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A new *Hyphessobrycon* (Characiformes: Acestrorhamphidae) from the rio Mamuru basin, Amazonas State, Brazil

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A new species of *Hyphessobrycon* from the rio Mamuru basin, Pará State, Brazil, is described. The new species is similar to two congeners, *Hyphessobrycon hildae* and *Hy. taguae*, and to a non-congener, *Hemigrammus bellottii*, by the presence of a conspicuous, vertically-elongated humeral blotch and the lack of other conspicuous dark color markings on body and fins, and by the presence, in life, of a bicolor longitudinal pattern dorsal to the longitudinal dark stripe composed by a dorsal thin red stripe and a ventral thin iridescent stripe. It differs from the abovementioned species by the shape of the humeral blotch. DNA barcoding methodology also distinguished the new species from *He. bellottii* sampled populations by 14.97 to 16.8% genetic distance in the cytochrome c oxidase I gene, and indicate the species as part of the subfamily Hyphessobryconinae and sister species of *Hyphessobrycon montagi* with genetic distance of 9.33%. Comments on the taxonomic status of *Hy. hildae* and *Hy. taguae* are made.

Keywords: DNA barcoding, *Hemigrammus bellottii*, *Hyphessobrycon hildae*, *Hyphessobrycon taguae*, Hyphessobryconinae.

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Uma nova espécie de *Hyphessobrycon* da bacia do rio Mamuru, Estado do Pará, é descrita. A nova espécie é similar a dois congêneres, *Hyphessobrycon hildae* e *Hy. taguae*, e ao não-congênere *Hemigrammus bellottii* pela presença de uma mancha umeral conspícua e verticalmente alongada, e pela ausência de outras estruturas de coloração escura conspícuas no corpo e nadadeiras, e pela presença, em vida, de um padrão bicolor longitudinal, composto por uma faixa vermelha dorsal e uma faixa iridescente ventral, posicionado dorsalmente a à faixa escura longitudinal. A nova espécie difere de todas estas espécies pela forma da mancha umeral. A metodologia DNA barcoding também distingue a nova espécie das populações amostradas de *He. bellottii* com distâncias genéticas de 14,97 a 16,8% no gene citocromo c oxidase I, e indica também que a espécie é parte da subfamília Hyphessobryconinae e é espécie-irmã de *Hyphessobrycon montagi* com distância genética de 9,33%. Comentários sobre o status taxonômico de *Hy. hildae* e *Hy. taguae* são apresentados.

Palavras-chave: DNA barcoding, *Hemigrammus bellottii*, *Hyphessobrycon hildae*, *Hyphessobrycon taguae*, Hyphessobryconinae.

INTRODUCTION

The genus *Hyphessobrycon* Durbin, 1908, is the most species rich in Acestrorhamphidae, with 146 species currently recognized as valid (Melo *et al*., 2024; Toledo-Piza *et al*., 2024; Lima *et al*., 2025a,b). The high number of species is related with the high number of lineages included in the genus, which is not only polyphyletic (Mirande, 2019; Ohara *et al*., 2019; Melo *et al*., 2024) but also is diagnosed with characters widespread among small acestrorhamphids, *i.e*., incompletely pored lateral line, caudal fin with scales restricted to its base, two teeth rows on premaxilla with five teeth in the inner row and presence of an adipose fin.

Due to the historic lack of comprehension about the phylogenetic relations of species in *Hyphessobrycon*, different authors have proposed groups intended as monophyletic within the genus using different combinations of characters, mostly related to color patterns and/or sexual dimorphic characters (*e.g*., Géry, 1977; Weitzman, Palmer, 1997; Ingenito *et al*., 2013; Ota *et al*., 2020). Two of these putative monophyletic groups, the *Hyphessobrycon heterorhabdus* species-group (Lima *et al*., 2014; Moreira, Lima, 2017; Faria *et al*., 2020, 2021) and the *Hy. agulha* species-group (Géry, 1977; Ohara, Lima, 2015; Faria *et al*., 2020) are especially relevant in the present context due to their color pattern similarities with the new species described here.

The *Hyphessobrycon heterorhabdus* species-group is composed, in its most recent proposition (Faria *et al*., 2021), by *Hy. amapaensis* Zarske & Géry, 1998, *Hy. cantoi* Faria, Guimarães, Rodrigues, Oliveira & Lima, 2021, *Hy. ericae* Moreira & Lima, 2017, *Hy. heterorhabdus* (Ulrey, 1894), *Hy. montagi* Lima, Coutinho & Wosiacki, 2014, *Hy. sateremawe* Faria, Bastos, Zuanon & Lima, 2020, and *Hy. wosiackii* Moreira & Lima, 2017. This species-group is diagnosed by the presence of a tricolor longitudinal pattern composed by: a dorsal red stripe, a middle iridescent stripe and a ventral dark longitudinal pattern composed by a black humeral blotch, which is well-defined anteriorly and

diffuse posteriorly, followed posteriorly by a black stripe that becomes blurred towards the caudal peduncle (the latter absent in most *Hy. ericae* populations and in *Hy. wosiackii*; see Moreira, Lima, 2017). In its turn, the *Hy. agulha* species-group is characterized by the presence of a dark, broad, and diffuse longitudinal stripe that occupies most of the ventral half of the body. Currently, the following species are considered to belong to this group: *Hy. agulha* Fowler, 1913, *Hy. clavatus* Zarske, 2015, *Hy. eschwartzae* García-Alzate, Román-Valencia & Ortega, 2013, *Hy. herbertaxelrodi* Géry, 1961, *Hy. klausanni* Garcia-Alzate, Urbano-Bonilla & Taphorn, 2017, *Hy. loretoensis* Ladiges, 1938, *Hy. lucenorum* Ohara & Lima, 2015, *Hy. margitae* Zarske, 2016, *Hy. metae* Eigenmann & Henn, 1914, *Hy. mutabilis* Costa & Géry, 1994, *Hy. peruvianus* Ladiges, 1938, *Hy. wadai* Marinho, Dagosta, Camelier & Oyakawa, 2016 and *Hy. zoe* Faria, Lima & Wosiacki, 2020 (Faria *et al*., 2020).

However, the recent broad phylogenetic analysis of the former family Characidae presented by Melo *et al*. (2024) has not recovered either the *Hy. heterorhabdus* (*sensu* Faria *et al*., 2021) nor the *Hy. agulha* (*sensu* Faria *et al*., 2020) as monophyletic. Melo *et al*. (2024:19, fig. 6) analyzed three species assigned to the *Hy. heterorhabdus* species group (*sensu* Faria *et al*., 2021), *i.e*., *Hy. amapaensis*, *Hy. ericae*, and *Hy. heterorhabdus*, and six species belonging to the *Hy. agulha* species group (*sensu* Faria *et al*., 2020), *i.e*., *Hy. agulha*, *Hy. herbertaxelrodi*, *Hy. margitae*, *Hy. mutabilis*, *Hy. peruvianus*, and *Hy. wadai*. Species of both the *Hy. heterorhabdus* species group and the *Hy. agulha* species-group were recovered intermigled in a clade within the newly proposed subfamily Hyphessobryconinae that also included *Hy. rubrostriatus* and *Hemigrammus bellottii*, and in addition several unidentified *Hyphessobrycon* species. A single species, *Hy. wadai*, was recovered outside this clade, within its sister-clade, as the sister-species of *Hy. cyanotaenia*. In the present work, we describe a new species of *Hyphessobrycon*, which is part of subfamily Hyphessobryconinae (*sensu* Melo *et al*., 2024), specifically of the clade that includes species belonging to the *Hy. heterorhabdus* and *Hy. agulha* species groups. We use DNA barcoding methodology to investigate its phylogenetic relations with the most similar species of the clade, including different populations of *He. bellottii*, a similar-looking syntopic species, and *Hy. montagi*, a species suggested to be related to the *Hy. heterorhabdus* species group on its original description (Lima *et al*., 2014). The new taxon is also the first species described from the rio Mamuru basin, a small tributary of the Amazon basin draining an area immediately west to the rio Tapajós basin and discharging into the Paraná de Ramos channel, a ria lake situated in the intervening area between the lower rio Tapajós and the lower rio Madeira.

