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Morphological and molecular evidence reveal three new species of *Imparfinis* (Heptapteridae: Heptapterini) from the Amazon River basin

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Abstract

The integration of morphological and molecular data for *Imparfinis* species from Amazonian drainages of the Brazilian Shield revealed the presence of three previously undescribed species, which are formally described herein. These species are readily distinguished from their congeners by characters related to coloration: *I. melanopterus*, from the middle Araguaia River, has a distinctly darker lower caudal-fin lobe; *I. nigropunctatus*, from the upper Araguaia River, possesses conspicuous black spots on the body; and *I. tessellatus*, from the upper Tapajós River, is characterized by dark blocks of chromatophores on the body, forming a variegated color pattern. Additionally, our species-delimitation analysis recovered these three morphotypes as independent genetic lineages, exhibiting high levels of genetic divergence. A discussion of distributional patterns of *Imparfinis* within the Amazon River basin is provided.

Key words: Diversity, Taxonomy, mitochondrial lineages, species delimitation

Introduction

Imparfinis is a genus of small-sized heptapterid catfishes typically inhabiting shallow streams and rapids where they are closely associated with rocky bottoms or marginal vegetation (Silva *et al.* 2025). Within the tribe Heptapterini, *Imparfinis* stands out as the most widely distributed genus, occurring longitudinally from Ecuador to the Atlantic coastal drainages and latitudinally from Costa Rica to Argentina (Fricke *et al.* 2025). In addition to being the most broadly distributed, it is also the most diverse genus, comprising 22 valid species. However, phylogenetic studies (Bockmann, 1998; Silva *et al.* 2021) have demonstrated that *Imparfinis* is not a natural group, and species such as *I. pristos*, *I. pseudonemacheir*, *I. microps*, *I. stictonotus* and *I. longicauda* should be reassigned to new genera in future classifications. *Imparfinis* sensu stricto (Silva *et al.*, 2021) is characterized by the presence of a series of dusky middorsal saddles; a subterminal mouth; open anterior cranial fontanel; a posterior process of the parieto-supraoccipital not reaching the anterior nuchal plate; the first pectoral-fin ray mostly flexible except proximally; an adipose fin with a free posterior lobe not fused with the caudal fin; and a deeply forked caudal fin (Bockmann & Slobodian 2018).

In the Amazon River basin, five species are assigned to *Imparfinis* sensu stricto (Silva *et al.*, 2021): *Imparfinis guttatus* (Pearson 1924) from the Rio Beni; *I. cochabambae* (Fowler 1940) also from the Rio Beni; *I. hasemani* Steindachner, 1915 from the Rio Branco; and two recently described species, *I. munduruku* Castro & Wosiacki, 2019 from the Tapajós river basin, and *I. arceae* Silva, Sabaj, Rodrigues & Oliveira, 2025 from the Xingu

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River basin. Recent expeditions to the Amazon basin have revealed additional new species of *Imparfinis*, which are formally described below.

Material and Methods

Taxon sampling

We combined newly generated mitochondrial sequences with those previously generated by Ferreira *et al.* (2014), Aguilera *et al.* (2022), Cortés-Hernández *et al.* (2023), Silva *et al.* (2023) and Silva *et al.* (2025). Sequences were analyzed for a total of 71 specimens spanning 16 of the 18 valid species of *Imparfinis* stricto sensu (Supplemental Table 1). Eight species of Heptapterinae were included as outgroup taxa: *Cetopsorhamdia iheringi*, *Chasmocranus longior*, *Heptapterus longicauda*, *Heptapterus mustelinus*, *Leptorhamdia marmorata*, *Nemuroglanis pauciradiatus*, *Rhamdiopsis microcephala*, and *Taunayia bifasciata*.

Molecular analysis

DNA extraction followed Ivanova *et al.* (2006). Partial sequences of the mitochondrial gene cytochrome oxidase C subunit I (COI) were amplified by polymerase chain reaction (PCR) using primers FishF6/R7 described by Jennings *et al.* (2019). Reactions were carried out in a 12.5 µL reaction volume containing 1.25 µL of 10X PCR buffer, 0.40 µL $MgCl_2$ (50 mM), 0.30 µL dNTPs (2 mM), 0.25 µL of each primer (5 lM), 0.20 µL of PHT Taq DNA polymerase (Phoneutria), 2 µL DNA template (200 ng), and 7.85 µL of ddH_2O. The PCR consisted of initial denaturation (5 min at 958C) followed by 30 cycles with a chain denaturation (1 min at 958C), primer hybridization (45 sec at 528C), nucleotide extension (1 min at 688C), and final extension (10 min at 688C). All PCR products were checked using 1% agarose gel and purified with ExoSap-IT (USB Corporation) following the manufacturer's instructions. The purified PCR products were sequenced using the Big DyeTM Terminator v3.1 Cycle Sequencing Ready Reaction Kit (Applied Biosys- tems, Austin, TX), purified through ethanol precipitation and loaded onto an ABI 3500 Genetic Analyzer (Applied Biosys- tems), in the Instituto de Biotecnologia (IBTEC), Universidade Estadual Paulista Júlio de Mesquita Filho, Botucatu, Brazil.

All individual sequences were initially assembled using the software Geneious 7.1.4 (Kearse *et al.* 2012) and aligned by Muscle (Edgar 2004) under default parameters. To evaluate the occurrence of substitution saturation in our molecular data, we estimated whether the Iss (index of substitution saturation) was significantly lower than Iss.cAsym (assuming asymmetrical topology) using the method described by Xia *et al.* (2003) and Xia & Lemey (2009) with the software DAMBE 7.2.1 (Xia 2018). Nucleotide variation, substitution patterns, and best-fit model of nucleotide evolution were estimated using MEGA X (Kumar *et al.* 2016). The overall mean genetic distances (between all specimens), as well as interspecific (between species groups) and intraspecific distances (between specimens of each species group), were estimated with 1,000 pseudoreplicates without the root. Maximum likelihood (ML) analysis was performed in RaxML PTHREADSSSE3 v8 (Stamatakis 2014) using the GTRGAMMA model on the *Gymnotus* server at LBP-UNESP. The best tree was accessed through ten random searches with 1,000 pseudoreplicates using the autoMRE function (Pattengale *et al.* 2020) with bootstrapping criteria which ran 850 pseudoreplicates. The analysis of assembled species by automatic partitioning (ASAP; Puillandre *et al.* 2020) is available via the ASAP webserver. The analysis was run using just the internal group and under defaut parameters.

Morphological data

Counts and measurements were taken from the left side of specimens following Lundberg & McDade (1986) and Bockmann (1994), except for body depth and caudal peduncle depth, the measurements of the pelvic-fin origin and pre-adipose length followed Ortega-Lara *et al.* (2011). Specimens were cleared and stained (CS) according to Taylor & Van Dyke (1985). The number of vertebrae, ribs, and supporting elements of dorsal and anal fins position in relation to vertebral number were determined from CS specimens and radiographs. Osteology follows Bockmann & Castro (2010); caudal-fin terminology follows Lundberg & Baskin (1969) and Sabaj and Arce H. (2021). Vertebral counts include the Weberian apparatus counted as five and the compound caudal centrum counted as one. Institutional acronyms follow Sabaj (2025). Specimens were deposited at the Laboratório de Biologia e Genética de Peixes, Universidade Estadual Paulista, Botucatu, Brazil (LBP); Departamento de Ciências Biológicas da UNESP, São José do Rio Preto (DZSJRP), Museu de Zoologia, Universidade de São Paulo, São Paulo (MZUSP) and Museu Nacional do Rio de Janeiro (MNRJ).

