

# A new species of *Inpaichthys* from the rio Canamã, rio Aripuanã basin, Mato Grosso State, Brazil, with a redefinition of the genus (Characidae: Stethaprioninae)

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A new species of *Inpaichthys* is described from a tributary of the rio Canamã, rio Aripuanã basin, Mato Grosso State, Brazil. The new species can be diagnosed from its congeners by the color pattern in life and by morphometric and meristic features. A comprehensive phylogenetic analysis of the Characidae, conducted to assess the generic placement of the new species, revealed that *Hasemania nambiquara* is also a member of *Inpaichthys* and thus transferred to this genus. A monophyletic group composed of the three known species of *Inpaichthys* is hypothesized to be related to *Nematobrycon* and a clade composed of *Carlana*, *Pseudochalceus*, and *Rhoadsia*, among the taxa herein analyzed. A diagnosis for *Inpaichthys* and morphometric and meristic data of *I. kerri* are also presented.

**Keywords:** *Hasemania nambiquara*, *Inpaichthys kerri*, rio Madeira basin, Phylogeny, Taxonomy.

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Uma espécie nova de *Inpaichthys* é descrita de um tributário do rio Canamã, bacia do rio Aripuanã, estado de Mato Grosso, Brasil. A espécie nova pode ser diagnosticada de suas congêneres por seu padrão de colorido em vida e por caracteres morfométricos e merísticos. Uma ampla análise filogenética de Characidae, conduzida para avaliar o posicionamento genérico da nova espécie, demonstrou que *Hasemanian nambiquara* também é um membro do gênero *Inpaichthys* e esta espécie é aqui transferida a esse gênero. Um grupo monofilético composto pelas três espécies de *Inpaichthys* é hipotetizado como sendo relacionado a *Nematobrycon* e o clado composto por *Carlana*, *Pseudochalceus* e *Rhoadsia*, entre os táxons aqui examinados. Uma diagnose para *Inpaichthys* e os dados morfométricos e merísticos de *I. kerri* também são apresentados.

**Palavras-chave:** Bacia do rio Madeira, Filogenia *Hasemanian nambiquara*, *Inpaichthys kerri*, Taxonomia.

## INTRODUCTION

*Inpaichthys* Géry & Junk, 1977 is currently a monotypic genus of Characidae. It was described by Géry, Junk (1977) to include *Inpaichthys kerri* Géry & Junk, 1977. The generic name honors the Instituto Nacional de Pesquisas da Amazônia (INPA), which had a research station in the Aripuanã city, above the great falls of Dardanelos and Andorinhas, on the upper rio Aripuanã, the type-locality of *I. kerri*.

*Inpaichthys kerri* is a small-sized species, not surpassing 28 mm SL, with a unique life color pattern among characids composed of a wide, conspicuous longitudinal black stripe from the jaw to the caudal fin, and the dorsal half of the body is bright blue and glows like “neon tubes” (Géry, Junk, 1977). Despite uncertainties regarding its relationship within Characidae, Géry, Junk (1977) proposed the genus *Inpaichthys* based on a combination of non-exclusive morphological characters, *viz.*, a subsuperior mouth, tricuspid teeth arranged in two very irregular series on the premaxilla, the inner series generally composed of only two median teeth on each side, maxilla with 7–8 conical to tricuspid teeth, third infraorbital (“suborbital” of Géry, Junk, 1977) large and in contact with the preopercular canal, absence of infraorbitals 5 and 6 (single postorbital of Géry, Junk, 1977), dorsal fin slightly behind the middle of the body, a deep caudal peduncle, and a peculiar coloration consisting of a wide and conspicuous longitudinal stripe extending from the dentary to the caudal fin, curved ventrally (Géry, Junk, 1977). According to a recently published phylogenetic hypothesis based on combined morphological and molecular data, *Inpaichthys* belongs to the tribe Rhoadsiini, being closely related to the genera *Nematobrycon* Eigenmann, 1911, *Pseudochalceus* Kner, 1863, and the clade of *Carlana* Strand, 1928, and *Rhoadsia* Fowler, 1911 (Mirande, 2019).

Recent collecting efforts at the rio Canamã, a tributary of the rio Aripuanã (the river basin where *Inpaichthys kerri* occur) revealed an additional, very distinctive, new *Inpaichthys* species. During our investigation on this new species, we tested our suspicion based on color pattern and distribution that *Hasemanian nambiquara* Bertaco & Malabarba, 2007, would be actually a species of *Inpaichthys*, which was corroborated by including

morphological data of the species into a phylogenetic analysis including both *I. kerri* and the new species, thus raising the number of species within this genus from one to three. We also present a hypothesis about the phylogenetic relationships between the species of genus using the framework provided by Mirande (2019), expanded in Terán *et al.* (2020) and subsequent articles (Lima *et al.*, 2021; Ferreira *et al.*, 2023).

## MATERIAL AND METHODS

**Morphological analysis.** Counts and measurements follow Fink, Weitzman (1974) and Menezes, Weitzman (1990), except for counts of the horizontal scale rows below the lateral line, that were counted to the pelvic-fin insertion. In the description, presented counts are followed by the number of specimens presenting a specific count in parentheses. Asterisks indicate values of the holotype. Counts of vertebrae and supraneurals are taken from cleared and stained (c&s) specimens; total vertebrae counts include the four vertebrae of the Weberian apparatus and the terminal centrum. *Circuli* and *radii* counts are taken from scale row immediately above the lateral line. Specimens were cleared and stained following the method of Taylor, Van Dyke (1985). Osteological terminology follows Weitzman (1962) with the modifications listed by Vari, Harold (2001). Institutional abbreviations follow Sabaj (2020). In the original description, the morphometrics of *Inpaichthys kerri* deviate from standard established by Fink, Weitzman (1974) and followed ever since in most of the literature on Characiformes systematics. For this reason, the morphometrics data of *I. kerri* were also obtained and presented in Tab. 1 for comparison reasons. Data on *Hasemania nambiquara* was obtained both from the direct examination of two paratypes, and from the original description (Bertaco, Malabarba, 2007).

**Extraction of the DNA, amplification, purification, and sequencing.** The DNA of seven specimens of the new species of *Inpaichthys* was extracted using the saline extraction protocol of Aljanabi, Martinez (1997). We amplified two mitochondrial molecular markers, Cytochrome c Oxidase I (COI) and 16S rRNA with primers described by Ward *et al.* (2005) and Palumbi, 1996, respectively. The Polymerase Chain Reaction (PCR) was prepared in a final volume of 25 µL containing: 12,5 µl GoTaq® DNA Polymerase (Promega), 0,5 µl of the each primer (10 mM), 1 µl of DNA, and ultrapure water to complete the final volume. The reactions were processed in a thermocycler (Applied Biosystems, Veriti), with initial denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 45 seconds, annealing at 53 °C for 45 sec, and extension at 72 °C for 60 sec, with a final extension at 72 °C for 5 min. The amplicons of the genes COI and 16S rRNA were purified and sequenced by Biotecnologia Pesquisa e Inovação (BPI, <https://bpibiotecnologia.com.br>). The samples were purified using a magnetic bead kit of the AMPure XP type, and sequenced with a BigDye® Terminator v. 3.1 Cycle Sequencing kit (Applied Biosystems), following the manufacturer's protocols. The samples were sequenced automatically by capillary electrophoresis in an ABI3730xl Genetic Analyzer (Applied Biosystems). The new sequences were deposited in the Genbank (16S rRNA: OR502673, OR502674, OR502675, OR502676, OR502677, OR502678) and BOLD Systems (COI: INPAI001–23, INPAI002–23, INPAI003–23, INPAI004–23).