MATERIAL AND METHODS

Counts and measurements follow Fink, Weitzman (1974), except for the number of horizontal scale rows below lateral line, which are counted to the pelvic-fin insertion (excluding the axillary scale) rather than to the anal-fin origin, and the addition of three measurements: distance from pelvic-fin origin to anal-fin origin, dorsal-fin base length, and anal-fin base length. Standard length (SL) is expressed in millimeters (mm) and all other measurements are expressed as percentages of SL, except subunits of the head, which are expressed as percentages of head length (HL). In the description, counts

are followed by their absolute frequency in parentheses. Asterisks indicate the counts of the holotype. *Circulii* and *radii* were counted on scales from the row immediately dorsal to the lateral line at the vertical through the dorsal-fin origin. Counts of supraneurals, branchiostegal rays, gill-rakers of the first branchial arch, teeth counts (with exception of premaxillary teeth) and morphology, unbranched anal-fin rays, procurrent caudal-fin rays and position of pterygiophores were taken from cleared and stained (c&s) specimens prepared according to Taylor, Van Dyke (1985). Vertebrae of the Weberian apparatus were counted as four elements and the compound caudal centrum (PU1+U1) as a single element. Catalog numbers are followed by the total number of specimens and their SL range. The number of c&s specimens is given in parentheses, followed by their respective SL range. Institutional abbreviations follow Sabaj (2020, 2023).

Molecular analysis. DNA extraction followed Ivanova *et al*. (2006) and partial sequences of the mitochondrial gene cytochrome c oxidase subunit I (COI) were amplified by polymerase chain reaction (PCR), with primers FishF1/R1 described by Ward *et al*. (2005). Reactions were carried out in a 12.5 µL reaction volume containing 1.25 µL of 10× PCR buffer, 0.40 µL MgCl2 (50 mM), 0.30 µL dNTPs (2 mM), 0.25 µL of each primer (5 µM), 0.20 µL of PHT Taq DNA polymerase (Phoneutria), and 2 µL DNA template (200 ng), and 7.85 µL of ddH2O. The PCR consisted of denaturation (5 min at 95°C) followed by 30 cycles of denaturation (1 min at 95°C), primer hybridization (45 sec at 52°C), nucleotide extension (1 min at 68°C), and a final extension (10 min at 68°C). 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 v. 3.1 Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Austins, USA), and purified through ethanol precipitation. Amplified fragments were then loaded into an ABI 3500 Genetic Analyzer (Applied Biosystems), in the Instituto de Biotecnologia (IBTEC), Instituto de Biociências, Universidade Estadual Paulista "Júlio de Mesquita Filho", Botucatu, Brazil. For this study, we generated two sequences of the new species and 13 sequences of other nine nominal species of *Hyphessobrycon* and *Hemigrammus*. We also used two sequences of *Hy. heterorhabdus* obtained from Genbank. For more details about sequences and Genbank numbers, see Tab. 1. The sequences were assembled using the software Geneious v. 7.1.4 (Kearse *et al*., 2012) and aligned with Muscle (Edgar, 2004) under default parameters. The best-fit model of nucleotide evolution was selected according to Akaike Information Criterion with corrections for small sample sizes (AICc). The overall mean genetic distances (among all specimens), as well as interspecific (among species group) and intraspecific distances (among specimens of each species group), were estimated with 1.000 pseudoreplicates and without root. These previous analyses were estimated using MEGA v. 11. Maximum likelihood (ML) analysis was performed in RAxML-HPC v. 8 on ACCESS using the GTRGAMMA model in the CIPRES server. The best tree was accessed through ten random searches with 1,000 bootstrap pseudoreplicates. The resulting ML tree was used as an input tree for the Poisson Tree Process model (PTP) analysis (Zhang *et al*., 2013), which was performed on the PTP web server (https://species.h-its.org), with the option "remove outgroup" and the others parameters in default. The analysis of Assemble Species by Automatic Partitioning (ASAP) (ASAP; Puillandre *et al*., 2021) is available in the ASAP webserver (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html) with model Jukes-Cantor (JC69).

TABLE 1 | Voucher information for analyzed sequences, and Genbank or BOLD numbers.

Species	Collection	Voucher	River basin	Specific location	Municipality/ State	Coordinates	BOLD	Genbank
Hemigrammus bellottii	LBP 33007	112819	Rio Abacaxis	Rio Abacaxis	Maués, Amazonas	06°41'51.58"S 58°51'36.13"W		PP786517
Hemigrammus bellottii	LBP 33193	110911	Rio Mamuru	Rio Mamuru	Itaituba, Pará	03°59'51.13"S 56°16'54.15"W		PP786518
Hemigrammus bellottii	LBP 33193	110910	Rio Mamuru	Rio Mamuru	Itaituba, Pará	03°59'51.13"S 56°16'54.15"W		PP786519
Hemigrammus bellottii	LBP 22476	86809	Rio Amazonas	Quebrada La Ponderosa	Leticia, Colombia	04°08'24.4"S 69°56'53.4"W		PQ044052
Hyphessobrycon agulha	LBP 30463	50120	Rio Madeira	Igarapé da UNIR	Porto Velho, Rondônia	08°49'36.1"S 63°56'04.2"W		PP786516
Hyphessobrycon amapaensis	LBP 30508	116901	Rio Amazonas	Igarapé affluent of rio Pedreira	Ferreira Gomes, Amapá	00°41'44.0"N 51°21'39.0"W		PP372830
Hyphessobrycon cf. *ericae*	LBP 31628	110207	Rio Curuá-Una	Rio Moju	Belterra, Pará	03°25'05.6"S 54°54'46.50"W		PP372834
Hyphessobrycon cf. *ericae*	LBP 31628	110208	Rio Curuá-Una	Rio Moju	Belterra, Pará	03°25'05.6"S 54°54'46.50"W		PP372835
Hyphessobrycon eschwartzae	ROMCID 134066	10194	Rio Madre de Dios	Rio Planchon	Tambopata, Madre de Dios, Peru*	12°16'37.67"S 69° 9'8.53"W		PQ044050
Hyphessobrycon herbertaxelrodi	LBP 8387	40453	Rio Paraguai	Córrego Águas Claras	Tangará da Serra, Mato Grosso	14°21'03.2"S 57°33'07.2"W		PP372838
Hyphessobrycon heterorhabdus	LBP 9451	45139	Rio Guamá	Igarapé affluent of igarapé São José	Santa Isabel, Pará	01°16'54.1"S 48°10'09.9"W	ACD9730	
Hyphessobrycon heterorhabdus	LBP 9451	45140	Rio Guamá	Igarapé affluent of igarapé São José	Santa Isabel, Pará	01°16'54.1"S 48°10'09.9"W	ACD9730	
Hyphessobrycon montagi	LBP 31642	110260	Rio Arapiuns, Tapajós	Aquarium specimen				PP786520
Hyphessobrycon mamuruensis	LBP 33015	112842	Rio Mamuru	Igarapé affluent of rio Mamuru	Itaituba, Pará	04°04'46.03"S 56°11'45.41"W		PP786521
Hyphessobrycon mamuruensis	LBP 33015	112841	Rio Mamuru	Igarapé affluent of rio Mamuru	Itaituba, Pará	04°04'46.03"S 56°11'45.41"W		PP786522
Hyphessobrycon pulchripinnis	LBP 32962	112719	Rio Tapajós	Igarapé do Abacaxi	Jacareacanga, Pará	06°08'51.9"S 57°43'44.3"W		PP372832
Hyphessobrycon sateremawe	INPA 50729	30449	Rio Abacaxis	Igarapé affluent of rio Abacaxis	Nova Olinda do Norte, Amazonas	04°17'5"S 58°34'44"W		PQ044051