Results

Molecular analysis. The final matrix comprises 613 bp with 213 variable sites. The frequency of nucleotides obtained was 23.1% adenine, 28.8% cytosine, 17.8% guanine, and 30.3% thymine, GC: 46.6%. The best-fit model estimated was K2+G+I with BIC value = 7786.099. The genetic distances were calculated by K2 model. The overall mean of genetic distance was 11% for the ingroup. Interspecific genetic distances ranged from 3.1% to 17.3% (Table 1). The ASAP method delimited 20 species (score = 2.0, Probability = 1.13 e-01): *I. usmai*, *I. timana*, *I. spurrellii*, *I. lineata*, *I.* cf. *hasemani*, *I. pjipersi*, *I. hasemani*, *I. tessellatus* (new species), *I. guttatus*, *I. arceae*, *I. melanopterus* (new species), *I. schubarti*, *I. nigropunctatus* (new species), *I. lepturus*, *I. mirini*, *I. piperatus*, *I. minutus*, *I. mishky*, *I. munduruku* and *I. robustus*. Our ML analysis (lnL = -4780.178863) indentified four major mitochondrial clades: (1) trans-andean clade, composed by *I. linetus*, *I. spurreli*, *I. timana* and *I. usmai*; (2) Orinoco clade, composed by *I. robustus*; (3) the Amazon-Guyana clade, composed by *I. pjipersi*, *I.* aff. *pjipersi*, *I. hasemani*, *I. variegatus*, *I. arceae*, *I. guttatus*, *I. araguaia*; and (3) the southeast clade, composed by *I. munduruku*, *I. shubarti*, *I. minutus*, *I. mishky*, *I. piperatus*, *I. mirini*, *I. punctatus* and *I. lepturus* (Fig. 1).

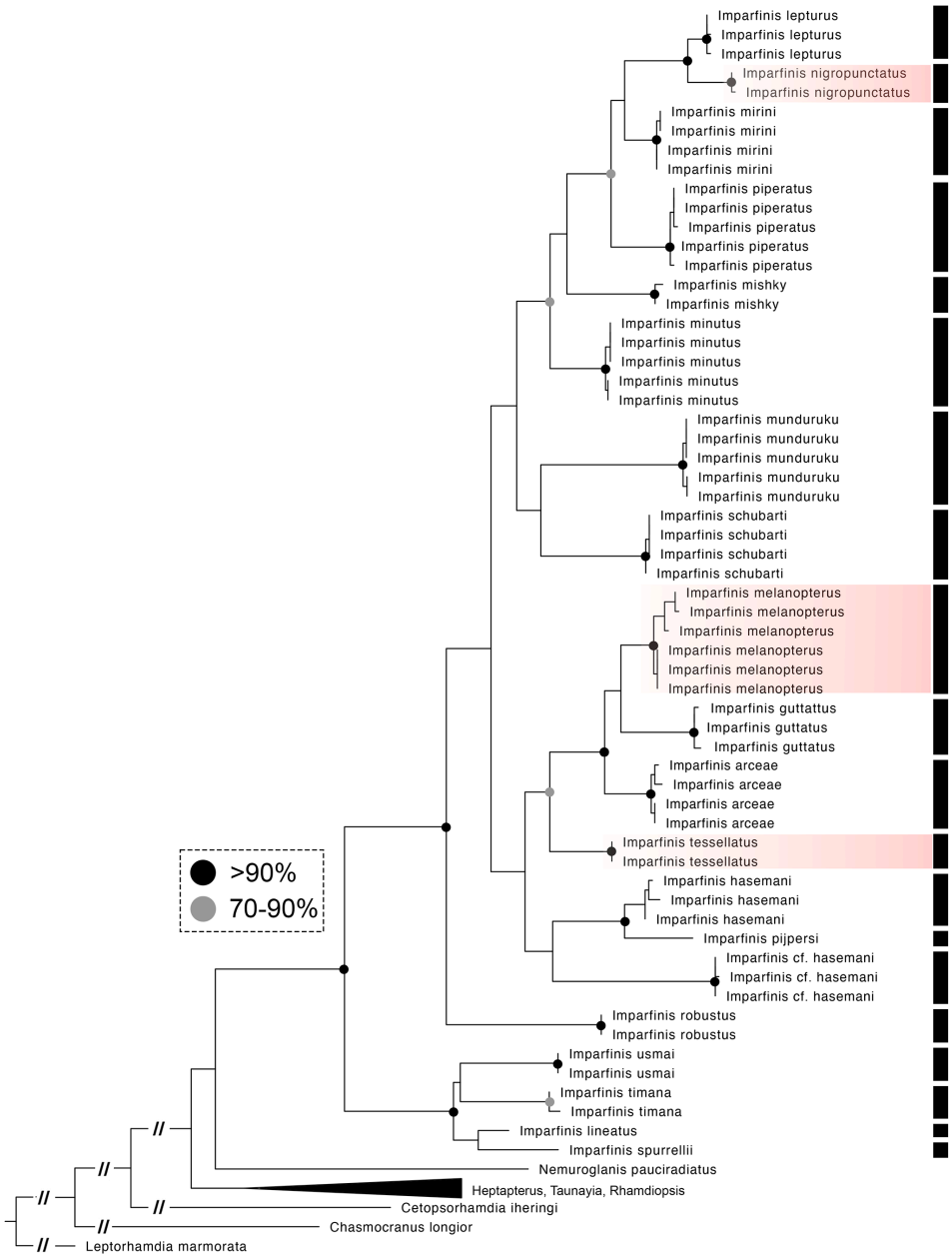

FIGURE 1. Maximum likelihood tree based on COI marker. Black nodes indicate>90% bootstrap values from 1,000 pseudoreplicates; gray nodes indicate support between 70% and 90% bootstrap values. Bars represent the species delimitation using ASAP.

TABLE 1. Genetic distances among lineages of *Imparfinis*, based on K2 model.

	1.	**2.**	**3.**	**4.**	**5.**	**6.**	**7.**	**8.**	**9.**	**10.**	**11.**	**12.**	**13.**	**14.**	**15.**	**16.**	**17.**	**18.**	**19.**
1. *I. usmai*																			
2. *I. timana*	0.075																		
3. *I. spurrelli*	0.080	0.072																	
4. *I. lineatus*	0.066	0.063	0.047																
5. *I. cf. hasemani*	0.139	0.136	0.134	0.139															
6. *I.pjpersi*	0.146	0.131	0.139	0.141	0.109														
7. *I. hasemani*	0.146	0.135	0.154	0.155	0.093	0.043													
8. *I. tessellatus*	0.142	0.131	0.141	0.146	0.110	0.095	0.082												
9. *I. guttatus*	0.145	0.132	0.143	0.149	0.108	0.134	0.117	0.088											
10. *I. arceae*	0.146	0.127	0.143	0.144	0.106	0.108	0.097	0.067	0.061										
11. *I. melanopterus*	0.144	0.125	0.154	0.142	0.110	0.107	0.094	0.074	0.058	0.047									
12. *I. robustus*	0.151	0.140	0.140	0.139	0.140	0.109	0.111	0.122	0.137	0.129	0.122								
13. *I. munduruku*	0.150	0.123	0.144	0.141	0.138	0.120	0.118	0.120	0.145	0.124	0.131	0.139							
14. *I.schubarti*	0.123	0.132	0.144	0.148	0.140	0.137	0.112	0.103	0.133	0.118	0.113	0.127	0.096						
15. *I. nigropunctatus*	0.147	0.151	0.159	0.140	0.128	0.145	0.120	0.129	0.133	0.122	0.116	0.127	0.116	0.097					
16. *I. lepturus*	0.153	0.158	0.173	0.154	0.136	0.146	0.128	0.128	0.140	0.130	0.120	0.128	0.113	0.091	0.312				
17. *I. mirini*	0.145	0.148	0.166	0.141	0.116	0.122	0.115	0.113	0.126	0.122	0.096	0.114	0.114	0.112	0.061	0.052			
18 *I. piperatus*	0.145	0.149	0.147	0.137	0.103	0.110	0.108	0.032	0.130	0.115	0.105	0.106	0.108	0.104	0.073	0.065	0.048		
19. *I. minutus*	0.137	0.141	0.140	0.134	0.127	0.115	0.104	0.084	0.109	0.103	0.098	0.112	0.091	0.081	0.090	0.078	0.067	0.066	
20. *I. mishky*	0.162	0.153	0.154	0.161	0.128	0.109	0.103	0.105	0.121	0.118	0.116	0.120	0.117	0.114	0.087	0.089	0.073	0.075	0.065