**Phylogenetic analysis.** Phylogenetic relationships of the new species were evaluated through the analysis of a dataset combining morphological and molecular evidence of the Characidae. The dataset included 520 morphological characters and nine blocks of molecular data. The morphological dataset was firstly defined by Mirande (2009, 2010), and had several stages of addition and revision of data (Mirande *et al.*, 2013, 2023; Ohara *et al.*, 2017, 2019; Mirande, 2019; Terán *et al.*, 2020; Lima *et al.*, 2021; Ferreira *et al.*, 2023). The molecular data included mitochondrial ribosomal 12S and 16S, ATP synthase F0 subunit 6 (ATP6), cytochrome c oxidase subunit I (COI), cytochrome b (CYTB) and the nuclear coding markers myosin heavy chain 6 (MYH6), patched domain containing 4 (PTCHD4) [mentioned as PTCHD1 in Thomaz *et al.* (2015)], and recombination activating 1 and 2 (RAG1 and RAG2). Sequences were aligned with Muscle (Edgar, 2004) through its implementation in Aliview (Larsson, 2014). The latter program was also used to corroborate codon positions, in order to prevent problems with reading frames of protein-coding sequences. Most of the molecular data were extracted from previous articles (*e.g.*, Javonillo *et al.*, 2010; Oliveira *et al.*, 2011; Thomaz *et al.*, 2015; Terán *et al.*, 2020) and curated through the corroboration of vouchers identification in collection databases or personal examination of the specimens, when possible. The list of morphological characters was provided in Mirande (2010, 2019) and a table with the Genbank ([www.ncbi.nlm.nih.gov/nucleotide](http://www.ncbi.nlm.nih.gov/nucleotide)) or BOLD ([www.boldsystems.org/](http://www.boldsystems.org/)) accessions herein analyzed was published in Terán *et al.* (2020). Herein, we added new molecular data available in Genbank since Terán *et al.* (2020) both for the Characidae and outgroup families (Tab. S1), in addition to the sequences of the new species, listed in the previous section. The complete dataset herein analyzed, with data for 578 species of Characiformes, is provided as supplementary data (S2). Relative to previous articles, we added herein the new species and *Hasemanian nambiquara*.

All analyses were performed with parsimony under extended implied weighting (Goloboff, 1993, 2014) in TNT v. 1.6 for Linux (Goloboff, Morales, 2023). Analyses followed the same procedure than in Ferreira *et al.* (2023), exploring a broad range of conditions combining five weighting schemes (general ways of weighting characters against their homoplasy) and six weighting strengths (values of K), resulting then in 30 analyses. In the different weighting schemes, molecular characters were weighted according to (1) BLK: the average homoplasy of entire block of data (marker), (2) COD: the average homoplasy of three contiguous characters (a codon; applicable for coding sequences), (3) GRO: the average homoplasy of groups formed by 30 contiguous characters (10 codons, for coding sequences), (4) SEP: the homoplasy of each separate character, and (5) POS: the average homoplasy of characters from each codon position for each coding marker, with the ribosomal characters weighted according to their own homoplasy. Weighting schemes were combined with six strengths determined for different K-values (Goloboff, 1993, 2014) in which an averagely homoplastic character had 70, 74, 78, 82, 86, and 90% of the weight of a character with no homoplasy. The analyzed K-values (16, 20, 25, 32, 43, and 64) sample regularly decreasing weighting strengths (Mirande, 2009). Each analytical condition is expressed as the abbreviation of the weighting scheme followed by the weighting strength (value of K). For instance, in COD64, three contiguous sites (a codon) are grouped to be collectively weighted (COD scheme) with the homoplasy downweighted according to a K = 64. After searching for the most parsimonious trees on each condition, a metacriterion based on

global parsimony was used to select the final hypothesis (Terán *et al.*, 2020; Mirande *et al.*, 2023). According to that criterion, the optimality of each most parsimonious tree is evaluated according to all the explored parameters, selecting the one that is better in the average of conditions. Clade supports were estimated through symmetric resampling (300 replicates and the values are represented as GC-values (difference of frequencies between the obtained clade and its most frequent alternative)).

Supplementary files provided include: the analyzed GenBank accessions and their vouchers, when known (Tab. S1); the analyzed dataset combining all the morphological and molecular data (S2); the scripts for TNT software to reproduce searches and trees comparisons herein performed (S3); a collection of all trees obtained under the complete range of explored analytical conditions, formatted for TNT software (S4); the list of autapomorphies and synapomorphies of the obtained nodes of the phylogenetic hypothesis herein proposed (S5); and our final hypothesis, as cladograms in vectorial graphic format, containing node numbers (corresponding to those listed in S5), frequencies, and support values (Fig. S6).

## RESULTS

### *Inpaichthys* Géry & Junk, 1977

**Type-species.** *Inpaichthys kerri* Géry & Junk, 1977

**Diagnosis.** We found eight morphological non-exclusive synapomorphies supporting the monophyly of *Inpaichthys* that, in combination, could be useful to diagnose the genus: nasal septum of mesethmoid formed by two parallel lamellae (9:1), absence of a dorsal expansion of rhinosphenoid projected medial to olfactory nerves (35:0), short supraoccipital spine covering dorsally only anterior axis of neural complex of Weberian apparatus (62:1), articulation between second and third infraorbitals anteroventrally angled (86:1), absence of anguloarticular portion of mandibular laterosensory canal (105:1), frontal and periotic laterosensory canals forming an angle on pore receiving infraorbital canal (118:1), maxillary teeth extended approximately to half maxillary length (191:0), and presence of 24 or fewer branched anal-fin rays, with a reversal to 21–25 in the new species herein described (420:0). Species of *Inpaichthys* can also be recognized by the combination of the following characters: two or more maxillary teeth with larger one, tri or pentacuspitate, ten or fewer gill rakers on first hypobranchial and ceratobranchial, interrupted lateral line, lack of parietal branch of supraorbital cephalic laterosensory canal, pore of the supraorbital cephalic laterosensory canal situated just anterior to dilatator fossa oriented dorsomedially (Mirande, 2018: S11, figure 11), *circuli* absent on posterior field of scales, iii+9 dorsal-fin rays with the anterior one visible only in c&s specimens, lack of secondary-sexual hooks on males, and lack of pseudotympanum.