RESULTS

Hyphessobrycon mamuruensis, new species

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(Figs. 1–2; Tab. 2)

Holotype. LBP 34880, 32.4 mm SL, Brazil, Pará State, Itaituba, igarapé tributary of rio Mamuru, near comunidade Mamuru, 04°02'19.66"S 56°15'24.5"W, T. C. Faria & I. L. P. Monteiro, 12 Dec 2022.

Paratypes. All from Brazil, Pará State, Itaituba. LBP 33134, 53, 16.5–32.0 mm SL, MPEG 39787, 5, 25.2–29.1 mm SL, same data as holotype. LBP 33024, 148, 15.4–32.8 mm SL, ZUEC 17660, 10, 22.4–31.2 mm SL, INPA 61051, 10, 23.7–30.6 mm SL, MZUSP 130842, 5, 19.8–30.9 mm SL, Igarapé tributary of rio Mamuru, 04°04'46"S 56°11'45.41"W, T. C. Faria & I. L. P. Monteiro, 12 Dec 2022. LBP 33188, 27, 18.6–26.8 mm SL, rio Mamuru, 03°59'51"S 56°16'54.5"W, T. C. Faria & I. L. P. Monteiro, 2 Dec 2022. LBP 33177, 23, 21.0–30.4 mm SL, Igarapé tributary of rio Mamuru, 04°03'29.3"S 56°13'24.2"W, T. C. Faria & I. L. P. Monteiro, 12 Dec 2022. LBP 33388, 107, 15.9–35.5 mm SL, 4 c&s, same locality and collectors as holotype, 2 Dec 2022.

Diagnosis. *Hyphessobrycon mamuruensis* can be distinguished from all congeners, except *Hy. bussingi* Ota, Carvalho & Pavanelli, 2020, *Hy. columbianus* Zarske & Géry, 2002, *Hy. condotensis* Regan, 1913, *Hy. daguae* Eigenmann, 1922, *Hy. ecuadorensis* (Eigenmann, 1915), *Hy. eilyos* Lima & Moreira, 2013, *Hy. hildae* Fernandez-Yépez, 1950, *Hy. igneus* Miquelarena, Menni, López & Casciotta, 1980, *Hy. itaparicensis* Lima & Costa, 2001, *Hy. panamensis* Durbin, 1908, *Hy. pinnistriatus* Carvalho, Cabeceira & Carvalho, 2017, *Hy. platyodus* Ohara, Abrahão & Espínola, 2017, *Hy. pulchripinnis* Ahl, 1937, *Hy. rheophilus* Ohara, Teixeira, Albornoz-Garzón, Mirande & Lima, 2019, and *Hy. taguae* García-Alzate, Román-Valencia & Taphorn, 2010, by the combination

FIGURE 1 | *Hyphessobrycon mamuruensis*. **A.** LBP 34880, holotype, 32.4 mm SL, female; **B.** LBP 33134, paratype, 24.4 mm SL, male, Brazil, Pará, rio Mamuru.

FIGURE 2 | *Hyphessobrycon mamuruensis*. Live specimen, paratype, LBP 33024, SL uncertain, same locality as holotype.

of the following color pattern features: presence of a single humeral blotch, lack of a conspicuous caudal-peduncle blotch, lack of a conspicuous blotch on the dorsal fin and lack of a conspicuous longitudinal dark stripe (*vs.* presence of two humeral blotches, or absence of any humeral blotch, presence of a conspicuous dark blotch on the caudal peduncle, presence of a conspicuous blotch on the dorsal fin and/or presence of a conspicuous longitudinal dark stripe). *Hyphessobrycon mamuruensis* can be distinguished from all species belonging to the *Hy. panamensis* species-group (*sensu* Ota *et al*., 2020; *i.e*., *Hy. bussingi*, *Hy. columbianus*, *Hy. daguae*, *Hy. ecuadorensis,* and *Hy. panamensis*) by lacking bony hooks on the anal fin of dimorphic males (*vs.* presence of individual large bony hooks on each anterior large ray the anal fin). *Hyphessobrycon mamuruensis* can be additionally distinguished from *Hy. bussingi*, *Hy. columbianus*, *Hy. condotensis*, *Hy. daguae*, *Hy. ecuadorensis*, *Hy. eilyos*, *Hy. igneus*, *Hy. itaparicensis*, *Hy. panamensis*, *Hy. pinnistriatus*, *Hy. platyodus*, *Hy. pulchripinnis*, *Hy. rheophilus*, by the presence well-defined humeral blotch in preserved specimens (*vs.* presence of a relatively inconspicuous, diffuse humeral blotch). *Hyphessobrycon mamuruensis* can additionally be distinguished from *Hy. platyodus* by presenting the anal fin in mature males with anteriormost anal-fin rays distinctly longer forming an anterior lobe (*vs*. mature males with anal-fin rays roughly equal in size along its length and lacking any distinct fin lobe). *Hyphessobrycon mamuruensis* can be distinguished from *Hy. hildae*, *Hy. taguae*, and from the non-congener but similar-looking *Hemigrammus bellottii*, by the presence of a well-developed, vertically elongated humeral blotch considerably higher than wide (*vs*. humeral blotch only slightly higher than wide in *Hy. hildae*, *Hy. taguae*, and *He. bellottii*; see Fig. 3). It is further distinguished from *Hy. taguae* and *He. bellottii*, by the absence of a posterior extension of the humeral blotch (*vs.* presence of a thin, short posterior extension of the humeral blotch; see Fig. 3), and by lacking bony hooks on the anterior rays of the anal fin of mature males (*vs.* presence of bony hooks on the anterior rays of the anal fin of mature males). See the Discussion, for further notes on both *Hy. hildae* and *Hy. taguae*.

