



# Integrative taxonomy reveals a new species of Neotropical headstanding fish in genus *Schizodon* (Characiformes: Anostomidae)

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*Schizodon* encompasses approximately 15 species of Neotropical headstanding fishes. Integrative taxonomy, combining molecular and morphometric analyses with traditional taxonomic methods, was used to investigate *Schizodon vittatus* and its potential new sister species. Molecular differences between the two species in the barcode are greater than intra-specific variation recovered in species of *Schizodon*, and the two species represent distinct lineages for approximately one million years. The two species are morphologically very similar, and the meristic data showed great overlap. Morphometric analyses also showed overlap among the putative species but indicated differences in caudal-peduncle depth, orbital diameter, and length of anal-fin rays. Color pattern seems to provide a clear diagnostic feature for the two species. *Schizodon vittatus* usually has four dark brown transversal bars on body, and its sister species has three conspicuous bars, with the fourth, if present, inconspicuous and dorsal to the lateral line. *Schizodon vittatus* is redescribed based on the type and recently collected specimens, its type locality is revisited, and its known distribution restricted to the Araguaia and Tocantins drainages. The new species, sister to *S. vittatus*, distributed in the Xingu and Tapajós drainages, is described. A key for the identification of the Amazon clade species of *Schizodon* is provided.

**Keywords:** Amazon, Identification key, Ostariophysi, Systematics, Taxonomy.

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*Schizodon* engloba aproximadamente 15 espécies de peixes neotropicais. A taxonomia integrativa, combinando análises moleculares e morfométricas com métodos taxonômicos tradicionais, foi utilizada para investigar *Schizodon vittatus* e sua potencial espécie irmã. As diferenças moleculares (DNA barcoding) entre as duas espécies são maiores do que a variação intraespecífica observada em espécies congêneres, e as duas espécies representam linhagens distintas por aproximadamente um milhão de anos. As duas espécies são morfologicamente muito similares e os dados merísticos mostram grande sobreposição. As análises morfométricas também mostraram sobreposição entre as duas espécies, mas indicaram diferenças na altura do pedúnculo caudal, no diâmetro interorbital, e no comprimento dos raios da nadadeira anal. O padrão de colorido parece fornecer uma característica diagnóstica clara para as duas espécies. *Schizodon vittatus* normalmente possui quatro faixas escuras transversais no corpo e sua espécie irmã tem três faixas, com a quarta, se presente, inconspícua e dorsal à linha lateral. *Schizodon vittatus* é redescrita com base no tipo e em espécimes coletados recentemente; sua localidade tipo é revisitada e a sua distribuição conhecida é restringida às drenagens do Araguaia e Tocantins. A nova espécie, irmã de *S. vittatus* e distribuída nas drenagens do Xingu e Tapajós, é descrita. Uma chave para a identificação das espécies do clado amazônico de *Schizodon* é apresentada.

**Palavras-chave:** Amazônia, Chave de identificação, Ostariophysi, Sistemática, Taxonomia.

## INTRODUCTION

Integrative taxonomy is a comprehensive framework to delimit and describe taxa by integrating data from different character sources, usually combining molecular and morphological data (Dayrat, 2005; Pante *et al.*, 2015). The general idea is that by applying multiple tests, stronger species hypotheses are recovered (de Queiroz, 2007; Schlick-Steiner *et al.*, 2010). This new approach has been successfully applied to Neotropical freshwater fishes, including erythrinids (Rosso *et al.*, 2018), characids (Guimarães *et al.*, 2019), and serrasalmids (Ota *et al.*, 2020), among others.

Anostomidae is the second richest family of Characiformes (Fricke *et al.*, 2020) and, as generally occurs in Neotropical freshwater fish groups, anostomid species are still being discovered and described at exponential rates (Reis *et al.*, 2016; Birindelli, Sidlauskas, 2018). The traditional taxonomy for Anostomidae is based mainly on the color pattern, teeth number, morphology, and scale counts (Steindachner, 1875; Garavello, Britski, 1990; Garavello, 1994; Britski *et al.*, 2012). Combining features from these morphological character complexes was sufficient to recognize almost all species considered valid today. However, with the advance of molecular data, a few studies focused on investigating species diversity applying DNA barcoding and species delimitation analyses have revealed species that are not easily distinguished based exclusively on traditional characters (*e.g.*, Ramirez *et al.*, 2017a, 2020). Concomitantly, some taxa were recently investigated and described using the combination of morphological and molecular data

(e.g., Burns *et al.*, 2017; Ramirez *et al.*, 2017b; Birindelli *et al.*, 2020a,b).

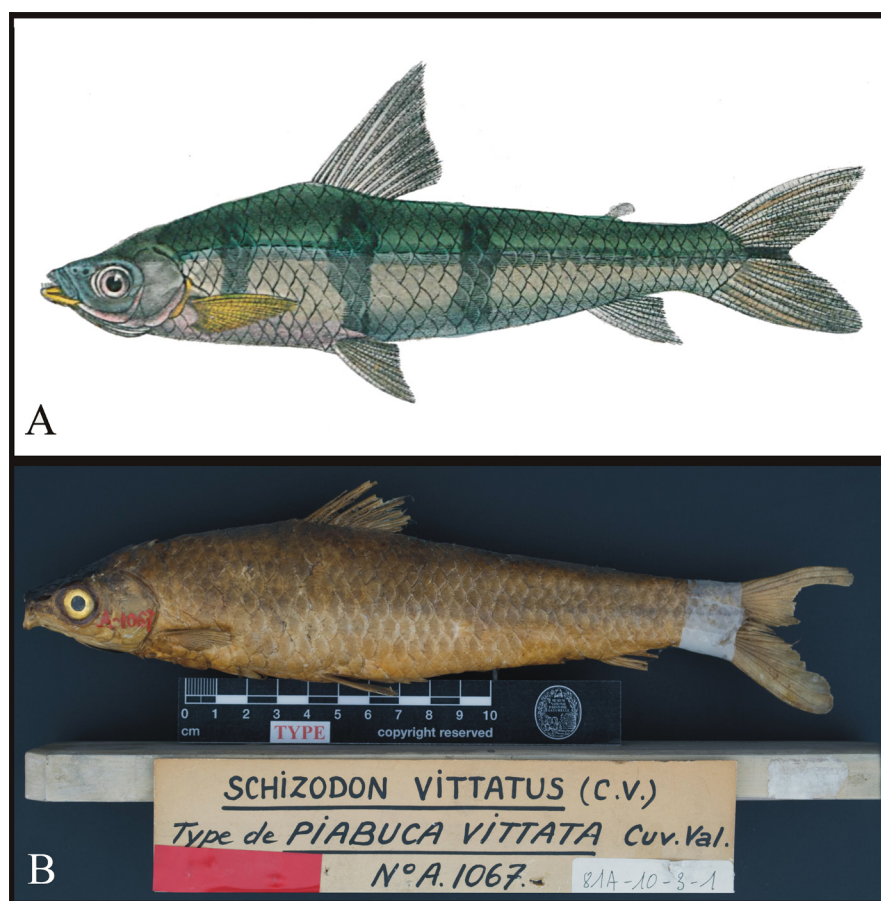
DNA barcoding and species delimitation analyses applied to investigate the species diversity in the anostomid genus *Schizodon* Agassiz, 1829 revealed hidden, unknown or underestimated diversity, as well as a possible case of synonymy (Ramirez *et al.*, 2020). *Schizodon* is the second most diverse genus of the family, encompassing 15 valid species (Bergmann, 1988; Garavello, Britski, 1990; Garavello, 1994; Garavello, Britski, 2003; Sidlauskas *et al.*, 2007; Garavello, Britski, 2019). Firstly, the species of the genus were split by Garavello (1994) into four groups according to color pattern. Then, the species were rearranged into two groups, recovered as monophyletic in a molecular phylogenetic analysis (Ramirez *et al.*, 2020). The first of these groups, named the Amazonas clade, includes seven species with disjunct distributions: *S. borellii* (Boulenger, 1900) occurring in the Paraguay basin, *S. corti* Schultz, 1944 (tentatively assigned to that group based on its similarity to *S. fasciatus* Spix & Agassiz, 1829) occurring in the lake Maracaibo, *S. dissimilis* (Garman, 1890) occurring in the Pindaré-Mearim, Itapecuru, and Parnaíba basin, in northeastern Brazil, *S. fasciatus* widespread in the Amazon basin and coastal rivers of the Guianas, *S. intermedius* Garavello & Britski, 1990 endemic to the upper Paraná basin, *S. scotorhabdotus* Sidlauskas, Garavello & Jellen, 2007 distributed in the Orinoco basin, and *S. vittatus* (Valenciennes, 1850) from the Araguaia and Tocantins drainages. The Amazonas clade is characterized by conspicuous dark vertical bars on flanks formed by epidermal pigments. On the other hand, the La Plata clade is diagnosable by lacking such conspicuous dark bars, and by the presence of inconspicuous dark vertical bars formed by dermal pigment, associated with a conspicuous dark horizontal blotch at the base of median caudal-fin rays. This latter group includes *S. altoparanae* Garavello & Britski, 1990, *S. australis* Garavello, 1994 (herein tentatively assigned based on its similarity to *S. platae* (Garman, 1890)), *S. isognathus* Kner, 1858, *S. jacuiensis* Bergmann, 1988, *S. knerii* (Steindachner, 1875), *S. nasutus* Kner, 1858, and *S. platae*.

The taxonomic history of *Schizodon vittatus* started more than 150 years ago when Valenciennes (1850) described *Piabuca vittata* as a new species based on material collected by François de Laporte, Comte de Castelnau, in the Araguay (=Araguaia) river, Brazil. Shortly after, Castelnau (1855) illustrated the species (Fig. 1), described the living coloration and transcribed Valenciennes's original description. The species was transferred to *Anostomus* Scopoli, 1777 by Günther (1864), along with *Schizodon fasciatus*. In that contribution, Günther (1864) classified all known anostomids into three genera: *Anostomus* (8 species), *Rhytiodus* Kner, 1858 (2 species), and *Leporinus* Agassiz, 1829 (14 species). Garman (1890) provided the first taxonomic revision of *Anostomus sensu* Günther (1864), mainly based on specimens collected by Louis Agassiz's Thayer Expedition and deposited at the Museum of Comparative Zoology (Harvard University). He considered *Anostomus vittatus* closely allied to *A. fasciatus* and *A. dissimilis*, all belonging to the subgenus *Schizodon*. Garman (1890) listed specimens of *S. vittatus* from two localities: Porto de Moz (MCZ 19385, MCZ 19386) and Goyaz (MCZ 19391, MCZ 19390, MCZ 30915). Whereas the first locality is in the Xingu basin, the second is likely in the Araguaia or Tocantins drainages (Isbrücker, 1973; Lima, 2004). Eigenmann's classification raised *Schizodon* to generic rank (Eigenmann, 1910, 1912).

Géry (1977:154) suggested that *S. vittatus* was a variation of *S. fasciatus*, in which the dark stripe on the caudal peduncle would mask the caudal-fin blotch characteristic of

the latter species. Similarly, Sidlauskas, Vari (2012) tentatively identified some specimens from the Guianas as *S. vittatus* noticing a variation in the color pattern mixing specimens of *S. fasciatus* and *S. vittatus*. Although the blotch at the base of the caudal fin is typical in large (more than 150 mm SL) specimens of *S. fasciatus*, small specimens (up to 130 mm SL) may or may not have a dark lateral stripe on the flanks and caudal peduncle. It is likely that the specimens previously identified as *S. vittatus* by Sidlauskas, Vari (2012) were small specimens of *S. fasciatus*.