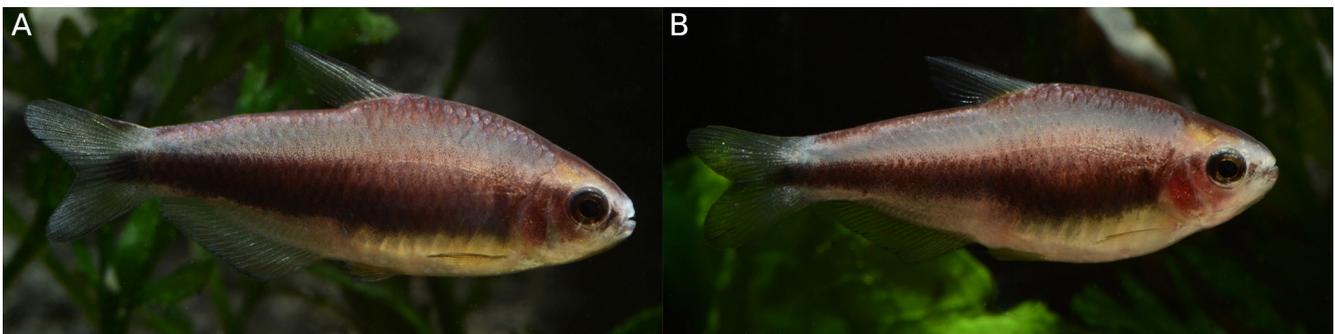
*Inpaichthys nambiquara* (Bertaco & Malabarba, 2007), new combination

(Fig. 1)

*Hasemania nambiquara* Bertaco & Malabarba, 2007:350–53 (Type-locality: “Brazil, Mato Grosso, Comodoro, rio Doze de Outubro on Highway BR-364 between Comodoro and Vilhena, tributary of rio Juruena, upper rio Tapajós drainage, 12°58'39”S 60°00'30”W”; see Remarks below). —Ohara, Loeb, 2016:3–6 (Brazil, Mato Grosso State, Igarapé Mutum, rio Juruena basin; photo in life, abundance).

**Diagnosis.** Five morphological autapomorphies were found for *Inpaichthys nambiquara*: third infraorbital not reaching horizontal arm of preopercle in its anterior margin (88:1), presence of (a reduced, in this species) fourth infraorbital (90:0), three or fewer maxillary teeth (190:0), five or more cusps on anterior maxillary teeth (193:1), and the possession of four or fewer supraneurals (392:0). *Inpaichthys nambiquara* can be easily distinguished from both *I. kerri* and the new taxon herein described by the absence of an adipose fin (*vs.* adipose fin present in other *Inpaichthys* species), and by having a conspicuous dark stripe along predorsal area (*vs.* absence of a conspicuous dark stripe along predorsal area in the remaining *Inpaichthys* species). *Inpaichthys nambiquara* can additionally be distinguished from the new species by the following combination of characters: presence of a conspicuous, broad, ventrally curved midlateral stripe extending from snout to caudal peduncle (*vs.* presence of a narrow, straight dark midlateral stripe along the longitudinal septum of body, extending from second humeral blotch to median caudal-fin rays), absence of six red dotted longitudinal stripes on the body flanks in living specimens (*vs.* presence), 16–18 branched anal-fin rays (*vs.* 21–25 branched anal-fin rays), presence of a single humeral blotch (*vs.* two humeral blotches), and largest dentary teeth with five cusps (*vs.* largest dentary teeth with three cusps). *Inpaichthys nambiquara* can additionally be distinguished from *I. kerri* by the presence of a humeral blotch (*vs.* absence of any humeral blotch), and 2–3 maxillary teeth, largest one pentacuspoid (*vs.* 6–9 maxillary teeth, largest tricuspid), respectively.

**Description.** See Bertaco, Malabarba (2007) for a complete description of the species.



**FIGURE 1** | *Inpaichthys nambiquara*, new combination, in life. **A.** Male; **B.** Female. Photos by Hans-Georg Evers.

**Remarks.** The type-locality of *Inpaichthys nambiquara* was originally indicated to be at the rio Doze de Outubro at the road BR-364. The rio Doze de Outubro is a tributary of the rio Camararé, a major tributary of the rio Juruena. Ohara, Loeb (2016) sampled extensively some of the headwater tributaries of the rio Camararé crossing the highlands of the Chapada dos Parecis at the road BR-364, including the rio Doze de Outubro, and only collected the species at the rio Mutum, another tributary of the rio Camararé, which runs parallel to the rio Doze de Outubro, roughly 20 km apart along their lengths (> 100 km) before joining the rio Camararé. Despite their proximity and the fact that they both belong to the same sub-basin, they are apparently quite distinct in the composition of their ichthyofaunas (Ohara, Loeb, 2016). The type-locality of *I. nambiquara* has been recently recognized as being incorrectly stated in the original description, and to be indeed the rio Mutum (V. A. Bertaco, 2023, pers. comm.). In fact, one of the authors (FCTL) participated in the field expedition where the type-material of *I. nambiquara* was obtained and photographed specimens sampled at the rio Mutum, including a specimen of *I. nambiquara*, which lends support to the idea that the locality was incorrectly stated at the original description. We take this opportunity to amend the type-locality of the species to “Brazil, Mato Grosso, Comodoro, rio Mutum, tributary of rio Camararé, at highway BR-364 between Comodoro and Vilhena, rio Juruena basin, 13°05'08”S 59°53'32”W”. In the original description, Bertaco, Malabarba (2007) did not mention the presence of sexual dimorphism in the species. However, H.-G. Evers (2023, pers. comm.), who bred the species in captivity, noticed that males are slightly larger than females, presenting a dark margin on the anal fin, and present a broader midlateral stripe (compare Figs. 1A–B). *Inpaichthys kerri* apparently possesses a similar sexual dimorphism, with males presenting a broader midlateral stripe and an anal-fin margin straighter than females (see Pastana *et al.*, 2017:1308, figs. 3E–F).

**Material examined.** *Inpaichthys nambiquara*. Brazil, Mato Grosso State, Comodoro, upper rio Tapajós basin: MCP 38038, paratypes, 2 of 4, 1 c&s, 21.1–23.5 mm SL.

### *Inpaichthys parauapiranga*, new species

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(Figs. 2–4; Tab. 1)

**Holotype.** CPUFMT 7908, 25.4 mm SL, Brazil, Mato Grosso State, Aripuanã, tributary of the rio Canamã, rio Aripuanã basin, upper rio Madeira basin, 10°24'40”S 58°54'13”W, 14 Mar 2021, A. C. Ribeiro & H. Pains da Silva.