TABLE 2 | Morphometric data for *Hyphessobrycon mamuruensis*. N = number of specimens measured; SD = Standard deviation.

	Holotype	Range	Mean±S.D.	N
Standard length(mm)	32.4	20.0–32.8	–	–
Percents of standard length				
Depth at dorsal-fin origin	34.6	27.5–35.0	32.1±1.7	29
Snout to dorsal-fin origin	49.7	48.4–50.6	49.7±0.7	29
Snout to pelvic-fin origin	47.5	44.9–49.3	47.2±1.1	29
Snout to anal-fin origin	62.3	60.5–65.4	62.7±1.1	29
Caudal peduncle depth	8.9	7.0–10.0	8.6±0.8	29
Caudal peduncle length	14.8	10.5–15.2	13.3±1.1	29
Pectoral-fin length	22.8	20.1–24.1	22.8±0.7	29
Pelvic-fin length	18.2	15.2–20.7	19.1±1.2	29
Dorsal-fin base	13.9	12.4–14.7	13.8±0.6	29
Dorsal-fin length	32.7	29.5–33.6	32.3±0.9	29
Anal-fin base	29.0	26.5–29.5	28.1±0.8	29
Head length	26.8	26.5–29.0	27.7±0.7	29
Percents of head length				
Horizontal orbital diameter	40.2	36.9–44.3	41.6±1.7	29
Snout length	23.0	20.0–25.9	22.9±1.7	29
Least interorbital width	31.0	28.4–33.3	30.7±1.3	29
Upper jaw length	43.7	40.5–47.4	44.8±1.6	29

Description. Morphometric data for holotype and paratypes in Tab. 2. Body compressed. Greatest body depth at vertical through dorsal-fin origin. Dorsal profile of the head slightly convex from upper lip to vertical through posterior nostril, straight from that point to tip of supraoccipital spine. Dorsal profile of body slightly convex from latter point to anterior terminus of dorsal fin. Dorsal-fin base straight, posteroventrally slanted, slightly convex from posterior terminus of dorsal fin to adipose-fin insertion and slightly concave between adipose-fin insertion and origin of anteriormost dorsal procurrent caudal-fin ray. Ventral profile of head and body convex from tip of lower jaw to anal-fin origin. Anal-fin base straight, posterodorsally slanted. Ventral profile of caudal peduncle slightly concave.

Jaws equal, mouth terminal. Posterior terminus of maxilla reaching vertical through anterior margin of iris. Maxilla approximately at 45 degrees angle relative to longitudinal axis of body. Nostrils close to each other, anterior opening oval, posterior opening crescent-shaped. Premaxillary teeth in two rows. Outer teeth row with 2(2), 3(10), or 4(2) conic to tricuspid teeth. Inner row with 5(13) or 6(1) bi- to pentacuspid teeth, symphyseal tooth narrower than neighbor tooth. Maxilla with 2(2) or 3(2), conical to tricuspid teeth. Dentary with 10(1), 12(1) or 13(2) teeth, anteriormost 3–4 teeth larger, bi- to tricuspid, one teeth uni- to tricuspid intermediary in size, remaining teeth considerably smaller and conical. Central cusp of all teeth more developed than lateral cusps.

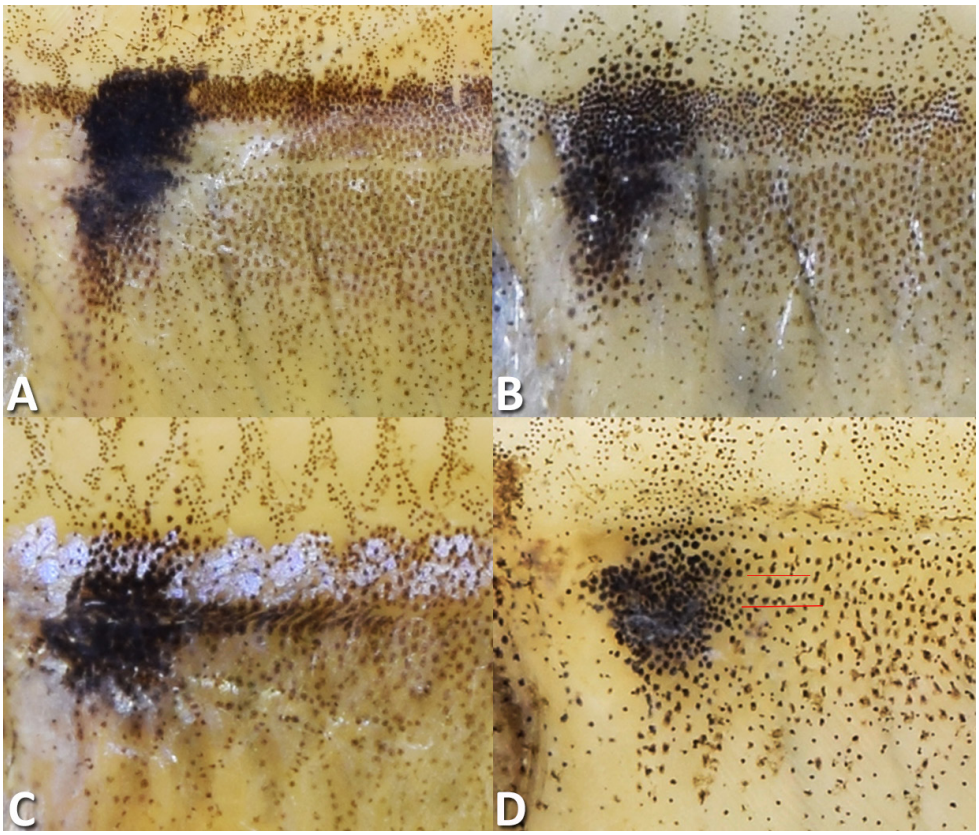

FIGURE 3 | Humeral blotches of *Hyphessobrycon mamuruensis* (**A**, **B**) and *Hemigrammus bellottiii* specimens (**C**, **D**). **A.** LBP 34880, holotype, 32.4 mm SL, showing no posterior extension. **B.** LBP 33134, paratype, 24.4 mm SL, showing no posterior extension. **C.** LBP 34342, 37.2 mm SL, showing conspicuous posterior extension. **D.** LBP 34285, 28.7 mm SL, showing inconspicuous posterior extension (between red lines).

Scales cycloid. Two to seven *radii* strongly marked, *circulii* well-marked anteriorly, weakly marked posteriorly. Lateral line slightly deflected downward and incompletely pored, with 7(6), 8*(18) or 9(5) perforated scales. Longitudinal scales series including lateral-line scales 32*(10), 33(10), 34(6) or 35(2). Longitudinal scale rows between dorsal-fin origin and lateral line 5*(28) or 6(1). Longitudinal scale rows between lateral line and pelvic-fin origin 3(18) or 4*(11). Predorsal scales 9(7), 10*(18) or 11(4). Circumpeduncular scales 12*(26). Caudal fin with few small scales basally.