***Imparfinis melanopterus* sp. nov.**
(Figs 2, 3a Tab. 2)

Imparfinis mirini—Venere & Garutti, 2011: page 151 [Check list]. Lima *et al.*, 2021: page 11 [citation. Figure 4]. Lima *et al.*, 2025: page 234 [citation. Figure 6F]

Holotype. LBP 38226, 57.9 mm SL, Rio Corrente, Barra do Garça, Mato Grosso, 15°29'57.3"S 52°12'10.4" W, 09 December 2002, C Oliveira.

Paratypes. Brazil, Araguaia River basin: LBP 1512, 1, 50.5 mm SL, Córrego Fundo, Barra do Garça, Mato Grosso, 15°52'40.4"S 52°18'15.5"W, 10 December 2002, C Oliveira *et al.* LBP 1528, 2, 42.9–60.8 mm SL, Ribeirão Insula, Barra do Garça, 15°40'57.7" S 52°13'24.8"W, 09 December 2002, C Oliveira *et al.* LBP 1548, 3, 37.2–43.7 mm SL, Córrego das Mulas, Aragarças, Goiás, 15°54'23.4"S 52°05'39.4"W, 12 December 2002, C Oliveira *et al.* LBP 1563, 12, 35.0–55.3 mm SL, 1 c&s 54.9 mm SL, same data a holotype. LBP 1605, 15, 40.6–82.7 mm SL, Aragarças, Goiás, 15°54' 24.8"S 52°09'05"W, 12 December 2002, C Oliveira et al; LBP 1809, 7, 38.6–51.5 mm SL, Córrego Fogaça, Barra do Garças, Mato Grosso, 15°40'53.9"S 52°13'21"W, 27 August 2003, C Martins *et al.* LBP 2419, 6, 40.8–55.3 mm SL, 2 c&s, 43.0–46.1 mm SL, Córrego Fundo, Barra do Garça, Mato Grosso, 15°52'40.4"S 52°18'15.5"W, 05 October 2004, C Oliveira, AO Shibatta, MA Spadella, GF França, EMR Martinez; LBP 2467, 1, 50.9 mm SL, Córrego Fundo, Barra do Garça, Mato Grosso, 15°52'40.4"S 52°18'15.5"W, 07 October 2004, C Oliveira, AO Shibatta, MA Spadella, GF França, EMR Martinez; LBP 5718, 4, 32.2–54.0 mm SL, Córrego Taquaral, 15°40'67.8"S 52°17'86.3"W, 21 Jan 2008, C Oliveira, JCO Santana, PC Venere, M Taylor, M Alexandrou; LBP 15653, 7, 31.0–40.4 mm SL, Rio das Mortes, Nova Xavantina, Mato Grosso, 14°40'44.8"S 52°21'53.5"W, 29 July 2012, C Oliveira, M Taylor, GJC Silva, JHM Martinez; LBP 20796, 2, 35.4–35.5 mm SL, Córrego Taquaralzinho, 15°42'43.4"S 52°15'32.1"W, 22 Out 2015, C Oliveira, M Taylor, AC Souto, VF Sene; LBP 25688, 1, 39.8 mm SL, Rio Corrente, Barra do Garça, Mato Grosso, 15°29'58.4"S 52°12'11.9"W, R Devidé, BF Melo, C Araya, GSC Silva. LBP 36347, 1, 49.7, mm SL, Córrego Vazantão, Crixás, Goiás, 14°57'53.1"S 50°14'04" W, 11 Ago 2024, BF Melo, L Reia, LP Ramos, B Coelho; MNRJ 56167, 2, 57.9–67.4 mm SL, Aragarças, Goiás, 15°54'24.8"S 52°09'05"W, 12 December 2002, C Oliveira *et al.* MZUEL 7738, 33, 42.4–34.8 mm SL, Rio Taquarizinho, Barra do Garças, Mato Grosso, 15°42'40.5"S 52°35'28.6"W, 30 July 2008, Jarduli LR, Ruiz WBG, Santana E; MZUEL 7740, 15, 34.7–44.3 mm SL, Rio Taquaral, Barra do Garça, Mato Grosso, 15°40'41.4" S 52°17'52.3"W, 30 July 2008, Jarduli LR, Ruiz WBG. MZUSP 131563, 2, 50.7–54.6 mm SL, same date of holotype.

FIGURE 2. Left column: *Imparfinis melanopterus*, holotype, LBP 38226, 57.9 mm SL. Right column: *Imparfinis melanopterus,* LBP 1563, from top to bottom: 54.5 mm SL; 51.2 mm SL; 40.8 mm SL.

FIGURE 3. Live specimens of a) *Imparfinis melanopterus*, LBP 36347; b) *Imparfinis nigropunctatus*, LBP 32067; c) *Imparfinis tessellatus*, LBP 37269.

Diagnosis. The new species differs from all congeners, except *I. cochabambae*, *I. guttatus*, *I. robustus*, *I. schubarti* by having the lower lobe of caudal-fin darker than upper lobe (vs. both lobes similarly pigmented). Moreover, the new species differs from its congeners by having 38 vertebrae (vs. 39 in *I. arceae*, 39–30 in *I. munduruku* and *I. piperatus*; 40 in *I. hasemani* and *I. variegatus*; 40–41 in *I. schubarti*; 42–43 in *I. cochabambae*, *I. guttatus*, *I. robustus*, *I. minutus* and *I. lineatus*; 42–43 in *I. timana*, and 45 in *I. spurreli*); by absence of a conspicuous longitudinal dark stripe along flank (vs. present in *I. arceae*, *I. hasemani*, *I. pjipersi*, *I. munduruku*, *I. schubarti*, *I. usmai*, *I. timana* and *I. spurreli*); by having 10–13 gill rakers on the first ceratobranchial (vs. 6–8 in *I. punctatus*, 6–7 in *I. munduruku*, 7–8 in *I. mirini* and *I. usmai*, *I. piperatus*, 5–7 in *I. minutus*, 5–6 in I. *lepturus*; 9 in *I. mishky*; 8–9 in *I. lineatus*; 5–6 in *I. timana*); by absence of a short extension of the pectoral, dorsal, and upper caudal-fin rays (vs. present in *I. usmai*, *I. nemacheir*, *I. guttatus,* and *I. robustus*); and by having maxillary barbel surpassing vertical through dorsal-fin origin (vs. maxillary barbel not suppressing vertical through dorsal-fin origin in *I. variegatus*, *I. nigropunctatus*, *I. mirini*, *I. minutus*, *I. pjipersi,* and *I. tessellatus*).

