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Karyotype characterization and ZZ/ZW sex chromosome heteromorphism in two species of the catfish genus *Ancistrus* Kner, 1854 (Siluriformes: Loricariidae) from the Amazon basin

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We present karyotypic characteristics and report on the occurrence of ZZ/ZW sex chromosomes in *Ancistrus ranunculus* (rio Xingu) and *Ancistrus* sp. "Piagaçu" (rio Purus), of the Brazilian Amazon. *Ancistrus ranunculus* has a modal number of 2n=48 chromosomes, a fundamental number (FN) of 82 for both sexes, and the karyotypic formula was 20m+8sm+6st+14a for males and 19m+9sm+6st+14a for females. *Ancistrus* sp. "Piagaçu" presented 2n=52 chromosomes, FN= 78 for males and FN= 79 for females. The karyotypic formula was 16m+8sm+2st+26a for males and 16m+9sm+2st+25a for females. The high number of acrocentric chromosomes in karyotype of *Ancistrus* sp. "Piagaçu" differs from the majority of Ancistrini genera studied so far, and may have resulted from pericentric inversions and translocations. The lower number of chromosomes in *A. ranunculus* indicates that centric fusions also occurred in the evolution of *Ancistrus* karyotypes. We conclude that karyotypic characteristics and the presence of sex chromosomes can constitute important cytotaxonomic markers to identify cryptic species of *Ancistrus*. However, sex chromosomes apparently arose independently within the genus and thus do not constitute a reliable character to analyze phylogenetic relations among *Ancistrus* species.

Nós apresentamos características cariotípicas e registramos a ocorrência de cromossomos sexuais ZZ/ZW em *Ancistrus ranunculus* (rio Xingu) e *Ancistrus* sp. "Piagaçu" (rio Purus), da Amazônia Brasileira. *Ancistrus ranunculus* teve um número modal de 2n=48 cromossomos, um número fundamental (NF) de 82 para ambos os sexos, e a fórmula cariotípica 20m+8sm+6st+14a para machos e 19m+9sm+6st+14a para fêmeas. *Ancistrus* sp. "Piagaçu" apresentou 2n=52 cromossomos, NF=78 para machos e NF= 79 para fêmeas. A fórmula cariotípica foi de 16m+8sm+2st+26a para machos e 16m+9sm+2st+25a para fêmeas. O alto número de cromossomos acrocêntricos no cariótipo de *Ancistrus* sp. "Piagaçu" difere da maioria dos gêneros de Ancistrini estudada até o momento, e pode ter resultado de inversões pericêntricas e translocações. O número mais baixo de cromossomos em *A. ranunculus* indica que fusões cêntricas também ocorreram na evolução dos cariótipos de *Ancistrus*. Nós concluímos que as características cariotípicas e a presença de cromossomos sexuais podem constituir marcadores citotaxonômicos importantes para identificar espécies crípticas de *Ancistrus*. Entretanto, cromossomos sexuais aparentemente surgiram de forma independente dentro do gênero e, deste modo, não constituem um caráter confiável para ser usado em análises de relações filogenéticas entre espécies de *Ancistrus*.

Key words: Hypostominae, Ancistrini, Cytogenetics, Evolution, Heterochromatin.

Introduction

Loricariidae is the largest family in the Siluriformes, with 683 valid species distributed across the entire Neotropical region (Isbrücker, 1980; Reis *et al*., 2003). The family is currently divided into six subfamilies: Delturinae, Hypoptopomatinae, Hypostominae, Lithogeneinae, Loricariinae, and Neoplecostominae (Reis *et al*., 2006). Within the Hypostominae, the tribe Ancistrini has been the subject of few taxonomic studies and its position within the subfamily is controversial (Isbrücker, 1980; Howes, 1983; Schaefer, 1987; Montoya-Burgos *et al*., 1998).

Ancistrini presently includes 217 valid species in 27 genera (Fish-Muller, 2003). Cytogenetic studies of this tribe, as well as of Loricariids overall, are scarce relative to the number of species involved. Only 23 species from seven genera (*Ancistrus*, *Baryancistrus, Hemiancistrus, Megalancistrus, Panaque, Parancistrus*, and *Peckoltia*) have been analyzed

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cytogenetically, most of then exhibiting the supposedly ancestral diploid number of 2n=52 chromosomes, predominantly meta- and submetacentrics (Artoni & Bertollo, 2001; Souza, 2003; Souza *et al*., 2004; de Oliveira *et al*., 2006). Only species of the genus *Ancistrus* have shown diploid numbers that deviate from this condition, and the presence of a high number of acrocentric chromosomes, *e.g. Ancistrus* n. sp. (Alves *et al*., 2003), *Ancistrus* cf. *dubius* (Mariotto *et al*., 2004), *Ancistrus* n. sp.1 (Alves *et al*., 2006) and *Ancistrus* cf. *dubius* (Mariotto & Miyazawa, 2006).

