

A new species of *Moenkhausia* (Characiformes: Characidae) from the rio Madeira basin, Brazil, with comments on the evolution and development of the trunk lateral line system in characids



Correspondence:
Manoela Maria Ferreira Marinho
manoela.marinho@gmail.com

Manoela Maria Ferreira Marinho¹, Willian Massaharu Ohara² and Fernando Cesar Paiva Dagosta³

A new species of *Moenkhausia* is described from the rio Machado drainage, Amazon basin, Brazil. It is diagnosed from congeners by its color pattern, consisting of the concentration of chromatophores on the anterior portion of body scales, the horizontally elongate blotch on caudal peduncle, a bright golden coloration of the dorsal portion of eye when alive, and a dark line crossing the eye horizontally. The new species has variable morphology regarding trunk lateral-line canals. Most fully grown individuals do not have enclosed bony tube in many lateral line scales, resembling early developmental stages of tube formation of other species. This pedomorphic condition is interpreted as a result of developmental truncation. Such evolutionary process may have been responsible for the presence of distinct levels of trunk lateral line reductions in small characids. Variation in this feature is common, even between the sides of the same individual. We reassert that the degree of trunk lateral-line tube development must be used with care in taxonomic and phylogenetic studies, because reductions in the laterosensory system may constitute parallel loss in the Characidae. We suggest the new species to be categorized Near Threatened due to the restricted geographical distribution and continuing decline in habitat quality.

Keywords: Developmental Truncation, Evolution, Intraspecific Variation, Pedomorphy, Scale.

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¹ Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, Cidade Universitária, s/n, Castelo Branco, 58051-900 João Pessoa, PB, Brazil. (MMFM) manoela.marinho@gmail.com (corresponding author).

² Laboratório de Ciências Ambientais, Universidade Federal de Rondônia, Av. da Paz, 4376, Lino Alves Teixeira, 76916-000 Presidente Médici, RO, Brazil. (WMO) ohara@unir.br.

³ Faculdade de Ciências Biológicas e Ambientais, Universidade Federal da Grande Dourados, Rodovia Dourados/Itahum, km 12, 79804-970 Dourados, MS, Brazil. (FCPD) ferdagosta@gmail.com.

Uma espécie nova de *Moenkhausia* é descrita da drenagem do rio Machado, bacia Amazônica, Brasil. É diagnosticada das congêneres pelo padrão de coloração, que consiste na concentração de cromatóforos na porção anterior das escamas do corpo, em uma mancha horizontalmente alongada no pedúnculo caudal, na coloração dourada brilhante da porção dorsal do olho quando vivo e na faixa escura que atravessa o olho horizontalmente. A nova espécie apresenta variação na morfologia do canal da linha lateral do corpo. A maioria dos indivíduos totalmente desenvolvidos não possuem tubo ósseo fechado em muitas escamas da linha lateral, assemelhando-se aos estágios iniciais do desenvolvimento da formação do tubo de outras espécies. Essa condição pedomórfica é interpretada como resultado do truncamento do desenvolvimento. Tal processo evolutivo pode ter sido responsável pelos diferentes níveis de redução do canal sensorial de pequenos caracídeos. A variação neste caráter é comum, até entre os lados do mesmo indivíduo. Por isso, reafirmamos que o grau de desenvolvimento do canal sensorial do corpo deve ser usado com cuidado em estudos taxonômicos e filogenéticos, porque reduções no sistema látero-sensorial podem significar perdas paralelas em Characidae. Sugerimos que a espécie nova seja categorizada como Quase Ameaçada devido à distribuição geográfica restrita e ao declínio contínuo da qualidade do habitat.

Palavras-chave: Desenvolvimento Truncado, Escama, Evolução, Pedomorfose, Variação Intraespecífica.

INTRODUCTION

Moenkhausia Eigenmann, 1903 is the third most species-rich genus among Amazonian fishes, behind only of *Corydoras* Lacepède, 1803 and *Hyphessobrycon* Durbin, 1908 (Dagosta, de Pinna, 2019). It is widely distributed in the Neotropical region (Fricke *et al.*, 2020), with its greatest diversity housed within the limits of the Amazon basin, which contains more than 80% of the *Moenkhausia* species (Dagosta, de Pinna, 2019). The genus has a remarkable diversity of shapes and colors, including some of the most beautiful characids, such as *Moenkhausia agnesae* Géry, 1965, *M. cosmops* Lima, Britski & Machado, 2007, and *M. heikoi* Géry & Zarske, 2004.