New records of *Schizodon vittatus* were published by Camargo *et al.* (2004, 2005), and Dagosta, de Pinna (2017) expanding the known distribution to the Tapajós and Xingu drainages. In Ramirez *et al.* (2020), the specimens previously identified as *S. vittatus* from the Xingu and Tapajós river drainages were recovered as a distinct molecular operational taxonomic unit (MOTU) relative to those of the Araguaia and Tocantins basins. Herein, we combine morphometric and molecular-based analyses with traditional taxonomy (based on color pattern and meristic data) to evaluate the putative distinction between the Xingu-Tapajós and the Araguaia-Tocantins samples previously identified as conspecific. As results, *S. vittatus* is herein redescribed, and a new species from Xingu-Tapajós basins is described and named.



**FIGURE 1** | *Schizodon vittatus*. **A.** drawing published by Castelnau (1855) illustrating the holotype; **B.** holotype of *Piabuca vittata*, MNHN-IC-A-1067, 285.0 mm SL, Brazil, Araguaia River (source: <http://coldb.mnhn.fr/catalognumber/mnhn/ic/a-1067>).

## MATERIAL AND METHODS

**Sampling.** We focused our analyses on the specimens previously identified as *Schizodon vittatus* in the literature (see Introduction), thus encompassing individuals from the Araguaia, Tocantins, Tapajós, and Xingu drainages in Brazil. Specimens were gathered into two groups (Xingu and Tapajós *vs.* Araguaia and Tocantins), as slight variation was observed among specimens of each of these groups, whereas considerable differences were observed between these groups. Nevertheless, comparisons included all congeners, especially those of the Amazonas clade of *Schizodon sensu* Ramirez *et al.* (2020): *S. borellii*, *S. corti*, *S. scotorhabdotus*, *S. dissimilis*, *S. intermedius*, *S. fasciatus*, and *S. vittatus*. Even though *S. corti* is herein tentatively assigned to this group based on its similarity to *S. fasciatus* (see Vari, Raredon, 1991 for details on the similar features), the species is lacking in our analyses due to absence of specimens and tissue samples. Also, the putative specimens of *S. vittatus* from Guianas (Sidlauskas, Vari, 2012) were considered specimens of *S. fasciatus* in our study. A total of 73 specimens of *S. vittatus* from the Araguaia and Tocantins drainages were examined, from which measurements and meristic data were taken from 20. A total of 49 specimens from the Xingu and Tapajós basins were examined from which measurements and meristic data were taken from 41.

Institutional abbreviations include: Museum of Comparative Zoology, Cambridge (MCZ); National Museum of Natural History, Smithsonian Institution, Washington DC. (USNM); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Museu Nacional, Universidade Federal Rio de Janeiro, Rio de Janeiro (MNRJ); Muséum national d'Histoire naturelle, Paris (MNHN); The Academy of Natural Sciences of Drexel University, Philadelphia (ANSP); Field Museum of Natural History, Chicago (FMNH); Museu de Zoologia da Universidade Estadual de Londrina, Londrina (MZUEL); Laboratório de Ictiologia Sistemática do Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Carlos, São Carlos (LISDEBE); Coleção de Peixes da Universidade Federal do Mato Grosso, Cuiabá (CPUFMT); and Laboratório de Ictiologia de Altamira, Altamira (LIA).

**Traditional methods.** Meristic data, including scale and rays counts, were taken according to Garavello (1994). Clear and double-stained specimens (c&s) prepared according to Taylor, van Dyke (1985) were used for counts, and descriptions of position and shape of the infraorbital series bones, premaxillary and dentary teeth, branchiostegal rays, and unbranched and branched fin rays. Meristic counts include the number of teeth in each maxilla, unbranched and branched fin rays, lateral-line scales, transverse scales (from dorsal-fin origin to pelvic-fin), predorsal scales, preanal scales and circumpeduncular scale series. Specimens were photographed live in the field or preserved and immersed in ethanol solution in a fish tank with black or white background. Photographs were edited and combined into plates to maximize comparisons of color pattern.

**Morphometric analyses.** Measurements were taken following Garavello (1994) and include fifteen point-to-point variables: standard length, head length, trunk length, body depth, predorsal distance, snout length, interorbital width, orbital diameter,



caudal peduncle depth, first anal-fin ray length, ninth anal-fin ray length, inter-opercle width, head depth, maxillary length and mandible width. All measurements were taken preferably on the left side of the specimen using a digital caliper with a precision of 0.1 mm.

Morphometric data were submitted to multivariate analyses. Principal Component Analysis (PCA) with log-transformed measurements of both species and using the covariance matrix was applied according to Bookstein *et al.* (1985), and sheared *a posteriori* following MacLeod (1990). Shearing method creates a set of principal components in which the second and higher components index size-independent variation among groups. Additionally, log-transformed measurements of specimens with more than 200 mm SL were submitted to a Canonical Variate Analysis (CVA) that evaluated whether *a priori* groups (samples of *S. vittatus* and of the new species from Xingu and Tapajós drainages) were diagnosable. The CVA was performed using PAST software version 4.03 (Hammer *et al.*, 2001) as did the assignment of specimens to each *a priori* group cross-validation by jackknife procedure.

**Molecular analyses.** All molecular procedures regarding extraction, amplification and sequencing were detailed in Ramirez *et al.* (2020). The genetic data used therein and herein included the DNA barcoding sequence, in our case, a fragment of approximately 698 bp of cytochrome C oxidase subunit I (COI), and partial sequences of cytochrome B (CytB, ~1110 bp), myosin heavy chain 6 of cardiac muscle alpha gene (Myh6, ~750 bp), recombination-activating gene 1 (RAG1, ~1500 bp), and recombination-activating gene 2 (RAG2, ~1100 bp). DNA barcoding sequence (COI) was obtained from five specimens from the Xingu-Tapajós, and eight from the Araguaia-Tocantins. Other genetic markers were sequenced for one specimen of each group. A complete list of specimens and GenBank accession numbers used in the genetic analyses are available in Ramirez *et al.* (2020: tabs. 1–2). A subset of the COI sequences matrix used in Ramirez *et al.* (2020) including exclusively 60 samples of the Amazonas clade species, was submitted to two analyses. The first included a Pairwise K2 P genetic distance analysis, calculating standard error via bootstrap procedure with 1.000 replicates. The second included an evolutionary analysis by Maximum Likelihood (ML) method and General Time Reversible G+I model (Nei, Kumar, 2000). Six *Schizodon platae* sequences were added to the matrix and that taxon was used as the tree root. Support values were assessed using 1.000 bootstrap replicates. Both analyses were performed in MEGA X (Kumar *et al.*, 2018; Stecher *et al.*, 2020). To illustrate the phylogenetic relationships of the species of the Amazonas clade, the species tree obtained in Ramirez *et al.* (2020) via calibrated Bayesian analysis performed in \*BEAST v2.6 (Star-BEAST) (Heled, Drummond, 2010) and using sequences of COI, RAG1, RAG2, CytB and Myh6 were edited in FigTree v1.4.3 (Rambaut, 2016). Details on the parameters used in the dated Bayesian analysis are available in Ramirez *et al.* (2020).

## RESULTS

Based on molecular and morphometric analyses and study of color patterns, our results are congruent and strongly support the hypothesis that specimens previously identified

as *Schizodon vittatus* actually represent two distinct species. Because the type locality of *S. vittatus* is in the Araguaia River, specimens from Araguaia and Tocantins drainages are identified as *S. vittatus*, whereas those from the Xingu and Tapajós are described further below as a new species named *Schizodon trivittatus*. The new species-name is used in the subsequent sections.

**Molecular analyses.** The overall mean genetic distance in the COI sequence among the seven species of the Amazonas clade of *Schizodon* is 3.4% (Tab. 1). The genetic distance is greatest (over 4%) between *S. scotorhabdotus* and *S. dissimilis*, and smaller among the five remaining species (up to 3.8%). The genetic distance is lowest between *S. borellii* and *S. intermedius*, with a mean of 1.1%. The genetic distance among the three other species (*S. fasciatus*, *S. trivittatus* and *S. vittatus*) is also relatively low, ranging from 1.9% to 2.9%. Each one of the *S. fasciatus* group species has an average intraspecific genetic distance much lower than any average distance between species (interspecific distances). The genetic distances among the fourteen specimens of *Schizodon fasciatus* from distinct locations along the Amazon basin is 0.2%.

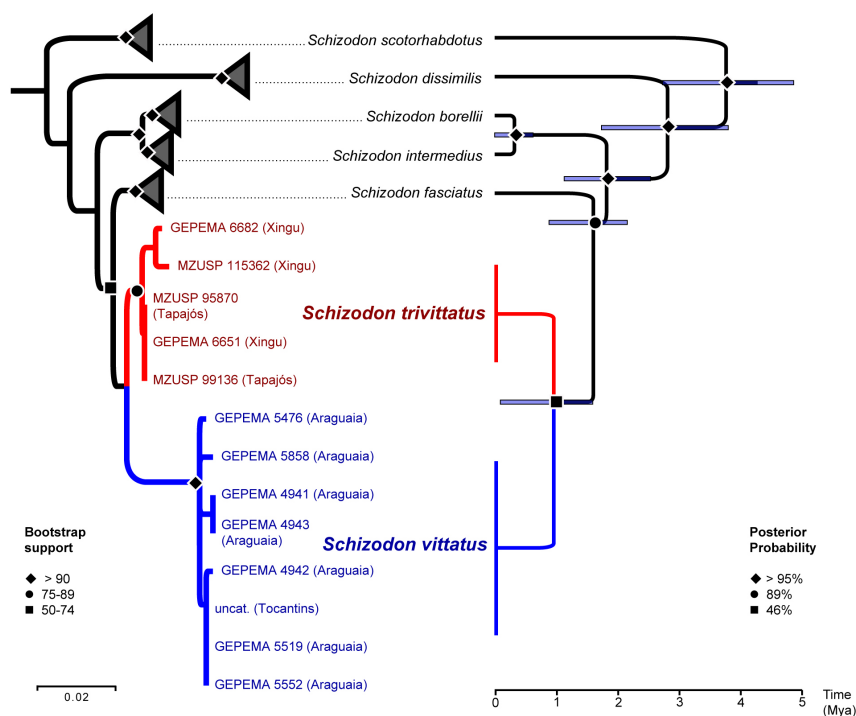
The ML analysis based on COI and the dated Bayesian analysis based on COI and other genes recovered *Schizodon trivittatus* and *S. vittatus* as sister taxa. Moreover, both species share the presence of a dark midlateral stripe on the caudal peduncle that is not present in other closely related species. The monophyly of *S. vittatus* have more than 90% bootstrap support whereas *S. trivittatus* monophyly have 75–89% (Fig. 2). The age of the most recent common ancestor of *S. vittatus* and *S. trivittatus* was calculated as approximately 1.0 Mya (mean of 1.03, 95% height between 0.01 and 1.67).

**Morphometric analyses.** In the principal components analysis, PC1 explained 93.84% of variance and PC2 and PC3 explained 1.83% and 1.17% of the total variance, respectively (Tab. 2). There is an overlap between *S. vittatus* and *S. trivittatus* along the sheared PC2 and sheared PC3 (Fig. 3). The heaviest loadings on PC2 were: ninth anal-fin ray length (-0.7743), trunk length (0.3232), maxillary length (0.2791) and first anal-

**TABLE 1 |** Pairwise K2P genetic distances among species of the Amazonas clade of *Schizodon* based on COI sequences (603 base pairs). Numbers in bold (diagonal) represent the genetic distance within sample, whereas the mean genetic distances among samples are indicated below diagonal, with values of standard error above diagonal. Groups were ordered based on Maximum Likelihood analysis. The overall mean genetic distance equals 3.4% ±0.5%.