In Neotropical freshwater fishes, the most frequent morphologically differentiated sex chromosome system is ZZ/ZW, making up 63% (39 of 62) of described cases (Galetti *et al*., 1981; Haaf & Schmid, 1984; Feldberg *et al*., 1987; Bertollo & Cavallaro, 1992; Moreira-Filho *et al*., 1993; Centofante *et al*., 2002). Five occurrences of this type of sex chromosome system have been observed in the Loricariidae, of which two refer to species of Ancistrini: *Ancistrus* cf. *dubius* and *Hemiancistrus spilomma* (Andreata *et al*., 1993; Scavone & Julio Jr., 1995; Artoni *et al*., 1998; Mariotto *et al*., 2004; de Oliveira *et al*., 2006).

Here we present the karyotypic structure and record the occurrence of ZZ/ZW sex chromosomes of two species of the genus *Ancistrus* and discuss possible mechanisms involved in the differentiation of this sex chromosomes.

Material and Methods

Ancistrus ranunculus Muller *et al*., 1994: five specimens (three males and two females) acquired from ornamental fish exporters (Turkys Aquarium, Manaus), from the rio Xingu, Altamira, Pará (03º15'21"S, 52º12'45"W) (Fig. 1a).

Ancistrus sp. "Piagaçu": seven specimens (three males and four females) collected in lago Aiapuá, on the left bank of the rio Purus, in the Piagaçu-Purus Sustainable Development Reserve (04º27'26"S, 62º11'56"W). This apparently undescribed species (S. Fish-Muller, pers. comm.) presents the following color pattern: dorsal region dark grey with small white spots; ventral region yellowish grey with well-defined stipples, that in smaller specimens resemble ocelli; dorsal fin dark grey with pale stipples (Fig. 1b).

Voucher specimens were deposited in the fish collection at the Instituto Nacional de Pesquisa da Amazônia (INPA) (*Ancistrus ranunculus*: INPA 25624; *Ancistrus* sp. "Piagaçu": INPA 25630).

Chromosomal preparations were obtained from kidney cells, following the "air-drying" technique of Bertollo *et al*. (1978). Approximately 30 metaphasic plates were analysed for each individual. The constitutive heterochromatin was identified according to Sumner (1972) and the nucleolar organizing regions (NORs) were detected using the technique