**Paratypes.** All from the same locality of the holotype. CI-FML 7946, 4, 14.3–16.0 mm SL; CPUFMT 7891, 51, 10.3–25.4 mm SL (8 c&s, 16.1–24.4 mm SL); ZUEC 17698, 4, 13.7–16.1 mm SL; collected with the holotype; CPUFMT 7892, 10, 12.9–23.6 mm SL, 20 Aug 2021, H. Pains da Silva. CPUFMT 7893, 11, 13.1–24.2 mm SL, 20 Aug 2021, H. Pains da Silva. MUBIO 113, 5, 19.0–26.3 mm SL; ZUEC 17920, 4, 20.9–22.4 mm SL, 25 Oct 2022, F. C. P. Dagosta, T. J. Seren, B. A. Nagamatsu & J. Damasceno.

**Diagnosis.** *Inpaichthys parauapiranga* can be easily distinguished from both *I. kerri* and *I. nambiquara* by its life color pattern. *Inpaichthys parauapiranga* has six red dotted longitudinal stripes on the flanks that are absent in *I. kerri* and *I. nambiquara*. Additionally, *I. parauapiranga* has a narrow dark midlateral stripe along the longitudinal septum of body, extending from second humeral blotch to median caudal-fin rays (*vs.* a large dark midlateral stripe along longitudinal septum of body extending from snout to caudal peduncle in *I. kerri* and *I. nambiquara*). *Inpaichthys parauapiranga* can also be distinguished from *I. kerri* by the following combination of characters: presence of two humeral blotches (*vs.* absence of humeral blotches); five scale rows between dorsal-fin origin and lateral line (*vs.* six scale rows between dorsal-fin origin and lateral line); and 12–14 circumpeduncular scales (*vs.* 16 circumpeduncular scales). *Inpaichthys parauapiranga* is also distinguished from *I. nambiquara* by the following combination of characters: adipose fin present (*vs.* adipose fin absent); 21–25 anal-fin branched rays (*vs.* 16–18 anal-fin branched rays); two humeral blotches (*vs.* a single humeral blotch), and largest dentary teeth with three cusps (*vs.* largest dentary teeth with five cusps). We found three morphological autapomorphies for *I. parauapiranga*: the absence of a bony rhinosphenoid (34:0), the absence of a conspicuous ethmopalatine cartilage (208:0), and the absence of denticles on gill rakers (300:1).

**Description.** Morphometric and meristic data for holotype and paratypes in Tab. 1. Largest specimen examined 26.3 mm SL. Body laterally compressed. Greatest body depth slightly anterior to vertical through dorsal-fin origin. Dorsal profile of head convex from tip of upper jaw to vertical through anterior nostril; slightly convex from that point to tip of supraoccipital spine. Dorsal body profile slightly convex from tip of supraoccipital spine to dorsal-fin origin; straight along dorsal-fin base; straight from terminus of dorsal-fin base to adipose-fin insertion, and slightly concave posteriorly from that point to anteriormost procurrent caudal-fin ray. Ventral profile of head and body convex from tip of lower jaw to pelvic-fin insertion, straight from that point to anal-fin origin, straight along anal-fin base and slightly concave along caudal peduncle.

Mouth slightly sub-superior, with dentary protruding slightly over anterior tip of premaxilla. Posterior terminus of maxilla surpassing vertical through anterior margin of eye. Premaxillary teeth in single misaligned row (Fig. 3), with 7(8), 8\*(6) or 9(6) tricuspid teeth, with median cusps slightly more developed and the third tooth usually positioned more externally. Maxilla with 6(3), 7(8), 8(4), 9\*(1), or 10(2) teeth, the first tooth tricuspid, remaining teeth conical. Dentary with four tricuspid teeth, followed by eight to twelve smaller conical teeth.

Scales cycloid. Three to five *radii*, and inconspicuous *circuli* anteriorly. Lateral line incomplete, with 6(7) or 7\*(14) perforated scales. Longitudinal scale series including lateral-line scales 31\*(9), 32(1), 33(7), 34(2), or 35(1). Five\* (20) scale rows between dorsal-fin origin and lateral line. Four\* (20) scale rows between lateral line and pelvic fin insertion. Predorsal scales 11(6), 12(9), 13(4), or 14\*(1). Circumpeduncular scales 12(3), 13(12), or 14\*(2). Single row of 11–16 scales covering base of anal-fin rays. Presence of two rows of scales extending over caudal-fin lobes; squamation covering evenly both caudal lobes.

**TABLE 1** | Morphometric data of *Inpaichthys parauapiranga* (N = 20) and *I. kerri* (N = 10; CPUFMT 4869; CPUFMT 4988; CPUFMT 5066). Range of *I. parauapiranga* includes the holotype. SD = standard deviation.