Description. Morphometric data summarized in Table 2. Head relatively short (18.5–25.0% of SL) and weakly depressed; body elongate, nearly cylindrical anteriorly, gradually compressed posteriorly. Dorsal profile convex from snout to dorsal-fin origin, straight to barely descending along dorsal-fin base, then convex (ascending) to adipose-fin origin, straight (descending) along adipose-fin base, and finishing more or less straight (ascending)

along caudal peduncle. Ventral profile convex from snout to pelvic-fin origin, then straight to pelvic-fin origin to anal-fin origin, straight ascending along anal-fin base, finishing gently concave to lower procurrent caudal-fin rays. Snout moderately long and rounded in dorsal view. Body width greatest across cleithral region, gradually tapering posteriorly to caudal peduncle.

Eyes large and horizontally elliptical, dorsolaterally positioned. Mouth subterminal with upper jaw longer than lower. Premaxilla and dentary with three to four irregular rows of small conical teeth. Maxillary barbel surpassing vertical through dorsal-fin origin. Outer mental barbel, surpassing pectoral-fin origin and longer than inner mental barbel and finishing short of pectoral-fin origin. Branchiostegal membranes with seven rays and joined to isthmus only at anterior point. 10–13 gill rakers along anterior border of first ceratobranchial. Total vertebrae 38 with 15 precaudal (nine or ten supporting pleural ribs) and 23 caudal.

Pectoral fin with first ray simple and eight or nine branched rays (i,8–9). First pectoral-fin ray stiffened proximally and flexible distally, lacking filamentous extension. Pelvic fin i,5; first ray shorter than second and third rays. Dorsal-fin i,6; first basal radial inserted on 7th vertebra and last basal radial anterior to neural spine of 13th vertebra (Fig. 4). Adipose fin long (16.0–20.3% of SL). Anal fin iv,7. Caudal skeleton composed of a plate formed by parhypural + hypurals 1 and 2 fused in lower lobe, upper lobe plate formed by hypurals 3 and 4 fused, hypural 5 free, and pleurostyle fused to compound centrum. Caudal fin with i,7,8,i principal rays. Upper and lower caudal-fin lobe approximately symmetrical. Dorsal and ventral caudal-fin lobes with 13–12 procurrent rays, respectively.

Coloration. In preserved specimens, background color of body yellowish. Interorbital and occipital regions of dorsal head dusky, followed by six evenly spaced dusky saddles; first saddle across nape, second at dorsal-fin origin, third below posterior insertion of dorsal fin; fourth saddle below distal margin of dorsal fin (about halfway between third saddle and adipose-fin origin) fifth saddles at adipose-fin origin, and sixth on adipose-fin end. Fins hyaline except for dark pigmentation on lower lobe of caudal fin. (Fig. 3a).

Distribution and habitat. The new species is known from the Middle Araguaia River including the Rio Corrente, Córrego Fundo, Ribeirão Insula, Córrego das Mulas, Córrego Fogaça, Córrego Taquaral, Rio das Mortes, Córrego Taquaralzinho, Córrego Vazantão (Fig. 4). It was collected in fast-flowing rivers, associated with a bottom of rocks (Fig. 5b).

Etymology. The specific name *melanopterus* is from Greek *melano* meaning black, and *pterus* meaning fin, in reference to the dark lower lobe of the caudal fin. An adjective.

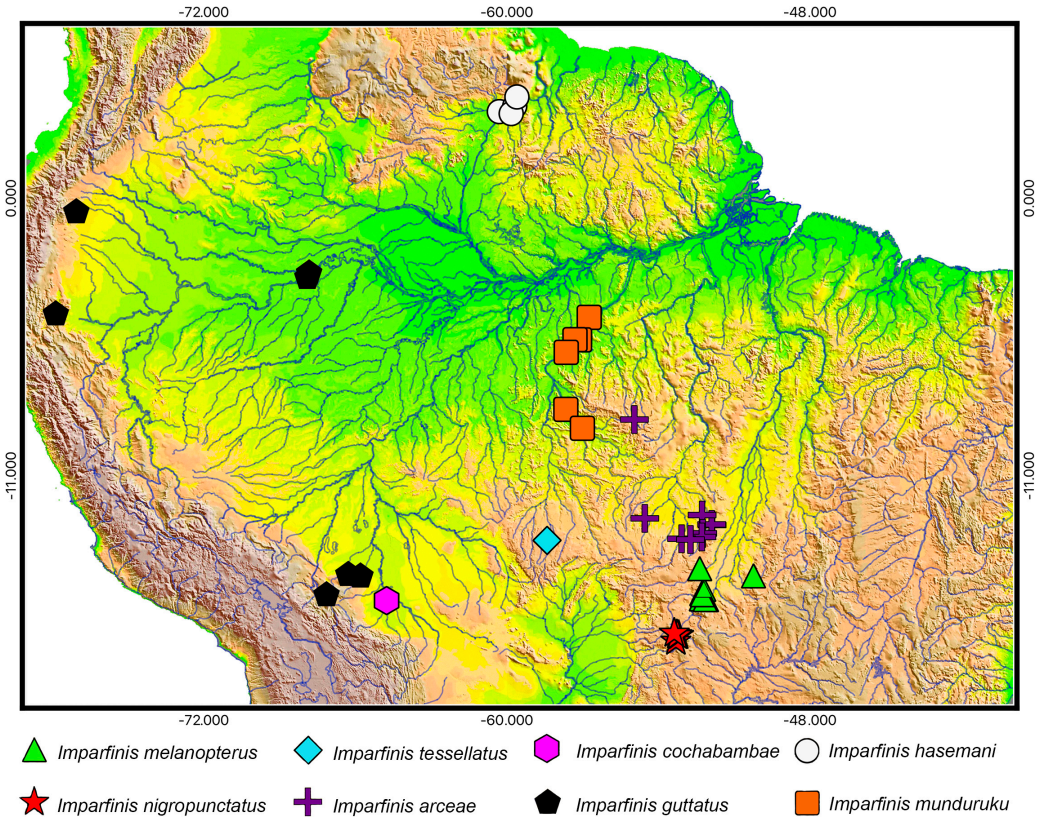

FIGURE 4. Geographic distribution of *Imparfinis* from Amazon river basin.