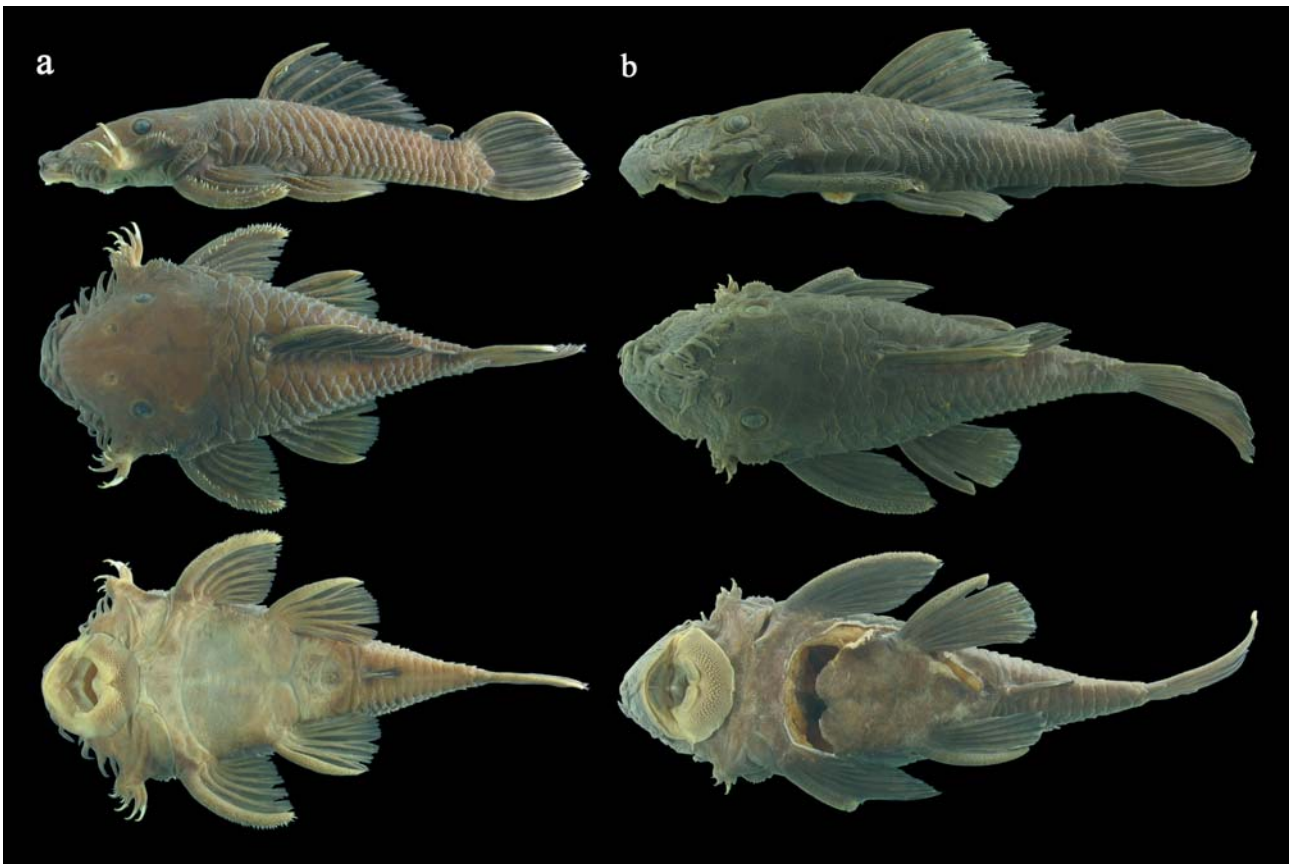

Fig. 1. Lateral, dorsal and ventral views of *Ancistrus ranunculus*, INPA 25624, 103 mm SL (a), and of *Ancistrus* sp. "Piagaçu", INPA 25630, 128 mm SL (b).

described by Howell & Black (1980). Chromosome morphology was based on arm ratios (long arm length divided by short arm length), as proposed by Levan *et al*. (1964). Chromosomes were classified as metacentric (m), submetacentric (sm), subtelocentric (st), or acrocentric (a). The fundamental number (FN) or arm number was determined by considering meta-, submeta- and subtelocentric chromosomes with two arms and acrocentrics with only one.

Results

Ancistrus ranunculus has a modal number of 2n=48 chromosomes and a fundamental number of 82 for both sexes; however, the karyotypic formula was different for males (20m+8sm+6st+14a) and females (19m+9sm+6st+14a). Sex chromosomes of the type ZZ/ZW were found in this species, with the Z being a small metacentric, and the W a medium sized submetacentric. The NORs are located in the region proximal to the long arms of pair 16. We also observed a size heteromorphism of the NORs between the homologues (Fig. 2).

