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One species, two basins: a new *Hyphessobrycon* (Characiformes: Acestrorhamphidae) from the upper rio Juruena and rio Guaporé basins, Mato Grosso, Brazil

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A new species is described from the upper rio Juruena and rio Guaporé basins from the Chapada dos Parecis, Mato Grosso State, Brazil. The new species can be distinguished from all its congeners by the absence of both a humeral spot and a caudal-peduncle blotch and by the anal fin with 15–18 branched rays. Populations from Juruena and Guaporé river basins exhibit subtle differences in body proportions, coloration, and dentition; however, in our assessment, these variations are insufficient to warrant recognition as distinct species. The putative evolutionary relationships and historical biogeography of the species are discussed.

Keywords: Chapada dos Parecis, Hyphessobryconinae, Intraspecific variation, River capture, Tetra.

Uma nova espécie é descrita das bacias dos rios Juruena e Guaporé, na Chapada dos Parecis, estado de Mato Grosso, Brasil. A nova espécie pode ser distinguida de todos os seus congêneres pela ausência de mancha umeral e de mancha no pedúnculo caudal, além de possuir nadadeira anal com 15–18 raios ramificados. As populações das bacias dos rios Juruena e Guaporé apresentam diferenças sutis nas proporções corporais, coloração e dentição; entretanto, em nossa avaliação, essas variações são insuficientes para justificar o reconhecimento como espécies distintas. As possíveis relações evolutivas e a biogeografia histórica da espécie são discutidas.

Palavras-chave: Captura de cabeceira, Chapada dos Parecis, Hyphessobryconinae, Tetra, Variação intraespecífica.

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INTRODUCTION

Hyphessobrycon Durbin, 1908 is one of the most species-rich genera of Neotropical freshwater fishes, comprising nearly 150 valid species (Toledo-Piza *et al*., 2024; Fricke *et al*., 2025; Lima *et al*., 2025). The genus is diagnosed by the following combination of morphological characters: two teeth rows on the premaxilla with the innermost row with five teeth, incomplete lateral line, and caudal fin not scaled (Eigenmann, 1918). Although broadly distributed across the Neotropical realm, the majority of its diversity is concentrated within the Amazon Basin (Ohara, Lima, 2015; Dagosta, de Pinna, 2019; Toledo-Piza *et al*., 2024). In addition to its taxonomic richness, the genus exhibits remarkable morphological variation. Among all characids (*sensu* Mirande, 2019) and related groups, *Hyphessobrycon* stands out as one of the least morphologically homogeneous groups, particularly with respect to coloration patterns. Several species display dark lateral stripes, which vary from narrow and sharply defined (*e.g*., Dagosta *et al*., 2016; Ohara *et al*., 2017) to broad and diffuse (*e.g*., Ohara, Lima, 2015; Ohara *et al*., 2019). Others are vividly pigmented, exhibiting intense orange to red hues (*e.g*., Carvalho *et al*., 2014; Marinho *et al*., 2016; Camelier *et al*., 2018). Many species are sexually dimorphic, with males possessing bony hooks on fins (*e.g*., Vieira *et al*., 2016) and modified fin shapes, filamentous extensions, and/or distinct coloration compared to females (*e.g*., Lima, Gerhard, 2001; Moreira *et al*., 2002; Dagosta *et al*., 2014; Pastana *et al*., 2017). A unifying trait among species of *Hyphessobrycon* is their small body size. While some species may reach up to 60 mm in standard length (SL), the majority remain significantly smaller, with many recognized as miniature species (Weitzman, Vari, 1988; Toledo-Piza *et al*., 2014; Pastana *et al*., 2017).

Due to their vibrant coloration, peaceful behavior, and small size, several species of *Hyphessobrycon* possess traits highly valued by aquarium enthusiasts. Consequently, dozens of species within the genus have gained worldwide popularity in the ornamental fish trade, with interest continuing to grow as new graceful species are described each year. In fact, some species enter the aquarium market even prior to formal scientific description (Marinho *et al*., 2016), which is precisely the case for the species described herein. Recent ichthyofaunal surveys conducted in central Brazil, particularly in the Chapada dos Parecis region and adjacent areas drained by the upper rio Juruena and upper rio Guaporé, have revealed populations of a yet-undescribed *Hyphessobrycon* species already present in the aquarium trade. In this study, we formally describe this new species and provide brief remarks on its phylogenetic relationships and biogeographic context.

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 origin, not including the small scale at pelvic-fin origin and with the addition of distance from pelvic-fin origin to anal-fin origin. Standard length (SL) is given in millimeters and all other measurements are expressed as percentage of SL, or of head length (HL) for head subunits. In the description, the frequency of each count is provided in parentheses after the respective count, with the count of the holotype indicated by an asterisk. Number of cusps, small dentary teeth, supraneurals, branchiostegal rays, gill rakers, vertebrae, unbranched anal-fin rays and procurrent caudal-fin rays are obtained only from cleared and stained specimens (c&s) prepared according to Taylor, Van Dyke (1985). *Radii* and *circuli* counts were taken from the scale row immediately above the lateral line. Vertebrae of the Weberian apparatus are counted as four elements and the compound caudal centra (PU1+U1) as one element. The sex of specimens was confirmed in ten specimens by dissection and direct examination of the gonads. In the list of types and comparative material, catalog numbers are followed by the number of specimens in alcohol, their SL range, and if any, the number of c&s specimens and their respective SL range. Institutional abbreviations follow Fricke, Eschmeyer (2025). Lot MZUEL 17771 was not designated as paratype because it originated from the aquarium trade and lacks a known locality.

RESULTS

Hyphessobrycon plumbellus, new species

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(Figs. 1–4, 5A, B; Tab. 1)

Holotype. MZUSP 112070, 23.6 mm SL, Brazil, Mato Grosso State, Comodoro, tributary from rio Juína near of BR-364, 13°47'59.33"S 59°29'17.69"W, 21 Oct 2018, F. C. P. Dagosta, A. Ferreria & H. Lenza.

Paratypes. All from Brazil, Mato Grosso State, Comodoro Municipality. Rio Juruena basin: MUBIO 699, 558, 10.2–29.1 mm SL; MZUSP 124997, 229, 11.6–25.1 mm SL, 4 dna (MZICT 5207, 5208, 5209, 5210), 16.7–22.8 mm SL; INPA 62046, 20, 16.7–23 mm SL, MZUEL 24462, 20, 13.5–28.1; CITL 1571, 20, 14.8–25.8 mm SL, collected with the holotype. MZUSP 115691, 23, 17.6–25.1 mm SL, rio Juína, tributary of the rio Juruena, recreational site of the rio Juína, between Comodoro and Campos de Júlio, 13°47'41.2"S 59°27'19.6"W, 29 Sep 2012, O. T. Oyakawa, F. C. P. Dagosta, M. M. Marinho, P. Camelier. Rio Guaporé basin: MUBIO 698, 65, 12.2–26.2 mm SL, Comodoro Municipality, tributary of the rio Piolho, at the bridge on road BR-174, 13 km from Comodoro, upper rio Guaporé, rio Madeira basin, 13°46'50.5"S 59°46'10.3"W, 28 Oct 2022, F. C. P. Dagosta, T. J. Seren, B. A. Nagamatsu & J. Damasceno; UFRO 12313, 72, 17.8–37.6 mm SL, 5 c&s, 24.9–26.1 mm SL, 11 Dec 2012, W. M. Ohara, F. G. Vieira, J. A. Filho; INPA 61816, 40, 19.7–31.4 mm SL, 3 Aug 2018, W. M. Ohara.

Non-type material. MZUEL 17771, 2, 21.1–22.2 mm SL, Brazil, Mato Grosso State, Campo Novo dos Parecis, uncertain locality, H. Lenza.