The genus was defined in a precladistic view, considering a combination of characters of common occurrence in the Characidae, which are premaxillary teeth in two rows, with at least five teeth in the inner row, caudal fin partially covered by scales, and all scales of the lateral line trunk canal pored (Eigenmann, 1917). This classification criterion of Eigenmann (1917, 1918, 1921), although efficient for decades, has been subject to criticism since most of the characters used to diagnose genera are known to have independently evolved within the family (Mirande, 2010, 2018).

Starting with Costa (1994), many authors have assigned species with an incompletely pored lateral line in *Moenkhausia*, arguing those were probably more closely related to species nowadays included in *Moenkhausia* than to species of *Hemigrammus* Gill, 1858, which are diagnosed from the former by having an incomplete lateral line (*e.g.*, Lima,

Toledo-Piza, 2001; Lima *et al.*, 2007; Benine *et al.*, 2009; Marinho, Langeani, 2010; Ohara, Lima, 2015a). A further issue of criticism is that the trunk lateral line canal may vary within species and even at the same individual. Such observations are not recent. Lütken (1875) mentioned that some specimens of *Psalidodon rivularis* (Lütken, 1875) have complete lateral line, others incomplete. Even Eigenmann (1917:83, 1918:110) pointed out reductions in the perforation of the lateral line scales in some populations of *Moenkhausia sanctaefilomenae* (Steindachner, 1907) and *M. cotinho* Eigenmann, 1908. Eigenmann, Henn (1914) documented variation in the development of the lateral line in *Hemigrammus barrigonae* Eigenmann & Henn, 1914. For decades later, several authors have mentioned variation in this character in many species of Characidae, which we summarized in this paper.

Field expedition to upper portions of the rio Machado, rio Madeira drainage, Amazon basin, Brazil and fish collections analysis revealed a new characid with variably developed bony tube along the lateral line length, with specimens failing to develop tube in some scales of the lateral line. This paper aims to describe the new species in detail and to discuss trunk lateral-line morphology in the Characidae, considering the evolutionary development of this character and the systematic of the family.

MATERIAL AND METHODS

Counts and measurements follow Fink, Weitzman (1974) and Menezes, Weitzman (1990), except for the number of horizontal scale rows below the lateral line counted to the pelvic-fin insertion, but not including the axillary scale, and with the addition of the pelvic-fin origin to anal-fin origin distance. Standard length (SL) and notochord length (NL) is expressed in millimeters (mm) and all other measurements are expressed as percentage of SL, except for subunits of head, which are expressed as percentage of head length (HL). In the description, counts are followed by their frequency of occurrence in parentheses. Asterisk indicates the counts of the holotype. Counts of supraneurals, tooth cusps, small dentary teeth, unbranched anal-fin rays, procurrent caudal-fin rays, and the position of the pterygiophores were taken from cleared and stained (CS) specimens prepared according to Taylor, Van Dyke (1985). Vertebrae of the Weberian apparatus were counted as four elements and the compound caudal centra (PU1+U1) as a single element. Abdominal vertebrae include the Weberian apparatus and the vertebrae associated with ribs or hemal arches without hemal spine. Caudal vertebrae are vertebra associated with hemal spine. *Circuli* and *radii* counts were taken from scale row immediately above the lateral line. Catalog numbers are followed by the number of specimens in alcohol, number of specimens measured and counted in parentheses, SL range of all specimens of the lot, and if any, the number of CS specimens and their respective SL range. Map was generated in the QGIS 3.14.16 program. Institutional abbreviations follow Sabaj (2019).

RESULTS

Moenkhausia cambacica, new species

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(Figs. 1–5; Tab. 1)

Holotype. MZUSP 125792, 34.8 mm SL. Brazil, Rondônia State, Municipality of Vilhena, rio Madeira basin, upper rio Machado, tributary of igarapé Ávila, near BR-364 road, 12°30'36.9"S 60°28'20.29"W, 12 Nov 2014, W. M. Ohara, F. C. P. Dagosta & V. Giovannetti.

Paratypes. All from Brazil, Rondônia State, Municipality of Vilhena, upper rio Machado, rio Madeira basin. MCP 39852, 19, 16.2–28.5 mm SL, rio Ávila at BR-364 road between Vilhena and Pimenta Bueno, 12°30'18"S 60°28'15"W, 14 Sep 2004, P. Lehmann, V. A. Bertaco & F. C. T. Lima. MZUSP 125793, 12, 27.2–35.9 mm SL, 2 CS, 26.5 and 29.0 mm SL, same data of holotype. MZUSP 115277, 1, 26.1 mm SL, upper rio Machado, tributary of igarapé Piracolina, near BR-364 road, 12°48'56.5"S 60°6'37.6"W, 14 Sep 2014, W. M. Ohara, D. Hungria & B. Barros. MZUSP 118576, 5, 23.7–29.3 mm SL, BR-364 road, km 60 to Porto Velho, 12°30'37.2"S 60°28'20.9"W, 19 Nov 2013, W. M. Ohara, D. Hungria & B. Barros.