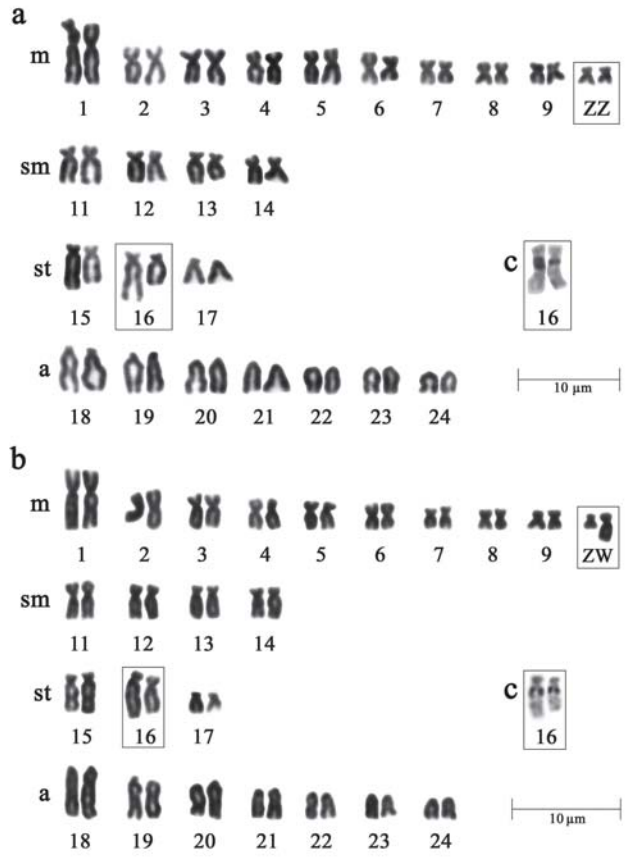

Fig. 2. Karyotypes of male (a) and female (b) *Ancistrus ranunculu*s after conventional Giemsa-staining, evidencing the sex chromosomes (box) and the NOR-bearing chromosomes after silver-staining (c). m= metacentric; sm= submetacentric; st= subtelocentric; a= acrocentric.

Ancistrus sp. "Piagaçu" has a modal number of 2n=52 chromosomes and a fundamental number of 78 for males and 79 for females. The karyotypic formula is 16m+8sm+2st+26a for males and 16m+9sm+2st+25a for females. ZZ/ZW chromosomes were also found in this species, the Z chromosome being a large acrocentric, and the W a small submetacentric. The NORs are found on the short arms of pair 26 (Fig. 3).

Ancistrus ranunculus has conspicuous blocks of heterochromatin in the distal region of pairs 18, 20, 21, and 24; smaller blocks in the proximal region of pair 16; and a small pericentromeric block on pair 9. One of the chromosomes of pair 10 has, along with the small pericentromeric blocks observed in its homologue, a considerable portion of heterochromatin on the long arm in the female karyotype (Fig. 4a). In *Ancistrus* sp. "Piagaçu" we found small pericentromeric blocks on pairs 1, 9, 14, 15, 17, 22, 23, 24, and 25; interstitial blocks on the long arms of pairs 2 and 4 and on the short arm of pair 2; small distal blocks on the short arms of pair 1; and conspicuous distal blocks on the short arms of pair 26 (Fig. 4b). In this species, sex chromosomes did not exhibit heterochromatin blocks. In both species, the NORs were coincident with blocks of heterochromatin (Fig. 4).

Discussion

The Ancistrini has the supposedly ancestral diploid number of 2n=52 chromosomes, the majority of which are meta- and submetacentric (Artoni & Bertollo, 2001; Alves *et al*., 2003). We found *Ancistrus* sp. "Piagaçu" to have the supposedly ancestral diploid number, yet its karyotype is composed of a high number of acrocentric chromosomes, a characteristic different from the majority of the Ancistrini species that have been studied so far. Pericentric inversions and translocations may be the principal rearrangements responsible for the differentiation of the karyotype in this species. The presence of 2n=48 chromosomes in *A. ranunculus* corroborates the hypothesis of Alves *et al*. (2003), who suggest that centric fusions, like chromosome rearrangement, predominate in the evolution of *Ancistrus* karyotypes.

In a comparative karyotypic analysis of males and females, we found morphologically differentiated sex chromosomes of the type ZZ/ZW in both studied species. In *A. ranunculus* the Z chromosome is represented by a small metacentric (corresponding to one of the homologues of pair 10 of the complement), and the W chromosome by a medium sized submetacentric. In *Ancistrus* sp. "Piagaçu" the Z chromosome is a large acrocentric (pair 16) and the W is a small submetacentric.

The initial heterochromatization seems to be the principal factor in the differentiation of the majority of ZZ/ZW systems in fish, generally resulting in an increase in the size of the W chromosomes. Examples of this can be found in some species in the anostomid genus *Leporinus* (Galetti *et al*., 1981; Galetti & Foresti, 1986; Galetti *et al*., 1995; Venere *et al*., 2004); in the prochilodontid *Semaprochilodus taeniurus* (Feldberg *et al*.,

1987) and in the Hypoptopomatinae loricariid *Microlepidogaster leucofrenatus* (Andreata *et al*., 1993); and in two species of the parodontid genus *Parodon* (Moreira-Filho *et al*., 1993; Centofante *et al*., 2002). However, past structural rearrangements seem to have occurred and many times are associated with repetitive sequences of DNA, as suggested for the differentiation of the W chromosome in species of the genus *Triportheus* (Artoni *et al*., 2001; Artoni & Bertollo, 2002).

