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New reddish species of *Moenkhausia* Eigenmann (Characiformes: Characidae) from the upper rio Xingu basin, Brazil

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A new species of *Moenkhausia* from the rio Culuene, rio Xingu basin, in Mato Grosso State is described here through genetic and morphological data. This new species differs from all congeners by the following combination of characters: the presence of reddish color on the posterior portion of the body, as well as on the base of anal, adipose, and pelvic fins in live specimens; a conspicuous midlateral dark stripe, which extends from posterior margin of opercle to the middle of caudal-fin rays, becoming wider and more conspicuous from the vertical through the dorsal-fin origin; absence of humeral blotch; absence of blotches on caudal-fin lobes; by having the concentration of dark pigments on the anterior margin of the caudal-fin rays; and presence of 2–3 maxillary teeth. A brief discussion about its putative relationships with other congeners is presented.

Keywords: Amazon basin, Mitochondrial DNA, *Moenkhausia lopesi*, Taxonomy, Tetra.

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Uma nova espécie de *Moenkhausia* do rio Culuene, bacia do rio Xingu é descrita aqui através da utilização de dados morfológicos e genéticos. Esta nova espécie difere de todas as suas congêneres por possuir a seguinte combinação de caracteres: a presença da porção posterior do corpo e a base das nadadeiras anal, adiposa e pélvicas avermelhadas em espécimes vivos; uma faixa meio-lateral escura que se estende da margem posterior do opérculo até os raios medianos da nadadeira caudal, tornando-se larga a partir da origem da nadadeira dorsal; ausência de uma mancha na região umeral; ausência de mancha nos lobos da nadadeira caudal; por ter uma concentração de pigmentos escuros na margem anterior dos raios da nadadeira caudal; e presença de 2–3 dentes no maxilar. Uma breve discussão sobre suas prováveis relações com as demais congêneres é apresentada.

Palavras-chave: Bacia Amazônica, DNA mitocondrial, *Moenkhausia lopesi*, Taxonomia, Piaba.

INTRODUCTION

Moenkhausia was proposed by Eigenmann (1903) and defined by himself (Eigenmann, 1917) by the following character combination: a complete pored lateral line, premaxillary teeth in two rows, with at least five teeth in the inner row, and a caudal fin partially covered by scales. Nevertheless, phylogenetic studies established the homoplastic condition of those characters and the non-monophyly of *Moenkhausia* (Mirande, 2010, 2019; Mariguela *et al*., 2013). Currently, *Moenkhausia* comprises 100 valid species widely distributed across the main South American rivers (Fricke *et al*., 2023), with its greater diversity in the cis-Andean region, being considered the third most species-rich genus in the Amazonian basin (Marinho *et al*., 2016; Dagosta, de Pinna, 2019).

A recent expedition to the rio Culuene, upper rio Xingu basin, revealed the existence of a new species of *Moenkhausia*, which is described here using the integrative approach. In addition to the description, we provide a discussion on its possible phylogenetic relationships.

MATERIAL AND METHODS

Morphological analysis. Counts and measurements follow Fink, Weitzman (1974), and Menezes, Weitzman (1990) with the exception of the counts of the horizontal scales series below the lateral line, which was counted at the row below the lateral line to the pelvic-fin origin and addition of the head depth, which was measured at the vertical through the middle of the orbit. Measurements were taken point to point using a digital caliper (0.1 mm) on the left side of specimens whenever possible and, as well as the counts, performed under a stereomicroscope. Specimens were cleared and counterstained (c&s) following the procedure of Taylor, Van Dyke (1985). The number of vertebrae, supraneurals, procurrent, and caudal-fin rays were taken from two c&s specimens and posterior small dentary teeth from four specimens, which were dissected, clear, and stained only jaws. The four vertebrae of the Weberian apparatus were counted as four separate elements, and the fused PU1+U1 as a single element. The frequency of each count is provided in parentheses after the respective range, with the count of the holotype marked by an asterisk. The sex was determined based on pelvic-fin elongation and confirmed by direct examination of gonads, under a stereomicroscope, which follows the methodology of Vazzoler (1996). The covariance analysis was realized with eight males and eight females using the package "car" (Fox, Weisberg, 2019) in the software RStudio v. 2023.06.1 (RStudio Team, 2020). Data of *Moenkhausia iris* Marinho & Dagosta, 2023 and *M. rubra* Pastana & Dagosta, 2014 were taken in the original description. Institutional abbreviations follow Sabaj (2020).

Molecular data and 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/R1and FishF2/R1 described by Ward *et al.* (2005) and FishF6/R7 described by Jennings *et al.* (2019). 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 ddH_2O. 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 three sequences of the new species and 22 sequences of the other three valid species of *Moenkhausia*. We also used three sequences obtained from Genbank, including the root *Psellogrammus kennedyi* (Eigenmann, 1903). For more details about sequences and Genbank numbers, see Tab. 1. The sequences were assembled using the software Geneious 7.1.4 (Kearse *et al*., 2012) and aligned with Muscle (Edgar, 2004) under default parameters. To evaluate the occurrence of substitution saturation in our molecular data, we estimated the index of substitution saturation (Iss) using the method described by Xia *et al.* (2003) and Xia, Lemey (2009) with the software DAMBE 7.2.1 (Xia, 2018).

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 (Tamura *et al*., 2021). Maximum likelihood (ML) analysis was performed in RaxML PTHREADS-SSE3 v. 8 (Stamatakis, 2014) using the GTRGAMMA model in the *Gymnotus* server at LBP-UNESP. The best tree was accessed through ten random searches with 1,000 bootstrap pseudoreplicates using the autoMRE function with bootstopping criteria (Pattengale *et al*., 2010), which ran 800 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*., 2020) is available in the ASAP webserver (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html) with model Jukes-Cantor (JC69).