Diagnose. *Moenkhausia cambacica* is distinguished from all congeners, except *M. chlorophthalma* Sousa, Netto-Ferreira & Birindelli, 2010, *M. petymbuaba* Lima & Birindelli, 2006, *M. plumbea* Sousa, Netto-Ferreira & Birindelli, 2010, and *M. parecis* Ohara & Marinho, 2016 by the presence of a large dark blotch on each scale of the second to seventh longitudinal series of body which are formed by a higher concentration of chromatophores on the anterior portion of scales (*vs.* pigmentation absent or, when present, concentrated at the middle or posterior margin of scales, forming stripes or a reticulate pattern). *Moenkhausia cambacica* can be readily distinguished from all the aforementioned species by having a conspicuous, well-defined, horizontally elongate blotch on the caudal peduncle, extending to middle caudal-fin rays, not reaching the upper and lower edges of the caudal peduncle (*vs.* caudal peduncle blotch absent or poorly defined, continuous with the longitudinal stripe of body in *M. chlorophthalma*, *M. petymbuaba*, and *M. plumbea*; round blotch in *M. parecis*). Additionally, it can be distinguished from *M. petymbuaba* by the absence of a conspicuous longitudinal black stripe on body (*vs.* black stripe present), from *M. plumbea* and *M. chlorophthalma* by the absence of a dark, diffuse, slightly concave midlateral stripe on body in live specimens (*vs.* dark stripe present), and from *M. parecis* by a shorter upper jaw length (41.5–48.8% HL *vs.* 50.6–55.0% HL), and, in life, by having a bright golden coloration of the dorsal portion of the eye and a dark shaded line crossing the eye horizontally (*vs.* eye entirely bright blue, with no horizontal dark line).

Description. Morphometric data of the holotype and paratypes presented in Tab. 1. Body moderately elongate, laterally compressed. Largest specimen examined 35.9 mm SL. Greatest body depth slightly anterior to the vertical through dorsal-fin origin.

Dorsal profile of head convex from anterior tip of upper jaw to vertical through anterior nostril. Straight or slightly convex from that point to tip of supraoccipital spine. Dorsal body profile straight or slightly convex from tip of supraoccipital spine to dorsal-fin



FIGURE 1 | Holotype of *Moenkhausia cambacica*, MZUSP 125792, 34.8 mm SL, Brazil, Rondônia State, Municipality of Vilhena, rio Madeira basin, upper rio Machado drainage.

TABLE 1 | Morphometric data of *Moenkhausia cambacica*. Range includes the holotype. SD = Standard deviation.

	Holotype	n	Specimens range	Mean	SD
Standard length (mm)	34.8	25	22.9 – 35.9	28.6	–
Percents of standard length					
Depth at dorsal-fin origin	35.5	25	31.7 – 37.3	34.7	1.4
Snout to dorsal-fin origin	53.6	25	51.3 – 54.9	53.4	1.0
Snout to pectoral-fin origin	30.2	25	28.7 – 35.1	31.0	1.3
Snout to pelvic-fin origin	52.6	25	50.9 – 56.7	53.5	1.2
Snout to anal-fin origin	69.5	25	67.2 – 73.2	69.5	1.3
Caudal-peduncle depth	12.6	25	11.2 – 17.4	12.7	1.1
Caudal-peduncle length	12.9	25	10.6 – 13.9	12.7	0.8
Pectoral-fin length	20.1	25	18.9 – 24.8	22.4	1.5
Pelvic-fin length	17.0	25	15.8 – 19.0	17.6	0.8
Pelvic-fin origin to anal-fin origin	19.6	25	16.0 – 20.3	18.0	1.1
Dorsal-fin length	25.7	25	25.7 – 30.0	28.1	1.1
Dorsal-fin base length	15.4	25	12.7 – 15.9	14.3	0.8
Anal-fin length	19.1	25	18.3 – 23.3	20.2	1.2
Anal-fin base length	21.0	25	20.4 – 23.5	21.7	0.8
Eye to dorsal-fin origin	38.4	25	36.7 – 39.0	37.9	0.7
Dorsal-fin origin to caudal-fin base	48.6	25	44.7 – 51.3	48.8	1.7
Head length	29.0	25	28.4 – 31.7	29.7	0.9
Percents of head length					
Horizontal eye diameter	35.6	25	35.6 – 43.0	39.3	2.3
Snout length	27.6	25	21.8 – 27.6	24.3	1.6
Interorbital width	35.6	25	32.9 – 39.8	35.9	1.8
Upper jaw length	45.9	25	41.5 – 48.8	45.2	1.9

origin, straight along dorsal-fin base, straight from base of last dorsal-fin ray to adipose-fin insertion and slightly concave along caudal peduncle. Ventral profile of body convex from anterior tip of dentary to anal-fin origin, straight at anal-fin base and slightly concave along caudal peduncle.