FIGURE 1 | *Hyphessobrycon plumbellus*, MZUSP 112070, holotype, 23.6 mm SL, from the upper rio Juruena, rio Tapajós basin, Comodoro Municipality, Mato Grosso State, Brazil.

Diagnosis. *Hyphessobrycon plumbellus* differs from all congeners, except *H. amandae* Géry & Uj, 1987, *H. axelrodi* (Travassos, 1959), *H. bayleyi* Lima, Bastos, Rapp Py-Daniel & Ota, 2022, *H. brumado* Zanata & Camelier, 2010, *H. compressus* (Meek, 1904), *H. diancistrus* Weitzman 1977, *H. eilyos* Lima & Moreira, 2003, *H. eos* Durbin, 1909 *H. gracilior* Géry, 1964, *H. georgettae* Géry, 1961, *H. juruna* Faria, Lima & Bastos, 2018, *H. minimus* Durbin, 1909, *H. parvellus* Ellis, 1911, *H. piabinhas* Fowler, 1941, *H. procerus* Mahnert & Géry, 1987, *H. saizi* Géry, 1964, *H. scutulatus* Lucena, 2003, *H. taurocephalus* Ellis, 1911, and *H. tukunai* Géry, 1965 by the absence of a dark humeral blotch (*vs.* presence of a dark humeral spot and/or presence of a dark longitudinal stripe covering the humeral region). It can be distinguished from *H. amandae*, *H. axelrodi*, *H. compressus*, *H. georgettae*, and *H. milleri* by the absence of concentration of dark chromatophores in the dorsal fin forming a blotch (*vs.* presence). From all the remaining species, except *H. bayleyi*, *H. diancistrus*, *H. eilyos*, *H. gracilior*, *H. otrynus* and *H. procerus* by not having a delimited caudal-peduncle blotch (*vs.* presence of concentration of chromatophores forming a distinct caudal-peduncle blotch). The new species differs from *H. bayleyi*, *H. diancistrus* and *H. otrynus* by the caudal-fin pigmentation (hyaline *vs.* two symmetrical dark blotches at the distal portion of the caudal-fin lobes in *H. bayleyi* and black at distal third of their length in *H. otrynus*), from *H. gracilior* and *H. procerus* by having fewer branched anal-fin rays (15–18 *vs.* 18–20 in *H. gracilior*; 22–26 in *H. procerus*). It can be further distinguished from *H. gracilior* by the presence of inner premaxillary, maxillary, and dentary teeth with five to seven cusps (*vs.* conical to three). It differs from *H. eilyos* by the presence of a midlateral stripe extending from the middle of the body to the middle caudal-fin rays (*vs.* uniformly dense body pigmentation without the formation of a midlateral stripe). Additionally, *H. plumbellus* can be diagnosed from its congeners by having four (rarely five) teeth in inner row of premaxillary. A further useful diagnostic feature is the presence of inner premaxillary, maxillary, and dentary teeth with up to seven cusps (*vs.* up to five cusps in most congeners).

Description. Morphometric data for the holotype and paratypes presented in Tab. 1. Body compressed, moderately short and deep. Greatest body depth slightly anterior to dorsal-fin origin. Dorsal profile of head convex from tip of upper jaw to vertical through posterior nostril; straight to slightly concave from that point to tip of supraoccipital spine. Dorsal profile of body convex from supraoccipital spine tip to dorsal-fin origin; straight to slightly concave along dorsal-fin base; straight to slightly concave from terminus of dorsal-fin to adipose-fin origin and concave between adipose-fin origin, and concave along caudal peduncle. Ventral profile of head and body convex from tip of lower lip to pelvic-fin origin; slightly convex from that point to anal-fin origin; straight and posterodorsally inclined along anal-fin base, and concave along caudal peduncle.

Jaws equal, mouth terminal. Posterior terminus of maxilla reaching vertical through anterior margin of pupil. Maxilla approximately at 45 degree angle relative to longitudinal axis of body. Nostrils close to each other, anterior opening circular, posterior opening crescent-shaped. Nostrils separated by narrow flap of skin.

Premaxillary teeth in two rows; outer teeth row with 2(22) or 3*(31) tricuspid teeth; inner row with 4(50) or 5*(4) teeth with five to seven cusps, symphyseal tooth of inner series narrower and laterally asymmetric. Maxilla with 1(12), 2*(38), or 3(4) teeth with five to seven cusps (Fig. 2); anteriormost tooth larger. Dentary with 4(40) or 5*(35) penta- to heptacuspid larger teeth, followed by series of 4(1), 6(3), or 7(1) small conical or tricuspid teeth. Central cusp of all teeth longer than lateral cusps. Branchiostegal rays 4(5). First gill arch with 2(5) gill rakers on hypobranchial, 8(5) on ceratobranchial, 1(5) on intermediate cartilage, and 5(3) or 6(2) rakers on epibranchial.

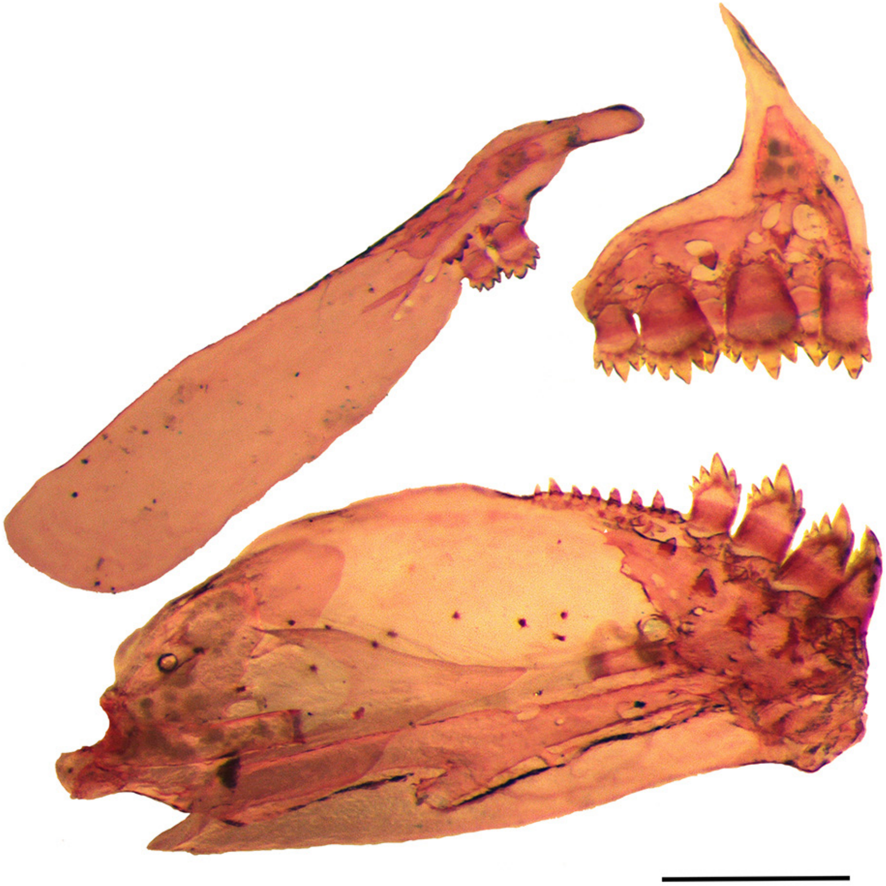

FIGURE 2 | Medial view of left side of the jaws of *Hyphessobrycon plumbellus*, UFRO 12313, paratype, 25.3 mm SL. Scale bar = 200 m.

TABLE 1 | Morphometric data of the holotype and paratypes of *Hyphessobrycon plumbellus*. Range not includes the values of the holotype. Number of specimens: rio Guaporé n = 42; rio Juruena n = 12; SD = Standard deviation.