	1	2	3	4	5	6	7
1. <i>S. borellii</i> (Paraguay, n = 7)	<b>0.2%</b>	1.0%	0.7%	0.4%	0.9%	0.7%	0.8%
2. <i>S. dissimilis</i> (Pindaré-Mearim, n = 18)	5.1%	<b>0.5%</b>	0.9%	1.0%	1.0%	0.9%	1.0%
3. <i>S. fasciatus</i> (Amazonas, n = 14)	2.7%	4.7%	<b>0.2%</b>	0.6%	0.8%	0.5%	0.7%
4. <i>S. intermedius</i> (upper Paraná, n = 8)	1.1%	5.1%	2.6%	<b>0.0%</b>	0.9%	0.6%	0.8%
5. <i>S. scotorhabdotus</i> (Orinoco, n = 4)	4.8%	5.5%	4.0%	4.3%	<b>0.1%</b>	10.8%	0.9%
6. <i>S. trivittatus</i> (Tapajós-Xingu, n = 5)	2.9%	4.7%	1.9%	2.5%	4.0%	<b>0.4%</b>	0.6%
7. <i>S. vittatus</i> (Araguaia-Tocantins, n = 8)	3.8%	5.5%	2.9%	3.6%	5.2%	2.3%	<b>0.4%</b>

fin ray length (-0.2704). The heaviest loadings on PC3 were first anal-fin ray length (-0.9170) and ninth anal-fin ray length (0.3177) (Tab. 2).

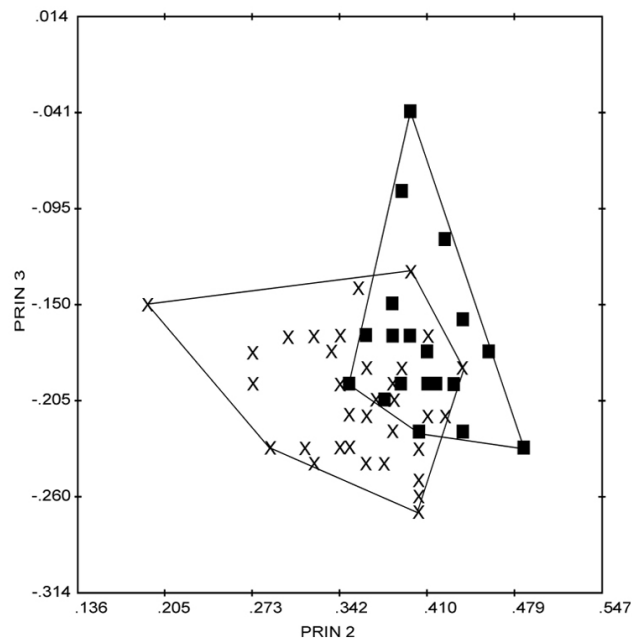


**FIGURE 2** | Phylogenetic relationships among species of the Amazonas clade of *Schizodon* based on: (left) Maximum Likelihood analysis using COI sequences, (right) dated Bayesian analysis using COI, RAG1, RAG2, Cytb, and Myh6 sequences. Node bars on the right consist of 95% confidence age height.

**TABLE 2** | Loadings of variance and eigenvalues of morphometric measurements of *Schizodon vittatus* and *S. trivittatus* used in the Principal Component Analysis (PCA). Discriminant characters in bold.

	PC 2	PC 3
Eigenvalue	0.003	0.002
Variance	1.83	1.17
Standard length	0.2558	0.0006
Head length	0.0217	0.0524
Trunk length	<b>0.3232</b>	-0.0154
Body depth	-0.2348	0.0145
Predorsal distance	0.1133	0.0474
Snout length	-0.0069	0.1144
Interorbital width	-0.0652	0.0779
Orbital diameter	0.0335	-0.0064
Caudal peduncle depth	0.0182	0.0481
First anal-ray length	<b>-0.2704</b>	<b>-0.9170</b>
Ninth anal-ray length	<b>-0.7743</b>	<b>0.3177</b>
Interopercular width	0.0710	-0.0157
Head depth	0.0060	0.1262
Maxillary length	<b>0.2791</b>	0.0249
Mandible width	-0.0133	0.1202





**FIGURE 3 |** Scatter plot of Sheared Principal Component Analysis (PCA) in adults of *Schizodon vittatus* (squares) and *S. trivittatus* (X). Logarithm transformed data of total specimens.

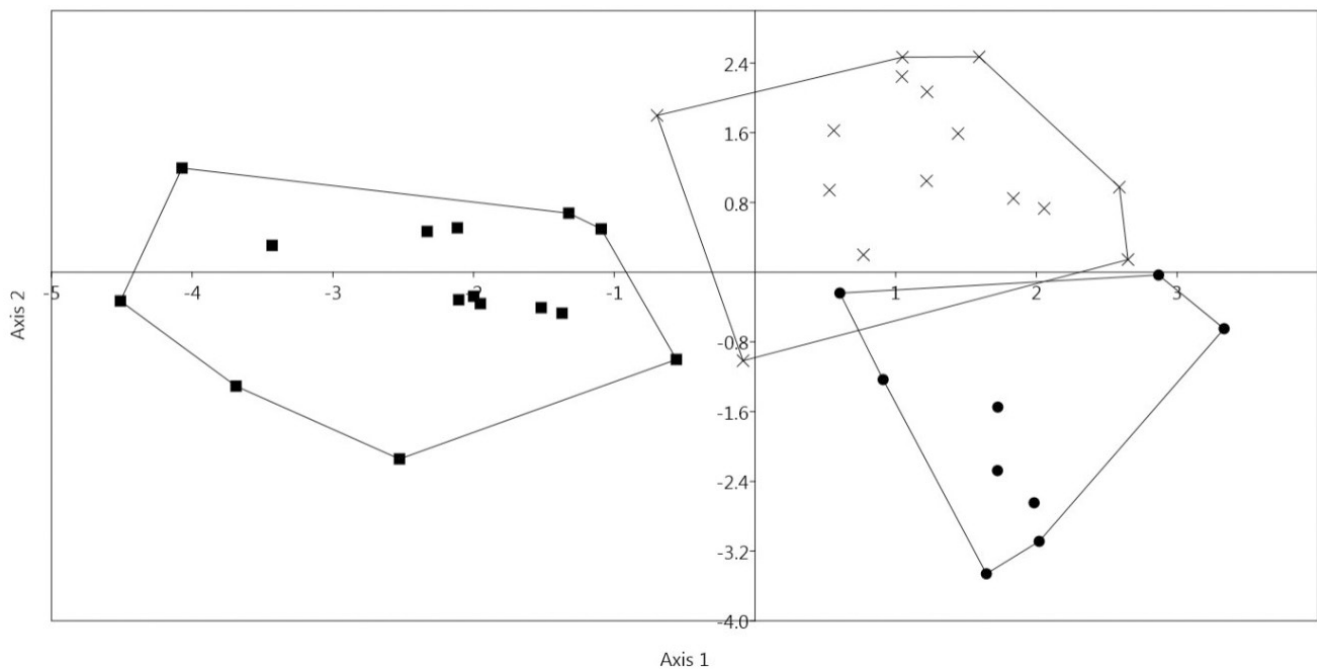
The Canonical Variates Analysis revealed that *S. vittatus* and *S. trivittatus* are diagnosable by some morphometric variables. The CVA analysis performed with the three groups (one of *S. vittatus* from Araguaia-Tocantins, and two of *S. trivittatus*, from Xingu and Tapajós) indicates the CV1 retaining 73.34% of the data variance (Tab. 3), discriminating the two studied species (Fig. 4). The following variables were the most important to specimens' distribution along the CV1: body depth (0.0143), ninth anal-fin ray length (0.0125), first anal-fin ray (0.0109) and orbital diameter (0.0101). The CV2 retained 26.66% of the variance and better discriminated the populations of *S. trivittatus* from Xingu and Tapajós rivers. Along the CV2, the ninth anal-fin ray length (0.0189) has the largest loadings. The jackknife procedure resulted in 64.1% correctly classified specimens. Most of the incorrectly classified specimens are from the Xingu and Tapajós samples of *S. trivittatus*. Twelve of the 15 specimens of *S. vittatus* from the Araguaia-Tocantins basin were correctly classified.

**Meristic data and coloration.** Meristic data are summarized in Tab. 4. All counts of scales and fin rays show a considerable overlap when comparing *S. trivittatus* and *S. vittatus*. Teeth count and teeth morphology are also identical between the two species. Both have four spatulate teeth on the premaxillary and dentary, teeth bearing three to five similarly sized cusps.

*Schizodon vittatus* and *S. trivittatus* have a dark midlateral stripe on the caudal peduncle that is unique among congeners and absent in other species of the Amazon clade. Most species of this clade and *S. vittatus* have four dark bars on body, the first located between the opercular opening and the vertical through the dorsal-fin origin, the second below the dorsal-fin base, the third in the vertical through the adpressed dorsal-fin terminus, and the fourth dorsal to the anal-fin base (ventral to adipose fin).

**TABLE 3** | Loadings of variance and eigenvalues of morphometric measurements used in the Canonical Variate Analysis (CVA) of *Schizodon vittatus* and *S. trivittatus*. The main discriminate characters are in bold.

	Axis 1	Axis 2
Eigenvalue	3.6743	1.3356
% variance	73.34	26.66
Standard length	0.0012	0.0031
Head length	0.0046	0.0094
Trunk length	0.0003	0.0014
Body depth	<b>0.0143</b>	0.0092
Predorsal distance	0.0054	0.0069
Snout length	0.0037	0.0109
Interorbital width	0.0087	0.0089
Orbital diameter	<b>0.0101</b>	0.0015
Caudal peduncle depth	0.0077	0.0033
First anal-fin ray length	<b>0.0109</b>	0.0025
Ninth anal-fin ray length	<b>0.0125</b>	<b>0.0189</b>
Interopercular width	0.0062	0.0028
Head depth	0.0079	0.0095
Maxillary length	0.0047	0.0022
Mandible width	0.0059	0.0101



**FIGURE 4** | Scatter plot of Canonical Variate Analysis (CVA) in adults of *Schizodon vittatus* (squares) and *S. trivittatus* from Tapajós (dots) and Xingu (X) rivers. Logarithm-transformed data from specimens with more than 200 mm SL.

The color pattern of *S. trivittatus* is distinct from that of *S. vittatus*. The fourth dark bar is absent and, if present, restricted to the dorsal trunk (*i.e.*, dorsal to the lateral line) in *S. trivittatus*, whereas it is usually conspicuous and extended in the dorsal and ventral trunk in *S. vittatus*. This seems to be the most conspicuous phenotypic difference between these two species.

Besides the four dark vertical bars, the base of the median caudal-fin rays bears a single dark spot in *S. fasciatus* and *S. corti*, whereas it is completely pale in *S. borellii*, *S. dissimilis*, and *S. intermedius*. *Schizodon scotorhabdotus* has a complete dark midlateral stripe, a condition also distinct from that of the new species and *S. vittatus*.

Our study, especially based on series of specimens of *Schizodon vittatus* from distinct locations in the Araguaia and Tocantins drainages (n = 73, 89.0–316.0 mm SL), shows that the dark midlateral stripe is indeed variable. Small specimens of *S. vittatus* (up to 120 mm SL) have a conspicuous dark midlateral stripe formed mainly by the dermal pigment (epidermal pigment absent on midlateral stripe, but present forming transversal bars) (Fig. 5A). The dark midlateral stripe dermal pigmentation becomes inconspicuous in specimens larger than 120 mm SL (Figs. 5B–F). Some specimens around 160 mm SL lack almost entirely epidermal pigments on the midlateral stripe (Fig. 5B), and show a pale caudal peduncle, a condition similar to *S. borellii*, *S. dissimilis* and *S. intermedius*. However, other specimens of similar size (*i.e.*, ranging from 120 to 160 mm SL) possess a thin and small midlateral stripe, consisting of epidermal pigment that rarely reaches the third dark bar on the trunk (Fig. 5C). Larger specimens (> 160 mm SL) always have a conspicuous midlateral stripe formed by the epidermal pigment (Figs. 5D–F), extending from the head to the caudal-fin base in some specimens (around 180 mm SL, see Fig. 5D) or restricted to the trunk posterior to the dorsal-fin (Figs. 5E–F). This condition seems persistent and consistent among *S. vittatus* and *S. trivittatus* specimens.