Mouth terminal, jaws equal. Posterior terminus of maxilla at the vertical through middle of pupil. Maxilla approximately at 45 degrees angle relative to longitudinal axis of body. Frontals with a triangle-shaped fontanel; parietal fontanel large, extending from epiphyseal bar to supraoccipital spine. Infraorbital series with six elements. Nostrils close to each other, anterior opening circular and small, crescent-shaped posterior one, twice in size. Nostrils separated by narrow skin flap.

Premaxillary teeth in two rows. Outer tooth row with 3*(1), 4(25) or 5(1) tricuspid teeth; inner tooth row with 4(1) or 5*(25) teeth with three to five cusps, symphyseal tooth of inner series narrow, asymmetric, with four cusps. Tooth cusps of inner premaxillary tooth row directed outward and arranged in an arched series. Maxilla with 2*(9), 3(17), or 4(1) teeth along its anterodorsal margin, with one to three cusps (Fig. 2). Dorsalmost tooth usually larger. Dentary with 4*(26) or 5(1) larger tri- to pentacusp teeth, followed by a series of 9(1) or 11(1) diminute conical teeth. Tooth cusps of larger dentary teeth arranged directed inward and arranged in an arched series. Central cusp of all multicusp teeth more developed than remaining lateral cusps.

Scales cycloid, moderately large, *circuli* distributed over whole area of scales. Three to seven *radii* well defined and slightly divergent posteriorly. Lateral line slightly curved downward anteriorly, with variably developed bony tube. Four specimens (including holotype) with fully developed tube in all lateral-line scales, terminating in a pore (*e.g.*, lateral line complete, with 31(1) and 32*(3) pored scales from supracleithrum to the end of caudal peduncle). Twenty-one specimens with fully developed tube in all lateral-line scales of the anterior and posterior portions of body, and, at the level of the anal-fin base, tubed scales interspersed by scales without bony tube and/or scales with poorly developed tube, with variable count (*e.g.*, 22 tubed scales with pore + 2 scales without tube or pore + 3 scales with poorly developed tube and no pore + 3 tubed scales with pore) (Fig. 3), with a total of 30(2), 31(8), 32(7), or 33(1) scales in the lateral series (see details in the Discussion). Longitudinal scale rows between dorsal-fin origin and lateral line 5*(24). Longitudinal scale rows between lateral line and pelvic-fin origin 3(7) or 4*(17). Predorsal area with 9(11) or 10*(13) scales arranged in one series. Horizontal scale rows around caudal peduncle 14*(24). Single row of 4(7), 5(7), 6(3), or 7*(2) scales covering base of anteriormost anal-fin rays. Caudal fin with small scales on the basal fourth of caudal-fin lobes.

Supraneurals 4(2) with narrow bony lamellae on upper portion. Dorsal-fin rays *i**(27), 9*(27). Dorsal-fin origin at middle of standard length and slightly posterior to vertical through pelvic-fin origin. First unbranched dorsal-fin ray shorter than second unbranched ray. First dorsal-fin pterygiophore located behind neural spine of 9th(2) vertebra. Adipose fin present. Anal-fin rays *v*(2), 15(4), 16(15), 17*(7), or 18(1); anteriormost rays longer, subsequent rays gradually decreasing in size. Anteriormost anal-fin pterygiophore inserted posterior to haemal spine of 16th(2) vertebra. Pectoral-fin rays *i**(27), 10(1), 11*(14), or 12(12). Tip of adpressed pectoral fin not reaching pelvic-fin origin in most specimens. Pelvic-fin rays *i**(27), 7*(27). Tip of adpressed



FIGURE 2 | Medial view of left side, premaxillary, maxillary, and dentary of *Moenkhausia cambacica*, MZUSP 125793, 27.1 mm SL, paratype. Scale bar: 1 mm.

pelvic fin reaching the anal-fin origin. Caudal-fin with $i^*(26)$, $9^*(26)$ rays on the upper and $i^*(26)$, $8^*(26)$ rays on the lower lobe. Caudal-fin forked, lobes somewhat pointed and of similar size. Twelve (1) or 13(1) dorsal procurrent caudal-fin rays and 10(2) ventral procurrent caudal-fin rays. Total vertebrae 31(2): precaudal vertebrae 16(2) and caudal vertebrae 15(2).