	Holotype	Rio Juruena basin			Rio Guaporé basin		
		Range	Mean	SD	Range	Mean	SD
Standard length (mm)	23.6	21.1–29.0	24.3	-	17.3–37.6	27.2	-
Percentage of standard length							
Depth at dorsal-fin origin	38.7	37.9–42.3	40.3	1.3	31.7–38.1	35.0	1.8
Snout to dorsal-fin origin	54.8	54.1–59.5	56.2	1.8	51.0–56.8	53.1	1.2
Snout to pectoral-fin origin	27.6	27.6–31.3	29.5	1.2	25.8–30.7	27.9	1.3
Snout to pelvic-fin origin	53.2	53.0–55.5	54.2	0.9	48.4–55.0	51.1	1.4
Snout to anal-fin origin	67.7	67.1–70.4	68.7	1.1	64.0–71.5	66.6	1.4
Caudal peduncle depth	13.0	12.3–14.4	13.5	0.7	11.5–14.7	12.8	0.7
Caudal peduncle length	12.2	9.8–12.6	11.0	0.9	7.9–15.4	13.2	1.9
Pectoral-fin length	24.0	19.6–24.0	21.6	1.4	18.0–21.9	20.5	0.9
Pelvic-fin length	20.6	17.3–20.6	18.7	1.1	16.0–18.4	17.2	0.6
Dorsal-fin base length	16.3	13.9–18.1	16.4	1.1	13.2–18.5	15.3	1.4
Dorsal-fin length	31.0	28.1–33.3	31.1	1.8	26.3–33.0	29.6	1.7
Anal-fin base length	24.7	24.4–28.2	26.6	1.2	22.9–29.8	25.5	1.6
Anal-fin length	19.5	17.6–22.3	20.1	1.5	15.0–21.1	18.0	1.5
Head length	26.8	26.7–28.6	27.8	0.6	24.1–29.4	26.3	1.2
Percentage of head length							
Horizontal length eye	38.9	35.9–41.7	38.5	1.7	32.3–42.6	37.9	2.6
Snout length	23.5	21.6–26.0	24.0	1.6	19.2–26.1	23.1	1.6
Least interorbital width	34.9	29.7–34.9	32.3	1.6	27.8–35.3	32.3	1.9
Upper jaw length	46.2	39.9–48.3	44.5	2.0	37.7–45.8	42.4	1.8

Scales cycloid, *circuli* distributed over whole area of scales with two to eight *radii* diverging nearly from anterior margin to posterior border. Perforated scales of lateral line 5(1), 6(5), 7*(10), 8(21), 9(14), 10(3), 12(2), or 16(1); longitudinal scales series including pored scales 30(3), 31(10), 32*(31), or 33(2). Longitudinal scale rows between dorsal-fin origin and lateral line 5*(57). Longitudinal scale rows between lateral line and pelvic-fin origin 4*(57). Scales in median series between tip of supraoccipital spine and dorsal-fin origin 8(4), 9(15), 10*(25), or 11(2). Horizontal scale rows around caudal peduncle 13(5) or 14*(45). Single row of 2(2), 3*(17), or 4(10) scales covering base of anterior most anal-fin rays. Caudal fin not scaled.

Dorsal-fin rays ii,8(2) or ii,9*(52). Dorsal-fin origin at middle of body and slightly posterior to vertical through pelvic-fin origin. First unbranched dorsal-fin ray shorter than second ray. First dorsal-fin pterygiophore inserted posterior to neural spine of 9th(3) or 10th(2) vertebra. Pectoral-fin rays i,9*(23), 10(35), or 11(1), not reaching pelvic-fin origin. Pelvic-fin rays i,6*(47) or i,7(6). Tip of pelvic fin reaching anterior portion of anal-fin. Adipose fin present. Anal-fin with iv(4) or v(1), 15(4), 16*(24), 17(23), or 18(6) rays. First anal-fin pterygiophore inserted posterior to haemal spine of 16th(3) or 17th(2) vertebra. Principal caudal-fin rays i,9,8,i*(51) or i,8,8,i(3). Caudal-fin forked, lobes somewhat pointed and of similar size. Dorsal procurrent caudal-fin rays 9(3) or 10(2); ventral procurrent caudal-fin rays 8(3) or 9(2). Total vertebrae 32(4) or 33(1): precaudal vertebrae 15(1) or 16(4) and caudal vertebrae 16(3) or 17(2). Supraneurals 4(1) or 5(4).

Coloration in alcohol. Overall ground coloration of body pale yellow. Dorsal portion of head and dorsal midline of body darker. Anterior portion of jaws, infraorbitals 1–2, snout and dorsal portion of head with concentration of small dark chromatophores. Opercle series and infraorbitals 2–4 with scattered dark chromatophores. Opercular series with guanine retention in some specimens. Humeral blotch absent. Muscle reduction at humeral region rendering darker coloration to the area. Narrow subjacent longitudinal dark line extending along horizontal septum, from vertical through middle pectoral fin to end of caudal peduncle. Superficially, a concentration of dark chromatophores is present along this dark line, beginning approximately at the vertical through the origin of the pelvic fin. This concentration becomes progressively denser posteriorly, reaching its greatest intensity on the caudal peduncle region, though without forming a distinct caudal-peduncle blotch. Dark midlateral longitudinal stripe narrower anteriorly and broader posteriorly, extending to tip of middle caudal-fin rays formed by concentration of dark chromatophores. Dorsal region with concentration of dark chromatophores. Abdominal region lighter with few small dark chromatophores; guanine retention in some individuals. Faint dark chromatophores on lower portion of body arranged along myosepta of the hypaxial muscle bundles from area above anal-fin end to caudal peduncle. Unpaired fins with concentration of dark chromatophores on interradial membranes, especially in males (see Sexual Dimorphism section). Paired and adipose fins with small, scattered chromatophores.

Coloration in life. Dorsal ground coloration sexually dimorphic (Fig. 3): blueish to greyish in males, greyish to olive in females. Abdominal region silvery; ventral portion occasionally light orange in mature males from rio Guaporé basin (Fig. 3A). Dorsal portion of eye red to orange. Head olive dorsally; silvery in infraorbital, jaws, gular, and opercular regions. Fin coloration sexually dimorphic: grayish in males, with yellowish portions in females (Figs. 3B, D). Midlateral golden stripe extending from head to caudal peduncle, more conspicuous in specimens from rio Guaporé basin.

Sexual dimorphism. Characteristics based on examination of fixed specimens, field observations and photographs of live specimens (Fig. 3). Although several morphological traits differentiate males from females, individuals at the extremes are more readily sexed. In many cases, however, sex identification is more challenging and may require gonadal examination for confirmation. Well-preserved specimens, particularly those with intact fins, greatly facilitate accurate sexual determination. Males with more conspicuous grayish pigmentation, extending over the dark midlateral stripe, which is more pronounced in females (Fig. 3). Males proportionally with deeper body than females (Figs. 6B, C). Live males with overall more vivid coloration; eyes with more intense reddish pigmentation. Presence of sexual dichromatism: dorsal region grayish to bluish in males, olive-colored in females (Fig. 3). Dorsal, anal, pelvic and caudal fins with denser dark pigmentation in males; less intense in females (Figs. 3–4). Branched anal-fin rays proportionally longer in males (Figs. 3–4). The distal profile of the anal fin is straighter in males and more concave in females, forming a more prominent anterior lobe (Figs. 3–4). Dorsal fin somewhat more rounded in males than in females (Figs. 3–4). Adipose and base of caudal fin grayish in males; yellowish in females (Fig. 3). Pelvic-fin rays proportionally longer in males.

Geographical distribution. The new species is known from three localities: a tributary of the rio Piolho in the upper rio Guaporé, rio Madeira basin, and two nearby sites in the rio Juína basin, upper rio Juruena, rio Tapajós basin. All localities are situated in the Chapada dos Parecis, Comodoro Municipality, Mato Grosso State, Brazil (Fig. 5).