TABLE 1 | Collection, vouchers, distributions, and Genbank number of species analyzed.

Species	Collection	Voucher	Locality (river/basin/city/state/country)	Geographic coordinates	Genbank
Moenkhausia aurantia	LBP 18999	75410	Roncador/Tocantins basin/São João da Aliança/GO/Brazil	14°43’51.3”S 47°32’34.0”W	OR922605
Moenkhausia sp. n.	LBP 16063	66490	Culuene/Xingu basin/Primavera do Leste/MT/Brazil	14°38’21.2”S 53°55’35.3”W	OR922604
Moenkhausia sp. n.	LBP 30660	105627	Culuene/Xingu basin/Primavera do Leste/MT/Brazil	14°38’21.2”S 53°55’35.3”W	OR922602
		105628	Culuene/Xingu basin/Primavera do Leste/MT/Brazil	14°38’21.2”S 53°55’35.3”W	OR922603
Moenkhausia bonita	CI-FML 7395	A-4	Bermejo basin/Orán/Salta/Argentina	23°07’00.0”S 64°30’00.0”W	MK928340
Moenkhausia bonita	LBP 3783	22244	Negro/Paraguai basin/Aquidauana/MS/Brazil	19°34’17.3”S 56°14’44.8”W	OR922616
		22246	Negro/Paraguai basin/Aquidauana/MS/Brazil	19°34’17.3”S 56°14’44.8”W	OR922619
Moenkhausia bonita	LBP 3740	22186	Negro/Paraguai basin/Aquidauana/MS/Brazil	19°34’54.6”S 56°15’16.5”W	OR922609
Moenkhausia bonita	LBP 8153	38041	Cacequi/Uruguai basin/Casequi/RS/Brazil	29°53’51.1”S 54°51’05.0”W	OR922607
Moenkhausia bonita	LBP 8546	43281	Sepotuba/Paraguay basin/Tangará da Serra/MT/Brazil	14°20’32.6” 57°31’22.5”W	OR922618
		43283	Sepotuba/Paraguay basin/Tangará da Serra/MT/Brazil	14°20’32.6” 57°31’22.5”W	OR922617
		43284	Sepotuba/Paraguay basin/Tangará da Serra/MT/Brazil	14°20’32.6” 57°31’22.5”W	OR922608
Moenkhausia bonita	LBP 9699	45818	São Bento/upper Paraná basin/Nova Andradina/MS/Brazil	22°08’56.9”S 53°25’34.8”W	OR922612
		45819	São Bento/upper Paraná basin/Nova Andradina/MS/Brazil	22°08’56.9”S 53°25’34.8”W	OR922615
Moenkhausia bonita	LBP 13171	55083	Uruguay basin/Uruguaiana/RS/Brazil	29°30’42.8”S 56°43’09.9”W	OR922610
		55084	Uruguay basin/Uruguaiana/RS/Brazil	29°30’42.8”S 56°43’09.9”W	OR922611
Moenkhausia bonita	LBP 13171	55085	Uruguay basin/Uruguaiana/RS/Brazil	29°30’42.8”S 56°43’09.9”W	OR922614
		55086	Uruguay basin/Uruguaiana/RS/Brazil	29°30’42.8”S 56°43’09.9”W	OR922613
Moenkhausia bonita	LBP 12158	51913	Paraguay basin/Cáceres/MT/Brazil	16°03’48.7”S 57°42’27.0”W	OR922620
		51914	Paraguay basin/Cáceres/MT/Brazil	16°03’48.7”S 57°42’27.0”W	OR922621
Moenkhausia aff. *lopesi*	LBP 8550	43297	Sepotuba/Paraguai basin/Tangará da Serra/MT/Brazil	14°20’32.6”S 57°31’22.5”W	OR922606
Moenkhausia aff. *lopesi*	LBP 30595	105766	Mutum/Juruena basin/Padronal/MT/Brazil	13°05’08.7”S 59°53’32.0”W	OR922601
Moenkhausia lopesi	LBP 33989	114736	Correntes/Piquiri basin/Paraguai/basin/Sonora/MS/Brazil	17°36’21.0”S 54°11’18.0”W	OR922622
		114737	Correntes/Piquiri basin/Paraguai/basin/Sonora/MS/Brazil	17°36’21.0”S 54°11’18.0”W	OR922623
Moenkhausia cf. *lopesi*	LBP 10237	47790	Manso/Paraguay basin/Campo Verde/MT/Brazil	15°30’17.2”S 55°21’53.9”W	OR922624
		47791	Manso/Paraguay basin/Campo Verde/MT/Brazil	15°30’17.2”S 55°21’53.9”W	OR922625
Hemigrammus marginatus	930249	DCC01369	São Francisco basin/MG/Brazil	19°46’26.4”S 45°27’46.8”W	HM906017
Psellogrammus kennedyi	LBP 5220	26408	upper rio Paraná basin/Porto Rico/MS/Brazil	22°47’29”S 53°20’58”W	JN989170

RESULTS

Moenkhausia aurora, new species

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(Figs. 1–3; Tab. 2)

Holotype. LBP 34895, 37.9 mm SL, Brazil, Mato Grosso State, municipality of Primavera do Leste, rio Culuene, upper rio Xingu basin, 14°38'21.2"S 53°55'35.3"W, 23 Aug 2021, L. Reia, G. S. C. Silva, C. S. Souza & E. V. Ywamoto.