Color in alcohol. Overall ground color pale, with small dark chromatophores spread at the entire head and body, except the ventral portion of abdominal region, and densely concentrated in its dorsal portion, gradually fading ventrally (Fig. 1). Dorsal midline of head and body dark brown. Jaws, opercular, and infraorbital areas pigmented with dark chromatophores. Single, dark humeral blotch, vertically oriented, extending vertically two scale rows above and one scale row below the lateral line. Dorsal portion of humeral blotch wider, over three scales horizontally. Ventral portion narrow, slightly turned anteriorly, over one scale. Thin longitudinal dark stripe at horizontal septum, formed by underlying chromatophores extending from vertical through dorsal-fin origin to caudal peduncle. Conspicuous dark horizontal blotch on caudal peduncle, extending to base of middle caudal-fin rays, never reaching the upper and lower edges of caudal peduncle. Horizontal blotch on caudal peduncle frequently extending to tip of

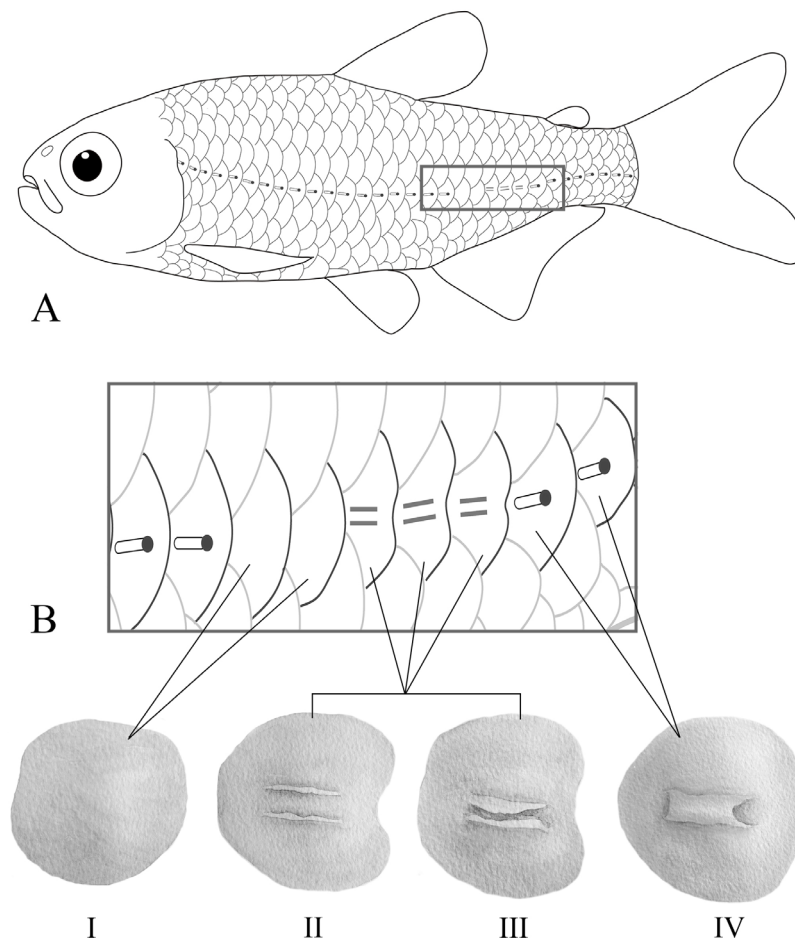


FIGURE 3 | Schematic drawing of *Moenkhausia cambacica* showing **A.** lateral-line perforation pattern observed in most specimens. **B.** Morphology of the lateral-line scales above anal fin: I – scale lacking tube and pore; II – scale with poorly developed tube, with small tube walls; III – scale with poorly developed tube, walls larger but not enclosed; IV – scale with fully developed bony tube, tube walls enclosed, with a posterior pore.

middle caudal-fin rays. Lower portion of caudal peduncle with a clear area. Second to seventh horizontal scale rows with scales bearing dark blotches on its anterior portion. All fins with scattered dark chromatophores on interradial membranes. Distal portion of interradial membranes of dorsal fin with concentration of dark chromatophores.

Color in life. Dorsal portion of head and body light brown. Ventral half of head and body pale yellow (Fig. 4). Infraorbital and opercular areas silvery. Dorsal portion of eye bright golden, ventral portion silvery with blue hue. Dark shaded line crossing the eye horizontally (Fig. 5). Vertical arm of preopercle yellow golden. Bright yellow to orange blotch anterior and posteriorly to the humeral blotch (Fig. 5). Second to seventh horizontal scales row with scales bearing brown blotches on its anterior portion. Humeral blotch and caudal-peduncle spot conspicuous in life. All fins with orange to yellow coloration, more intense at the anterior half of caudal-fin lobes. Posterior tip of caudal and dorsal fins hyaline.