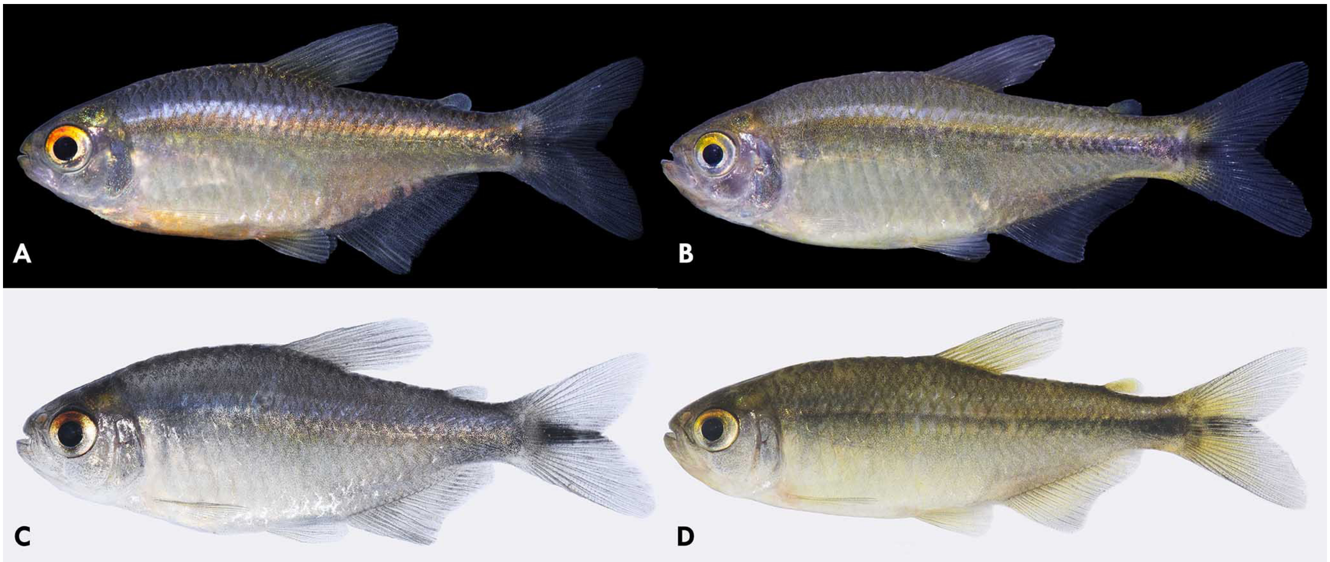

FIGURE 3 | Live specimens of *Hyphessobrycon plumbellus* from the rio Guaporé basin (MUBIO 698, **A.** Male; **B.** Female) and from the rio Juruena basin (MUBIO 689, **C.** Male; **D.** Female). Specimens not measured.

FIGURE 4 | Preserved specimens of *Hyphessobrycon plumbellus* from the rio Guaporé basin (UFRO 12313, **A.** Male, 31.4 mm SL; **B.** Female, 31.8 mm SL) and from the rio Juruena basin (MUBIO 699, **C.** Male, 21.7 mm SL; **D.** Female, 25.6 mm SL).

Ecological notes. The population of *Hyphessobrycon plumbellus* from the rio Guaporé basin inhabits both a small clearwater tributary, 3–5 m wide and 0.5–2 m deep, characterized by swift current and a substrate composed of rocks, sand, and submerged vegetation, as well as an upstream reservoir formed by a hydroelectric power plant. The reservoir features transparent water, an average depth of 1.5 m, and sparse aquatic vegetation. The species is by far the most abundant species in this region. Downstream of the hydroelectric plant, the species was collected syntopically with *Saxatilia lepidota* (Heckel, 1840), *Crenicichla* sp., *Characidium nambiquara* Zanata & Ohara, 2020, *Hoplias malabaricus (Bloch, 1794)* and *Moenkhausia rubra* Pastana & Dagosta, 2014. In contrast, only *Aequidens* sp. and *S. lepidota* were recorded in the reservoir. The analysis of the stomach contents of five cleared and stained paratypes revealed mostly filamentous algae, and smaller quantities of ants, spider, Odonata, larvae of Diptera (Chironomidae), nematoids, Ephemeroptera, unidentified insect fragments, and sand. Some individuals of *H. plumbellus* possess a bulge on the side of the body, caused by a nematode endoparasite.

Conservation status. The species is known only from the municipality of Comodoro, Mato Grosso State, Brazil, in three localities: one in a tributary of the rio Piolho, upper rio Guaporé, rio Madeira basin, and two closely situated sites in the rio Juína basin, upper rio Juruena, rio Tapajós basin. In the Guaporé locality, specimens were collected both immediately downstream and upstream of a small hydroelectric power plant. The species appears to have adapted well to the small reservoir formed by the dam, where it is by far the most abundant fish. Thus, the species shows high adaptability to such altered environment. Another potential threat is collection for the ornamental fish trade. However, according to ornamental fishers, the species currently has low commercial value due to its successful captive breeding by aquarists, and there is little remaining demand for wild-caught specimens. Additionally, the species occurs in the main channel of the rio Juína, a large river that enters the Nambikwara Indigenous Territory just over 10 km downstream from the collection site, where it likely finds pristine habitat conditions. Therefore, *Hyphessobrycon plumbellus* should be classified as Least Concern (LC) under the categories and criteria of the International Union for Conservation of Nature (IUCN, 2024).

Etymology. The specific name *plumbellus* is derived from the Latin *plumbeus*, meaning “leaden,” in reference to the grayish-blue coloration of the males, which has led to the species being popularly known in the aquarium trade as the “tetra chumbinho” in portuguese (= “little lead tetra in english”).The suffix *-ellus* is a Latin diminutive indicating a reduced expression of a quality, here referring to the subtle plumbaceous coloration. In addition, the diminutive may also allude to the small body size of the species. An adjective.

Intraspecific variation. The golden midlateral stripe is markedly more conspicuous in specimens from the rio Guaporé population. Specimens from the rio Juruena population have proportionally deeper bodies: depth at dorsal-fin origin 37.9–42.3% SL (mean 40.3% SL) *vs*. 31.7–38.1% SL (mean 35.0% SL) (Fig. 6). Specimens from the rio Guaporé reach larger body sizes, up to 37.6 mm SL, whereas those from the rio Juruena attain only up to 29.1 mm SL. A meristic difference is also observed. Most specimens from rio Guaporé basin possess four large dentary teeth (n = 40), and only two with five, while all individuals from Juruena (n = 33) exhibit five large dentary teeth. Sexual dimorphism, although present in both populations, is more pronounced in specimens from the rio Juruena basin.