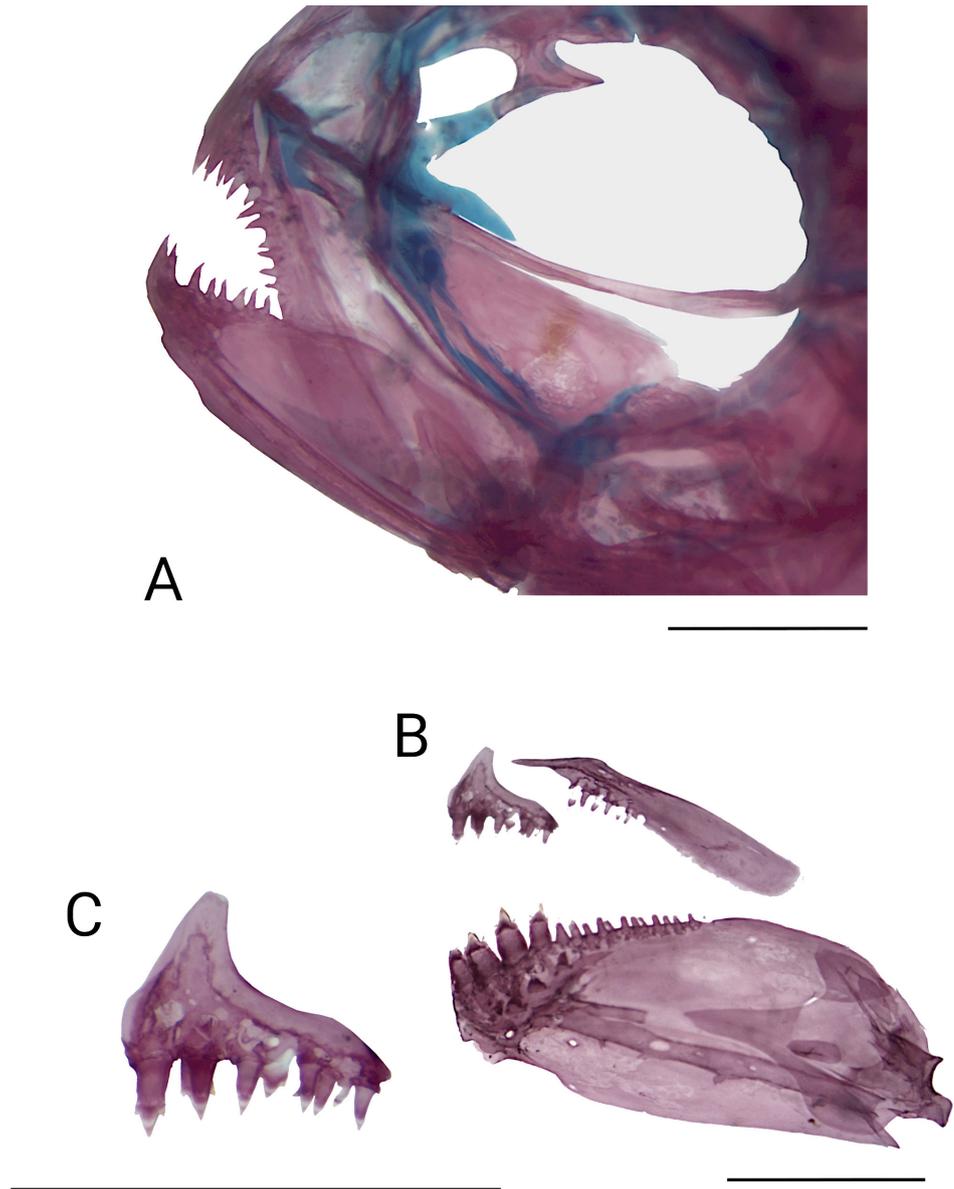
	<i>Inpaichthys parauapiranga</i>				<i>Inpaichthys kerri</i>		
	Holotype	Paratypes			Range	Mean	SD
		Range	Mean	SD			
Standard length	25.4	17.2–25.4	21.5	–	19.7–26.6	22.4	–
<b>Percentages of standard length</b>							
Body depth	32.5	32.1–36.4	34.7	1.1	30.6–36.3	32.7	1.8
Snout to dorsal-fin origin	54.7	53.1–57.6	55.1	1.1	51.6–55.9	54.1	1.3
Snout to pectoral-fin origin	25.5	25.5–28.3	26.7	0.9	24.9–27.3	25.7	1.1
Snout to pelvic-fin origin	43.6	43.6–47.6	46.0	1.1	42.9–47.1	44.6	1.4
Snout to anal-fin origin	56.9	53.3–57.6	56.1	1.3	56.2–60.5	59.1	1.2
Pelvic-fin insertion to anal-fin origin	13.9	11.8–15.3	13.7	1.0	11.3–15.8	13.6	1.3
Caudal-peduncle depth	13.9	11.6–14.0	12.6	0.7	10.0–11.7	11.2	0.5
Caudal-peduncle length	9.3	9.3–11.4	10.4	0.8	8.9–12.9	11.8	1.3
Dorsal-fin origin to caudal-fin base	51.4	46.8–51.5	49.3	1.2	46.4–49.4	48.3	1.0
Dorsal-fin base length	12.5	10.9–13.7	12.5	0.6	10.7–13.2	12.0	0.7
Anal-fin base length	34.9	31.3–37.1	34.3	1.4	29.4–32.7	31.3	1.2
Pectoral-fin length	20.6	18.2–23.9	21.3	1.6	18.3–22.6	20.2	1.3
Pelvic-fin length	14.3	12.6–15.9	14.7	0.9	14.0–16.8	15.1	0.8
Dorsal-fin length	29.6	26.4–34.6	29.9	1.8	26.1–30.6	28.5	1.8
Anal-fin length	18.5	17.1–23.9	20.5	1.8	17.4–21.3	19.1	1.4
Bony head length	25.7	25.6–29.5	27.5	1.3	24.3–28.0	25.8	1.1
Head depth	24.8	23.5–28.1	26.1	1.3	23.1–25.8	24.3	1.1
<b>Percentages of head length</b>							
Horizontal eye diameter	37.9	37.0–40.4	38.9	1.0	38.7–41.9	40.4	1.2
Snout length	20.9	19.7–24.5	22.2	1.3	20.1–23.6	21.9	1.2
Least interorbital distance	38.7	33.3–38.7	35.4	1.5	35.2–39.9	37.1	1.4
Upper jaw length	41.3	39.5–43.5	41.5	1.1	38.6–41.8	40.1	1.0

Supraneurals 7(7) or 8(1). Dorsal-fin rays iii, 9\*(20), first unbranched dorsal-fin ray visible only in c&s specimens. Dorsal-fin origin at midpoint of standard length. First dorsal-fin pterygiophore located after neural spine of 11<sup>th</sup> vertebra (8). First unbranched ray about half the length of second ray. Adipose fin present. Pectoral-fin rays i,10(20), its tip typically falling short before reaching vertical through pelvic-fin insertion, reaching that point in few (5) specimens. Pelvic-fin rays i,6(3) or i,7\*(17). Tip of adpressed pelvic fin not reaching origin of anal fin. Anal-fin rays iv(6), 21(1), 22(5), 23(5), 24\*(9), or 25(1). First anal-fin pterygiophore inserted behind haemal spine of 15<sup>th</sup> vertebra (8). Caudal fin forked, lobes similar in size; principal caudal-fin rays i,9/8,i (20). First gill arch with 10(15) gill rakers on hypobranchial and ceratobranchial, 6(2) or 7(9) on epibranchial, and one on cartilage between ceratobranchial and epibranchial. Four (1) branchiostegals, 3(1) on anterior ceratohyal, and 1(1) on posterior ceratohyal. Vertebrae 31(1), 32(3), or 33(4).

**Coloration in alcohol.** Overall basic color pale yellow (Fig. 2A). Dark chromatophores concentrated on the dorsal surface of the head, from tip of the snout to end of supraoccipital spine, and extend posteriorly over the predorsal scales. Small, scattered, dark chromatophores at infraorbitals, preopercle and opercle bones. Two diffuse humeral spots separated by a clearer area. Anterior humeral blotch located at level of second and third perforated scales of lateral line and extends to about one or two scales rows above lateral line. Second humeral blotch located at sixth and/or seventh perforated scales of lateral line and extending to approximately one row of scales above lateral line. Four brown diffuse lateral stripes present in the flanks, from dorsal profile to midline region. Body sides above midline with chromatophores in middle part of scales, chromatophores absent on posterior edges of scales. Scattered chromatophores below median stripe, with chromatophores concentrated at the edges of myosepta of posterior half of lower body above anal fin. All fins without pigmentation. Immediately after preservation (Fig. 2B), two conspicuous rectangular-shaped humeral blotches present, being the anteriormost blotch more diffuse when compared to the second humeral blotch, and still retaining five to six red dotted longitudinal stripes along body sides. Dorsal, adipose, pectoral, pelvic and anal fins yellow-orange at distal region. Caudal yellowish at the proximal region. Dorsal, caudal, and anal fins with scattered dark chromatophores along interradial membranes.