Sexual dimorphism. Secondary dimorphic characters were not found in the examined specimens.

Geographical distribution. The new species is so far only known from two headwater tributaries of the upper rio Machado at Chapada dos Parecis, Rondônia State, Brazil (Fig. 6). Intensive ichthyological collecting efforts in the rio Madeira basin (e.g., Queiroz *et al.*, 2013), including the rio Machado drainage (e.g., Perin *et al.*, 2007; Casatti *et al.*, 2013; Costa *et al.*, 2017) have failed to capture *M. cambacica* in other streams, indicating a very restricted distribution to the tributaries draining the Chapada dos Parecis.

Ecological notes. The type locality of *Moenkhausia cambacica* is a Balneário (recreation area) upstream the Cachoeira Small Hidroelectric Dam (PCH, Pequena Central Hidrelétrica), and is located at 415 m above sea level. The stream is small, 2–4



FIGURE 4 | Live coloration of *Moenkhausia cambacica*, paratype, MZUSP 125793, Brazil, Rondônia State, Municipality of Vilhena, rio Madeira basin, upper rio Machado drainage.



FIGURE 5 | Paratypes of *Moenkhausia cambacica*, MZUSP 125793, freshly collected, showing other aspects of its live coloration, Brazil, Rondônia State, Municipality of Vilhena, rio Madeira basin, upper rio Machado drainage.

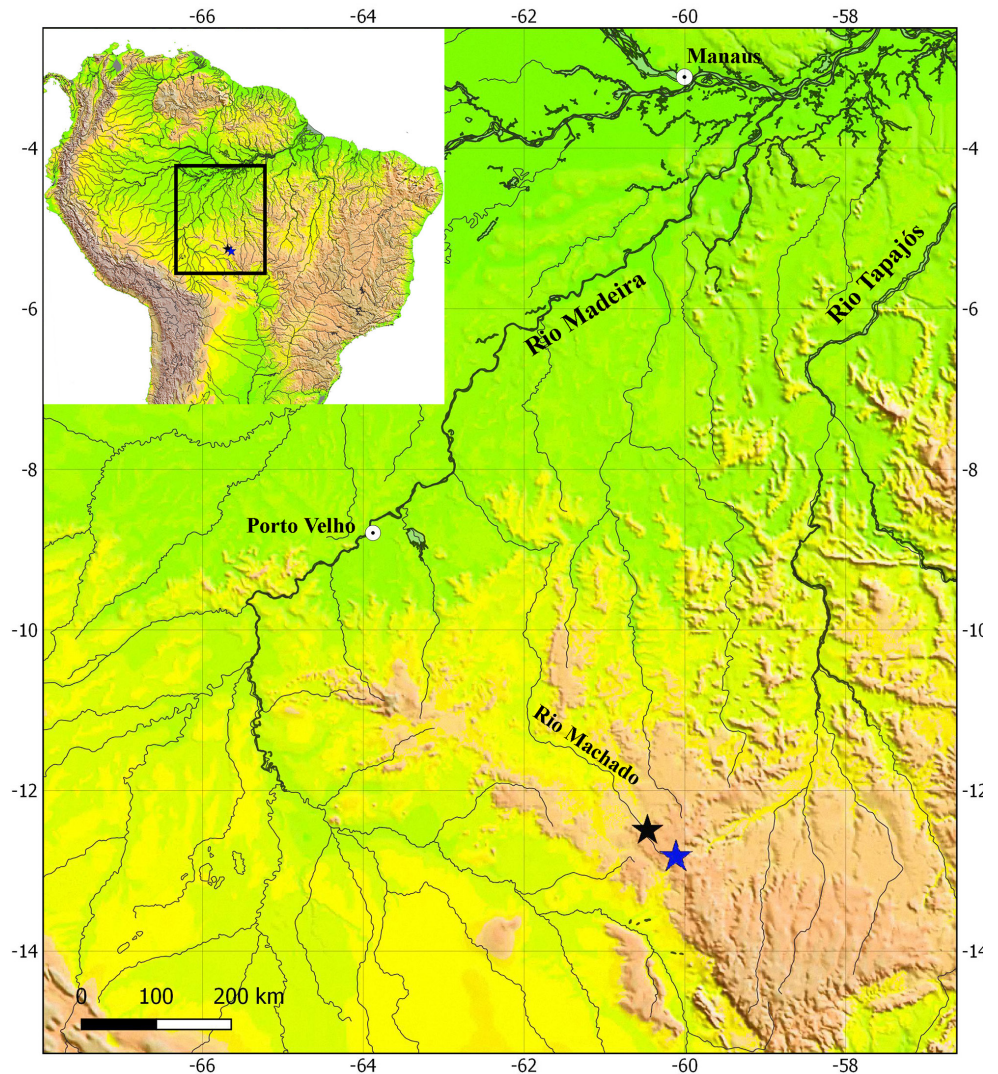


FIGURE 6 | Distribution of *Moenkhausia cambica* in the upper rio Machado, rio Madeira basin, Brazil. Black star (type-locality), blue star (other localities).