Paratypes. All from Brazil. LBP 16063, 26, 26.5–36.8 mm SL, same locality of the holotype, 5 Aug 2012, C. Oliveira, M. Taylor, G. J. C. Silva & J. H. M. Martinez. LBP 30660, 36, 23.3–36.7 mm SL, 2 c&s, 31.9–32.8 mm SL, same data of holotype. ANSP 208909, 3, 31.0–34.0 mm SL; MNRJ 54695, 3, 30.8–33.7 mm SL; MZUEL 23348, 3, 30.2–34.7 mm SL, MZUSP 118284, 194, 17.6–43.0 mm SL, Mato Grosso State, municipality of Primavera do Leste, stream tributary of rio Culuene, rio Xingu basin, 14°43'04.4"S 54°04'38.2"W, 17 Nov 2014, F. C. P. Dagosta, W. M. Ohara & V. Giovannetti.

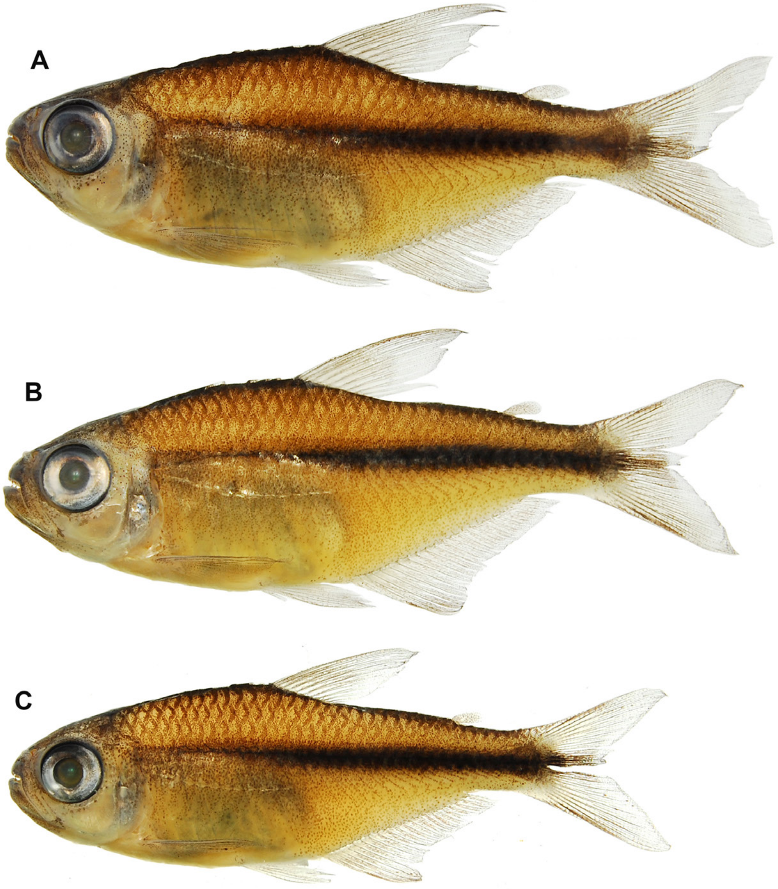

FIGURE 1 | *Moenkhausia aurora*, Brazil, Mato Grosso State, municipality of Primavera do Leste, rio Culuene. **A.** LBP 34895, 37.5 mm SL, holotype, male; **B.** LBP 30660, 34 mm SL, paratype, male; **C.** LBP 30660, 31.4 mm SL, paratype, male.

FIGURE 2 | Medial view of the left side of maxilla, premaxilla, and dentary. *Moenkhausia aurora*, paratype, LBP 16660, 34.8 mm SL, Brazil, Mato Grosso, Primavera do Leste, rio Culuene. Scale bar = 1 mm.

Diagnosis. *Moenkhausia aurora* is distinguished from all congeners, except *M. rubra*, and *M. iris* by the presence of reddish body color in life specimens. The new species can be readily distinguished from *M. rubra* by having the base of pelvic and anal fins reddish in live specimens (*vs*. pelvic and anal fins hyaline), and by the absence of dark pigmentation on anteriormost rays of the anal fin (*vs*. presence). *Moenkhausia aurora* differs from *M. iris* by lower number of scales between lateral line and pelvic-fin origin (4 *vs*. 5), and by a lower number of unbranched anal-fin rays (iii *vs*. iv–v). *Moenkhausia aurora* is also distinguished from all congeners, except *M. bonita* Benine, Castro & Sabino, 2004, *M. celibela* Marinho & Langeani, 2010, *M. dichroura* (Kner, 1858), *M. intermedia* Eigenmann, 1908, and *M. lopesi* Britski & Silimon 2001, by the absence of a humeral blotch (variable in *M. dichroura* and *M. intermedia* see Lima *et al*., 2020 *vs*. presence). The new species differs from *M. lopesi* by having, in life specimens, a reddish color on the posterior portion of the body, as well as on the base of the anal, adipose, and pelvic fins (Fig. 3A) (*vs*. yellowish, Fig. 3B), and by the lower number of maxillary teeth (2–3 *vs*. 3–7). *Moenkhausia aurora* can be distinguished from *M. bonita*, *M. celibela*, *M. dichroura*, and *M. intermedia* by the absence of dark pigmentation on caudal-fin lobes (*vs*. two black blotches on caudal fin, one on each lobe in *M. bonita*, *M. dichroura*, and *M. intermedia*, and one blotch on dorsal lobe in *M. celibela*). *Moenkhausia aurora* can be distinguished from *M. dichroura* and *M. intermedia* by a lower number of gill rakers on the first arch (9–14+1+ 6–8 *vs*. 18–22 +1+ 10–11). Additionally, *M. aurora* differs from *M. lopesi*, *M. bonita*, *M. celibela*, *M. dichroura*, and *M. intermedia* by having a concentration of dark pigments on the anterior margin of the caudal-fin rays (Figs. 1, 3A) (*vs*. scarcely pigmented).