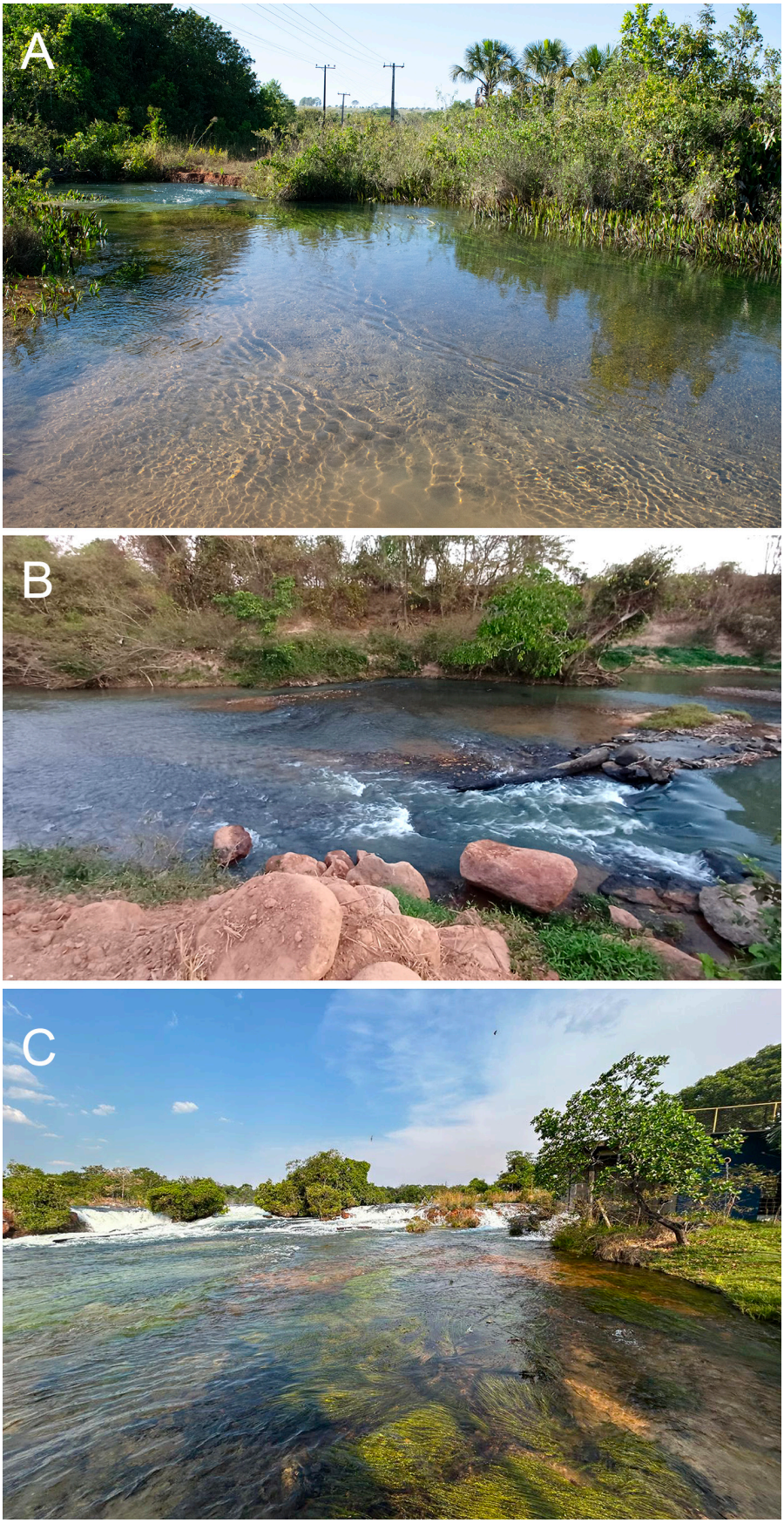

FIGURE 5. Habitat in which the species were collected: a) Córrego do Sapo, Upper Araguaia basin; b) Rio Corrente, Middle Araguaia basin; c) Rio Papagaio, Upper Tapajós basin.

TABLE 2. Morphometric data for *Imparfinis nigropunctatus* (n=16); *I. tessellatus* (n=15); *I. melanopterus* (n=31).

	Holotype	Min	Max	Mean	SD	Holotype	Min	Max	Mean	SD	Holotype	Min	Max	Mean	SD
Standard length (mm)	45.6	32.4	50.2	39.8		71.8	52.0	81.1	63.7	9.2	57.8	35.1	82.7	49.0	10.3
Percentages of standard length															
Body depth	17.5	14.0	19.6	16.5	1.4	16.4	15.0	18.9	16.8	0.9	19.0	14.6	23.1	18.1	1.4
Cleithral width	16.8	14.1	17.3	15.2	0.8	19.1	16.5	20.2	18.6	1.0	18.0	15.7	19.8	18.0	0.9
Predorsal length	34.9	29.0	37.5	35.6	1.9	39.1	37.3	41.3	39.4	1.1	37.7	33.2	40.2	37.5	1.5
Dorsal-fin base	14.0	11.3	14.0	12.4	0.7	12.1	11.0	13.9	12.3	0.7	11.5	9.4	16.3	12.2	1.2
Length of first dorsal-fin ray	16.7	13.4	18.2	16.1	1.2	19.6	14.6	20.3	18.5	1.3	18.8	14.8	20.2	17.9	1.1
Dorsal-adipose distance	31.9	26.8	32.7	30.1	1.6	25.5	28.7	33.1	31.2	1.2	30.8	30.2	36.3	32.5	1.3
Adipose-fin base	25.0	22.8	27.9	25.7	1.4	17.5	16.4	19.8	18.1	1.0	18.5	14.8	20.7	18.4	1.2
Adipose-fin depth	4.9	3.3	5.3	4.0	0.6	4.5	3.1	5.4	4.2	0.7	4.9	3.4	5.5	4.5	0.6
Head-pectoral length	22.2	19.2	22.2	20.6	0.7	24.4	22.3	25.4	24.2	0.9	21.8	21.0	26.0	23.5	1.4
Length of first pectoral-fin ray	11.4	11.4	15.9	13.4	1.5	15.9	13.8	17.4	16.3	0.9	16.5	12.2	18.1	15.6	1.4
Prepelvic length	40.8	38.2	45.0	40.3	1.6	43.9	41.2	45.6	43.8	1.3	44.4	47.2	46.5	44.8	0.9
Length of first pelvic-fin ray	11.9	11.5	14.9	13.1	0.9	12.1	10.3	14.7	12.5	1.0	12.7	9.8	18.0	13.5	1.6
Preanal length	63.4	63.4	68.5	66.7	1.3	70.2	69.0	73.2	70.5	1.0	69.5	65.3	74.3	70.1	1.9
Anal-fin base	16.8	12.0	16.8	14.0	1.4	11.5	9.8	13.4	11.5	1.0	11.7	9.7	14.5	11.8	0.8
Caudal-peduncle length	19.6	17.6	21.2	19.7	0.9	18.8	16.9	21.1	19.2	1.3	21.7	16.1	22.3	18.8	1.5
Caudal peduncle depth	8.0	6.5	8.0	7.1	0.4	6.9	6.0	7.0	6.6	0.2	8.1	7.6	11.0	9.0	0.9
Length of dorsal caudal-fin lobe	25.8	23.2	28.2	26.0	1.4	23.7	21.9	27.7	25.2	1.5	32.1	25.2	33.8	30.4	1.7
Length of ventral caudal-fin lobe	24.5	22.8	27.1	25.1	1.0	21.6	20.9	24.6	22.6	1.2	27.1	24.5	30.1	27.3	1.5
Head length	18.9	17.6	20.1	18.7	0.7	22.4	21.9	23.9	23.0	0.5	21.3	18.5	25.0	21.1	1.5
Head width	16.3	13.5	16.3	14.9	0.7	18.1	15.0	20.5	18.8	1.6	16.5	14.9	19.8	17.7	1.2
Maxillary-barbel length	36.3	23.5	36.3	29.3	3.0	24.6	21.1	27.5	24.3	1.7	34.5	30.2	40.6	34.4	2.5
Outer mental-barbel length	21.1	15.2	25.3	19.2	2.3	16.2	13.9	18.6	16.1	1.3	20.5	17.6	33.2	21.5	2.9
Inner mental-barbel length	14.4	10.9	17.1	14.3	1.4	11.7	10.5	15.3	12.2	1.2	14.7	11.6	18.1	15.4	1.4
Percentages of head length															
Mouth gap	39.4	39.4	47.2	42.7	2.0	49.3	36.3	46.9	43.1	2.9	38.6	32.9	45.7	40.7	3.7
Internarial length	14.0	14.0	22.3	18.9	2.4	20.2	17.9	22.6	20.0	1.4	18.1	14.7	21.4	18.0	1.4
Anterior internarial width	17.7	11.9	18.7	15.1	1.7	18.4	11.8	18.4	14.6	1.8	13.6	11.2	19.0	16.0	1.7
Posterior internarial width	19.5	18.8	22.6	20.8	1.1	18.2	15.3	18.8	17.1	1.0	16.8	16.5	23.1	19.5	1.6
Snout length	43.4	39.8	45.9	43.4	1.6	50.3	43.3	50.3	45.9	2.0	40.3	38.5	46.6	42.3	2.1
Interorbital distance	23.5	23.5	37.0	32.8	3.1	27.6	22.6	28.1	25.8	1.7	32.2	27.8	38.5	33.5	2.3
Eye diameter	17.6	16.9	20.4	18.8	1.0	18.5	15.9	19.6	17.9	1.1	18.2	17.1	22.8	19.3	1.4