Dorsal-fin rays ii, 8*(1) or 9(28). Dorsal-fin origin approximately at middle of standard length. First dorsal-fin pterygiophore inserting behind neural spine of 8th(1) or 9th(3) vertebrae. Adipose fin present. Anteriormost anal-fin pterygiophore inserting posterior to haemal spine of 15th(3) or 16th(1) vertebrae. Anal-fin rays iii(1) or iv(3), 18(3), 19(9), 20*(13), 21(3) or 22(1). Last unbranched and first to third anteriormost branched rays distinctly longer than remaining rays, subsequent rays gradually decreasing in size. Pectoral-fin rays i,9(3), 10*(15), 11(10) or 12(1). Pelvic-fin rays i,7*(29). Tip of pelvic fin reaching anteriormost anal-fin rays. Caudal fin forked, lobes roughly rounded and of similar size. Nine (1), 10(1) or 11(2) dorsal procurrent caudal-fin rays, and 8(3) or 9(1) ventral procurrent caudal-fin rays. Vertebrae 33(4).

Supraneurals 4(3) or 5(1), upper portion wider. Branchiostegal rays 4. First gill arch with 1(1) or 2(3) hypobranchial, 1(1) on cartilage between hypobranchial and ceratobranchial, 7(1), 8(2) or 9(1) ceratobranchial, 1(3) on cartilage between ceratobranchial and epibranchial, and 4(1), 5(2) or 6(1) epibranchial gill-rakers.

Coloration in alcohol. Overall body color beige. Dorsal half of body darker. Dorsal portion of head dark. Ventralmost portion of head and body with low concentration of scattered dark chromatophores. Snout and tip of dentary dark. Numerous dark chromatophores across infraorbitals, maxilla and opercle. Predorsal and preadipose scales with conspicuous central dark blotches. Predorsal-scale peripheral region less darker than its center. Scale rows dorsal to midbody with conspicuous reticulated pattern formed by dark chromatophores concentrated at scales margins. Humeral blotch vertically elongated, roughly triangular, about two scales high and one to one and a half wide, with smallest angle directed downward. Humeral blotch surrounded anteriorly and posteriorly by clear areas lacking melanophores. Narrow, ill-defined longitudinal stripe, conspicuous only in some specimens (*e.g.*, Fig. 1A), extending from upper portion of humeral blotch to vertical through adipose fin insertion, fading considerably after vertical through middle portion of dorsal fin. Relatively dense concentration of dark chromatophores along the midbody, after the humeral blotch, imparting an overall dark coloration and contrasting with the markedly clearer ventral area. Narrow dark line along midlateral septum extending from vertical through middle portion of dorsal fin to anterior portion of caudal peduncle. Dark chromatophores aligned along myocommata of hypaxial muscles above anal fin and parallel to anal fin base. Pectoral fin and pelvic fin hyaline with few scattered dark chromatophores. Dorsal-fin ray hyaline, with dark chromatophores concentrated on anteriormost rays and distal region. Anal fin hyaline, with dark chromatophores scattered along interradial membranes. Adipose fin with few scattered dark chromatophores, mainly at its base. Caudal fin mostly hyaline, with few dark chromatophores scattered on interradial membranes, with a higher concentration on distalmost regions and along ventralmost and dorsalmost region of fin lobes.

Coloration in life. Based on pictures of living specimens taken at the field (Fig. 2): overall body color olivaceous. Lower half of head and abdominal region silvery. Dorsal portion of eye red. Two longitudinal, juxtaposed stripes on flanks, one dorsal red stripe and one ventral iridescent stripe. Stripes extending on midlateral region immediately dorsal to darkened midbody area (see coloration in alcohol). Red stripe, anteriorly thicker and continuous, becoming row of red blotches after dorsal fin insertion, ending in large red blotch at posterodorsal region of caudal peduncle. Iridescent stripe golden, continuous, more diffuse on caudal peduncle, ending immediately before red blotch. Humeral blotch vertically elongated, conspicuous, and with diffuse borders. Humeral blotch dorsal expansion with about half the height of ventral expansion. Iridescent bluish chromatophores immediately ventral to midlateral golden stripe and scattered on dorsalmost portion of abdominal region. Dorsal and adipose fin, anterior lobe of anal fin, proximal half of caudal-fin lobes and anterior rays of pelvic fins yellow.

Sexual dimorphism. Females present the last unbranched and two anteriormost branched anal-fin rays longer, resulting in a more pointed and developed anal-fin lobe. Males present tiny bony hooks restricted to the pelvic fins, along all rays, an uncommon condition among acestrorhamphids recently discussed by Lima *et al*. (2025b:11). Females reach larger sizes than males (largest female 35.5 mm SL, largest male 26.5 mm SL). The presence of female-biased sexual size dimorphism in characiforms was recently discussed by Teixeira *et al*. (2025:140).

Geographical distribution. *Hyphessobrycon mamuruensis* is known only from the upper rio Mamuru basin, State of Pará, near the border with Amazonas State, Brazil (Fig. 4).

Ecological notes. *Hyphessobrycon mamuruensis* is known from moderate-flowing, clear water forest streams with sandy bottom (Fig. 5). Specimens were collected in both the main channel of upper rio Mamuru and in its small tributaries. It was the most common species in smaller tributaries, where larger specimens were also more abundant. *Hemigrammus bellottii*, the most similar-looking species to *Hy. mamuruensis* (see Discussion), was collected syntopically in most localities, but was less abundant than the latter at the rio Mamuru basin.

Etymology. The specific epithet is a reference to type-locality of the new species, rio Mamuru basin. A noun in apposition.