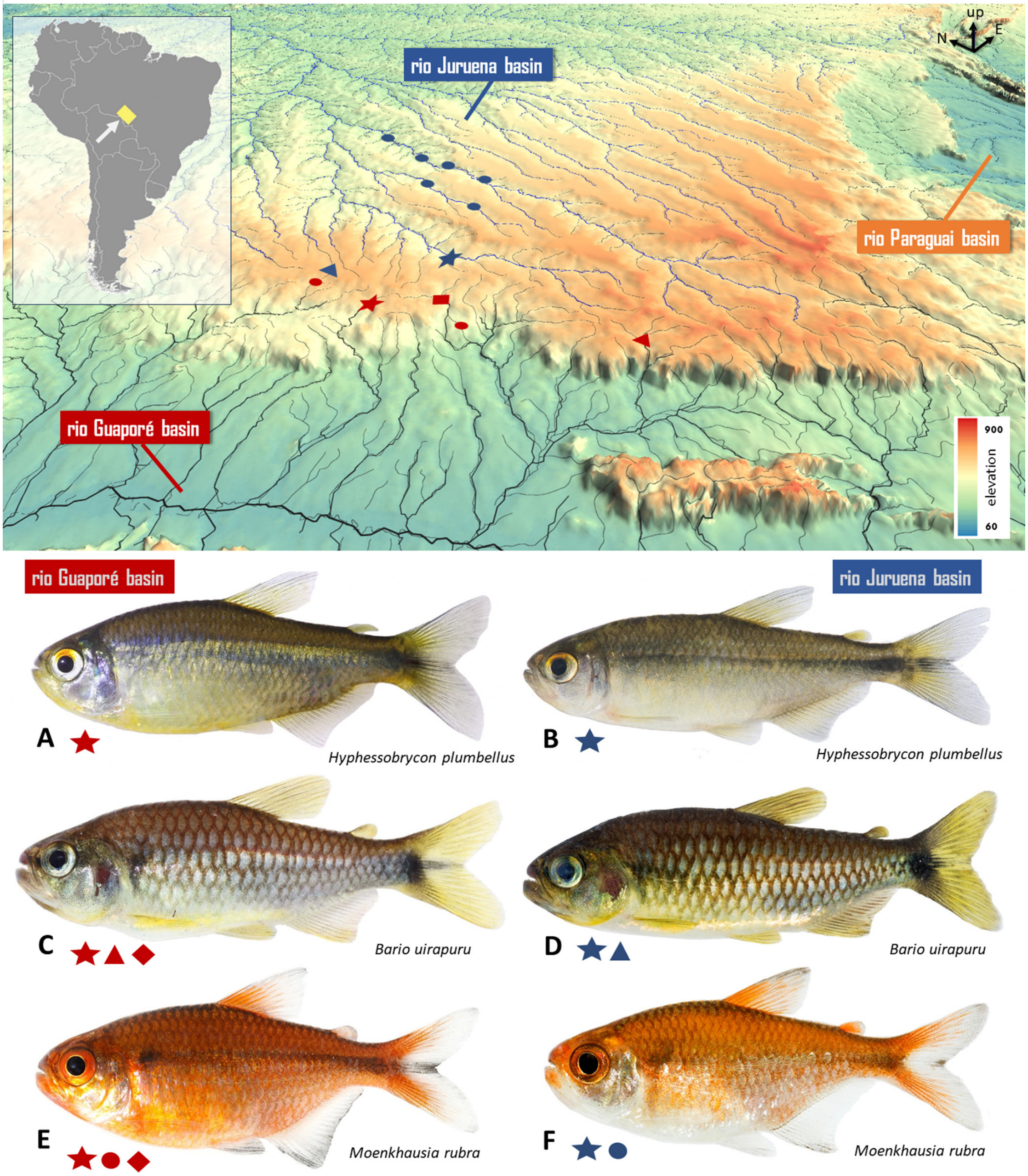

FIGURE 5 | Map of the Chapada dos Parecis, viewed from above and highlighting its western region. Stars indicate the distribution of *Hyphessobrycon plumbellus*, and the blue star representing the type-locality. Blue symbols represent collection sites within the rio Juruena basin, while red symbols correspond to localities in the rio Guaporé basin. Symbols may represent more than one collection event. Each locality on the map has its own ichthyofaunal composition, represented by different symbols (star, diamond, or triangle). These symbols are placed below each species to indicate their occurrence across the respective localities. Representative fish species shared between adjacent basins: **A.** *H. plumbellus* female (rio Guaporé basin); **B.** *H. plumbellus* female (rio Juruena basin); **C.** *Bario uirapuru* (rio Guaporé basin); **D.** *B. uirapuru* (rio Juruena basin); **E.** *Moenkhausia rubra* (rio Guaporé basin); **F.** *M. rubra* (rio Juruena basin).

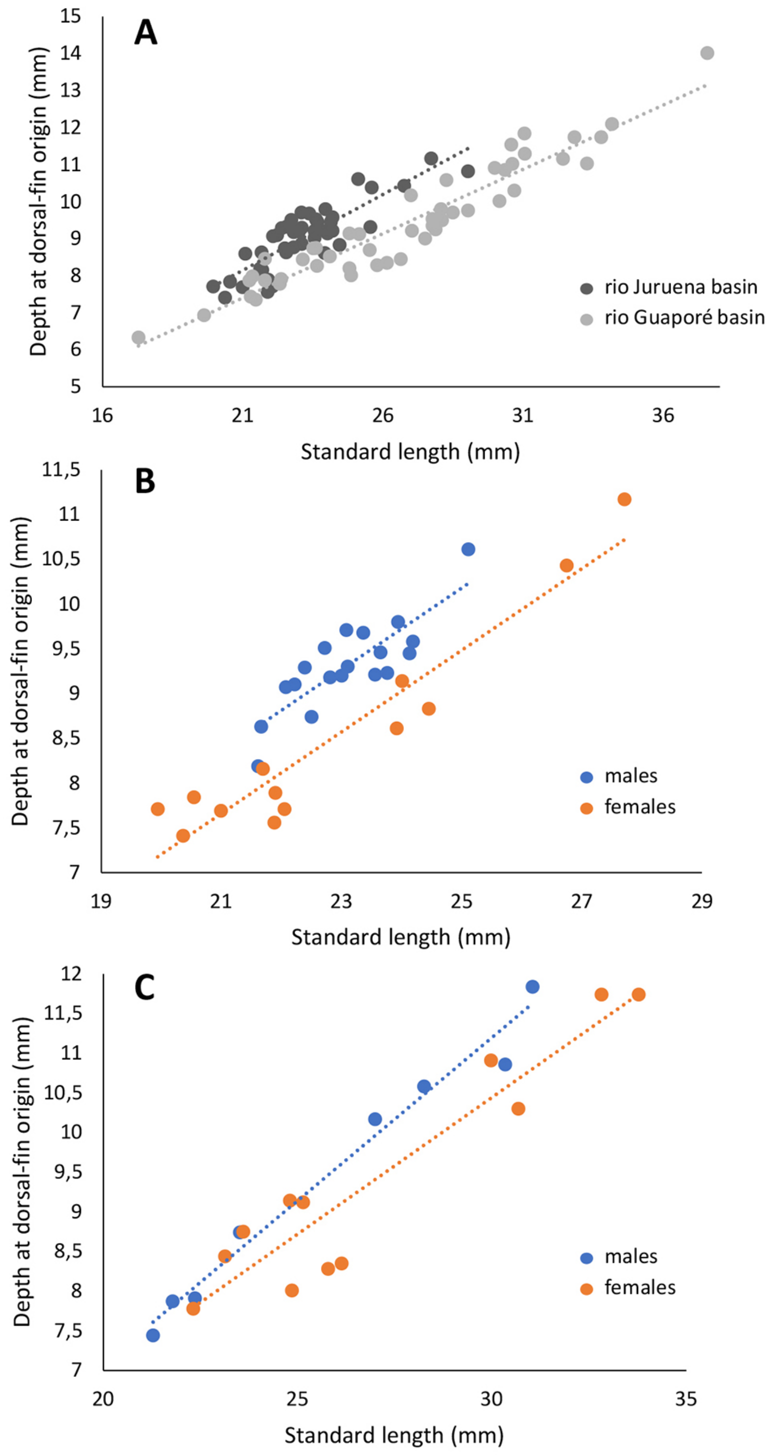

FIGURE 6 | Comparative regression analysis of body depth at the dorsal-fin origin (mm) as a function of standard length (SL, mm). **A.** Regression comparison between specimens from the rio Juruena (R^2 = 0.7314) and rio Guaporé (R^2 = 0.906) basins, with individuals of both sexes pooled. **B.** Sexual dimorphism within the rio Juruena population: females (n = 13, R^2 = 0.9087) and males (n = 19, R^2 = 0.692). **C.** Sexual dimorphism within the rio Guaporé population: females (n = 12, R^2 = 0.8776) and males (n = 8, R^2 = 0.9774).