**TABLE 4 |** Morphometric and meristic data of *Schizodon trivittatus* and *S. vittatus*.

	<i>Schizodon trivittatus</i> (n = 41)					<i>Schizodon vittatus</i> (n = 20)				
	Holotype	Mean	SD	Low	High	Holotype	Mean	SD	Low	High
Morphometry										
Standard length	285.0	228.0	–	149.0	330.5	223.0	230.4	–	128.0	303.0
<b>Percents of standard length</b>										
Head length	22.1	22.3	1.0	20.0	25.2	47.0	21.8	1.2	19.2	24.2
Trunk length	77.9	77.7	1.0	74.8	80.0		78.2	1.2	75.8	80.8
Body depth	26.4	26.6	1.9	22.7	33.3	52.0	24.3	1.8	19.0	27.2
Predorsal distance	41.7	42.5	1.3	40.1	46.4	92.0	41.5	1.7	38.6	45.4
Caudal peduncle depth	10.4	9.9	0.6	8.3	11.7	22.0	9.4	0.6	8.0	10.2
First anal-fin ray length	9.8	12.5	1.0	9.8	14.2		11.2	1.0	8.7	13.0
Ninth anal-fin ray length	3.9	4.4	0.6	3.4	6.7		4.0	0.5	3.0	4.9
<b>Percents of head length</b>										
Snout length	39.0	41.6	1.9	36.9	45.7	19.0	42.1	1.7	38.0	44.4
Interorbital width	48.6	51.5	2.8	44.0	57.5		50.1	2.3	45.0	55.3
Orbital diameter	20.2	21.1	1.5	17.1	24.5	11.0	20.4	1.6	17.8	24.0



TABLE 4 | (Continued)

Head depth	75.1	72.8	3.5	64.4	80.6		71.9	3.5	66.4	77.8
Interopercular width	64.4	62.9	3.6	55.1	70.3		61.8	4.7	52.9	73.5
Maxillary length	21.1	20.6	1.9	16.8	24.0		20.6	1.3	18.8	22.9
Mandible width	20.2	19.8	1.1	17.6	22.0		19.6	1.0	18.0	21.4
<b>Meristic counts</b>										
Premaxillary teeth	4	4.0	0.0	4	4		4.0	0.0	4	4
Mandible teeth	4	4.0	0.0	4	4		4.0	0.0	4	4
Lateral line scales	45	44.4	0.6	43	45	44	44.4	0.5	44	45
Scales above lateral line	4	4.0	0.0	4	4	4	4.0	0.0	4	4
Scales below lateral line	4	4.0	0.0	4	4	4	4.0	0.0	4	4
Predorsal scales	11	11.1	0.3	11	12		11.1	0.3	11	12
Preanal scales	32	33.4	1.0	31	35		33.4	0.8	32	35
Circumpeduncular scales	16	16.0	0.0	16	16		16.0	0.0	16	16
Unbranched dorsal-fin rays	ii	ii	0.0	ii	ii	ii	ii	0.0	ii	ii
Branched dorsal-fin rays	11	11.0	0.3	9	11	9	11.0	0.0	11	11
Unbranched pectoral-fin rays	i	i	0.0	i	i		i	0.0	i	i
Branched pectoral-fin rays	16	15.0	0.6	14	16		15.2	0.6	14	16
Unbranched ventral-fin rays	i	i	0.0	i	i		i	0.0	i	i
Branched ventral-fin rays	8	8.0	0.2	8	9		8.0	0.0	8	8
Unbranched anal-fin rays	ii	ii	0.0	ii	ii		ii	0.0	ii	ii
Branched anal-fin rays	9	9.0	0.0	9	9		9.0	0.2	8	9

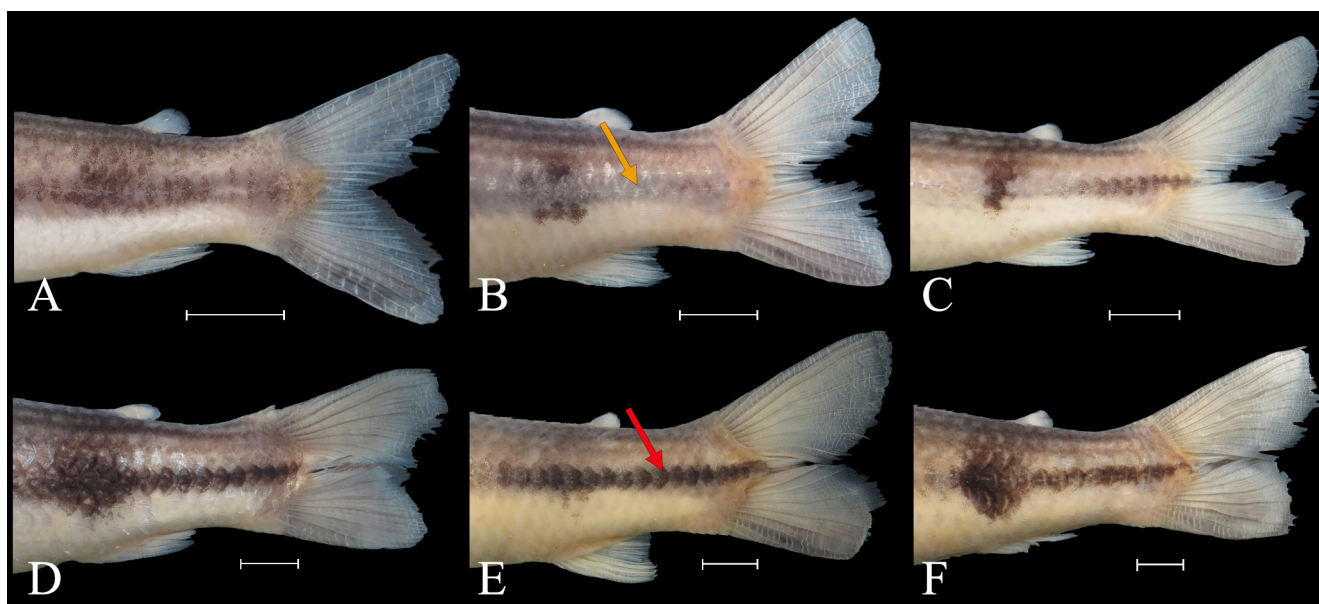


FIGURE 5 | Detail of the caudal peduncle's coloration in syntopic specimens of *Schizodon vittatus* collected in the Araguaia river basin (MZUEL 20693). A. 88.1 mm SL; B. 159.1 mm SL; C. 162.5 mm SL; D. 181.9 mm SL; E. 206.6 mm SL; F. 235.6 mm SL. Scale bars = 10 mm. Arrows indicate dermal (orange) and epidermal (red) pigmentation.

## *Schizodon vittatus* (Valenciennes, 1850)

(Figs. 1, 6; Tab. 4)

*Piabuca vittata* Valenciennes in Cuvier, Valenciennes, 1850:115 (original description, holotype unique, type locality “l’Amazone”). —Castelnau, 1855:64, pl. 23, fig. 1 (illustration of holotype in life, type locality restricted to “l’Araguay” [=Araguaia River, Brazil]).

*Anostomus vittatus*. —Günther, 1864:303 (literature compilation). —Borodin, 1931:44 (in part, Goyaz [=Araguaia or Tocantins river in Goiás, Brazil]).

*Anostomus* (*Schizodon*) *vittatus*. —Garman, 1890:21 (redescription, in part, Goyaz).

*Schizodon vittatus*. —Eigenmann, 1910:425 (citation). —Bertin, 1948 (catalog of type specimens). —Santos, Jégu, 1989: figs. 9, 22 (description, illustration of a preserved specimen, illustration of teeth, the lower portion of Tocantins river). —Garavello, Britski, 2003:80 (catalog of Neotropical Fishes).

**Diagnosis.** *Schizodon vittatus* is distinguished from *S. isognathus*, *S. jacuiensis*, *S. knerii*, *S. nasutus*, *S. platae*, and *S. scotorhabdotus* by having four conspicuous dark transversal bars on the trunk formed by the epidermal and dermal pigment (*vs.* vertical bars absent or inconspicuous and formed exclusively by dermal pigment); from *S. australis*, *S. borellii*, *S. corti*, *S. dissimilis*, *S. fasciatus* and *S. intermedius*, by having a dark midlateral stripe on caudal peduncle (*vs.* caudal peduncle and base of median caudal-fin rays pale in *S. borellii*, *S. dissimilis*, *S. intermedius*, or a single rounded spot in *S. australis*, *S. corti*, *S. fasciatus*); and from *S. trivittatus* by having a dark transversal bar dorsal to anal-fin conspicuous and extended ventral the lateral line (*vs.* a dark transversal bar dorsal to anal-fin absent or inconspicuous and restricted above the lateral line).

**Description.** Morphometric and meristic data in Tab. 4. Body compressed and fusiform, maximum depth ranging from 1.8 to 2.0 times of maximum width. Greatest depth of body at dorsal-fin origin. Lateral profile of head with dorsal slope of skull straight; predorsal region from supraoccipital to dorsal-fin origin slightly convex; dorsal-fin base straight; profile from dorsal-fin terminus to adipose fin more or less straight, slightly inclined; caudal peduncle concave. Ventral profile slightly convex from lower jaw to anal-fin insertion with an inflection at pelvic-fin origin; base of anal-fin straight; caudal peduncle concave. Adipose fin origin on vertical through base of first or second branched anal-fin ray; pelvic-fin origin on vertical through base of dorsal-fin terminus.

Mouth small and terminal, upper and lower jaws meeting at horizontal with median portion of orbit. Maxilla slightly curved and widening at ventral margin; upper and lower lips smooth. Each premaxillary and dentary with four compressed teeth without inner ridge. Teeth with four similarly sized cusps forming a serrated cutting edge (medial cusps slightly larger than lateral ones); teeth slightly graded in size from symphysis. Anterior nare tubular, posterior nare forming a rhomboid opening; nares horizontally aligned with dorsal portion of orbit. Six infraorbitals ring eye; supraorbital positioned along anterodorsal margin of orbit. Four medial branchiostegal rays anteriorly narrow; fleshy opercular membrane fused to isthmus.



Dorsal-fin ii,9. Adipose fin teardrop-shaped, longer than high. Pectoral-fin i,15 or i,16; fin slightly pointed dorsally. Pelvic-fin i,8. Anal-fin ii,7. Caudal-fin i,9,8,i, with six of seven median rays of lobe greatly ramified, lobes rounded. Fleshy tissue at base of anterior dorsal and anal-fin rays. Fins not scaled except base of caudal-fin, and bases of dorsal and anal-fin with incomplete series of scales. Lateral line with 44 or 45 perforated scales, including three on base of caudal-fin rays; 16 series of scales around caudal peduncle; four scale rows from dorsal-fin origin to lateral line; four scale rows from lateral line to pelvic-fin origin; 11 or 12 scales from supraoccipital to dorsal-fin origin.