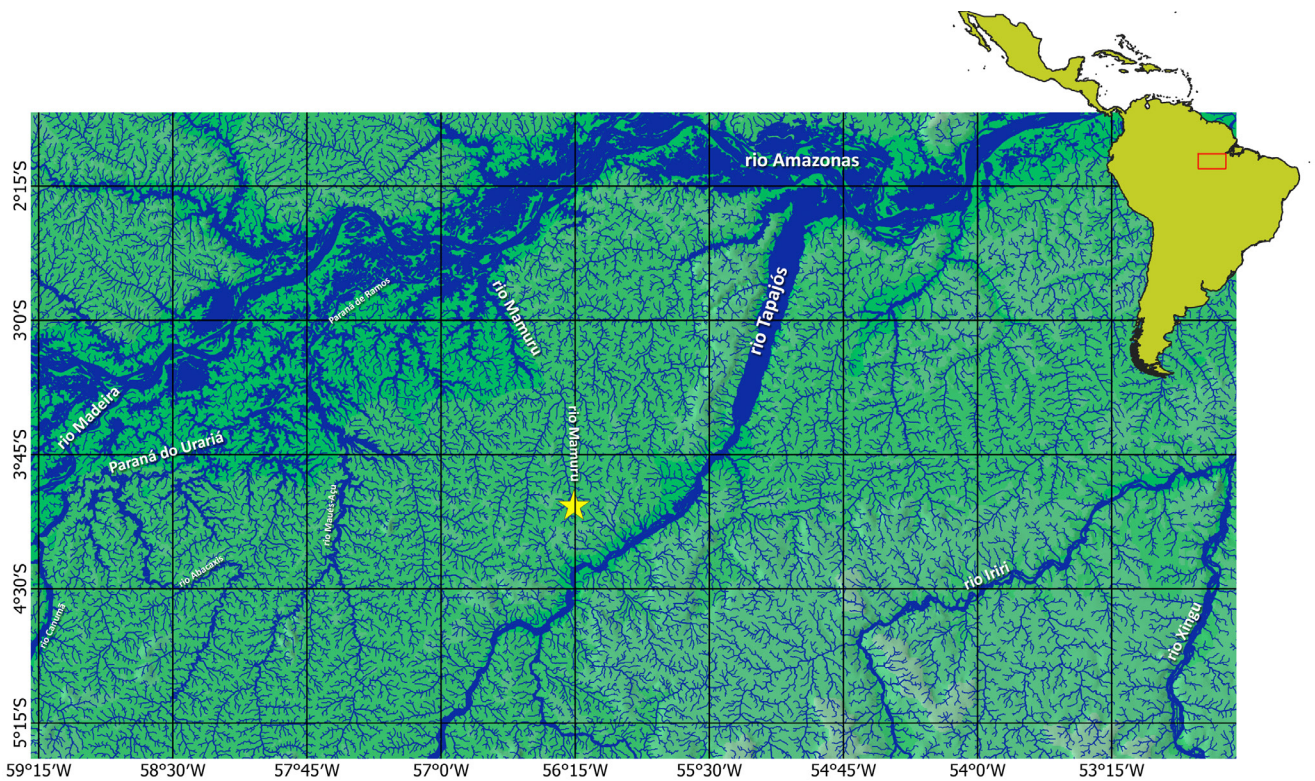

FIGURE 4 | Map of the central Amazon basin, showing the known distribution of *Hyphessobrycon mamuruensis* (yellow star comprises multiple localities).

FIGURE 5 | A and **B.** Type-locality of *Hyphessobrycon mamuruensis*, a small tributary of rio Mamuru. **C.** Main channel of rio Mamuru.

Conservation status. *Hyphessobrycon mamuruensis* is known only from the upper rio Mamuru basin. The region of occurrence of the species is right at the frontier of the Amazon's deforestation arc. In fact, Itaituba is a hotspot in the Amazon for gold mining and deforestation and there are roads connecting the city to the upper portion of rio Mamuru basin. Fortunately, the species' known range is very close to the Parque Nacional da Amazônia, which protects the left bank tributaries of rio Mamuru basin. Due to this, we suggest the conservation status of the new species as Low Concern (LC) according to the IUCN criteria and categories (2024).

Genetics. The recovered tree using DNA barcoding methology (Fig. 6) indicates *Hyphessobrycon mamuruensis* and *Hemigrammus bellottii* as not closely related, with the two belonging to different groups with high bootstrap support. This result contrasts with the fact that *He. bellottii* is the most similar-looking species to *Hy. mamuruensis* known to date.

Hemigrammus bellottii is recovered as monophyletic, but ASAP species delimitation method indicates each population sampled (from Tabatinga, its type-locality, rio Mamuru and rio Abacaxis basins) as different species while bPTP indicates all populations as a single species (Figs. **S1**, **S2**). All other nominal species are recovered as a single evolutionary lineage by both species delimitation methods. A clade consisting of *Hy. mamuruensis*, *Hy. herbertaxelrodi*, *Hy. ericae* and *Hy. montagi* is recovered with 78% bootstrap support, indicating a sister relation between *Hy. mamuruensis* and *Hy. montagi* with high bootstraps support (92%).

A sister clade relationship between *He. bellottii* and *Hy. heterorhabdus* is recovered with small bootstraps support (50%). The *Hy. heterorhabdus* species group (*sensu* Lima *et al*., 2014; Moreira, Lima, 2017; Faria *et al*., 2020, 2021) is recovered as non-monophyletic with the inclusion of *He. bellottii* and *Hy. eschwartzae* and exclusion of *Hy. montagi* and *Hy. ericae*. A clade consisting of *He. bellottii*, *Hy. sateremawe*, *Hy. heterorhabdus*, *Hy. amapaensis* and *Hy. eschwartzae* is recovered with bootstrap support of 98%.

The genetic distances among the ingroup samples (Tab. 3; not considering genetic distances between same species samples recovered by ASAP) ranged between 20.42% (between *Hy. agulha* and *He. bellottii* from rio Mamuru) and 2.97% (between *He. bellottii*

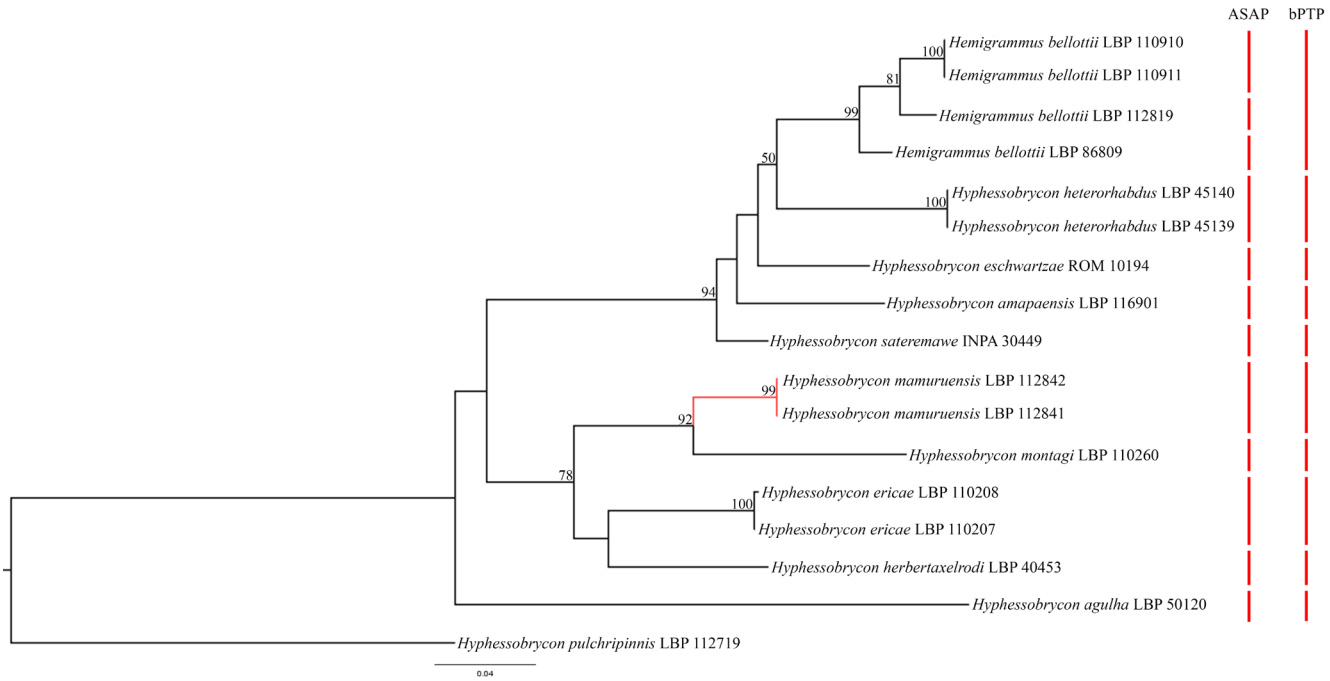

FIGURE 6 | RAxML tree based on DNA barcoding methodology showing *Hyphessobrycon mamuruensis* (red clade) and similar species. Species delimitation methods indicate the presence of 9 or 10 species in the ingroup.