In the genus *Ancistrus*, the heterochromatization process is involved in the differentiation of the sex chromosome system of *Ancistrus* cf. *dubius* (Mariotto *et al*., 2004) and *A. ranunculus* (present study), however, the suggested pathway for these two differentiations seems to be distinct. In *Ancistrus* cf. *dubius*, there was an accumulation of heterochromatin over chromosome Z, followed by the loss of this heterochromatin segment in W, in such a way that it appears much smaller and only possesses homology with the euchromatic segment of the Z chromosome. In *A. ranunculus*, the W chromosome is almost completely heterochromatic, with a considerable portion of heterochromatin on the long arm, while the Z chromosome is much smaller and has only a small block of heterochromatin in the centromeric position.

The differentiation of sex chromosomes may also be linked to structural rearrangements, resulting in the prevention of meiotic recombination (Beçak & Beçak, 1969; Almeida-Toledo *et al*., 2000). Nevertheless, these events are more related to the emergence of multiple sex chromosome systems, as seen in the parodontid *Apareiodon affinis* (Moreira-Filho *et al*., 1980), in the sternopygid *Eigenmania* sp. (Almeida-Toledo *et al*., 1984), and in some populations of the erythrinid *Hoplias malabaricus* (Bertollo *et al*., 1997). While uncommon among species that have the simple ZZ/ZW mechanism, structural rearrangements seem to play an important role in the differentiation of sex chromosomes in the loricariids *Loricariichthys platymetopon* (Scavone & Júlio Jr., 1995) and *Hypostomus* sp. (Artoni *et al*., 1998). For these species, it has been suggested that a pericentric inversion in an acrocentric chromosome similar to the Z chromosome, followed by a loss of chromosomic material, could have originated the W chromosome. We believe that a similar process has occurred in *Ancistrus* sp. "Piagaçu" since we did not find any heterochromatin blocks on the Z (large acrocentric) or W (small submetacentric) sex chromosomes.

The differentiation of sex chromosomes in Neotropical freshwater fish seems to have resulted from independent events, and its presence does not relate to species' phylogenetic relationships (Almeida-Toledo & Foresti, 2001).