***Imparfinis nigropunctatus* sp. nov.**
(Fig 6, 3b Tab. 2)

Imparfinis n.sp.1 'UA'– Silva *et al.*, 2023: fig.1 [phylogenetic relationships of *Imparfinis*].
Imparfinis sp "UA"– Silva *et al.*, 2025: fig.1 [phylogenetic relationships of *Imparfinis*]

Holotype. DZSJRP 3087, 45.6 mm SL, Alto Araguaia, 17°24'36.0" S 53°22'26" W, 11 November 1988, A Salino, JC Milani, SG Britto.

Paratypes. Brazil, Mato Grosso, Upper Araguaia River: LBP 1438, 7, 25.7–34.4 mm SL, Córrego do Sapo, Alto Araguaia, 17°33'42.4"S 53°18'29"W, 06 May 2003, C Oliveira et al; LBP 1445, 14, 29.8–47.6 mm SL, 2 c&s, 41.0–41.2 mm SL, Córrego Boiadeiro, Alto Araguaia, 17°19'19.4"S 53°14'25" W, 06 May 2003, C Oliveira et al; LBP 32056, 2, 30.7–33.1 mm SL, Córrego Sapão, Alto Taquari, 17°33'42.4"S 53°18'29"W, 16 July 2022. GSC Silva, L Crispim, L Reia. LBP 32067, 5, 31.7–34.06 mm SL, Córrego Sapão, Alto Araguaia, 17 July 2022, GSC Silva, J Crispim, L Reia; LBP 32076, 1, 38.2 mm SL, Córrego Aninha, Alto Araguaia, 17°19 19.3 S 53°14'26.8" S, 18 July 2022, GSC Silva, J Crispim, L Reia; LBP 37464, 3, 29.0–34.3 mm SL, Córrego gordura, Alto Araguaia, 17°18'20.3"S 53°16'22.3" W, 17 September 2025, BF Melo, L Reia, GSC Silva. MZUSP 41426, 5, 22.4–51.5 mm SL, Córrego Jacaré, Santa Rita do Araguaia, Goiás, 17°20'00"S 53°12'00"W; MZUSP 41840, 5, 38.7–62.8 mm SL, Córrego do Coqueiro, Santa Rita do Araguaia, Goiás, 17°18'53"S 53°12'55"W; MZUSP 73255, 46, 21.0–39.7 mm SL, Córrego Gordura, 17°18'20"S 53°16'22"W; MZUSP 73273, 110, 14.7–40.8 mm SL, Córrego Boiadeiro, 17°20'01"S 53°14' 53"W.

Diagnosis. The new species differs from all congeners by having a distinctive color pattern, consisting of concentrated chromatophores over a yellow-colored background, forming conspicuous black dots (vs. absence of this pattern). Additionally, the new species differs from all congeners, except *I. lineatus*, *I. lepturus*, *I. munduruku*, *I. mirini*, *I. minutus*, and *I. piperatus* by having 6–8 gill rakers on the first ceratobranchial (vs. 9–16); by having 39–40 vertebrae (vs. 38 in *I. lepturus*, *I. mirini*, and *I. melanopterus*, 41 in *I. guttatus* and, *I. minutus*, 42 in *I. lineatus*, 42–43 in *I. cochabambae* and *I. timana*, and 45 in *I. spurreli*); by the absence of a short, flexible extension of the pectoral- and dorsal-fin spines, and outermost primary rays of upper caudal-fin lobe (vs. extensions present in *I. usmai*, *I. nemacheir*, and *I. guttatus*); and by having the maxillary barbel not surpassing vertical through dorsal-fin origin (vs. maxillary barbel suppressing vertical through dorsal-fin origin in *I. arceae*, *I. cochabambae*, *I. guttatus*, *I. lepturus*, *I. longicauda*, *I. mishky*, *I. nemacheir*, *I. piperatus*, *I. robustus*, *I. schubarti*, *I. timana* and *I. usmai*).

FIGURE 6. Left column: *Imparfinis nigropunctatus*, holotype, DZSJRP 3087, 45.6 mm SL. Right column: *Imparfinis nigropunctatus,* LBP 32067, from top to bottom: 37.7 mm SL; LBP 1445, 43.2 mm SL; LBP 32067, 33.6 mm SL.

Description. Morphometric data summarized in Table 2. Head relatively short (20.2–25.8% of SL) and weakly depressed; body elongate, nearly cylindrical anteriorly, gradually compressed posteriorly. Dorsal profile broadly convex from snout to dorsal-fin origin, straight to barely descending along dorsal-fin base, then convex (ascending) to adipose-fin origin, straight (descending) along adipose-fin base, and finishing more or less straight (ascending) along caudal peduncle. Ventral profile gently convex from snout to vent, then straight to anal-fin origin, finishing gently concave to lower procurrent caudal-fin rays. Snout moderately short and rounded in dorsal view. Body width greatest across cleithral region, gradually tapering posteriorly to caudal peduncle.

Eyes horizontally elliptical, dorsolaterally positioned. Mouth subterminal with upper jaw longer than lower. Premaxilla and dentary with three to four irregular rows of small conical teeth. Maxillary barbel not surpassing vertical through dorsal-fin origin. Outer mental barbel, reaching pectoral-fin origin, longer than inner mental barbel, and finishing short of pectoral-fin origin. Branchiostegal membranes supported by seven rays and joined to isthmus only at anterior point. Six to eight gill rakers along anterior border of first ceratobranchial. Total vertebrae 39–40 with 12 precaudal (seven supporting pleural ribs) and 26–28 caudal (Fig. 4).

Pectoral fin with first ray simple and seven or eight branched rays (i,7–8). First pectoral-fin ray stiffened proximally and flexible distally, lacking filamentous extension. Pelvic fin i,5; first ray shorter than second and third rays. Dorsal-fin i,6; first basal radial inserted on 8th vertebra and last basal radial anterior to neural spine between 11th to 12th vertebra. Adipose fin long (22.8–27.9% of SL). Anal fin iii,9–10. Caudal skeleton composed of a plate formed by parhypural + hypurals 1 and 2 fused in lower lobe, upper lobe plate formed by hypurals 3 and 4 fused, hypural 5 free, and pleurostyle fused to compound centrum. Caudal fin with i,7,8,i principal rays. Upper and lower caudal-fin lobe approximately symmetrical. Dorsal and ventral caudal-fin lobes with 7–14 and 6–11 procurrent rays, respectively.