Description. Data summarized in Tab. 2. Small-sized species, largest specimen examined 43.0 mm SL. Body compressed laterally, moderately elongated, greatest body depth at dorsal-fin origin. Dorsal profile of head convex from its tip to vertical through posterior nostril; straight to slightly convex from that point to tip of supraoccipital spine. Dorsal profile of body convex from tip of supraoccipital spine to dorsal-fin origin; dorsal-fin base slightly convex to straight and posteroventrally inclined; slightly convex to straight from last dorsal-fin rays to adipose-fin insertion; adipose-fin base slightly inclined posteroventrally; slightly concave from terminus of adipose-fin base to anteriormost dorsal procurrent caudal-fin rays. Ventral profile of head slightly convex to straight from chin to isthmus. Ventral profile of body slightly convex to anal-fin origin; anal-fin base straight and inclined posterodorsally; slightly concave from terminus of anal fin base to anteriormost ventral procurrent caudal-fin ray.

TABLE 2 | Morphometric data for holotype and paratypes of *Moenkhausia aurora*. SD = Standard deviation.

	Holotype	N	Range	Mean	SD
Standart length	37.9	44	28.1-43.0	34.2	-
Porcentages of standart length					
Greatest depth	36.8	44	29.9-36.8	34.0	1.7
Snout to dorsal-fin origin	52.0	44	49.8-54.2	51.6	1.0
Snout to pelvic-fin origin	47.2	44	41.4-51.0	47.5	1.7
Snout to pectoral-fin origin	29.4	44	26.7-30.1	28.4	0.8
Snout to anal-fin origin	63.6	44	60.1-67.2	62.9	1.8
Caudal peduncle depth	11.8	44	10.4-12.3	11.4	0.5
Caudal peduncle length	11.4	44	9.7-13.9	11.4	0.9
Pectoral-fin length	25.3	44	21.1-26.3	23.8	1.2
Pelvic-fin length	21.0	44	15.5-21.6	18.3	1.5
Dorsal-fin length	32.4	43	25.5-33.5	29.5	1.9
Dorsal-fin base	14.5	44	12.4-15.7	13.9	0.7
Anal-fin length	20.8	43	16.9-22.8	19.5	1.4
Anal-fin base	30.8	44	26.9-34.0	30.3	1.8
Eye to dorsal-fin origin	36.6	44	34.0-38.9	36.7	1.2
Dorsal-fin origin to caudal-fin origin	53.7	44	50.6-55.3	52.7	1.2
Head depth	19.9	43	18.4-22.3	20.7	0.9
Head length	27.8	44	26.0-29.5	27.6	0.8
Porcentages of head length					
Orbital diameter	40.0	44	36.9-47.4	42.2	2.5
Interorbital distance	32.6	44	30.2-34.4	32.0	1.2
Snout length	27.2	44	20.0-31.6	26.7	3.3
Upper jaw length	48.4	44	46.8-53.3	50.3	1.7

Eyes large. Mouth terminal. Premaxillary teeth in two rows. Outer row with 3(6), 4*(26) or 5(10) tricuspid teeth; inner row with 5(40) or 6*(2) pentacuspid teeth, the last tooth varying from tricuspid to pentacuspid. Maxillary with 2*(27) or 3(14) pentacuspid to tricuspid teeth. Tip of maxilla through vertical reaching posterior half of second infraorbital. Dentary with 4*(42) pentacuspid teeth, followed by one small tricuspid tooth and a row varying between 5–13(4 c&s) small conic teeth. Central cuspid in all teeth more developed than lateral cusps (Fig. 2). First gill arch with 6(3), 7*(20), 8(5) gill rakers on upper limb, 1(28) gill raker on intermediate cartilage and 9(1), 11*(6), 12(20), 14(1) gill rakers on lower limb.

Scales cycloid. Lateral line complete, slightly curved with 34(12), 35*(22), or 36(8) pored scales. One specimen with interrupted lateral line. Longitudinal scale rows above lateral line 5*(43) or 6(1). Longitudinal scale rows below lateral line 4*(44). Circumpeduncular scale rows 13(10), 14*(30) or 15(1). Single row of scales overlaying basal portion of anterior anal-fin rays. Small scales covering proximal one-third of caudal-fin lobes.

Dorsal-fin rays ii,9*(43). Pectoral-fin rays i,10(23), 11*(9), 12(2), or i,10,i(8) with their tips surpassing pelvic-fin origin. Pelvic-fin rays i,6(2) or 7*(40), with their tips surpassing anal-fin rays only in males. Anal fin slightly falcate, last unbranched, and four first branched rays longest. Anal-fin rays iii,18(1), 19(9), 20*(24), 21(7) or 22(1). Caudal fin forked, lobes of similar size. Caudal-fin rays i,9,8,i. Dorsal procurrent caudal-fin rays 10(2). Ventral procurrent caudal-fins rays 8(2). Total vertebrae 33(2). Supraneurals 4(2).