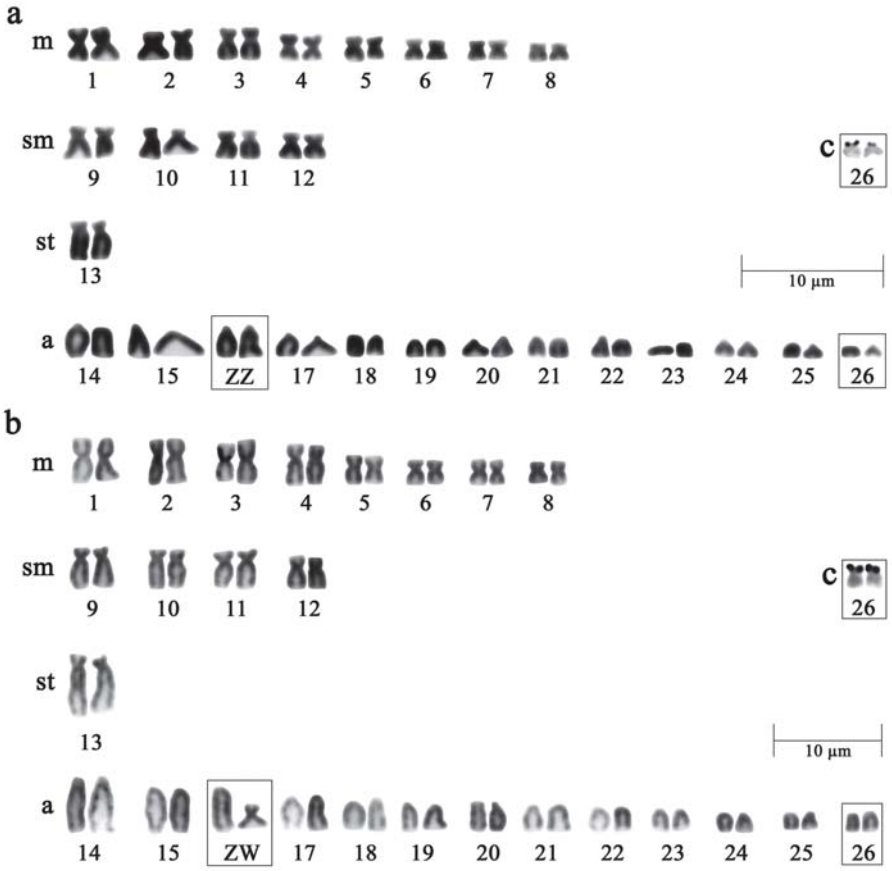

Fig. 3. Karyotypes of male (a) and female (b) *Ancistrus* sp. "Piagaçu" after conventional Giemsa-staining, evidencing the sex chromosomes (box) and the NOR-bearing chromosomes after silver-staining (c). m= metacentric; sm= submetacentric; st= subtelocentric; a= acrocentric.

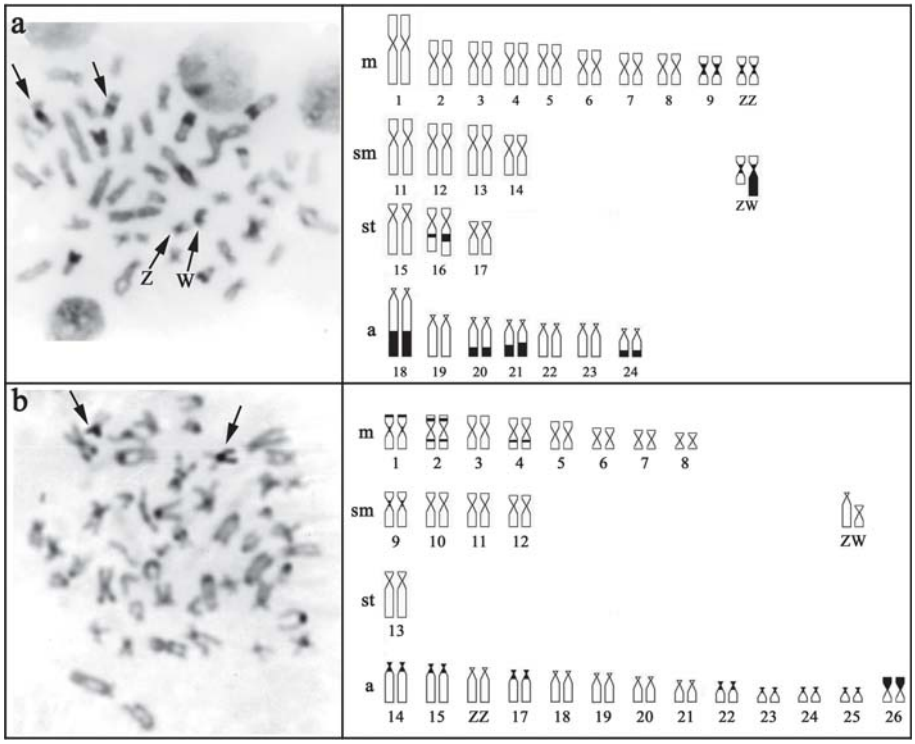

Fig. 4. Metaphase and idiogram showing the distribution of constitutive heterochromatin after C-banding technique in *Ancistrus ranunculus* (a) and in *Ancistrus* sp. "Piagaçu" (b). Arrows indicate the NOR-bearing chromosomes with positive C-banding. m= metacentric; sm= submetacentric; st= subtelocentric; a= acrocentric.

Nevertheless, in *Triportheus* (Characidae) all species analyzed share a ZZ/ZW mechanism that may have originated in a common ancestor for this genus (Artoni *et al*., 2001; Artoni & Bertollo, 2002). The occurrence of ZZ/ZW sex chromosomes in *Ancistrus* species probably do not represent a synapomorphy for the group, since they involve different chromosome pairs that vary in both size and morphology and probably resulted from distinct differentiation processes. Only *A. ranunculus* shows the most common mechanism observed among fish with ZZ/ZW sex chromosomes, characterized by an increase in the size of chromosome W through the accumulation of heterochromatin.

Ancistrus is a species-rich loricariid genus that seems to contain a large number of morphologically similar, undescribed species (S. Fish-Muller, pers. comm.). The results presented herein indicate that chromosome macrostructure, and especially the presence of sex chromosomes, represent important cytotaxonomic markers, which can help in the identification of cryptic species of that genus. However, sex chromosomes apparently arose independently within the genus and thus do not constitute a reliable character to analyze phylogenetic relations among *Ancistrus* species.

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