DISCUSSION

According to Durbin (1908), *Hyphessobrycon* differs from *Hemigrammus* Gill, 1858 solely by the absence of scales on the caudal-fin lobes, a definition that has remained in use to this day due to ongoing phylogenetic uncertainties within these groups. This character, however, is highly homoplastic among characids, and scales are easily lost through friction, even in recently collected specimens (Carvalho *et al*., 2010). As such, a formal diagnosis distinguishing the new species from all species of *Hemigrammus* is required. *Hyphessobrycon plumbellus* can be readily distinguished from all species of *Hemigrammus*, except *He. boesemani* Géry, 1959, *He. brevis* Ellis, 1911, *He. diagonicus* Mendonça & Wosiacki, 2011, *He. durbinae* Ota, Lima & Pavanelli, 2015, *He. filamentosus* Zarske, 2011, *He. hyanuary* Durbin, 1918, *He. mahnerti* Uj & Géry, 1989, *He. marginatus* Ellis, 1911, *He. matei* Eigenmann, 1918, *He. micropterus* Meek, 1907, *He. parana* Marinho, Carvalho, Langeani & Tatsumi, 2008, *He. rodwayi* Durbin, 1909, *He. silimoni* Britski & Lima, 2008, and *He. tridens* Eigenmann, 1907 by the absence of a humeral spot (*vs*. presence of a dark humeral spot and/or presence of a dark longitudinal stripe covering the humeral region). Beyond the lack of scales covering the caudal-fin lobes, *Hy*. *plumbellus* can be diagnosed from all aforementioned species, except *He. levis* Durbin, 1908, *He. mahnerti*, *He. rodwayi*, *He. silimoni*, and *He. tridens* by having 15–18 branched anal-fin rays (*vs*. 14 or less in *He. hyanuary* and *He. rhodostomus* (Ahl, 1924), 19 or more in other species). It differs from *He. levis*, *He. mahnerti*, *He. rodwayi*, and *He. tridens* by not having a dark well-delimited caudal-peduncle blotch (*vs*. presence) and from *He. silimoni* by the absence of an ocellated caudal-fin blotch on the dorsal caudal-fin lobe (*vs*. presence).

Generic allocation, evolutionary relationships and biogeography. Despite clear evidence that *Hyphessobrycon* is not a monophyletic group (Javonillo *et al*., 2010; Oliveira *et al*., 2011; Mirande, 2019; Melo *et al*., 2024), the genus continues to be defined according to the characters originally proposed by Durbin in Eigenmann (1908) and later followed by Eigenmann (1917, 1918). This persistence is largely due to the inability of available phylogenetic hypotheses to provide practical diagnostic characters for the clades recovered in their analyses. As a result, these clades cannot yet be translated into workable taxonomic units. This limitation reflects the extremely high complexity of the group, which is not only species-rich, but also exhibits a high degree of homoplasy.

According to the most recent phylogenetic hypothesis (Melo *et al*., 2024), *Hyphessobrycon* is highly polyphyletic, although most species are placed within the subfamily Hyphessobryconinae. The species of the genus that are endemic to the Chapada dos Parecis and included in the analysis of Melo *et al*. (2024, fig. 6) form a closely related group within a clade that also includes the genera *Erythrocharax* Netto-Ferreira, Birindelli, Sousa, Mariguela & Oliveira, 2013, *Dinotopterygium* Frainer, Carvalho, Bertaco & Malabarba, 2021, *Phycocharax* Ohara, Mirande & Lima, 2017, together with additional species of *Hyphessobrycon*. Notably, members of this clade exhibit teeth with up to seven cusps (except *Hyphessobrycon psittacus* Dagosta, Marinho, Camelier & Lima, 2016) and lack bony hooks on fins (except in species of *Dinotopterygium*), both of which are conditions present in *H. plumbellus*. This clade is sister to another composed mainly of lowland Amazonian species such as *H. heterorhabdus* (Ulrey, 1894) and *H. agulha* Fowler, 1913, and together these two clades form the sister group to the lineage that contains the type species of the genus, *H. compressus*. Although species of *Hyphessobrycon* are scattered across several unrelated lineages (see Melo *et al*., 2024), the clade to which *H. plumbellus* is most likely to belong is closely related to the type species of the genus. Given this proximity, and despite the availability of more recently described generic names such as *Dinotopterygium*, *Erythrocharax*, and *Phycocharax* that are more closely related, we adopt a conservative approach and retain the species within *Hyphessobrycon*.

In the absence of a formal hypothesis regarding the phylogenetic relationships of the species, we are limited to highlighting certain morphological traits that stand out and may carry evolutionary significance. These traits should ultimately be evaluated in the context of future phylogenetic analyses. Although it may be premature to propose a relationship between two species without analytical support, the aim here is merely to point out morphological, ecological, and biogeographical similarities that may suggest a potential close relationship.

Among all known species of *Hyphessobrycon*, the one that most closely resembles *H. plumbellus* is *H. myrmex* Pastana, Dagosta & Esguícero, 2017, particularly the females (see Fig. 7). This similarity is marked by a set of relatively uncommon traits among *Hyphessobrycon* species shared between the two species, which deserve special attention. Both exhibit a distinct black midlateral stripe accompanied dorsally by an orange band, a feature also observed in other species of *Hyphessobrycon* (*e.g*., *H. vilmae* Géry, 1966, species of the *H. heterorhabdus* group *sensu* Faria *et al*. (2021)). Both species exhibit a midlateral dark stripe that is narrower anteriorly and becomes progressively broader posteriorly, without forming a distinctly delimited caudal-peduncle blotch. Other traits are related to sexual dimorphism. Both *H. plumbellus* and *H. myrmex* display sexual

FIGURE 7 | Live coloration pattern of *Hyphessobrycon myrmex*, MZUSP 118672, paratypes: **A.** Male, 21.6 mm SL; **B.** Female, 19.5 mm SL.

dichromatism, although the pigments involved differ. In *H. plumbellus*, coloration is based on black and blue pigments, whereas in *H. myrmex*, it results from black and carotenoid-based pigments (Pastana *et al*., 2017). In both species, males exhibit significantly denser pigmentation in the anal fin compared to females, making the anal-fin rays more prominent. The shape of the anal fin is also sexually dimorphic, with females having a well-defined anterior lobe, while in males the distal profile of the fin is proportionally straighter and the anterior lobe is poorly developed or indistinct. Another shared feature is the reddish pigmentation on the dorsal portion of the eye, which is consistently more intense in males than in females. Notably, both species have become highly abundant in impounded environments formed by small hydroelectric power plants (PCHs). In many of these sites, they are the dominant or even the only species consistently recorded.

Biogeographic evidence for this relationship includes the observation that several tetra species endemic to the Chapada dos Parecis have sister taxa or closely related congeners distributed across neighboring basins, never occurring in sympatry. In the case of *H. plumbellus* and *H. myrmex*, the former occurs in the rio Juína basin, with a secondary presence in the rio Guaporé basin, while the latter inhabits the adjacent rio Formiga basin. Secondary occurrences likely represent recent range expansions due to headwater capture events along the Chapada escarpment and are discussed in the Biogeography section.

This pattern is not unique to *H. plumbellus* and *H. myrmex*. For example, *H. wadai* Marinho, Dagosta, Camelier & Oyakawa, 2016 is endemic to the rio do Sangue (Marinho *et al*., 2016), whereas its sister species *H. cyanotaenia* Zarske & Géry, 2006 (Melo *et al*., 2024) occurs in the rio Juruena basin, with secondary presence in the rio Guaporé (Dagosta *et al*., 2016). Similarly, *Bario uirapuru* (Ohara & Lima, 2015) inhabits the rio Juína basin with secondary presence in the rio Guaporé basin (Dagosta, de Pinna, 2019), and *B. cosmops* (Lima, Britski & Machado, 2007) occurs in the rio Juruena and rio Papagaio basins, with secondary presence in the Paraguay and Guaporé basins (Lima *et al*., 2007; Dagosta, de Pinna, 2019). The sister group to this clade is *Bario skolioplatus* (Bertaco & Carvalho, 2005) (Melo *et al*., 2024), endemic to the rio Mutum and rio Doze de Outubro basins.