**Coloration in alcohol.** Overall ground color tan or light brown, and countershaded (Figs. 6A–C). Ventral portion of head, trunk, and caudal peduncle pale. Dorsal surface of head dark brown. Lateral trunk with four conspicuous dark brown vertical bars extended from dorsum and falling shy of ventralmost portion of trunk by at least two scale series. Dark brown bars formed by dermal and epidermal pigmentation. First dark bar located two or three scales posterior to opercular membrane and above adpressed pectoral-fin. Second dark bar located beneath dorsal-fin base and above pelvic-fin. Third dark bar located between dorsal-fin terminus and anal-fin origin, and immediately posterior to terminus of adpressed dorsal-fin. Fourth dark bar located above anal-fin base and immediately anterior to adipose-fin origin; fourth bar often conspicuous and large, especially in specimens larger than 160 mm SL, but sometimes small, occupying a single scale below lateral-line scale series, and incorporated into the midlateral dark brown stripe, especially in specimens smaller than 160 mm SL. Head and trunk with a dark brown midlateral stripe formed by dermal pigment as deep as the lateral-line scale series running from snout tip to base of median caudal-fin rays in specimens of approximately 120 mm SL; midlateral stripe formed by dermal pigment becoming inconspicuous in larger specimens. Specimens from 120 to 160 mm SL possessing dark brown, thin and small (not reaching fourth dark bar) midlateral stripe on caudal peduncle formed by epidermal pigment; midlateral stripe formed by epidermal pigment entirely lacking in a few specimens. Larger specimens possessing a dark brown midlateral stripe from head to median caudal-fin rays; midlateral stripe usually restricted to caudal peduncle in specimens larger than 180 mm SL. Dorsal portion of trunk posterior to dorsal-fin with inconspicuous dark lines between scale series. Dorsal-fin dusky, pectoral, pelvic and anal fins hyaline. Adipose fin dusky with outline darker. Caudal-fin dusky with dorsal portion of dorsal lobe slightly darker, and ventral portion of ventral lobe conspicuously darker, almost black.

**Coloration in life.** Similar to described above for alcohol-preserved specimens, except for background color of the head and body silvery (Fig. 5D), head slightly green, ventral portion of the head and body white; fins slightly yellow-tan to light brown. Iris silvery or reddish-brown with orangish dorsal portion.

**Geographical distribution.** *Schizodon vittatus* occurs in the Araguaia and Tocantins river basins in Goiás, Tocantins and Maranhão states, Brazil (Fig. 7).

**Conservation status.** The species is widely distributed in the main channel and tributaries in the Araguaia and Tocantins river basins, and common, although not



**FIGURE 6** | *Schizodon vittatus*. **A.** MZUEL 20693, 206.6 mm SL; **B.** MZUEL 20693, 88.1 mm SL; **C.** MZUEL 20693, 159.1 mm SL; **D.** MZUEL 20693, 162 mm SL. Scale bars = 10 mm. Specimens A–C alcohol-preserved, **D** photographed live by José Birindelli.

abundant. Because there is no imminent threat to the species, it is recommended to consider it as Least Concern (LC) in the International Union for Conservation of Nature (IUCN) criteria (IUCN Standards and Petitions Subcommittee, 2019).

**Remarks.** The holotype of *Piabuca vittata*, MNHN A-1067, is a dry specimen prepared in a wood support and labeled as “*Schizodon vittatus* (Cuvier, Valenciennes), type of *Piabuca vittata* Cuvier, Valenciennes, Number A1067” (Fig. 1B). Even though the specimen was painted and varnished exhibiting bright colors during our examination in 1980 (made by HAB), the midlateral dark stripe was still visible from the vertical through the dorsal-fin terminus to the caudal-fin base. Nevertheless, it was impossible to distinguish any of the trunk’s transversal dark bars. In the original description (Cuvier, Valenciennes, 1850) and also in the drawing provided later by Castelnau (1855), the holotype exhibits three dark transversal bars on the trunk, the first dorsal to the addressed pectoral-fin, the second below the dorsal-fin base, and the third below the tip of the addressed dorsal-fin, thus lacking the fourth dark transversal bar above

the anal-fin. In addition, the holotype also has a dark midlateral stripe from head to the terminus of median caudal-fin rays. In Castelnau's drawing (Fig. 1A), the specimen also shows yellow lower jaw and pectoral-fin. That coloration is not entirely precise, based on our examination of an extensive series of alcohol-preserved and live specimens (Fig. 5D). First, the lower jaw and pectoral-fin are neither yellow nor distinctly colored than the rest of the head and fins. Second, specimens of *S. vittatus* rarely lack the fourth dark transversal bar (the one above anal-fin) entirely. However, discrepancies are not rare in those old species descriptions (Britski *et al.*, 2012; Birindelli, Britski, 2013). The holotype and its illustration combined with its type locality leave no doubt of the species identity.

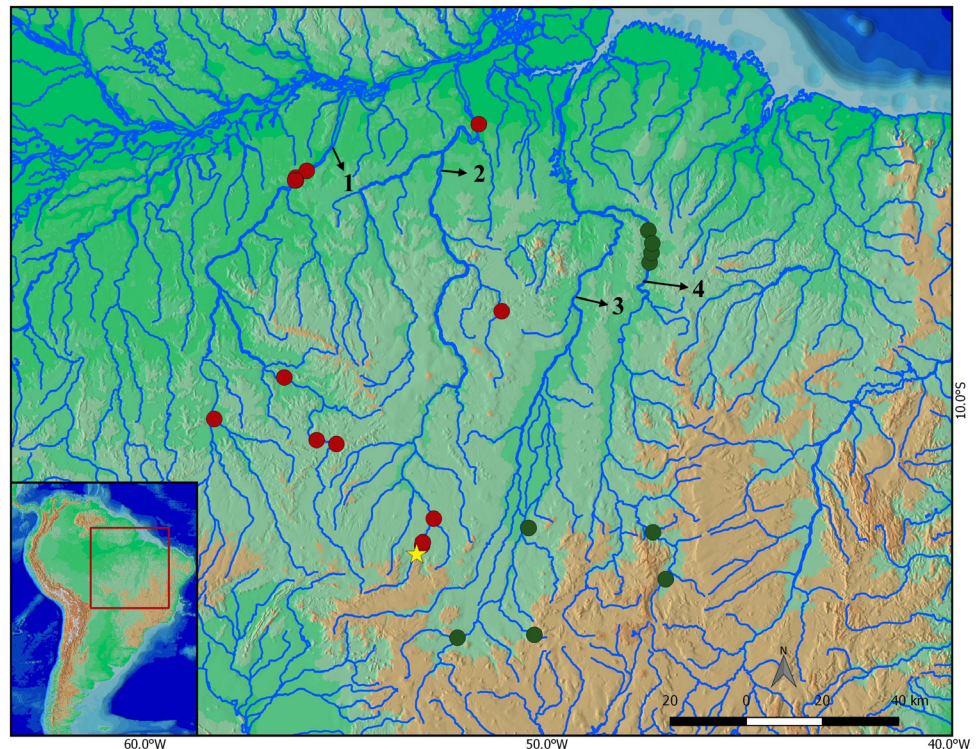
The type locality of *Piabuca vittata* is imprecise. Valenciennes indicates that Castelnau collected the holotype in the "l'Amazone" in the original description. However, Castelnau (1855) later reported that the specimen came from "l'Araguay" (= Araguaia river). According to Papavero (1971), Castelnau went down the Araguaia River via the Crixás River (thus entering the Araguaia river in the São Miguel do Araguaia municipality), departing from the city of Goiás (Goiás State) to the confluence of the Araguaia and Tocantins rivers, and then upstream the Tocantins River back to the city of Goiás. He departed in April 1844 and arrived back in Goiás in October 1844. Thus, the holotype of *Schizodon vittatus* was collected somewhere along the Araguaia River, from around the city of São Miguel do Araguaia, in Goiás State, or downstream in the Tocantins State.

The precise locality of the MCZ lots registered as Goyaz is suggested by Isbrücker (1973:174) as 'Rio Araguaia drainage, the upper course of Rio Vermelho at Goiás (15°57'S 50°07'W)', based on Eigenmann, Eigenmann's map. Examining the fishes collected by the Thayer Expedition, and catalogued as from "Goyaz", Lima (2004) concluded that most were collected in the Araguaia possibly in Goiás state, and a few were most likely collected near the mouth of the Tocantins river. Borodin (1931) mentioned 18 specimens from Cudajas (MCZ 19400), consequently possibly in the Solimões/Amazonas river. That lot was unfortunately lost (A. Williston, 2019, pers. comm. based on MCZ records), and the same MCZ number is currently used for a lot of *Cyphocharax* identified by Richard Vari and collected in the same locality. Given the locality, Borodin (1931) might have misidentified specimens of *S. fasciatus* as *S. vittatus*. Another erroneous record came from Argentina. Ringuélet *et al.* (1967:21) and then Menni (2004:72) mentioned the species occurring in the Rio de la Plata, Argentina. Even though we did not examine these specimens, we consider very unlikely that the species occur in Argentina.

**Material examined.** All from Brazil. MNHN-IC-A-1067 (dry), holotype of *Piabuca vittata* Valenciennes, 1850, "l' Amazone" (type locality posterior restricted to the Araguaia river, Brazil), François-Louis de Laporte, Comte de Castelnau, 223.0 mm SL. Goiás: MZUEL 20693, 22, 89.0–176.8 mm SL, Araguaia River at Luiz Alves, 13°10'35"S 50°36'25"W, São Miguel do Araguaia, 15 Oct 2019, J. L. O. Birindelli *et al.* MZUSP 26528, 1, 135 mm SL, Resende River, tributary of Vermelho and Araguaia rivers, 10 km near Buenolândia, 7–13 Dec 1981. LISDEBE 6985, 2, 236.0–242.0 mm SL, Vermelho River, tributary of Araguaia River, downstream of Barra do Bugre, 27–29 Nov 1983. LISDEBE 7306, 8, 159.0–199.0 mm SL, Córrego do Medo, tributary of Araguaia River, 13°09'36"S 50°27'36"W, São Miguel do Araguaia, 9 Jul



2008, L. H. da Silva. LISDEBE 7343, 6, 226.0–280.0 mm SL, Araguaia River, 15°53'20"S 52°13'48"W, Barra do Garças, no date, P. C. Venere. Tocantins: LISDEBE 6986, 1, 275.0 mm SL, Tocantins River between the mouth of Lageado River and Tocantinópolis, 06°19'12"S 47°24'00"W, 14–18 Jun 1988, UFSCar; LISDEBE 6987, 5, 240–295 mm SL, Tocantins River, between the mouth of Lageado River and Itaguatins, Itaguatins, 05°45'36"S 47°28'48"W, 7 Jun 1988, DMA-Themag and UFSCar. LISDEBE 7254, 3, 242.0–261.0 mm SL, Tocantins River, between Itaguatins and Cachoeira de Santo Antônio, Itaguatins, 14–18 Dec 1987, DMA-Themag and UFSCar. LISDEBE 7255, 10, 265.0–316.0 mm SL, Tocantins River, upstream Itaguatins, 22–26 Feb 1988, DMA-Themag and UFSCar. LISDEBE 7256, 8, 237.0–291.0 mm SL, Tocantins River, between Itaguatins and Porto Franco, Itaguatins, 16–20 Aug 1988, DMA-Themag and UFSCar. Maranhão: LISDEBE 7305, 1, 230.0 mm SL, Lajeado River, tributary of Tocantins, at the bridge of Rodovia Belém-Brasília, 06°04'48"S 47°24'00"W, Campestre do Maranhão, 18 Apr 1988, DMA-Themag and UFSCar. Pará: MZUSP 21334, 2, 173.0–192.0 mm SL, Tucuruí, lake near Tocantins River, 29 September 1970, H.A. Britski *et al.* MZUSP 21263, 3, 128.0–159.0 mm SL, lake near Tocantins River, between Baião and Tucuruí, 11 Sep 1970, H. A. Britski *et al.*



**FIGURE 7 |** Map of the northern portion of Brazil showing the distribution of *Schizodon vittatus* (green dots) and *Schizodon trivittatus* (red dots; yellow star = type locality). Rivers indicated as follows: 1. Tapajós, 2. Xingu, 3. Araguaia, 4. Tocantins. Some symbols may represent more than one sample locality.