Coloration in alcohol. Overall body coloration yellowish. Dorsal portions of head and body darkly pigmented. Lips and maxilla densely pigmented; infraorbitals, opercle, and preopercle light beige, with scattered melanophores. Dorsolateral portion of the body with scattered dark chromatophores concentrated on distal margin of scales, exhibiting a reticulated pattern on three first horizontal rows. Conspicuous midlateral dark stripe, extending from posterior margin of opercle to middle caudal-fin rays. Dark stripe narrow anteriorly, becoming wide from vertical line just anterior dorsal-fin origin region, with median portion darker than anterior and posterior ones. Melanophores scattered between midlateral dark stripe and second row of scales below lateral line horizontally. A thin black stripe on the base of anal fin. Pectoral, pelvic, and anal fins hyaline, with melanophores scattered. Anterior portion of caudal-fin rays with concentrated melanophores on lepidotrichia margins, more evident on medial rays, forming a dark stripe, and in the upper and lower unbranched rays. Posterior portion of caudal-fin rays entirely hyaline, without melanophores.

Coloration in life. Dorsal portion of head, lips and maxilla emerald green; first, second, and third infraorbitals silver; fifth and sixth infraorbitals gold. Gular region reddish. Laterodorsal portion of trunk emerald green, becoming reddish from dorsal-fin origin to caudal peduncle. Lateroventral portion of trunk from isthmus to pelvic-fin origin silver to gold became reddish from that point to caudal peduncle. Upper portion of eyes golden, ventral portion silver. Inconspicuous midlateral silver stripe becomes black from vertical line just last anal-fin rays to middle caudal-fin rays. A concentration of black pigments on the anterior margin of the caudal-fin rays. Pectoral fin yellow to red. Pelvic, dorsal, adipose, anal, and caudal fins red on base, orange in central, and white on their tips (Fig. 3A).

FIGURE 3 | Color in life of *Moenkhausia aurora* (**A**), paratype, LBP 30660, Brazil, Mato Grosso State, municipality of Primavera do Leste, rio Culuene. Specimen not measured. Photo by Eric V. Ywamoto; and *Moenkhausia lopesi* (**B**) from Mato Grosso State, municipality of Sonora, rio Piquiri drainage, rio Paraguay basin. Specimen not measured. Photo by Heriberto G. Junior.

Sexual dimorphism. Pelvic-fin length in adult males is proportionally longer than in adult females (19.4–21.6 *vs*. 15.5–17.5% of SL), with their tips surpassing anal-fin rays. This result was corroborated by covariance analysis (Fig. 4), which presents a strong relation between pelvic-fin length and standard length influencing the sex with p-value >0.05. Bony hooks were not found on fin rays.

Geographical distribution. *Moenkhausia aurora* is known from the upper rio Culuene drainage, rio Xingu basin, municipality of Primavera do Leste, Mato Grosso State, Brazil (Fig. 5).

Ecological notes. The type-locality of *M. aurora* is a tributary of the rio Culuene with about 10 m width, 1.5 m deep, and 470 m above sea level (Fig. 6). The stretch sampled presents riparian vegetation composed of trees and shrubs, fast and transparent water with the substrate formed by sand and submerged aquatic macrophytes. *Moenkhausia aurora* was collected syntopically with *Hyphessobrycon loweae* Costa & Géry, 1994, *Hemigrammus* sp., *Rhinotocinclus acuen* (Silva, Roxo & Oliveira, 2014), *Knodus* sp., and *Leporinus multimaculatus* Birindelli, Teixeira & Britski, 2016.

Etymology. The specific epithet *aurora* comes from Latin, which means dawn or sunrise. In allusion to the red, orange, and gold colors present in specimens in life. A noun in apposition.

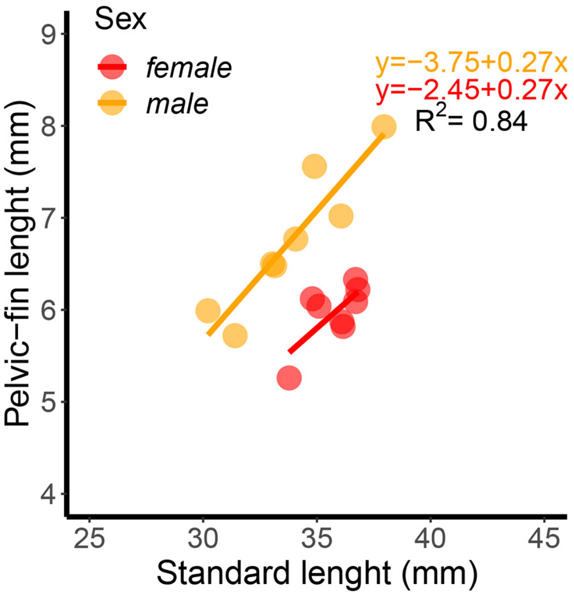

FIGURE 4 | The relationship between standard length and pelvic-fin length in *Moenkhausia aurora*.

