple NORs in the terminal position of their

chromosomes, as observed in other species of this genus (Table 2). In *H. cf. heraldoi*, NORs occurred on the long arm of an acrocentric chromosomal pair (pair 20) (Figure 2A, Table 2); in *H. regani*, NORs occurred on the short arms of two subtelocentric chromosomal pairs (pairs 15 and 16) (Figure 2B, Table 2); in *Hypostomus* sp., from the Mogi-Guaçu River, NORs occurred on the short arms of two subtelocentric chromosomal pairs (pairs 7 and 14) (Figure 2C, Table 2); in *H. aff. agna*, NORs occurred on the long arms of two chromosomal pairs, one submetacentric (pair 5) and one subtelocentric (pair 13) (Figure 3A, Table 2); finally, in *H. cf. topavae*, NORs occurred on two chromosomal pairs: on the short arms of a subtelocentric (pair 11) and on the long arms of an acrocentric pair (pair 30) (Figure 3B, Table 2). These findings highlight the extensive diversity in NOR phenotype among the Loricariidae.

Oliveira and Gosztonyi (2000) stated that in the Siluriformes the basal NOR condition was probably a single NOR at a terminal position on the chromosome. Artoni and Bertollo (1996) proposed that NORs located terminally on the long arm of a single metacentric chromosomal pair represented the primitive condition in the Hypostominae. Based on these hypotheses, species with multiple NORs

would be derived in a monophyletic group. Since most *Hypostomus* species studied here had multiple NORs, we suggest that these NORs either originated independently among *Hypostomus* species or originated only once in a monophyletic *Hypostomus* group.

The hypothesis that the five *Hypostomus* species analyzed here represent a derived cytogenetic condition is coherent with the available biogeographic data for *Hypostomus*. Based on geological and molecular data, Montoya-Burgos (2003) estimated that the origin of the main clade of *Hypostomus* was on the former Amazon River basin. According to this author, the vicariant and dispersal events from Amazonian areas to Paraná-Paraguayan areas occurred about 10-12 million years ago. Thus, if the cytogenetic hypotheses are congruent with the biological evolution of *Hypostomus*, then Amazon basin species should have chromosomal numbers close to $2n = 54$ and a single NOR in the terminal position. However, although *Hypostomus* species have been described from the Amazon River basin (Weber, 2003; Zawadzki *et al.*, 2008a) only *H. emarginatus* has been karyotyped. If we consider that some authors consider *H. emarginatus* as pertaining to the genus *Squaliforma* (Weber 2003; Ferraris 2007; Eschmeyer, 2011), then, to date, no nominal *Hypostomus* species from the Amazon River basin have been karyotyped. Clearly, an adequate understanding of the karyotypic evolutionary history of *Hypostomus* requires detailed cytogenetic studies of Amazonian species.

Acknowledgments

The authors thank Cristiane K. Shimabukuro-Dias and Osvaldo T. Oyakawa for their critic analysis and suggestions on the manuscript, José A. Senhorini for help in collecting samples from the Mogi-Guaçu River, José Carlos P. Alves for help in collecting samples from Carrapato Stream and Renato Devidé for technical assistance. We also thank Centro de Pesquisa e Treinamento em Aquicultura (CEPTA) and Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura (Nupelia) for logistic support. This study was partially supported by grants from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), Coordenadoria de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grant nos. 140644/2005-9, 300314/2003-5 and 306066/2009-2 to E.R.M.M., C.O. and C.H.Z., respectively).

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Associate Editor: Yatiyo Yonenaga-Yassuda

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