*Schizodon trivittatus*, new species

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(Fig. 8; Tab. 4)

*Anostomus* (*Schizodon*) *vittatus*. —Garman, 1890:21 (in part; Porto de Moz).*Anostomus vittatus*. —Borodin, 1931:44 (in part, Porto de Moz).*Schizodon vittatus*. —Camargo *et al.*, 2004:132 (lower and middle Xingu). —Camargo *et al.*, 2005:240 (Tapajós, Xingu). —Dagosta, de Pinna, 2017: Appendix 1 (Juruena and Teles Pires rivers, Tapajós basin).*Schizodon* aff. *vittatus*. —Ramirez *et al.*, 2020:1 (phylogeny and species delimitation analysis based on molecular data).**Holotype.** MZUSP 115362, 285.0 mm SL, Brazil, Mato Grosso, São José do Couto, Culuene River, a tributary of Xingu River, 13°49'01"S 53°14'45"W, 16 May 2013, H. Batista & J. Ramirez.**Paratypes. Brazil, Mato Grosso: Xingu drainage:** LIA 6562, 1, 86.4 mm SL, Altamira, Xingu River at Lago da Ilha Grande, 12 Jan 2014, P. Trindade *et al.* MZUSP 94296, 1, 194.0 mm SL, lake of Culuene River at Fazenda Luar do Sertão, 13°35'49"S 53°06'36"W, Gaúcha do Norte, 25 May 2007, F. C. T. Lima, F. Machado, C. Figueiredo & J. L. O. Birindelli. MZUSP 94935, 1, 192.0 mm SL, Culuene River, tributary of Xingu River, 13°30'50"S 53°05'34"W, Gaúcha do Norte, 19 Oct 2004, J. L. O. Birindelli, O. T. Oyakawa, & C. Nolasco. MZUSP 83551, 6, 270.0–330.5 mm SL, Xingu River, at the confluence between of Culuene and Sete de Setembro rivers, 12°55'48"S 52°49'12"W, 23 Aug 1984, M. Goulding, L. P. S. Portugal & M. L. Carvalho. **Pará:** MZUSP 31471, 1, 275.0 mm SL, Belo Monte, Xingu River, 03°07'12"S 51°42'00"W, Jul/Aug 1983, M. Goulding. MZUSP 36012, 1, 242.0 mm SL, Fresco River at Aldeia Gorotire, São Félix do Xingu, 07°46'12"S 51°07'48"W, Aug 1983, M. Petrere. MZUSP 106034, 1, 164.0 mm SL, Altamira, Boa Esperança, 12 Jan 2001, Eq. Ict. UFPA. MZUSP 36835, 3, 149.0–252.0 mm SL, Xingu River at Cachoeira do Espelho, 23–26 Oct 1986, P. E. Vanzolini. MZUSP 83544, 6, 180.0–235.0 mm SL, edge of the channel, 03°07'12"S 51°42'00"W, Belo Monte, Jul/Aug 1983, M. Goulding. CPUFMT 5152, 2, 260–320 mm SL, Culuene River, São José do Couto, 13°49'01"S 53°14'47"W, 16 May 2013, H. Batista, J. Ramirez.**Non-type specimens. Tapajós drainage:** MZUSP 21347, 2, 190.0–195.0 mm SL, Ilha Tapaiuna, 26–27 Oct 1970, Expedição Permanente da Amazônia (EPA). MZUSP 21406, 1, 265.0 mm SL, lake in Ilha Campinho, 23 Nov 1970, EPA. MZUSP 22108, 4, 168.0–185.0 mm SL, Tapajós River at Ilha da Barreirinha, near São Luís, 04°27'00"S 56°15'00"W, 21 Nov 1970, EPA. MZUSP 21906, 3, 230.5–250.2 mm SL, Maloquinha, near Itaituba, 04°16'48"S 55°58'48"W, Itaituba, 11–13 Nov 1970, EPA. MZUSP 25318, 2, 260.0–283.0 mm SL, Ilha Grande, upriver of Park headquarter, PARNA-PA, 04°31'12"S 56°15'00"W, 15–31 Jul 1979, J. C. Oliveira. MZUSP 25480, 2, 258.0–266.0



mm SL, left margin, opposite to PARNA headquarter, 04°31'12"S 56°16'12"W, 15–31 Jul 1979, J. C. Oliveira. MZUSP (not numbered), 5, 161.0–194.0 mm SL, lake in front of Monte Cristo, 8 Dec 1970, EPA. MZUSP 95870, 1, 310.0 mm SL, Teles Pires River, Itaúba, 10°58'30"S 55°44'03"W, J. L. O. Birindelli & P. H. Carvalho. MZUSP 99136, 1, 295.0 mm SL, Renato River, tributary of Teles Pires River, Itaúba, 11°04'24"S 55°14'35"W, P. H. Carvalho & S. Lima. MZUSP 99468, 1, Teles Pires River, Paranaíta, 09°25'05"S 56°32'21"W, R. Hilario. MZUSP 103676, 4, Arinos River, tributary of Juruena River, Juruena, 10°27'00"S 58°17'00"W, F. R. Machado *et al.*

**Diagnosis.** *Schizodon trivittatus* is distinguished from *S. isognathus*, *S. jacuiensis*, *S. knerii*, *S. nasutus*, *S. platae*, and *S. scotorhabdotus*, by having conspicuous dark transversal bars on the trunk formed by the epidermal and dermal pigment (*vs.* vertical bars absent or inconspicuous and formed exclusively by dermal pigment); from *S. australis*, *S. borellii*, *S. corti*, *S. dissimilis*, *S. fasciatus*, *S. intermedius*, by having a dark midlateral stripe on caudal peduncle (*vs.* caudal peduncle and base of median caudal-fin rays pale in *S. borellii*, *S. dissimilis*, *S. intermedius*, or a single rounded spot in *S. australis*, *S. corti*, *S. fasciatus*); and from *S. vittatus* by lacking a dark transversal bar ventral to the adipose fin or having an inconspicuous bar restricted to the region dorsal to the lateral line (*vs.* possessing a conspicuous dark transversal bar ventral to the adipose fin that extends ventral to the lateral line).

**Description.** Morphometric and meristic data in Tab. 4. Body compressed and fusiform, maximum depth ranging from 1.3 to 2.0 times of maximum width. Greatest depth of body at dorsal-fin origin. Lateral profile with skull's slope almost straight; predorsal region from supraoccipital to dorsal-fin origin slightly convex; dorsal-fin base straight; profile from dorsal-fin terminus to adipose fin almost straight, slightly inclined; caudal peduncle concave. Ventral profile slightly convex from lower jaw to anal-fin insertion with an inflection at pelvic-fin origin; base of anal-fin straight and from caudal peduncle concave. Adipose fin origin on vertical through base of first or second branched anal-fin ray; pelvic-fin origin on vertical through base of dorsal-fin terminus.

Mouth small and terminal, upper and lower jaws meeting at horizontal with median portion of orbit. Maxilla slightly curved and widening at ventral margin; upper and lower lips smooth. Each premaxillary and dentary with four compressed teeth without inner ridge. Teeth with four similarly sized cusps forming a serrated cutting edge (medial cusps slightly larger than lateral ones); teeth slightly graded in size from symphysis. Anterior nare tubular, posterior nare forming a rhomboid opening; nares horizontally aligned with dorsal portion of pupil. Six infraorbitals ringing eye; supraorbital positioned along anterodorsal margin of orbit. Four medial branchiostegal rays anteriorly narrow; fleshy opercular membrane fused to isthmus.

Dorsal-fin ii,9. Adipose fin teardrop-shaped, longer than high; origin on vertical through base of second or third branched anal-fin rays. Pectoral-fin i,15 or i,16; fin slightly pointed dorsally. Pelvic-fin i,8. Anal-fin ii,7. Caudal-fin i, 9, 8, i, with six or seven median rays of lobe greatly ramified, lobes rounded. Specimens larger than 200 mm SL with first six or seven dorsal caudal-fin rays and last six or seven ventral caudal-fin rays branched. Fleshy tissue at base of anterior dorsal and anal-fin rays. Fins not scaled except base of caudal-fin, and bases of dorsal and anal-fin with incomplete series

of scales. Lateral line with 44 or 45 perforated scales, including three on base of caudal-fin rays; 16 series of scales around caudal peduncle; four scale rows from dorsal-fin origin to lateral line; four scale rows from lateral line to pelvic-fin origin; 11 scales from supraoccipital to dorsal-fin origin.

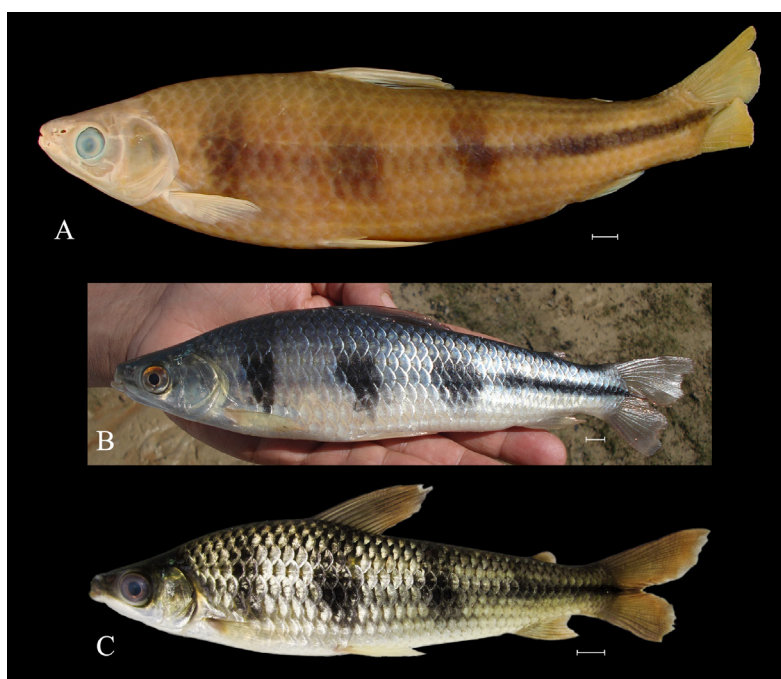
**Coloration in alcohol.** Coloration as described for *Schizodon vittatus*, except for lacking the fourth dark brown bar (dorsal to anal-fin and ventral to the adipose-fin origin) in almost all specimens. In the few specimens possessing the dark brown bar, that bar is inconspicuous and restricted to the dorsal trunk, above the lateral line (Fig. 8).

**Coloration in life.** Similar to described for alcohol-preserved specimens, except for background color of head and body silvery, head slightly green, ventral portion of head and body white; fins slightly yellow-tan to light brown. Iris silvery or reddish-brown with an orangish dorsal portion (Figs. 8B–C).

**Geographical distribution.** *Schizodon trivittatus* occurs widely in the Xingu and Tapajós drainages, including their tributaries, in Mato Grosso and Pará states, Brazil (Fig. 7).

**Etymology.** The name *trivittatus* is an adjective in allusion to the presence of three dark vertical bars on the trunk exhibited by the new species, its main diagnostic feature.

**Conservation status.** The species is widely distributed in the main channel and tributaries in the Tapajós and Xingu basins, and common, although not abundant.



**FIGURE 8** | *Schizodon trivittatus*, new species. **A.** holotype, MZUSP 115362, 285.0 mm SL, Brazil, Mato Grosso, São José do Couto, Culuene river, Xingu River tributary; **B–C.** LIA uncatalogued, Xingu river at Altamira, Pará. Scale bars = 10 mm. Specimen **A** alcohol preserved, **B–C** photographed live (**B**, photo by José Birindelli; **C**, photo by Leandro Sousa).