m wide and 0.5–2 m deep, with clear waters with swift current, and bottom composed of sand and dead leaves (Fig. 7). Other species collected syntopically were: *Ancistrus verecundus* Fisch-Muller, Cardoso, da Silva & Bertaco, 2005, *Astyanax* aff. *bimaculatus* (Linnaeus, 1758), *Bryconops piracolina* Wingert & Malabarba, 2011, *Erythrinus erythrinus* (Bloch & Schneider, 1801), *Cetopsorhamdia* sp. 3 (cf. Bockmann, Slobodian, 2013:25), *Aequidens* sp., and *Crenicichla* sp. A single *M. cambica* specimen was collected in a tributary of rio Piracolina near Vilhena at altitude 591 m a.s.l., in a small, clear water stream 1–1.5 m wide and 0.3–1.5 m deep, presenting swift water current and sandy bottom. This specimen was collected syntopically with *M. parecis* and other species (e.g., *A. verecundus*, *B. piracolina*, *Cetopsorhamdia* sp. 3, *Corydoras hephaestus* Ohara, Tencatt & Britto, 2016, *Hyphessobrycon lucenorum* Ohara & Lima, 2015, *Hyphessobrycon* aff. *melanostichos* Carvalho & Bertaco, 2006, *Hyphessobrycon* aff. *notidanus* Carvalho & Bertaco, 2006, and *Pyrrhulina* sp.).



FIGURE 7 | Type-locality of *Moenkhausia cambacica*, tributary of igarapé Ávila, upper rio Machado, rio Madeira basin, Vilhena, Rondônia, Brazil.

Etymology. The specific name, *cambacica*, is after the one of the Brazilian popular name for *Coereba flaveola* (Linnaeus, 1758), a small neotropical bird whose coloration resembles that of the new species, which is bright yellow underparts, dark back coloration and a dark line crossing the region of the eye horizontally, contrasting with a light area above it. A noun in apposition.

Conservation status. *Moenkhausia cambacica* is another endemic species from the ‘Chapada dos Parecis’ biogeographic region, characterized by high levels of endemism and large number of restricted-range species (Ohara, Lima, 2015a,b; Dagosta *et al.*, 2020). This biogeographic region was considered by latter authors as one of the Endemic Amazonian Fish Areas (EAFAs), *i.e.*, regions that should be considered as conservation priorities in the basin by presenting imminent threats and low cover of protected areas. *Moenkhausia cambacica* is endemic to Brazil, known by only two localities. One site is a tourist bathing resort and the other is entirely surrounded by monoculture plantation. Its area of occupancy (AOO) (B2) 8 km² is based on these two known records. The

AOO is likely underestimated, although the region has already been largely sampled. A continuing decline in habitat quality b(iii) is inferred based on the deforestation caused by still growing urbanization and agriculture activity in the region. It is not possible to meet subcriterion 'a' because the population is not necessarily fragmented. Therefore, we suggest this species is assessed as Near Threatened, close to meeting Critically Endangered (CR) by the following criteria B2b(iii) according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2019).

DISCUSSION

Moenkhausia cambacica presents a series of dark blotches on body, located at the anterior portion of scales, an unusual coloration within the Characidae. Sousa *et al.* (2010) used this feature to indicate a close relationship between *M. clorophthalma*, *M. petymbuaba*, and *M. plumbea*. Ohara, Marinho (2016), described the same character in *M. parecis* and considered it as closely related to that group of species. Additionally, Ohara, Marinho (2016) observed these species further share characters such as a relatively large head, round dorsal-fin profile, and a relatively short anal-fin base. These features are also observed in *M. cambacica*. These five species of *Moenkhausia* also have colored eyes (totally green in *M. clorophthalma*, partially green in *M. petymbuaba*, totally blue in *M. parecis*, yellowish with a longitudinal dark stripe in *M. plumbea* and *M. cambacica*) (Sousa *et al.*, 2010; Ohara, Marinho, 2016). Therefore, it is reasonable to assume *M. cambacica* is closely related to members of this group of species although a phylogenetic analysis is needed to corroborate this hypothesis.