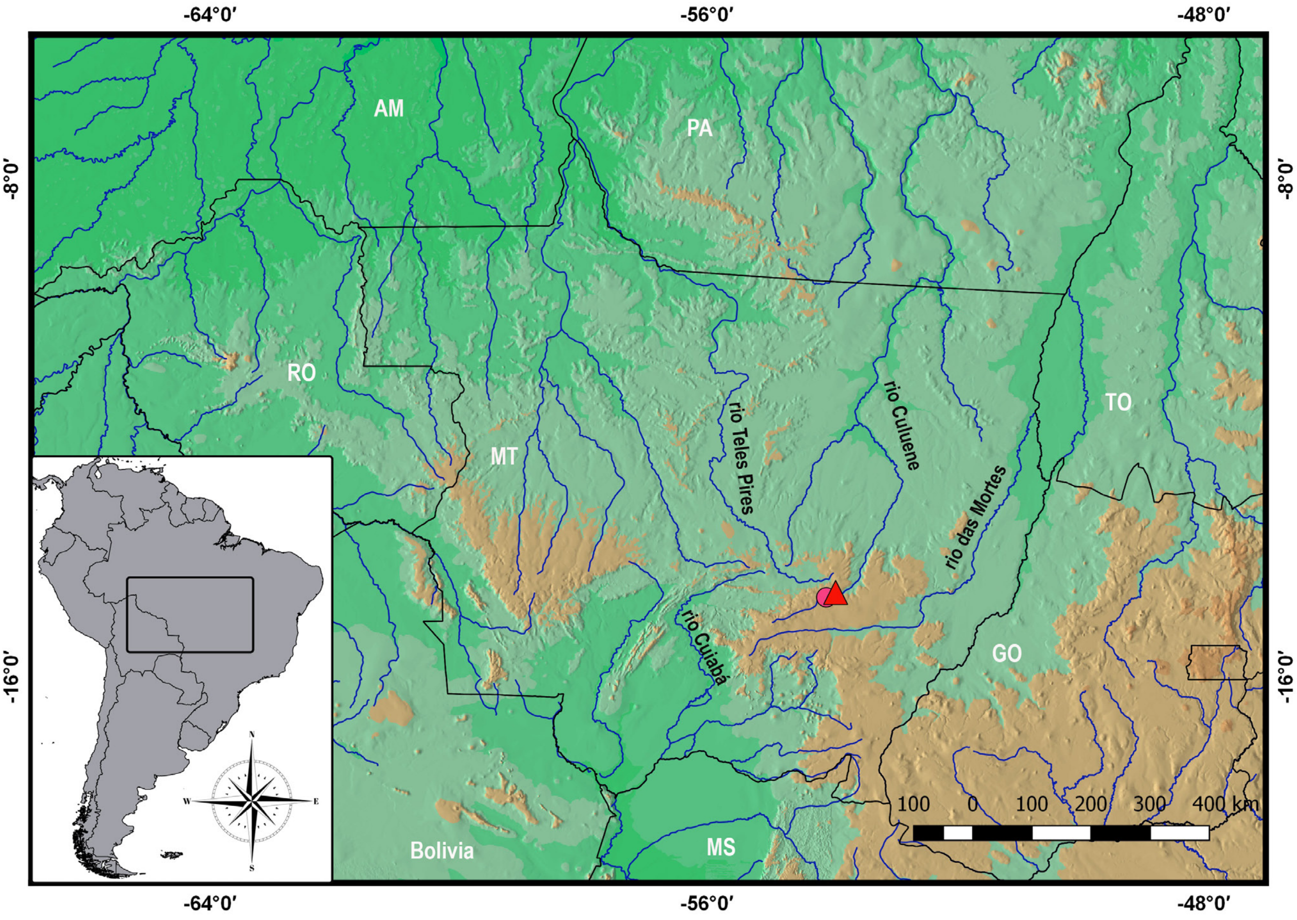

FIGURE 5 | Map of central South America indicating the type locality (triangle) of *Moenkhausia aurora*.

Conservation status. *Moenkhausia aurora* is known from two localities of the upper rio Culuene, rio Xingu basin, and its conservation status is uncertain based on the currently available geographic distribution. However, no imminent threats to the species were detected in the area of occurrence; we suggest that *M. aurora* should be classified as Least Concern (LC) according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2022).

Genetics. The final matrix comprehended 600 pb with 155 variable sites. The composition of frequency of nucleotides obtained was A = 25.2%, C = 25.1%, G = 18.3%, and T = 31.4%. The values of Iss. were lower than Iss.c, indicating an absence of saturation in our matrix. The best evolution nucleotide model was GTR+G (General Time Reversible + Gamma) with an AICc value = 3888.273. However, the genetic distances analysis did not include this model, so we used the third best model TN93+G (Tamura-Nei + Gamma) model, with an AICc value = 3901.128. Genetic analyses supported *Moenkhausia aurora* as a distinct lineage. Overall, the mean genetic distance was 5%±0.01 without the outgroup. The genetic distance interspecific ranged from 2.2%±0.6 between *M. bonita*, and *M.* aff. *lopesi* rio Sepotuba basin to 10.2%±1.6 between *M.* aff. *lopesi* rio Juruena basin and *M. lopesi* rio Piquiri basin (Tab. 3). *Moenkhausia aurora* has 5.9%±0.010 of genetic distance from *M. lopesi*, the most similar species in terms of morphology. The Asap (ASAP score = 2.00, Fig. **S1**) and PTP methods discriminate the same eight lineages for the data and supported the identity of *M. aurora* (Figs. 7 and **S2**).

FIGURE 6 | The type-locality of *Moenkhausia aurora*, rio Culuene, municipality of Primavera do Leste, Mato Grosso State, Brazil. Photo by Camila Souza.