**FIGURE 2 |** *Inpaichthys parauapiranga*, holotype, CUFMT 7908, 25.4 mm SL, Brazil, Mato Grosso State, Aripuanã, rio Canamã, rio Aripuanã basin. **A.** When transferred to alcohol after several days of fixation; **B.** Recently fixed in formaldehyde. Photos by Alexandre C. Ribeiro.



**FIGURE 3** | *Inpaichthys parauapiranga*, paratype, CUFMT 7891, 24.4 mm SL. **A.** Anterior region of cranium; **B.** Upper and lower jaws; **C.** Premaxillary; right side, lateral view. Scale bars = 1 mm.

**Coloration in life.** Description based on photographs taken in the field of two specimens (Fig. 4), and of a specimen photographed by Fernando C. P. Dagosta (MUBIO 113, SL undetermined). Overall body coloration silvery, grayish dorsally, with a reddish tint in the upper third of the facial bones, occupying the upper half of the operculum and infraorbital 3 to infraorbital 5 (apparently imparted by the transparency of these bones, exposing red pigmentation of the gills), upper margin of eye also red. Blue iridescence present on the flanks, longitudinally to opercle to caudal peduncle. Five red dotted longitudinal stripes along the body sides and a narrow iridescent midlateral

stripe along longitudinal septum of body, extending from first humeral blotch to median caudal-fin rays. Dorsal, anal, adipose, pectoral, and pelvic fins yellow-orange (being orange specially concentrated at posterior half of pectoral and anal-fin rays in some specimens) (Fig. 4B), caudal fin yellowish. Tip of anal fin white, forming a stripe along anal-fin margin.

**Sexual dimorphism.** Contrary to what is observed for *I. kerri* and *I. nambiquara* (see Remarks of *I. nambiquara*), no secondary sexual characters were detected on examined specimens of *I. parauapiranga*.

**Geographical distribution.** *Inpaichthys parauapiranga* is known from a tributary of the rio Canamã, a tributary of rio Aripuanã, itself a tributary of the rio Madeira, Amazon basin, Mato Grosso State, Brazil (Fig. 5).

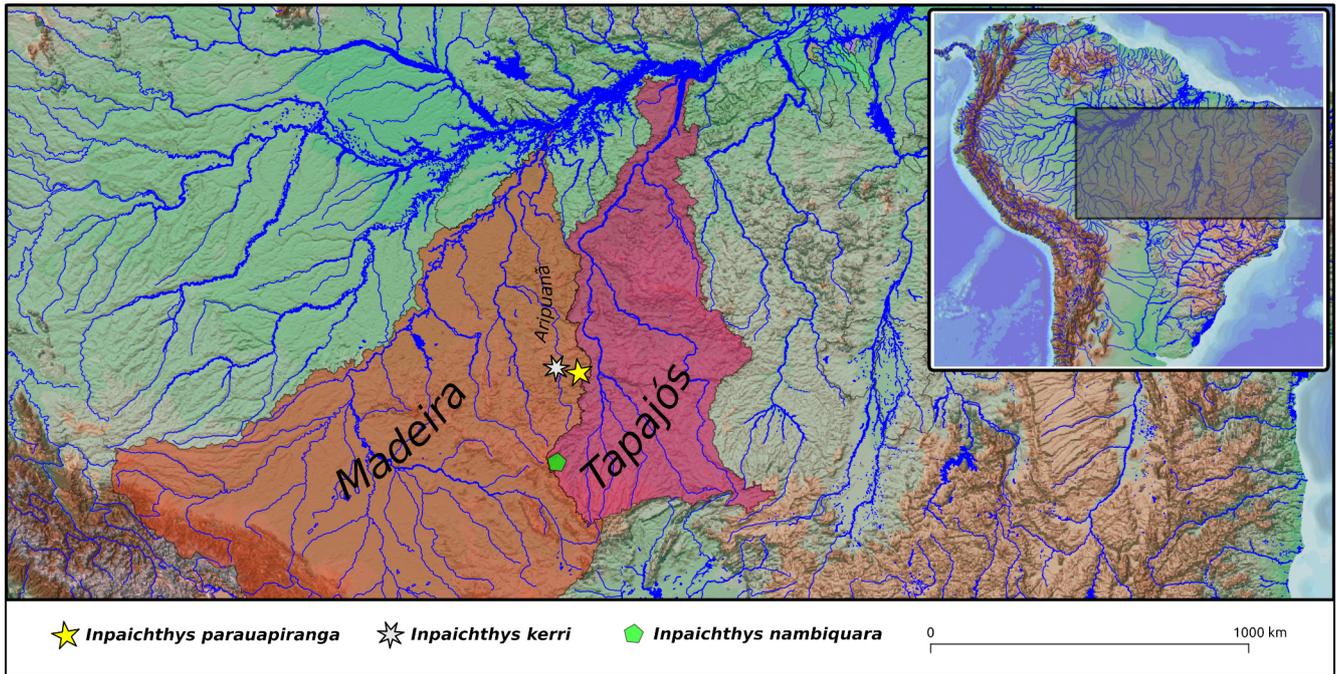
**Ecological notes.** The type-locality is a narrow and shallow stream (approximately 2 m wide and 60 cm deep), with clear water, slow to moderately-flowing current, and a sandy bottom with abundant aquatic vegetation, where specimens were typically captured (Fig. 6). Stomach contents of four paratypes revealed mainly remnants of insect larvae.

**Etymology.** The specific epithet *parauapiranga* derives from Tupi language, *paraua*, meaning blotch and *piranga*, meaning red, and it is in allusion to its color pattern in living specimens. A noun in apposition.

**Conservation status.** *Inpaichthys parauapiranga* was collected at only one sampling site. Several specimens were collected at the type-locality, indicating that the species is relatively common at this site, which is currently moderately well preserved. However,



**FIGURE 4** | *Inpaichthys parauapiranga*. **A.** CPUFMT 7891, paratype, 23.1 mm SL. **B.** CPUFMT 7908, holotype, 25.4 mm SL, immediately after capture. Photos by Alexandre C. Ribeiro.