Other morphologically similar pairs for which phylogenetic hypotheses are lacking follow the same trend. *Hyphessobrycon melanostichos* Carvalho & Bertaco, 2006 and *H. comodoro* Dagosta, Seren, Ferreira & Marinho, 2022 are found in adjacent basins (rio Doze de Outubro and rio Mutum, respectively) and are often traded under the same name in the ornamental fish market (Dagosta *et al*., 2022). Likewise, *Moenkhausia rubra* Pastana & Dagosta, 2014 inhabits the rio Juína and rio Juruena basins, with secondary occurrence in the rio Guaporé, whereas *M. nigromarginata* Costa, 1994 is recorded in the rio Papagaio and rio Sangue basins (Dagosta, de Pinna, 2019).

The two known populations of *H. plumbellus* do not constitute a metapopulation, as there is no gene flow between them. They inhabit separate drainage basins, and this distribution holds important implications for historical biogeography. It is crucial here to distinguish between dispersion and dispersal in the biogeographic sense (Platnick, 1976). Dispersion refers to the movement of individuals within their normal range as part of their life cycle (Platnick, 1976; Dagosta, de Pinna, 2017), whereas dispersal denotes the crossing of a pre-existing geographic barrier. Since freshwater fishes are confined to aquatic environments, river basin divides represent strict biogeographic barriers that lie outside their suitable range. Therefore, dispersion cannot account for the presence of freshwater fishes in separate basins; only dispersal or vicariance can explain such a distribution. The distinction between these two processes lies in the relative age of the geographic barrier and the taxa involved: if dispersal is invoked, the barrier must predate the divergence of the taxa; if vicariance is the explanation, then the barrier is as old as resulting taxa.

For freshwater fishes, which are incapable of aerial or terrestrial movement (Myers, 1947), dispersal is often considered an *ad hoc* explanation. As Nelson (1978) noted, dispersal is "the science of the rare, the mysterious, and the miraculous". Any distributional pattern can be attributed to dispersal, but such explanations typically lack mechanistic detail, predictive power, and falsifiability. Dispersal hypotheses are inherently species-specific, depending on the physiological or ecological traits of individual taxa, and thus do not account for broader biogeographic patterns (Croizat *et al*., 1974; Nelson, Platnick, 1981). As Rosen (1976) emphasized, while dispersal may enable a species to cross a barrier, it does not generate repeatable patterns across taxa. In contrast, as Croizat (1958) argued, vicariant events generate shared biogeographic patterns, while dispersal tends to obscure them. Dispersal hypotheses for freshwater fishes invoke mechanisms such as fish eggs attaching to (epizoochory or ectozoochory) or egestion from (endozoochory) waterbirds (Hirsch *et al*., 2018; Silva *et al*., 2019; Lovas-Kiss *et al*., 2020, 2024; Green *et al*., 2023; Yao *et al*., 2024) or fishes being transported by windstorms during extreme weather events. The scientific literature provides little convincing evidence that such events play a significant role in facilitating fish dispersal across drainage divides, and current explanations remain largely speculative, with little support from rigorous empirical data.

In contrast, multiple unrelated freshwater taxa, including *Bario uirapuru*, *Hyphessobrycon plumbellus*, and *Moenkhausia rubra* (Fig. 5), display the same disjunct distribution across the Guaporé and Juruena basins. Other tetras, such as *Hyphessobrycon cyanotaenia*, *H. hexastichos* Bertaco & Carvalho, 2005, *H. psittacus*, and *Bario cosmops*, are likewise confined to these two basins in other parts of the Chapada dos Parecis (Dagosta, de Pinna, 2019). Moreover, a putatively monophyletic species pair, *Melanorivulus modestus* (Costa, 1991) (rio Juruena basin) and *M. melanopterus* Nielsen & Ohara, 2024 (rio Guaporé basin), is also confined to these basins (Nielsen, Ohara, 2024). In this case, headwater capture is likely to have driven allopatric speciation.

The repeated pattern of species or lineages shared exclusively between the same drainages strongly suggests a common underlying mechanism. In historical biogeography, it is vicariance, rather than random species-specific dispersal, that gives rise to shared distributional patterns across taxa. Therefore, the occurrence of *H. plumbellus* in both the rio Guaporé and rio Juruena basins is best explained by a vicariant event. As previously discussed, because freshwater fishes are confined to aquatic corridors, their current biogeographic distributions must be interpreted in light of past drainage reorganizations that allowed for temporary hydrological connectivity, followed by subsequent isolation. Indeed, time-series remote sensing imagery, topographic analysis, and erosion rates show that drainage divides are not static but highly dynamic (Dahlquist *et al*., 2018; Scheingross *et al*., 2020; He *et al*., 2024).

Bishop (1995) identifies three mechanisms of drainage reorganization: Capture (bottom-up river capture), Diversion (top-down river capture), and Beheading. Bottom-up capture occurs when a stream at a lower elevation with a higher rate of erosion intercepts the flow of an adjacent stream at a higher elevation. This process is driven by asymmetric erosion, where one side of a drainage divide erodes more rapidly than the other. In tectonically inactive regions, drainage divides tend to migrate toward areas with lower erosion rates (Mudd, Furbish, 2005; He *et al*., 2024; Hoskins *et al*., 2024). Streams with steeper gradients and higher stream power are generally more erosive, carving deeper into the landscape and gradually shifting the divide in the direction of the less erosive basin. This shift is a key mechanism of headward erosion, through which a more energetic stream progressively expands into the neighboring basin, effectively 'stealing' drainage area. When this headward erosion reaches a tributary of the adjacent basin, a river capture event occurs: the intercepted stream is diverted, and its flow is rerouted into the capturing river (Prince *et al*., 2011; Stokes *et al*., 2018; He *et al*., 2024; Hoskins *et al*., 2024). This process fundamentally alters the hydrological connectivity between basins and may facilitate the exchange of aquatic biota across previously isolated drainage system. It also may promote allopatric speciation by fragmenting populations (*e.g*., Wilkinson *et al*., 2006; Albert, Crampton, 2010; Albert, Reis, 2011; Albert *et al*., 2020; He *et al*., 2024).

Another form of drainage reorganization is diversion, or top-down river capture, in which a stream at higher elevation redirects its flow into a lower-elevation drainage system by breaching the divide (Bishop, 1995; Shugar *et al*., 2017; He *et al*., 2024; Hoskins *et al*., 2024). In this case, the initiative comes from the stream that is eventually captured. Due to lateral erosion, channel instability, or avulsion, the stream gradually alters its course and begins to flow toward a neighboring valley. This redirection may naturally lead to a new connection with an adjacent drainage network. Unlike bottom-up capture, this process does not involve direct headward erosion from a neighboring basin; instead, the stream effectively abandons its original catchment and integrates into another. It redirects its flow to a different basin, driven by internal dynamics rather than external erosive forces (*e.g*., Bishop, 1995; Shugar *et al*., 2017; Hoskins *et al*., 2024).