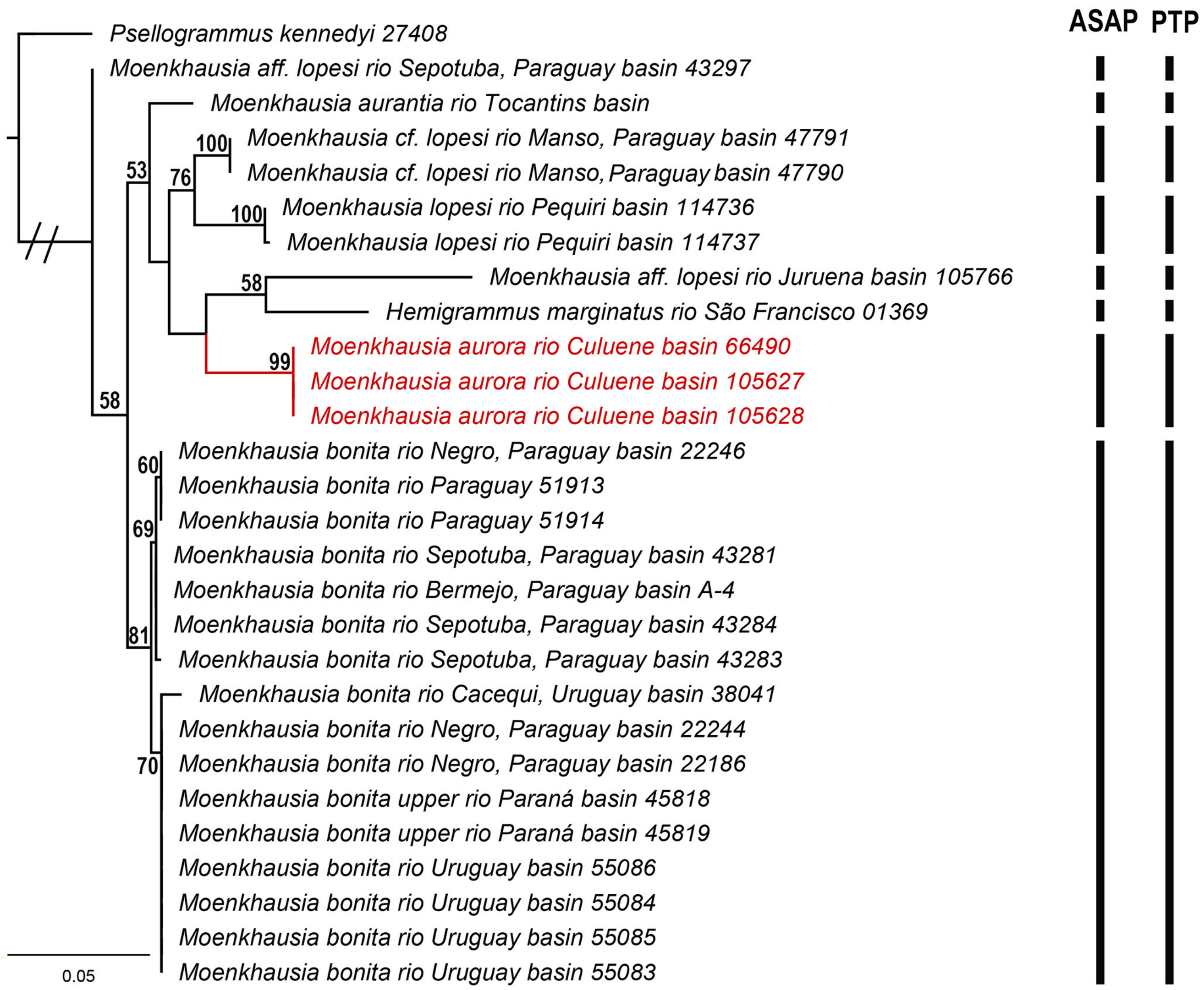

FIGURE 7 | Maximum likelihood tree of species of the group *Moenkhausia lopesi* based on the COI gene (600pb). Bars represent the number of species obtained by the ASAP and PTP analyses. Bootstrap values above 50% are represented by numbers near the nodes.

TABLE 3 | Genetic distances and S.D. of species analyzed in this study based on the TN93+G model. Intraspecific distances are marked in bold.

	1	2	3	4	5	6	7	8
1. *M.* aff. *lopesi* rio Juruena	-							
2. *H. marginatus*	0.085±0.013	-						
3. *M. aurora*	0.092±0.014	0.07±0.012	**0±0**					
4. *M. aurantia*	0.086±0.014	0.071±0.012	0.058±0.011	-				
5. *M.* aff. *lopesi* rio Sepotuba	0.099±0.015	0.072±0.012	0.056±0.010	0.026±0.007	-			
6. *M. bonita*	0.094±0.015	0.073±0.012	0.060±0.010	0.030±0.007	0.022±0.006	**0.004±0.001**		
7. *M.* cf. *lopesi* rio Manso	0.099±0.015	0.069±0.012	0.054±0.010	0.037±0.008	0.041±0.009	0.038±0.008	**0±0**	
8. *M. lopesi* rio Piquiri	0.102±0.016	0.080±0.013	0.059±0.010	0.044±0.009	0.053±0.010	0.045±0.009	0.034±0.008	**0.001±0.001**

DISCUSSION

Moenkhausia aurora, the new species described here, is morphologically similar to *M. lopesi* in terms of general color pattern in alcohol-preserved specimens. However, these two species can be readily distinguished by the coloration of live specimens. Individuals of *M. aurora* have a reddish coloration (trunk and base of fins) *versus* yellowish in *M. lopesi*. (Figs. 3A,B) (see Diagnosis section). Britski, Silimon (2001) described color variations in some freshly collected specimens of *M. lopesi*, with dorsal fin varying from yellow (Fig. 3B) to orange and caudal fin varying from yellow (Fig. 3B) to orange or red (Bertaco *et al*., 2011:36, fig. 6b), but they did not report any specimen with dorsal, pelvic, anal or adipose fins red, or even, the trunk reddish, as occurs in *M. aurora*. The color variation observed in *M. lopesi* is most likely associated with sexual dimorphism since orange and red (carotenoid-based) reported in fins are two of the sets of pigments more common to expressed sexual dichromatism in Characiformes species (Pastana *et al*., 2017). In contrast, all collected specimens of *M. aurora,* including males and females, and small individuals showed a reddish color pattern.