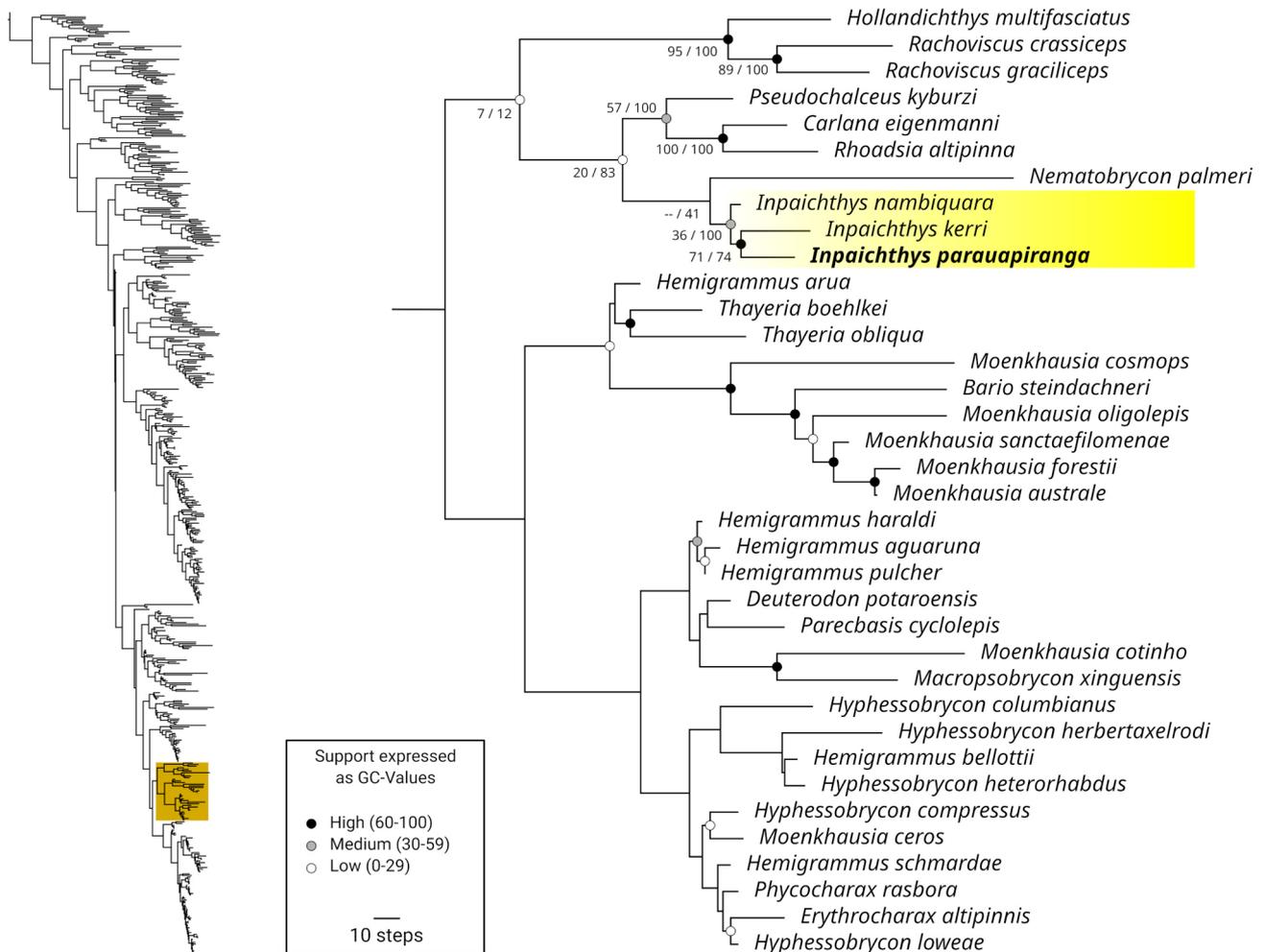
**FIGURE 5** | Map of South America with a detailed view of the southwestern portion of the Amazon basin, showing the distribution of the three *Inpaichthys* species (*I. kerri*, *I. nambiquara*, and *I. parauapiranga*) in the rio Madeira basin and rio Tapajós basin.



**FIGURE 6** | Type-locality of *Inpaichthys parauapiranga*, tributary of the rio Canamã, rio Aripuanã basin, Mato Grosso State, Brazil.

the species is already being targeted by fish collectors operating for the aquarium hobby and unsustainable levels of extraction of wild specimens may pose a threat to the species in the future. Thus, we suggest that pending more efforts to establish the distributional range, population, and impacts from capture for the aquarium hobby, *Inpaichthys parauapiranga* should be classified as Data Deficient (DD), according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2022).

**Remarks.** The phylogenetic hypothesis herein presented was obtained in SEP64 (i.e., each character weighted according to its own homoplasy and using a K-value of 64, the mildest explored). In these conditions we found three most parsimonious trees of 70439 steps (5600 of them morphological) and fit = 508.27677 (Fig. 7). The monophyly of *Inpaichthys*, including *I. nambiquara* as the sister group a clade composed of *I. kerri* and *I. parauapiranga*, was obtained in all performed analyses. In SEP64 the monophyly of the genus is moderately well supported (GC =36), while the relationships of *I. kerri* and *I. parauapiranga* have better support (GC =71). In the final hypothesis, *Nematobrycon palmeri* Eigenmann, 1911 was obtained as the sister group of *Inpaichthys*, but such relationship is weakly supported (negative GC value) and unstable among the most parsimonious trees of different analytical conditions (Freq = 41 and GC = -16 in the optimal trees of the explored conditions). Also with low support, we found as



**FIGURE 7** | Phylogenetic relationships of *Inpaichthys* in the tribe Stethaprionini, as obtained from the phylogenetic analysis under parsimony and extended implied weighting (SEP; K = 64; fit = 508.27677; length = 70435 steps). Support expressed as GC values (differences of frequencies “group present/contradicted”). Numeric values of support are shown only for the clade including *Inpaichthys*. Branches length represent the number of synapomorphies.

successive sister groups of *Inpaichthys* and *Nematobrycon* the clade composed of *Carlana*, *Pseudochalceus*, and *Rhoadsia*, and the group composed of *Hollandichthys* Eigenmann, 1909 and *Rachoviscus* Myers, 1926 (Fig. 7). The condition in which the number of morphological steps was lowest (5574) is SEP32. In the most parsimonious trees under SEP32 (70685 steps and fit = 738.45437), the relationships between *Inpaichthys* and *Nematobrycon* as the sister group of the clade of *Carlana*, *Pseudochalceus*, and *Rhoadsia* are the same than in SEP64. However, the sister group of this clade is composed of the genus *Jupiaba* Zanata, 1997 (*J. ajuricaba* (Marinho, Lima, 2009), *J. anterior* (Eigenmann, 1908), *J. anteroides* (Géry, 1965), *J. polylepis* (Günther, 1864), and *J. poranga* Zanata, 1997). In SEP64, we found eight morphological synapomorphies supporting the monophyly of *Inpaichthys*: nasal septum of mesethmoid formed by two parallel lamellae (9:1), absence of a dorsal expansion of rhinosphenoid projected medial to olfactory nerves (35:0), short supraoccipital spine covering dorsally only anterior axis of neural complex of Weberian apparatus (62:1), articulation between second and third infraorbitals anteroventrally angled (86:1), absence of anguloarticular portion of mandibular laterosensory canal (105:1), frontal and pterotic laterosensory canals forming an angle on pore receiving infraorbital canal (118:1), maxillary teeth extended approximately to half maxillary length (191:0), and presence of 24 or fewer branched anal-fin rays (420:0). The sister-group relationship of *I. kerri* and *I. parauapiranga* is supported by three morphological synapomorphies: three cusps on anterior dentary teeth (201:0), metapterygoid foramen as a simple rounded opening (228:0), and first anal-fin pterygiophore located ventral to last dorsal-fin pterygiophores (416:1).