Because there is no imminent threat to the species, it is recommended to consider it as Least Concern (LC) in the International Union for Conservation of Nature (IUCN) criteria (IUCN Standards and Petitions Subcommittee, 2019).

**Key to species identification.** The key below is restricted to the Amazonas clade of *Schizodon* species *sensu* Ramirez *et al.* (2020), with the addition of *Schizodon corti*, which is herein tentatively added as being similar to species included in this clade. Species of this clade, except for *S. scotorhabdotus*, are characterized by having conspicuous dark transversal bars formed by dermal and epidermal pigments.

1. Trunk with three or four conspicuous dark brown transversal bars in all specimens; an inconspicuous dark brown midlateral stripe from head to caudal-fin sometimes present in specimens smaller than 200 mm SL (stripe never as conspicuous as the transversal bars) .....2
- 1'. Trunk with three to five inconspicuous dark brown transversal bars in some specimens (bars never as conspicuous as the midlateral stripe); a conspicuous dark brown midlateral stripe from head to base of median fin rays in all specimens (stripe more conspicuous than the transversal bars) .....*Schizodon scotorhabdotus* (Orinoco)
2. Caudal peduncle and base of median caudal-fin rays pale (without a dark brown spot or a midlateral stripe).....3
- 2'. Caudal peduncle and base of median caudal-fin rays with a dark brown spot or a midlateral stripe.....5
3. Five scale rows between dorsal-fin origin to lateral line, and between the lateral line to pelvic-fin origin; eight branched anal-fin rays..... *Schizodon dissimilis* (Itapecuru, Mearim, Parnaíba, Pindaré, and Turiaçu, in northeast Brazil)
- 3'. Four scale rows between dorsal-fin origin to lateral line, and between the lateral line to pelvic-fin origin; seven branched anal-fin rays ..... 4
4. Fourth dark brown transversal bar (dorsal to anal-fin and ventral to adipose-fin origin) rectangular (*i.e.*, width at second scale row dorsal to lateral line similar to that at second scale row ventral to lateral line, especially in specimens larger than 150 mm SL) ..... *Schizodon borellii* (Paraguay)
- 4'. Fourth dark brown transversal bar (dorsal to anal-fin and ventral to adipose-fin origin) rounded or oval (especially in specimens larger than 150 mm SL) *Schizodon intermedius* (upper Paraná)
5. Caudal peduncle and base of median caudal-fin rays with a dark brown midlateral stripe .....6
- 5'. Caudal peduncle and base of median caudal-fin rays with a dark brown spot .....7
6. Dark brown transversal bar above anal-fin and below adipose fin usually present and extended above and below midlateral stripe *Schizodon vittatus* (Araguaia, Tocantins)
- 6'. Dark brown transversal bar above anal-fin and below adipose fin usually absent, or rarely present but not extended below midlateral stripe ..... *Schizodon trivittatus* (Tapajós, Xingu)
7. Teeth with three cusps; five scale series rows between dorsal-fin origin to lateral line, and between the lateral line to pelvic-fin origin.....*Schizodon corti* (Maracaibo)
- 7'. Teeth with four cusps; four scale series rows between dorsal-fin origin to lateral line, and between the lateral line to pelvic-fin origin ..... *Schizodon fasciatus* (Amazonas)

## DISCUSSION

**Integrative taxonomy.** The present contribution is another example of how combining data from different sources can help test and propose new species hypothesis (Costa *et al.*, 2014; Guimarães *et al.*, 2019). The discovery of the new species herein described resulted from a broad study based on species delimitation analyses using DNA barcoding (Ramirez *et al.*, 2020). Similar approaches were performed to other genera of Anostomidae, including *Megaleporinus* Ramirez, Birindelli & Galetti, 2017 (Ramirez *et al.*, 2017a) and *Laemolyta* Cope, 1872 (Ramirez, Galetti Jr., 2015). Those studies were critical to showing that the known diversity is yet far from being wholly described and to exposing species groups that should be focused on future studies combining multiple data sources. Integrative taxonomy could also be applied to widespread species complexes of Anostomidae such as *Leporinus fasciatus* (Bloch, 1794), *L. friderici* (Bloch, 1794), *Leporellus vittatus* (Valenciennes, 1850), and *Megaleporinus obtusidens* (Valenciennes, 1837), as well as to a few cases in which the geographical distribution indicates that there might be more than one species, *e.g.*, *Pseudanos winterbottomi* Sidlauskas & Santos, 2005 (Sidlauskas, Santos, 2005). In all these cases, the traditionally used phenotypic characters alone, including color pattern, scale counts, and jaws and teeth morphology, may not be enough to investigate species diversity and propose strong species hypotheses.

Molecular analyses supported the color evidence of the Amazon clade, formed by species with dark bars on body. Within this clade, the genetic distance between *S. fasciatus*, *S. trivittatus* and *S. vittatus* is relatively low. The three species have allopatric distributions and are morphologically distinguishable based mainly on the color pattern details. A similar morphology seems to be printed in the barcode genetic distance in these species. Nevertheless, the intraspecific genetic variation within each species of the *S. fasciatus* group is much lower than any variation observed between species. Our results indicate that the genetic differences observed among species are most likely due to distinct historical lineages that have evolved by allopatric speciation. This is also corroborated by *S. borellii* and *S. intermedius*, which have low genetic distance, are extremely similar in morphology, and distributed in distinct drainages, the Paraguay and the upper Paraná, respectively (Garavello, Britski, 1990).

Such allopatric speciation hypothesis was also corroborated in our previous study (Ramirez *et al.*, 2020) by four distinct species delimitation analyses, namely the general mixed Yule coalescent (GMYC) (Pons *et al.*, 2006), the Poisson tree processes (PTP) (Zhang *et al.*, 2013), the PTP model implemented in the Bayesian analysis (bPTP) (Zhang *et al.*, 2013), and the Barcode Index Number System (BIN) (Ratnasingham, Hebert, 2013). The results from those approaches strongly agree with the recognition of the seven species (mentioned above) comprising the *Schizodon fasciatus* species group as well as with the validity of the new species, *S. trivittatus*.

These results are also like those recently obtained for other anostomids. For example, the genetic distance between two closely related species of *Laemolyta*, *L. proxima* (Garman, 1890) and *L. fernandezii* Myers, 1950, varied between 0.92 and 1.7% (Ramirez, Galetti Jr., 2015). Similarly, the genetic distance between closely related *Megaleporinus*, *M. elongatus* (Valenciennes, 1850) and *M. obtusidens*, was 2.7% (Ramirez *et al.*, 2017a). Comparable results (2.6%) were observed between two closely related species of small-sized *Hypomasticus* Borodin, 1929, *Hypomasticus despaxi* (Puyo, 1943) and *H.*

*lineomaculatus* Birindelli, Peixoto, Wosiacki & Britski, 2013 (Birindelli *et al.*, 2020b). The genetic similarity between *Megaleporinus gaiero* Birindelli, Britski, Ramirez, 2020 and *M. obtusidens* is likely even smaller than that (although not calculated in Birindelli *et al.*, 2020a). In that case, these species are distinct from each other by two exclusive features of *M. gaiero*, an irregular dark longitudinal stripe and a partially closed anterior cranial fontanel. These comparisons strengthen the hypothesis that *Schizodon trivittatus* is a distinct and valid species.

The ML analysis recovered *Schizodon trivittatus* and *S. vittatus* as sister taxa, which is supported by the color pattern, as both species share the presence of a dark midlateral stripe on the caudal peduncle. The speciation event that separated *S. vittatus* and *S. trivittatus* was estimated as occurring approximately 1.0 Mya and is possibly related to the recent separation between Tapajós and Xingu basins. These drainages are thought to have been connected in the recent past through the headwaters of the Curuá (Xingu basin) and Jamanxim and Teles Pires (Tapajós basin) (Oliveira *et al.*, 2021).

**Variation in color patterns.** The color pattern is one of the main diagnostic features used in the systematics of fishes in general (*e.g.*, Grether *et al.*, 2004; Baldwin, 2013), and especially in the taxonomy of Anostomidae (*e.g.*, Géry, 1977; Garavello, 1979; Birindelli *et al.*, 2013). The two species studied here are unique among congeners and anostomids by their color pattern. Nevertheless, there is intraspecific variation due to development and differences among similar-sized specimens. Intra-specific variation due to development is always present and often quite impressive in Anostomidae, as previously described in detail for *Rhytiodus microlepis*, *Megaleporinus trifasciatus* (Steindachner, 1875), *Leporinus fasciatus* (Santos, 1980, 1982), *L. altipinnis* Borodin, 1929 (Britski, Birindelli, 2016) and *L. striatus* Kner, 1858 (Birindelli, Britski, 2013). Therefore, it is often necessary to inform the size of the specimens when referring to a diagnostic color pattern. For example, the color pattern of some *S. vittatus* around 160 mm SL may be indistinguishable from those of *S. fasciatus*, which could lead to the idea that these nominal species are synonymous, as proposed by Géry (1977). Furthermore, the coloration of specimens smaller than 120 mm SL in some species of *Schizodon* (as in *S. fasciatus* and *S. vittatus*) is also identical, leading to misidentifications, as in Sidlauskas, Vari (2012). For example, *Leporinus falcipinnis* Mahnert, Géry & Muller, 1997 (current synonym of *L. altipinnis*) was described and diagnosed from *L. altipinnis* based on a distinct color pattern (fourteen transversal bars *vs.* eight), which turned out to be due to ontogenetic change, the eight transversal bars of juveniles splitting into fourteen in large adults (Mahnert *et al.*, 1997; Britski, Birindelli, 2016). Therefore, extensive series of specimens encompassing different sizes are necessary for taxonomic studies of Anostomidae, and diagnostic color patterns should always be proposed considering the size of specimens.

The presence of dark transversal bars formed by dermal and epidermal pigment is characteristic of the Amazonas clade of *Schizodon*, being present in all species, except perhaps in *S. scotorhabdotus* (see Sidlauskas *et al.*, 2007). *Schizodon fasciatus* and *S. corti* are unique among the Amazonas clade congeners by possessing a dark rounded spot on the base of median caudal-fin rays. On the other hand, *S. borellii*, *S. dissimilis*, and *S. intermedius* share the lack of any dark marks on the caudal peduncle and caudal-fin rays. Four dark bars are present in *S. corti*, *S. dissimilis*, *S. fasciatus*, *S. intermedius*, and *S. vittatus*. *Schizodon scotorhabdotus* has a dark midlateral stripe, a condition also



distinct from that of *S. trivittatus* and *S. vittatus*. The dark midlateral stripe on the caudal peduncle was early recognized as a diagnostic feature of *S. vittatus* (Castelnau, 1855; Garman, 1890). This caudal peduncle stripe is useful in diagnosing *S. trivittatus* and *S. vittatus* from *S. fasciatus*, contrary to what was assumed by Géry (1977). However, it was considered variable when larger samples were made available (Géry, 1977; Sidlauskas, Vari, 2012).

Sidlauskas, Vari (2012) described variation in lateral dark stripe for specimens of *S. fasciatus*. Some individuals smaller than approximately 130 mm SL exhibited the dark stripe, however, such stripe is absent in individuals above that size. As in our study, this seems to be an ontogenetic variation, in which a conspicuous dark midlateral stripe formed by dermal pigment is present in small specimens (smaller than 120–130 mm SL). This stripe becomes faded in larger specimens and is partially replaced by a dark midlateral stripe formed by the epidermal pigment in *S. vittatus* and *S. trivittatus*, and by a small caudal blotch in *S. corti* and *S. fasciatus*. There seems to be intra-specific variation in medium-sized specimens (from 120 to 160 mm SL), with some lacking the dark epidermal pigment during this process. Be that as it may, the presence of a dark midlateral is a consistent feature of specimens larger than 160 mm SL in both *Schizodon trivittatus* and *S. vittatus*, and thus an essential diagnostic feature that distinguishes it from *S. fasciatus*. Based on that, it is likely that the specimens previously identified as *S. vittatus* by Sidlauskas, Vari (2012) were small specimens of *S. fasciatus*, and not *S. vittatus*.