Coloration. Background color of body yellowish. Dark-brown patches of melanophores forming conspicuous dark dots along lateral portion of body. Interorbital and occipital regions of dorsal head dusky, followed by six evenly spaced dusky saddles; first saddle across nape, second at dorsal-fin origin, third below posterior insertion of dorsal fin; fourth saddle below distal margin of dorsal fin (about halfway between third saddle and adipose-fin origin) fifht saddle at adipose-fin origin, and sixth on adipose-fin end. Fins hyaline.

Distribution and habitat. The new species is known from the Upper Araguaia River including the Córrego do Sapo, Córrego Boiadeiro, Córrego Aninha, Córrego Gordura, Córrego Jacaré, Córrego do Coqueiro (Fig. 4). It was collected in fast-flowing, clear waters associated with marginal vegetation (Fig 5a).

Etymology. The specific name *nigropunctatus* is from Latim *nigra* meaning black, and *punctum* meaning spot, in reference to the spotted body coloration. An adjective.

Imparfinis tessellatus sp. nov.

(Fig 7, 3c Tab. 2)

Imparfinis n.sp.3 Juruena–Silva *et al.*, 2021: fig.1 [phylogenetic relationships of Heptapteridae]

Holotype. LBP 38227, 79.0 mm SL, Brazil, Mato Grosso, Sapezal, Rio Papagaio, 13° 33’38.0”S 58°24’27.3”W, 11 September 2025, BF Melo, GSC Silva, L Reia.

Paratypes. Brazil, Mato Grosso, Juruena River basin: LBP 20906, 5, 56.4–64.5 mm SL, Mato Grosso, Sapezal, Rio Papagaio, 13°33’38.0”S 58°24’27.3”W, 31 October 2015, BF Melo, GJ Costa-Silva, GSC Silva, C Araya, NTB Mateussi. LBP 37291, 17, 26.3–81.0 mm SL, Brazil, Mato Grosso, Sapezal, Rio Papagaio, 13°33’38.0”S 58°24’27.3”W, 11 September 2025, BF Melo, GSC Silva, L Reia. LBP 37269, 4, 42.6–59.3 mm SL, Brazil, Mato Grosso, Sapezal, Rio Papagaio, 13°33’38.0”S 58°24’27.3”W, 11 September 2025, BF Melo, GSC Silva, L Reia. MZUSP 93517, 13, 29.9–39.6 mm SL, Rio Papagaio, Sapezal, 13°33.4’ S58°24.3’W. MNRJ 56176, 2, 52.0–57.1 mm SL, Brazil, Mato Grosso, Sapezal, Rio Papagaio, 13°33’38.0”S 58°24’27.3”W, 11 September 2025, BF Melo, GSC Silva, L Reia.

Diagnosis. The new species differs from all congeners by having a distinctive color pattern, consisting of dark blotches of chromatophores over a cream-colored background, forming a variegated color pattern (vs. absence of this pattern). Additionally, the new species differs from its congeners by having 10–11 gill rakers on the first ceratobranchial (vs. 5–6 in *I. lineatus and I. lepturus*, 6–8 in *I. nigropunctatus*; 7–8 in *I. usmai*, *I. mirini*, and *I. piperatus*, 9 in *I. mishky*; 12–16 *I. guttatus*, 14 in *I. cochabambae*, and 12–15 in *I. pjipersi*); 38 vertebrae (41 in

I. guttatus, *I. minutus* and *I. cochabambae*, 42 in *I. lineatus*, 42–43 in *I. timana*, 45 in *I. spurreli*); by having the maxillary barbel not surpassing vertical through the insertion of the last pectoral fin-ray (vs. surpassing the pectoral-fin base in *I. arceae*, *I. cochabambae*, *I. guttatus*, *I. lepturus*, *I. melanopterus*, *I. myshky*, *I. nemacheir*, *I. piperatus*, *I. nigropunctatus*, *I. robustus*, *I. schubarti*, *I. timana*, *I. usmai*) and absence of a short, flexible extension of the pectoral- and dorsal-fin spines, and outermost primary rays of upper caudal-fin lobe (vs. extension present in *I. guttatus*, *I. nemacheir*, and *I. usmai*).

Description. Morphometric data summarized in Table 2. Head relatively long (21.9–23.9% of SL) and weakly depressed; body elongate, nearly cylindrical anteriorly, gradually compressed posteriorly. Dorsal profile broadly convex from snout to dorsal-fin origin, straight to barely descending along dorsal-fin base, then straight to adipose-fin origin, straight (descending) along adipose-fin base, and finishing more or less straight (ascending) along caudal peduncle. Ventral profile gently convex from snout to vent, then straight to anal-fin origin, finishing gently concave to lower procurrent caudal-fin rays. Snout moderately long and rounded in dorsal view. Body width greatest across cleithral region, gradually tapering posteriorly to caudal peduncle.

Eyes large and horizontally elliptical, dorsolaterally positioned. Mouth subterminal with upper jaw longer than lower. Premaxilla and dentary with five irregular rows of small conical teeth. Maxillary barbel not surpassing the pectoral fin base. Outer mental barbel, reaching the pectoral-fin origin and longer than inner mental barbel which finishes short of pectoral-fin origin. Branchiostegal membranes supported by eight rays and joined to isthmus only at anterior point. Ten to eleven gill rakers along anterior border of first ceratobranchial. Total vertebrae 38 with 12 precaudal (seven supporting pleural ribs) and 26 caudal.

Pectoral fin with first ray simple and eight or nine branched rays (i,8–9). First pectoral-fin ray stiffened proximally and flexible distally, lacking filamentous extension. Pelvic fin i,5; first ray shorter than second and third rays. Dorsal-fin i,6; first basal radial inserted on eigth vertebra and last basal radial anterior to neural spine of 14th vertebra. Adipose fin long (16.4–19.8% of SL). Anal fin iii,9. Caudal skeleton composed of a plate formed by parhypural + hypurals 1 and 2 fused in lower lobe, upper lobe plate formed by hypurals 3 and 4 fused, hypural 5 free, and pleurostyle fused to compound centrum. Caudal fin with i,7,8,i principal rays. Upper and lower caudal-fin lobe approximately symmetrical. Dorsal and ventral caudal-fin lobes with 11–10 procurrent rays, respectively.

Coloration. Background color of body yellowish. Dark blotches of chromatophores over a cream-colored background, forming a variegated color pattern. Interorbital and occipital regions of dorsal head dusky, followed by six evenly spaced dusky saddles; first saddle across nape, second at dorsal-fin origin, third below posterior insertion of dorsal fin; fourth saddle below distal margin of dorsal fin (about halfway between third saddle and adipose-fin origin) fifth saddles at adipose-fin origin, and sixth on adipose-fin end. Fins hyaline.

FIGURE 7. Left column: *Imparfinis tessellatus*, holotype, LBP 38227, 79.0 mm SL. Right column: *Imparfinis tessellatus,* LBP 37291, from top to bottom: 81.5 mm SL; 58.7 mm SL; 61.1 mm SL.

Distribution and habitat. The new species is known from the Rio Papagaio (Fig. 4). It was collected in fast-flowing rivers, in clear waters associated with bottom rocks and submerged vegetation (Fig. 5c).