TABLE 3 | Genetic distances based on DNA barcoding using Maximum Composite Likelihood among species *Hyphessobrycon* and *Hemigrammus* similar to *Hyphessobrycon mamuruensis*.

	1	2	3	4	5	6	7	8	9	10	11	12
1- *Hy. pulchripinnis*												
2- *Hy. agulha*	24.14%											
3- *Hy. heterorhabdus*	21.56%	18.97%										
4- *Hy. amapaensis*	24.52%	18.74%	11.00%									
5- *Hy. eschwartzae*	22.66%	18.57%	9.26%	8.73%								
6- *Hy. sateremawe*	22.50%	18.78%	8.77%	7.39%	7.13%							
7- *He. bellottii* Leticia (type-locality)	22.85%	19.10%	9.30%	9.15%	8.17%	7.02%						
8- *He. bellottii* Abacaxis	23.18%	19.99%	9.86%	9.51%	9.47%	8.37%	3.98%					
9- *He. bellottii* Mamuru	23.18%	20.42%	10.43%	9.69%	9.66%	7.79%	4.17%	2.97%				
10- *Hy. montagi*	22.66%	18.08%	18.88%	18.43%	17.87%	16.40%	16.63%	18.26%	17.85%			
11- *Hy. mamuruensis*	21.12%	17.31%	15.83%	14.79%	15.26%	14.28%	14.97%	16.80%	15.98%	9.33%		
12- *Hy. herbertaxelrodi*	22.54%	19.20%	16.82%	16.61%	15.68%	14.66%	15.68%	15.05%	15.25%	13.65%	11.67%	
13- *Hy. ericae*	22.29%	17.70%	15.92%	16.97%	16.02%	14.79%	16.41%	16.19%	17.22%	12.35%	11.16%	9.56%

from rio Mamuru and *He. bellottii* from rio Abacaxis). The genetic distances between *He. bellottii* and *Hy. mamuruensis* range between 14.97% and 16.8% (respectively between *Hy. mamuruensis* and populations of *He. bellottii* from Tabatinga and rio Abacaxis). The genetic distance between *Hy. mamuruensis* and *Hy. montagi* is 9.33%.

DISCUSSION

Hyphessobryconinae, one of the recently proposed subfamilies of Acestrorhamphidae, was proposed using only the species relationships recovered in Melo *et al.* (2024) phylogenomic study of Characidae. This subfamily lacks a morphological diagnosis, and it is divided into four main unnamed clades. *Hyphessobrycon mamuruensis* possesses two of the three typical features of species recovered in one of these four clades, specifically the one comprising most sampled species of the *Hy. agulha* and all sampled species of *Hy. heterorhabdus* species groups (the least inclusive clade with *Hy. agulha* and *Hy. heterorhabdus*, which we propose to be informally named as "*Hy. agulha* lineage"). These features are: an midlateral iridescent stripe and teeth with up to five cusps (Melo *et al.*, 2024). Additionally, *Hy. mamuruensis* possesses a longitudinal narrow red stripe dorsally to the midlateral iridescent stripe as is typical for the species of the *Hy. heterorhabdus* species group (*sensu* Faria *et al.*, 2021).

Our resulting tree, using sequences of the cytochrome c oxidase subunit I, recovers *Hyphessobrycon mamuruensis* as the sister species of *Hy. montagi*, with a genetic distance of 9.33% between them. Melo *et al.* (2024) did not sample neither of these species, however, in the present study, these species were recovered as a sister group

of a clade containing *Hy. ericae* and *Hy. herbertaxelrodi*, studied by Melo *et al*. (2024), with moderate to strong bootstrap support (78%), suggesting that *Hy. mamuruensis* and *Hy. montagi* could be considered as part of the *Hy. agulha* lineage in the subfamily Hyphessobryconinae. Our molecular data also recover *He. bellottii*, *Hy. heterorhabdus*, *Hy. eschwartzae*, *Hy. amapaensis*, and *Hy. sateremawe* forming a well supported clade with 94% bootstrap support. This result agrees with that found by Melo *et al*. (2024) which found that *He.* cf. *bellottii*, *Hy. heterorhabdus*, and *Hy. amapaensis* belong to a lineage related with *Hy. ericae* and *Hy. herbertaxelrodi.*

The only congeners sharing a color pattern similar to *Hyphessobrycon mamuruensis* are *Hy. hildae* and *Hy. taguae*. *Hyphessobrycon hildae* is only known from its original description (Fernández-Yépez, 1950), and its holotype and only known specimen originated from the Río Autana, a tributary of the upper Río Orinoco basin in Venezuela, whereas *Hy. taguae* was described from localities in the Amazon and Orinoco basins in Colombia (García-Alzate *et al*., 2010). Additionally, a non-congener very similar to *Hy. mamuruensis* is *Hemigrammus bellottii*, a widely distributed species in the Amazon basin, and in fact both species were collected syntopically at the rio Mamuru. Both species share the presence of a conspicuous humeral blotch and the absence of any other conspicuous dark markings in the body or fins (compare Figs. 1 and 7). The diagnosis between *Hy. mamuruensis* from *He. bellottii* is essentially the same as its diagnosis from *Hy. hildae* and *Hy. taguae*, *i.e*., the presence of a distinctly vertically elongated humeral blotch in *Hy. mamuruensis*, *versus* a humeral blotch that is only slightly higher than wide in *He. bellottii, Hy. hildae*, and *Hy. taguae* (Fig. 3). In fact, even though currently not congeneric with *He. bellottii*, no diagnosis among these three nominal species is available. Fernandez-Yépez (1950) noticed that *Hy. hildae* presents a tiny blotch at the base of the caudal fin, a feature we have observed in specimens identified by us as *He.* cf. *bellottii* from the upper Río Orinoco in Colombia. The systematics of these three nominal species is currently being addressed (FCTL, TCF, and C. A. García-Alzate, work in progress) and for the time being we propose to consider them as belonging to a putative *Hemigrammus bellottii* species-complex.

Hyphessobrycon mamuruensis specimens used in this study were collected in the first ever ichthyological expedition to explore the rio Mamuru basin. There are six other main rivers in the same region, as rio Canumã, rio Abacaxis, rio Paraconi, rio Apoquitauá, rio Maués-Açu and rio Andirá, all of them presenting black water and discharging into the Paraná de Urariá and Paraná de Ramos. These represent two murky water channels, with the first one connecting the lower rio Madeira into the rio Amazonas and the second one connecting the eastern portion of the Paraná de Urariá to the rio Amazonas. The only other species previously described from this same region is *Hy. sateremawe* known from the rio Abacaxis and rio Maués-Açu basins. Some ichthyological surveys have been conducted at the rio Canumã, rio Abacaxis, rio Paraconi, rio Maués-Açu and rio Mamuru basins, but the whole area can still be considered sparsely sampled and consequently poorly known ichthyologically. Additional surveys in the area are necessary to fill this gap in the knowledge of Amazon fishes.