Finally, drainage reorganization may also occur through beheading, or divide migration, in which drainage area is gradually transferred from one basin to another without the preservation of original channels or flow paths (Bishop, 1995; Stokes *et al*., 2018; Hoskins *et al*., 2024). Unlike capture (bottom-up) or diversion (top-down), beheading does not involve the direct transfer of river channels. Instead, it results in the loss of drainage area from one catchment to another, without the migration of active stream courses. Another key distinction lies in the nature and tempo of these processes: capture and diversion typically occur over short timescales and are often considered abrupt, discrete events of drainage reorganization (Hoskins *et al*., 2024). In contrast, beheading is a gradual and continuous process, driven by the long-term shift of the drainage divide, often as a result of differential erosion or tectonic uplift (Hoskins *et al*., 2024). As the divide shifts, portions of the landscape are incrementally annexed by the expanding basin, while the neighboring basin progressively loses drainage area, particularly in its headwaters, without any direct re-routing of stream channels (*e.g*., Willett *et al*., 2014; Stokes *et al*., 2018; He *et al*., 2024; Hoskins *et al*., 2024).

The relative importance of drainage capture versus divide migration in driving drainage reorganization remains debated (Hoskins *et al*., 2024). From a biogeographic perspective, however, bottom-up and top-down river captures are far more relevant than divide migration for aquatic organisms, as only the former two involve shared connections between basins, which allow for faunal exchange. In contrast, divide migration typically does not preserve channel continuity, and thus does not enable passage for aquatic biota. Although identifying the specific mechanism responsible for a given instance of drainage reorganization can be challenging, biological evidence can offer valuable clues.

The presence of *H. plumbellus* in both the Guaporé and Juruena basins provides strong evidence for a historical headwater connection between these systems, indicating that one or more river capture events likely occurred. Faster erosion on one side of a drainage divide suggests that the divide migrates toward the side with slower erosion (Mudd, Furbish, 2005; He *et al*., 2024; Hoskins *et al*., 2024). In this region, the exposed escarpment indicates erosion is advancing from the lower-elevation Guaporé basin toward the higher-elevation Juruena basin. These observations support the hypothesis that bottom-up river captures account not only for the distribution of *H. plumbellus* across both basins but also for the shared occurrence of other tetra species (see Fig. 5).

The Fig. 5 shows that the northern segment of the western escarpment of the Chapada dos Parecis (left side of the image) is considerably more eroded, providing clearer geomorphological evidence of river capture from the rio Juruena by the rio Guaporé. In contrast, the southern segment remains comparatively intact. Species shared between the Guaporé and Juruena basins are more frequently recorded in the more eroded northern portion, reflecting this pattern of drainage reorganization. This suggests a long-term trend in which an increasing number of Juruena headwaters are progressively incorporated into the Guaporé basin. Consequently, the Guaporé may continue to capture sister populations from the Juruena, which over time could undergo genetic divergence and potentially speciation, generating additional biogeographic and evolutionary outcomes across the region.

The occurrence of *H. plumbellus* and other tetra species across multiple, unconnected river basins is not an unusual pattern. As discussed above, numerous studies have shown that drainage divides are not static but highly dynamic (Dahlquist *et al*., 2018; Scheingross *et al*., 2020; He *et al*., 2024). As a result, they are often poor predictors of freshwater fish distribution (Dagosta, de Pinna, 2017), since these boundaries are frequently breached by headwater capture events (Albert, Crampton, 2010; Albert, Reis, 2011; Lima, Ribeiro, 2011; Albert *et al*., 2020). Such events facilitate ichthyofaunal exchange between adjacent basins, resulting in hybrid drainages in both their species composition and biogeographic history (Dagosta, de Pinna, 2017). The rio Guaporé basin also fits this pattern: its ichthyofauna is of mixed origin, including several species that are exclusively shared with the rio Juruena basin (Fig. 5), among other sources such as the Amazonian lowlands (Ohara, 2018).

As discussed above, geological evidence strongly supports that the allopatric populations of *H. plumbellus* in the rio Guaporé and rio Juruena basins are sister lineages, separated by a vicariant event: capture of Juruena headwaters by the Guaporé drainage. As detailed in the "Intraspecific Variation" section, these populations exhibit differences expected from isolated groups, which diverge over time in the absence of gene flow. Determining whether they represent separate species requires careful consideration.

Debating the definition of a species, or precisely where species boundaries begin and end, falls outside the scope of this manuscript. Evolutionary processes give rise to a continuum of living organisms across space and time, and species represent segments of this continuum rather than universally discrete taxonomic entities. Nonetheless, it is well recognized that divergence times vary substantially among different lineages of sister taxa, as does the degree of phenotypic and genotypic differentiation observed. The diagrams in de Queiroz (2005, fig. 2; 2007, fig. 1) effectively illustrate this: in the early stages of divergence, populations may be indistinguishable, while over time they accumulate differences until a consensus emerges that they constitute separate species. Between these endpoints lies what de Queiroz termed the "gray zone": a phase during which diverging lineages become increasingly differentiated but have not yet reached clear diagnosability. This gray zone appears to characterize the relationship between the *H. plumbellus* populations occurring in distinct drainage basins.

Although the populations show measurable differences, none are fixed or exclusive; traits vary in frequency or intensity rather than kind. No combination of traits unambiguously separates all individuals of one population from the other, failing to meet the criterion of the smallest diagnosable units (*sensu* Nelson, Platnick, 1981; Cracraft, 1983; Nixon, Wheeler, 1990). This weakens the case for recognizing them as distinct species. Nevertheless, the populations are on independent evolutionary trajectories, and the absence of fixed traits does not preclude eventual species-level divergence. The shared disjunct distribution pattern in other tetras suggests that the river capture event may be relatively recent, insufficient for complete speciation.

A further critical point concerns the potential impact of taxonomic inflation (Isaac *et al*., 2004). The recognition of geographically isolated populations as distinct species can lead to an artificial inflation of species counts and a distorted understanding of evolutionary processes. Delimiting species based solely on minor geographic variation risks overestimating biodiversity, a practice with far-reaching implications, especially for conservation. Conservation strategies are typically grounded in species-based frameworks, where the legal status of threatened species is formally defined and substantial funding is allocated by governments and international agencies. Consequently, species counts often serve as a foundation for conservation assessments and management plans (Myers *et al*., 2000).

Landscapes evolve over time, reshaping watersheds and altering drainage divides (Bishop, 1995; He *et al*., 2024; Hoskins *et al*., 2024). Fish are participants in this dynamic history, and their populations inevitably reflect these geological changes. Morphological variation will always exist to some degree. Over-splitting taxa based on minor morphological differences risks overemphasizing the terminal branches of the tree of life, highlighting distinctions that are virtually imperceptible without detailed examination. Morphological evidence alone already indicates population-level differences, but regardless of what genetic analyses may uncover, diagnosing both populations as distinct species in practice would remain challenging, as they lack conspicuous morphological traits that would justify such separation. That difficulty in consistently separating these populations based on discrete traits should guide our taxonomic judgment.

Comparative material examined. *Hasemania negodagua*, MZUSP 54589, 111, paratypes, 19.4–29.1 mm SL, rio Paraguaçu drainage, Bahia State. *Hemigrammus silimoni*, all from rio Tapajós basin, Mato Grosso State. MZUSP 93559, holotype, 29.7 mm SL; MZUSP 93560, 1 of 2, paratypes, 32.7 mm SL. MZUSP 115874, 21, 16.3–25.1 mm SL. *Hyphessobrycon rutiliflavidus*, MUSP 92438, 4, paratypes, 35.5–37.1 mm SL, rio Paraguai, Mato Grosso State.

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AUTHORS’ CONTRIBUTION

Fernando Cesar Paiva Dagosta: Conceptualization, Data curation, Formal analysis, Funding acquisition, Project administration, Writing-original draft, Writing-review and editing.

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ETHICAL STATEMENT

Specimens were collected under IBAMA collection permits 83/2012 (May 2012 - September 2013) and 60634/2018.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article.

AI STATEMENT

The authors used AI-assisted technology (ChatGPT 4 - OpenAI) for grammatical revision.

COMPETING INTERESTS

The authors declare no competing interests.

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