## DISCUSSION

The phylogenetic position of the, until now, monotypic genus *Inpaichthys* was a subject of debate ever since its original description. Géry, Junk (1977:418) considered the genus “difficult to position”. These authors considered *Inpaichthys kerri* as similar and possibly related to *Coelurichthys tenuis* Nichols, 1913 [a synonym of *Mimagoniates lateralis* (Nichols, 1913)], a species currently included in the subfamily Stevardiinae. They also surmised putative relationships with the genera *Nematobrycon* (based mostly on color pattern), *Rachoviscus*, and *Bryconella* Géry, 1965 (the latter based on a similar arrangement of the premaxillary teeth).

The first study to include *I. kerri* within a phylogenetic framework was Calcagnotto *et al.* (2005) who, based on molecular data, recovered the species in a group with representatives of the genera *Astyanax* Baird & Girard, 1854; *Astyanacinus* Eigenmann, 1907; *Moenkhausia* Eigenmann, 1903; *Hemigrammus* Gill, 1858; and *Hyphessobrycon* Durbin, 1908. Miranda (2010) proposed the first phylogenetic hypothesis based only on morphological data that includes *I. kerri*, in which the species was considered to be a member of the subfamily Aphyocharacinae, as the sister group of the remaining members of the subfamily (*i.e.*, the genera *Aphyocharax* Günther, 1868; *Leptagoniates* Boulenger, 1887; *Paragoniates* Steindachner, 1876; *Prionobrama* Fowler, 1913; *Phenagoniates* Eigenmann & Wilson, 1914; *Rachoviscus*; and *Xenagoniates* Myers, 1942). However, subsequent molecular analyses (Javonillo *et al.*, 2010; Thomaz *et al.*, 2010; Oliveira *et al.*, 2011) did not confirm *I. kerri* as a member of the Aphyocharacinae, but

instead, proposed it to be more related to taxa classified in *Astyanacinus*; *Bario* Myers, 1940; *Ctenobrycon* Eigenmann, 1908; *Hyphessobrycon*; and *Moenkhausia*. Particularly, Oliveira *et al.* (2011) did not recover a subfamily Aphyocharacinae with the composition proposed by Miranda (2010), but rather they obtained *Inpaichthys* as the sister group of *Bario*, *Rachoviscus*, and *Hollandichthys*. Tagliacollo *et al.* (2012) corroborated that *Inpaichthys* [as well as *Rachoviscus* and *Protocheiroidon pi* (Vari, 1978)] did not belong to the subfamily Aphyocharacinae, but instead, to a clade comprised of *Astyanacinus*, *Carlana*, and *Nematobrycon*. Finally, Miranda (2019) published a comprehensive phylogenetic analysis of Characidae combining morphological and molecular data, in which *I. kerri* was recovered as belonging to the tribe Rhoadsiini within the subfamily Stethaprioninae, as the sister group of *Nematobrycon palmeri*, *Pseudochalceus kyburzi* Schultz, 1966, *Rhoadsia altipinna* Fowler, 1911, and *Carlana eigenmanni* Meek, 1912. Miranda *et al.* (2023) found a sister-group relationship of *Inpaichthys kerri* and the clade of *Hollandichthys* and *Rachoviscus* but, in that article, *Carlana*, *Nematobrycon*, *Pseudochalceus*, and *Rhoadsia* were not included. Our hypothesis, thus, corroborates the findings of Oliveira *et al.* (2011), Miranda (2019), and Miranda *et al.* (2023), in a more comprehensive analysis including, among other species, the three currently known species of the genus.

Weitzman, Vari (1988) circumscribed the term “miniature fish” to species that do not exceed 26 mm SL and that reach sexual maturity before 20 mm SL. Additionally, miniature fishes have in common numerous apparently paedomorphic morphological reductions, including the lower degree of development of the laterosensory canal system of the head and the body, reduction in the number of the fin rays, body scales, and loss of cranial bones which contribute to an overall simplification of the skeleton (Weitzman, Vari, 1988:445). Although *Inpaichthys* species are slightly larger than the arbitrary cut-off standard length (*I. kerri*: 28 mm SL; *I. nambiquara*: 27.0 mm SL; *I. parauapiranga*: 26.3 mm SL) proposed by Weitzman, Vari (1988) and still in use in the literature (*e.g.*, Toledo-Piza *et al.*, 2014), they exhibit some reductive features, such as the absence of the fourth and sixth infraorbitals (the fourth is present but much reduced in *I. nambiquara*), and an interrupted lateral line.

Despite *Inpaichthys* being composed of species with restricted distributional ranges, the discovery of *I. parauapiranga* and the new generic assignment of *I. nambiquara* imply that the genus *Inpaichthys* as a whole, now exhibits a relatively broad distribution across the northwestern portion of the Brazilian Shield, in both the upper rio Madeira (rio Aripuanã basin) and the adjacent upper rio Tapajós basin (rio Juruena basin). The sister-group relationship between *I. parauapiranga* and *I. kerri* is congruent with the fact that both species occur relatively close to each other (*ca.* 60 km in a straight line), within the rio Aripuanã basin. On the other hand, *I. nambiquara* occurs at the westernmost portion of the rio Juruena basin, roughly 300 km southwest from the type-locality of *I. parauapiranga* (Fig. 5). There are additional undescribed species of *Inpaichthys* occurring in the same general area (F. C. P. Dagosta, 2023, pers. comm.), which, once described, will add more information to this increasingly complex and interesting biogeographic scenario.

**Comparative material examined.** *Inpaichthys kerri*: All from Brazil, Mato Grosso State, rio Aripuanã basin: CPUFMT 4869, 5, 22.1–23.9 mm SL (2 c&s, 21.0–25.5 mm SL); CPUFMT 4897, 2, 18.9–20.29 mm SL; CPUFMT 4933, 4, 16.3–19.6 mm SL; CPUFMT 4988, 3, 22.7–27.0 mm SL; CPUFMT 5001, 1, 12.3 mm SL; CPUFMT 5020, 2, 23.2–24.5 mm SL; CPUFMT 5038, 4, 17.2–19.4 mm SL; CPUFMT 5066, 5, 20.5–20.7 mm SL; CPUFMT 5083, 2, 18.5–20.1 mm SL; ZUEC 9775, 62, 9.5–27.9 mm SL (11 c&s, 16.2–21.8 mm SL); ZUEC 13433, 1, 14.5 mm SL. Specimens of other characiform genera, examined and coded for the phylogenetic analysis, are listed in Terán *et al.* (2020), with additions in Lima *et al.* (2021) and Ferreira *et al.* (2023).

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**ETHICAL STATEMENT**

The specimens were collected under a collection permit authorized by Sistema de Autorização e Informação em Biodiversidade (SISBIO processes #18454-2 and 71172-2).

**COMPETING INTERESTS**

The author declares no competing interests.

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