**Distribution patterns.** The disjunct distribution of all species of the Amazonas clade of *Schizodon* is an interesting biogeographical matter. The species herein described fits that pattern. In the Amazon basin, the most widespread species is *Schizodon fasciatus* occurring from Peru to near the mouth of the Amazonas and in the major tributaries, including the Madeira (Santos, Feitosa, 2013) and Negro (Beltrão *et al.*, 2019) rivers. *Schizodon fasciatus* also occurs in the Essequibo, Corantjin, and Maroni rivers in Suriname and French Guiana (Sidlauskas, Vari, 2012). This widespread distribution in the Amazon basin was considered as a lowland distribution pattern by Lima, Ribeiro (2011). Other anostomids that exhibit the Amazon basin distribution pattern are *Rhytiodus* spp., and *Megaleporinus trifasciatus* (Lima, Ribeiro, 2011).

On the other hand, *Schizodon vittatus* seems to be restricted to the Araguaia and Tocantins drainages. Several species of fish are also endemic to the Araguaia and Tocantins basins including *Moenkhausia alesi* Petrolli & Benine, 2015, *Serrapinnus aster* Malabarba & Jerep, 2014, *Hypostomus delimai* Zawadzki, de Oliveira & Debona, 2013, *Harttia duriventris* Rapp Py-Daniel & Oliveira, 2001, *Hassar wilderi* Kindle, 1895, anostomid *Leporinus unitaeniatus* Garavello & Santos, 2009 (Garavello, Santos, 2009), *L. santosi* Bristki & Birindelli, 2013 (Britski, Birindelli, 2013) and at least one other aquatic vertebrate (Hrbek *et al.*, 2014). Furthermore, *Megaleporinus* cf. *trifasciatus* (*sensu* Ramirez *et al.*, 2017a) is endemic to the Araguaia-Tocantins, and closely related to a species more widespread in the Amazon basin.

Similarly, the distribution of *Schizodon trivittatus* seems to be restricted to the Xingu and Tapajós basin, a pattern exhibited by at least a few other species, including *Leptodoras oyakawai* Sousa & Sabaj Pérez, 2008, *Corydoras benattii* Espíndola, Tencatt, Pupo, Villa-Verde & Britto, 2018, *Bryconops gracilis* (Eigenmann, 1908), *Moenkhausia*

*pirauba* Zanata, Birindelli & Moreira, 2010, *Spatuloricaria taira* Fichberg, Oyakawa & de Pinna, 2014, *Retroculus xinguensis* Gosse, 1971, and *Rivulus kayabi* (Costa, 2008).

The distribution pattern observed in the three species above of *Schizodon* is also congruent with the ecoregions, as delimited by Abell *et al.* (2008), who considered the Tapajós (their ecoregion number 322), Xingu (320), and Tocantins-Araguaia (324), as three distinct ecoregions. These ecoregions share several species, including *Argonectes robertsi* Langeani, 1999, *Microchemobrycon elongatus* Géry, 1973, *Leporacanthicus* spp., *Scobinancistrus* spp., *Roeboexodon guyanensis* (Puyo, 1948), and *Tocantinsia piresi* (Miranda Ribeiro, 1920), indicating that they have a history of connection. In addition, the close relationships between the Araguaia, Tocantins, Tapajós and Xingu basins were recovered based on an area cladogram (Lima, Ribeiro, 2011: fig. 9.5), and on a Brooks Parsimony Analysis (BPA, Dagosta, Pinna, 2017: fig. 4), both considering the fish species shared by these basins. The group formed by these drainages was named the Brazilian Shield drainages by Dagosta, Pinna (2017). Lima, Ribeiro, (2011) considered that the species in this area exhibit a shield distribution pattern. In both of those studies, part of the Madeira basin that drains the Brazilian shield's uplands was considered to form that group. Some of the species that occur in the Araguaia, Tocantins, Tapajós, and Xingu also occur in the Madeira drainage (especially in the Aripuanã River), such as *Archolaemus blax* Korrington, 1970, *Pachyurus junki* Soares & Casatti, 2000, and *Jupiaba acanthogaster* (Eigenmann, 1911). *Schizodon fasciatus* is the only species among congeners occurring in the Madeira basin, but not in the highlands of the Aripuanã River, where no congener is currently known to occur.

On the other hand, additional areas of endemism within the distribution areas of *S. vittatus* and *S. trivittatus*, such as those formed by sub-basins of the Tapajós and Xingu (Curuá River, Jamanxim River, or headwaters of Serra do Cachimbo, Goulding *et al.*, 2003, Lima, Birindelli, 2006; Birindelli, Britski, 2009; Birindelli *et al.*, 2009), are not consistent with the distribution observed for the species here studied. This could be related to the fact that these are medium to large-sized fishes that occur in the main channels and larger tributaries, have high vagility and can travel a long way without geographical barriers.

*Schizodon trivittatus* is the first species of the genus revealed using an integrative taxonomy framework, and perhaps the second species complex of the family investigated using such approach (Burns *et al.*, 2017). The differentiation of *S. vittatus* and *S. trivittatus* based on meristic and morphometric characters is hampered by their great morphological similarity. On the other hand, comparative analyses using DNA barcode (Ramirez *et al.*, 2020), and a detailed study of the coloration pattern securely revealed a species pair occurring in the tributaries of the right margin of the lower Amazonas River. This is an example of the success of the integrative taxonomy framework, an approach that can help to solve the taxonomy of other species that have similarly broad distributions.

**Comparative material examined.** *Schizodon nasutus*: **Brazil:** MZUSP 2023, 5, 87.0–100.8 mm SL; MZUSP 42844, 17, 96.0–206.0 mm SL; MZUSP 51457, 13, 98.0–115.0 mm SL; LISDEBE 6979, 3, 184.0–216.0 mm SL; LISDEBE 6980, 7, 204.0–252.0 mm SL; LISDEBE 749, 1, 241.0 mm SL; LISDEBE 994, 1, 188.0 mm SL; LISDEBE 1027, 2, 198.0–215.0 mm SL; LISDEBE 1274, 1, 260.0 mm SL; LISDEBE 4986, 1, 190.0 mm SL; LISDEBE 5861, 9, 210–229.0

mm SL. *Schizodon fasciatus*: **Peru**: MZUSP 21464, 1, 191.0 mm SL. **Brazil**: MCZ 19365, 3, 172.0–224.0 mm SL; MCZ 19336, 3, 194.0–262.0 mm SL; MZUSP 20972, 15, 170.0–295.0 mm SL; MZUSP 7518, 5, 110.0–130.0 mm SL; MZUSP 62720, 5, 115.0–240.0 mm SL; MZUSP 62722, 3, 240.0–275.0 mm SL; LISDEBE 6981, 19, 94.4–316.0 mm SL; MZUSP 9188, 3, 140.0–230.0 mm SL; MCZ 19329, 2, 100.0–285.0 mm SL. *Schizodon isognathus*: **Brazil**: MZUSP 4397, 1, 307.0 mm SL; MZUSP 36719, 1, 176.0 mm SL; LISDEBE 6977, 1, 230.0 mm SL; LISDEBE 6978, 1, 207.0 mm SL. *Schizodon intermedius*: **Brazil**: MZUSP 41123, 280.0 mm SL, holotype; MZUSP 41125–41137, 13, 145.0–280.0 mm SL, paratypes; LISDEBE 6984, 6, 210.0–291.0 mm SL. *Schizodon altoparanae*: **Brazil**: MZUSP 41102, 282.0 mm SL, holotype; MZUSP 41103 to 41120, 28, paratypes, same locality as holotype; LISDEBE 5830, 1, 230 mm SL; MZUSP 41122, 3, Tietê River, Barra Bonita; MZUSP 4018, 1, 66 mm SL; LISDEBE 6983, 2, Ilha Solteira, Paraná River, Ilha Solteira dam. **Paraguay**: LISDEBE 6988, 4, 128.0–225.0 mm SL. *Schizodon australis*: **Brazil**: MCP12931, 260.0 mm SL, holotype 4; Paratypes: MCP12793, 1, São Nicolau, Uruguai River, Santo Izidro; MCP 12936, 3, São Nicolau, Uruguai River, Santo Izidro; MCP 12929, 2, Roque Gonzales, mouth of Ijuí River, tributary of Uruguai River; MCP 13279, 1, São Nicolau, Uruguai River, Santo Izidro; MZUSP 47445, 1, São Nicolau, Uruguai River, Santo Izidro; MZUSP 47446, 1, São Nicolau, Uruguai River, Santo Izidro. *Schizodon dissimilis*: **Brazil**: MCZ 19383, 264.6 mm SL, lectotype, Puty (= Poti) River, Parnaíba basin; MCZ 19381, 5 (3 measured), 152.0–260.0 mm SL; MCZ 19382, 2 (1 measured), 252.5 mm SL; MCZ 19384, 1, not measured; USNM 120238, 3, 166.0–211.0 mm SL, all paralectotypes, same data as lectotype; ANSP 69491, 3, 40.0–80.0 mm SL; ANSP 69494, 1, (c&s); MZUSP 55143, 4, 196.0–220.0 mm SL; MZUSP 55144, 1, 155.0 mm SL; MZUSP 35763, 4, 195.0–292.0 mm SL; MZUSP 21386, 4, 141.0–249.0 mm SL; MZUSP 5074, 1, 272.0 mm SL; MZUSP 3558, 1, 185.0 mm SL; MNRJ 51527, 1, 181.0 mm SL; CPDOL 98287, 10, 155.0–187.0 mm SL; MNRJ 51528, 1, 201.0 mm SL; MNRJ 51529, 1, 274.0 mm SL; MNRJ 51530, 1, 215.0 mm SL; LISDEBE 6976, 2, 221.0–229.0 mm SL; MZUSP 5101, 4, 61.0–114.0 mm SL. *Schizodon knerii*: **Brazil**: MZUSP 94051, 4, Formoso River, tributary of Corrente River, at Colônia do Formoso, Coribe, BA; LISDEBE 7001, 1, 187.0 mm SL LISDEBE 7321, 2, 188.0–190.0 mm SL; LISDEBE 7322, 5, 176.0–205.0 mm SL; MZUSP 95159, 2; MZUSP 73762, 1; MZUSP 90841, 1. *Schizodon borellii*: **Brazil**: MZUSP 2908, 1, Coxim, Piqueri River; MZUSP 62715, 1, Cuiabá, mouth of Varadouro, near 25 km from Barão de Melgaço; MZUSP 41146, 2, 290.0–298.0 mm SL, Cuiabá, Coxipó da Ponte River, São Gonçalo; MZUSP 41147, 2, Cuiabá, Cuiabá River, Sangradouro Grande, Barão de Melgaço; MZUSP 41148, 9, Miranda, marginal ponds of Transpantaneira road; MZUSP 62439, 1, Sangradouro Grande, Barão de Melgaço; MZUSP 62714, 2, Barão de Melgaço; MZUSP 41151, 1, mouth of Croará; LISDEBE 6977, 13, 227.0–271.0 mm SL; **Paraguay**: MZUSP 41144, 4. *Schizodon corti*: **Venezuela**: USNM 121300, 257.0 mm SL, holotype. *Schizodon jacuiensis*: **Brazil**: MZUSP 38864, 1, paratype; MZUSP 62748, 2, 107.0–196 mm SL.

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