Etymology. The specific name *tessellatus* is derived from the Latin, meaning mosaic, in reference to the mosaic-like color pattern found in this species. An adjective.

Discussion

The three new species described herein exhibit markedly distinct coloration patterns: *Imparfinis tessellatus* exhibits a variegated body coloration pattern, characterized by irregular blotches of dark pigment over a cream-colored background (Fig 7, 3c); *Imparfinis nigropunctatus* bears a series of small dark spots scattered over a yellow background (fig 6, 3b) and *Imparfinis melanopterus* is distinguished by the prominently darkened lower lobe of the caudal fin (Fig 2, 3a). The ASAP analysis supported that these morphotypes represent distinct and independent evolutionary lineages (Fig 1). Furthermore, comparisons of genetic distances between each of the three new species and their genetic closest congeners revealed high levels of molecular divergence: *I. melanopterus* vs. *I. guttatus* = 5.8%; *I. nigropunctatus* vs. *I. lepturus* = 3.1%, and *I. tessellatus* vs. *I. arceae* = 6.7% (Tab. 1).

Imparfinis nigropunctatus and *I. melanopterus* are the first species of the genus formally described from the Araguaia River basin. They are readily distinguished by morphological traits (see Diagnosis) and exhibit pronounced genetic divergence (12%), being placed in distinct clades (Fig. 1). *Imparfinis nigropunctatus* occurs in the upper portion of the Araguaia River, whereas *I. melanopterus* inhabits the middle basin. These regions are separated by the Couto Magalhães waterfall, a geomorphological barrier with an estimated 40-meter drop that effectively restricts upstream dispersal of most fish species. As a result, the upper Araguaia harbors a disproportionately high number of endemic fishes (Lima & Moreira 2003; Dagosta *et al.* 2019; Melo *et al.* 2021).

Similarly, the Tapajós River basin harbors two distinct species of *Imparfinis*: *I. tessellatus*, restricted to upland river above 400 m on the Chapada dos Parecis, and the recently described *I. munduruku* (Castro & Wosiacki 2019), which inhabits lowland regions below 150 m, including the Teles Pires and Tapajós Rivers. As in the previous case, these species are clearly differentiated from each other in morphology, genetic divergence, and phylogenetic placement (Fig 1). *Imparfinis tesselatus* is endemic to the Upper Rio Tapajós; other species such as *Astyanax utiariti* Bertaco & Garutti 2007 and *Crenicichla chicha* Varella, Kullander & Lima, 2012 are also known only for the Rio Papagaio, a tributary of the upper Rio Juruena, drainage of the upper Rio Tapajós. According to Bertaco & Garutti (2007), the ichthyofauna of the upper Rio Tapajós drainage (upstream from the confluence with the Teles Pires and Juruena rivers) is little known, so that apart from the descriptions of new species, there are no published data on the species composition of this drainage. Other species endemic to Upper Tapajós include *Hemigrammus skolioplatus* Bertaco & Carvalho 2005 (Characidae), *Hasemania nambiquara* Bertaco & Malabarba 2007 (Characidae), *Moenkhausia andrica* Reia, Oliveira & Benine 2021 (Characidae), *Gelanoglanis pan* Calegari, Reis & Vari 2014 (Auchenipteridae), *Tatia melanoleuca* Vari & Calegari 2014 (Auchenipteridae), *Hisonotus bockmanni* Carvalho & Datovo 2012 (Loricariidae) and *Corydoras apiaka* Espíndola, Spencer, Rocha & Britto 2014 (Callichthyidae).

Imparfinis is an interesting group to study evolutionary radiation, with remarkable contemporary richness and deserving a biogeographical history to be understood. The distribution of *Imparfinis* in the Amazon basin reveals a clear east-west contrast. In the highlands of the cratonic areas of the eastern Amazon, the genus reaches its greatest diversity, with six described species (*I. arceae, I. hasemani, I. melanopterus, I. munduruku, I. nigropunctatus,* and *I. tessellatus*), all with highly restricted ranges (Fig. 4). By contrast, the western Amazon, a younger region dominated by sedimentary plains and whitewater rivers, harbors a single widespread species, *I. guttatus*, distributed from southern Bolivia to Ecuador. The presence of waterfalls and rapids in the eastern cratonic highlands promotes population isolation, endemism, and ultimately speciation. In contrast, the western Amazon is dominated by lowland rivers with high hydrological connectivity facilitating gene flow and dispersal, reducing opportunities for isolation and favoring the persistence of generalist species with broad distributions. (Hoorn *et al.* 2010; Oberdorff *et al.* 2019).

Other groups of small catfishes have shown similar patterns, with a single species occurring in the lowland regions of the western Amazon and multiple species restricted to the Brazilian Shield. In *Phenacorhamdia*, for example, *P. nigrolineata* is widely distributed throughout the western Amazon, whereas several species are confined to the amazonian Brazilian Shield (Castro & Woziaki 2023; Silva *et al.* 2025, 2022). A comparable case is observed in *Microglanis*, where *M. poecilus* inhabits lowland regions, while multiple species occur in the shield areas.

Comparative material examined

Imparfinis minutus: Brazil, Minas Gerais, rio São Francisco basin: LBP 6504, 1, 63.8 mm SL; *Imparfinis mirini*: Brazil, São Paulo, Rio Parana basin: LBP 930 1 c&s (56.0 mm SL); LBP 2898, 7, 46.2−71.9 mm SL; LBP 32005, 1 c&s (51.3 mm SL); DZSJRP 3309, 2, 44.1−50.8 mm SL; DZSJRP 11932, 2, 40.9−42.0 mm SL; DZSJRP 19210, 7, 45.6−78.8 mm SL; *Imparfinis piperatus*: Brazil, São Paulo, Upper Tietê River basin: LBP 1025, 8, 48.9−66.4 mm SL; LBP 1057, 4, 48.9−59.8 mm SL, 3 c&s (45.1−50.3 mm SL); DZSJRP 12846, 4, 56.4−65.3 mm SL; *Imparfinis schubarti*: Brazil, São Paulo, rio Grande basin: LBP 32932, 10, 46.5−83.5 mm SL, 2 c&s (40.5−49.5 mm SL); *Imparfinis lepturus*: Brazil, Goias, rio Corrente basin: holotype, MZUSP 127602, 44.9 mm SL; *Imparfinis hasemani*: Guiana, Takutu river: ANSP 179747, 2, 58.1–58.4 mm SL; ANSP 180938, 1, 59.0 mm SL; ANSP 179748, 1, 56.1 mm SL; ANSP 180957, 1, 51.1 mm SL. Brazil, Para, Lower Xingu basin. *Imparfinis guttatus*: Bolivia, Rio Mamore, AMNH 077485, 1, 60.1 mm SL; Brazil, Rio Solimões: ANSP 206935, 56.8 mm SL; FMNH 97019, 2, 98.1–102.0 mm SL; FMNH 103255, 1, 98.8 mm SL; *I. muduruku*: Brazil, PA, Tapajos River basin: LBP 24703, 28.1–35.5 SL. *I. cochabambae*: Bolivia, Beni River basin: Holotype, ANSP 699066. *Imparfinis lineatus*: Panama, Chiriqui, Balneario Las Fuentes: ANSP 151053, 50.8 mm SL. *Imparfinis longicaudus*: Equador, Napo, Rio Aguarico: ANSP 130602, 54.6 mm SL.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

Supplementary Table 1. Species and specimens included in the molecular study. The order of the species in the table follow the order of taxa in Fig 1.