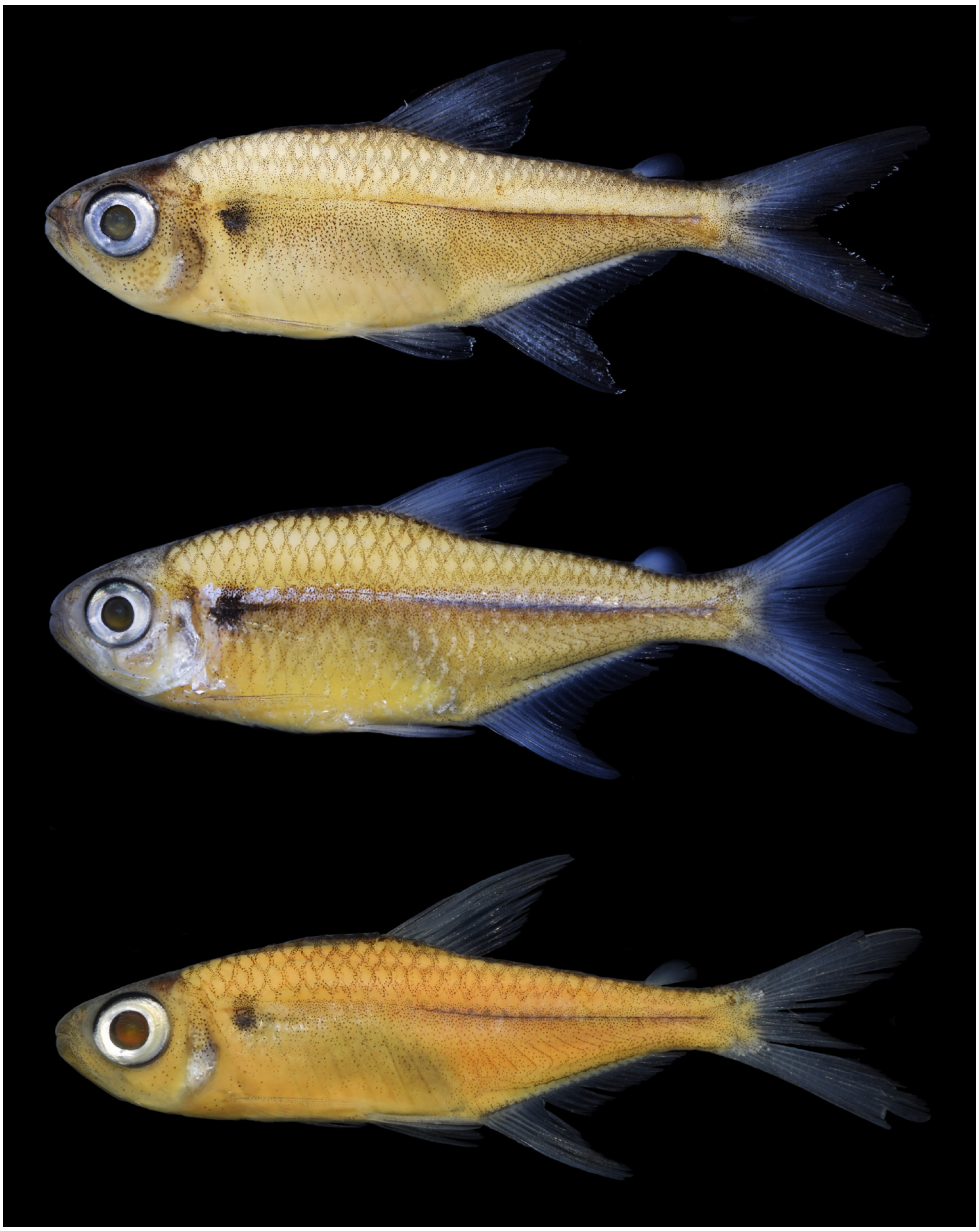

FIGURE 7 | *Hemigrammus bellottii* color variation. Top: LBP 34285, 28.7 mm SL, Brazil, Pará, rio Trombetas basin near Floresta Estadual do Trombetas. Middle: LBP 34342, 37.2 mm SL, Brazil, Pará, igarapé tributary of rio Amazonas at Santarém-Mirim. Bottom: LBP 33135, 28.3 mm SL, Brazil, Pará, rio Mamuru basin.

Comparative material examined. *Hemigrammus bellottii*: all from Brazil, river basins: Abacaxis: LBP 33007, 41, 16.6–28.4 mm SL. Amazonas (direct affluents): LBP 34342, 154, 20.7–36.8 mm SL; LBP 34476, 207, 18.9–33.1 mm SL; NMW 57254, 4, 24.6–29.8 mm SL, syntypes. Javari: ZUEC 16987, 206, 19.8–31.7 mm SL. Juruá: ZUEC 13717, 122, 16.5–31.5 mm SL. Madeira: ZUEC 7237, 39, 20.0–30.7 mm SL. Mamuru: LBP 33022, 1, 21.0 mm SL; LBP 33135, 1, 28.5 mm SL; LBP 33193, 15, 16.5–30.7 mm SL; LBP 33412, 46, 16.2–25.5 mm SL. Negro: ZUEC 18232, 45, 21.1–27.1 mm SL. Paraconi: MPEG 16045, 23, 27.4–33.1 mm SL. Solimões: ZUEC 15338, 145, 22.2–30.1 mm SL. Tefé: ZUEC 15360, 136, 20.1–

32.3 mm SL. Trombetas: LBP 34285, 40, 23.8–30.4 mm SL. Urubu: ZUEC 11407, 5, 27.8–34.3 mm SL. *Hemigrammus* cf. *bellottii*: all from Colombia, river basins: Inirida: MPUJ 995, 18 of 35, 16.2–29.0 mm SL; MPUJ 1493, 7 of 13, 25.4–28.4 mm SL; MPUJ 1494, 4 of 7, 23.0–25.8 mm SL. Vichada: IAvH-P 10196, 7 of 15, 23.1–26.6 mm SL. *Hyphessobrycon heterorhabdus*: Brazil, rio Acará: LBP 35036, 411, 17.0–30.9 mm SL. *Hyphessobrycon taguae*: Colombia, rio Inirida: MPUJ 919, 10 of 49 paratypes, 24.3–26.3 mm SL.

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AUTHORS' CONTRIBUTION

Tiago C. Faria: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing-original draft.
Claudio Oliveira: Data curation, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing-review and editing.
Iann Leonardo Pinheiro Monteiro: Methodology.
Flávio César Thadeo de Lima: Conceptualization, Data curation, Investigation, Supervision, Writing-review and editing.

ETHICAL STATEMENT

No experiments involving live animals were conducted for this study. All specimens were obtained through field collection under the permanent license for biological material collection issued to Claudio Oliveira (SISBIO license number 13843-5).

DATA AVAILABILITY STATEMENT

The authors confirm that the molecular data supporting the findings of this study are available in Genbank and/or BOLD with access numbers available in Tab. 1. Morphological data and distributions are available within the article.

COMPETING INTERESTS

The authors declare no competing interests.

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