Recent phylogenetic studies recovered a subclade of *Moenkhausia* composed of *M. bonita*, *Hemigrammus marginatus* Ellis, 1911, and *Moenkhausia* aff. *lopesi* (this paper, voucher 43297, Tab. 1) (Mariguela *et al*., 2013; Britzke *et al*., 2018). *Moenkhausia aurora*, *M. lopesi*, and *M. aurantia* are genetically close to the aforementioned species (Fig. 7) and probably also belong to this clade. Additionally to molecular data, this cluster of species, which include *M. bonita*, *H. marginatus*, *M. aurora*, *M. lopesi*, and *M. aurantia*, share a set of characters that can be putative synapomorphies for this group, such as (1) presence of a dark midlateral stripe, which extends from the posterior margin of the opercle (or from the vertical line just anterior to dorsal-fin origin, in *M. aurantia*) to middle caudal-fin rays, becoming wide from dorsal-fin origin; (2) dorsolateral portion of the body with concentrated chromatophores along distal margin of scales resulting in a reticulated pattern along the first three horizontal rows of scales; (3) absence of humeral blotch or inconspicuous in *M. aurantia*; (4) a thin black stripe on base of anal fin; (5) proximal portion of fins colorful (yellow, orange or red) and their distal portion usually white in life specimens.

Our molecular delimitation analysis was useful in discriminating eight mitochondrial lineages within this putative monophyletic group: *Moenkhausia aurora*, *M. bonita*, *Hemigrammus marginatus*, *M. aurantia*, *M. lopesi*, and more three other species that are probably new to science (revision in progress by the first author) morphologically similar to *M. lopesi*: *Moenkhausia* aff. *lopesi* from rio Juruena, *Moenkhausia* cf. *lopesi* from rio Manso, and *Moenkhausia* aff. *lopesi* from rio Sepotuba (Fig. 5). Additionally, our molecular results corroborated that *M. bonita* a species that occurs throughout Paraguay, Uruguay, and upper Paraná river basins (Vanegas-Ríos *et al*., 2019), is a unique widespread evolutionary lineage.

The overall mean of genetic distance found for this group is relatively low (mean~5%) when compared with values found in other monophyletic and genetically well-studied groups of Characidae, such as *Tetragonopterus* Cuvier, 1816 (mean~11%) (Melo *et al*., 2011; Silva *et al*., 2013), *Moenkhausia oligolepis* group (mean~19.0%) (Benine *et al*., 2009; Reia *et al*., 2021), and *Priocharax* Weitzman & Vari, 1987 (mean~22%) (Mattox *et al*., 2020, 2023). In other words, we can find evident morphological diagnostic characters even in lineages within a few DNA changes (*e.g.*, 2.2% between *M. bonita* and *Moenkhausia* cf. *lopesi*). Certainly, intrinsic and/or extrinsic mechanisms are involved in the degree of morphological diversification in different rates for different clades of Characidae, constraining the phenotypic disparity (*e.g.*, *Moenkhausia oligolepis* group) or promoting fast morphological diversification, as in the case of the group herein studied.

Comparative material examined. Brazil. *Moenkhausia aurantia*: rio Tocantins basin: LBP 18999, 4, 26.9–45.4. *Moenkhausia bonita*: rio Uruguay basin: ANSP 168836, 5, 25.2–32.5 mm SL. *Moenkhausia celibela*: rio Xingu basin: ANSP 194586, 6, 21.4–26.8 mm SL. ANSP 197467, 24, 15.5–31.1 mm SL. *Moenkhausia lopesi*: MZUSP 64480, 1, 36.5 mm SL, holotype; MZUSP 64481, 4 of 410, 29.6–34.9 mm SL, paratypes. *Moenkhausia* aff. *lopesi*: rio Sepotuba basin: LBP 8550, 1, 44.4 mm SL. *Moenkhausia* aff. *lopesi*: rio Juruena basin: LBP 30595. *Hemigrammus marginatus*: rio Itapecuru basin: ANSP 187197, 50, 14.4–31.6 mm SL; ANSP 187198, 49, 16.9–30.1 mm SL. Rio São Francisco basin: ANSP 171945, 29, 25.1–31.4 mm SL. **Colombia.** *Moenkhausia intermedia*: rio Amazonas basin: ANSP 135936, 28.5–31.8 mm SL. **Guyana.** *Moenkhausia shideleri*: rio Essequibo basin: ANSP 177002, 1, 64.6 mm SL. **Paraguay.** *Moenkhausia bonita*: rio Paraguay basin: ANSP 168836, 5, 25.2–32.3 mm SL; ANSP 175110, 5, 22.1–32.3 mm SL. Rio Paraná basin: ANSP 170335, 19, 23.4–31.7 mm SL. *Moenkhausia dichroura*: rio Paraguay basin: ANSP 169719, 51, 44.8–78.1 mm SL.

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AUTHORS' CONTRIBUTION

Lais Reia: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Writing-original draft, Writing-review and editing.

Gabriel de Sousa Costa e Silva: Conceptualization, Investigation, Writing-original draft, Writing-review and editing.

Claudio Oliveira: Data curation, Funding acquisition, Methodology, Resources, Writing-review and editing.

Ricardo C. Benine: Data curation, Formal analysis, Investigation, Methodology, Validation, Writing-review and editing.

ETHICAL STATEMENT

Collecting permits were issued by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio 13843–5). The use of animals in this research was conducted under Brazilian animal welfare laws, and the research was approved by the Ethics Committee on Animal Use of the Instituto de Biociências, UNESP (protocol number 1058/2020).

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The author declares no competing interests.

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