Trunk lateral line and the systematics of the Characidae. The mechanoreceptive lateral-line system in fishes is typically composed of a series of neuromasts included in pored canals and of superficial neuromasts in the head and body (Webb, 1989; Pastana *et al.*, 2019). Scaled fishes generally present the trunk canal contained within scales of the lateral-line series bearing tubes, which are bony canal walls and roofs that extend upward from the scale plate, surrounding the canal lumen. Adjacent lateral-line scales overlap, forming a continuous tube that is pored periodically, connecting the canal lumen to the environment (Wonsettlar, Webb, 1997).

Eight trunk canal patterns are identified among teleosts (Coombs *et al.*, 1988; Webb, 1989): 1) complete and straight, 2) complete and arched, 3) complete with dorsal displacement, 4) complete with ventral displacement, 5) multiple, 6) disjunct, 7) incomplete, and 8) absent. Among characids, are found (1) complete and straight, with tubed scales with a pore, extending from the supracleithrum to the caudal peduncle, (7) incomplete, with only the anteriormost scales of the lateral line tubed, from the supracleithrum to a variable extent on body, (8) absent, with scales lacking any tube or pore, and an additional condition, which is (9) discontinuous lateral line scale, with tubed scales interspersed by non-tubed scales. As discussed below, intraspecific variation can be found, *i.e.*, species presenting complete, discontinuous, incomplete lateral line, in the same population.

Analyzed specimens of *M. cambacica* have variable morphology regarding trunk lateral line: four specimens (including the holotype) have a fully developed tube in all

scales of the lateral-line series, which are pored posteromedially; remaining specimens (21) have scales with distinct levels of tube development along the lateral-line length (Fig. 3A). In these specimens, the anteriormost scales near supracleithrum and the posteriormost scales at the caudal peduncle bear fully developed tube with a pore (Fig. 3B, scale IV), whereas the scales located approximately at the level of the anal-fin base frequently lack tube and pore (Fig. 3B, scale I) or have poorly developed tube (*i.e.*, tube not fully enclosed, represented by a superficial groove, frequently with a posterior slit and no apparent pore, Fig. 3B, scales II and III). In this specific area above anal-fin level, scales bearing a groove without fully developed tube are interspersed with tubed scales and/or scales lacking tube or pore, characterizing a discontinuous lateral line. Specimens with incomplete lateral line were not found.

Poorly developed bony tube of lateral line scales, *i.e.*, those scales bearing a groove present in most specimens of *M. cambacica* (Fig. 3B, scales II and III), resembles early stages of formation of the bony tube of the trunk lateral line of other fish species. In both the scorpaeniform Hexagrammidae and the cypriniform zebrafish *Danio rerio* (Hamilton, 1822), bony tube development of lateral line scales starts as a pair of ridges that protrude outward forming a longitudinal groove which later fuses at the apical region to form the tube roof (Wonsettlar, Webb, 1997; Wada *et al.*, 2014). The same pattern of tube formation at scale level was observed in the development of *Paracheirodon innesi* (Myers, 1936) and *Moenkhausia pittieri* Eigenmann, 1920 (Marinho, 2017). Also, all specimens examined are fully grown individuals, with other morphological aspects fully formed. Additionally, individuals of *Moenkhausia cambacica* with complete lateral line are of 28.6 to 35.9 mm SL and individuals with discontinuous lateral line are of 22.9 to 33.1 mm SL, not showing correlation between size and completeness of lateral line at this range of size.

Lack of tube formation has been repeatedly documented in Euteleostei and interpreted as a derived paedomorphic condition in many lineages (Myers, 1958; Webb, 1990; Montgomery *et al.*, 1994; Coombs *et al.*, 1998; Wellenreuther *et al.*, 2010). The same has been interpreted for characid lineages (Myers, 1958; Weitzman, 1962; Weitzman, Fink, 1983; Weitzman, Vari, 1988; Mattox *et al.*, 2016; Marinho, 2017; Pastana *et al.*, 2017; Camelier *et al.*, 2018; Jerep *et al.*, 2018; Abrahão *et al.*, 2019). Therefore, we consider the scales with a longitudinal groove, observed in most fully grown specimens of *M. cambacica*, as a paedomorphic condition, a character resulted from the loss of terminal stages of development.

As widely discussed in the literature, the traditional classification of Characidae by Eigenmann (1917) is based on features known to occur independently in numerous lineages within the family (Weitzman, Fink, 1983; Costa, 1994; Mirande, 2010; Dagosta *et al.*, 2015; Marinho, 2017), resulting in non-monophyletic assemblages. One of the characters used in this classification system for establishing generic limits is the completeness of the trunk lateral line. Morphological reductions in many characids are result of loss of terminal stages in the developmental sequence that compromises late-forming structures, such as trunk lateral-line canals, resulting in incompletely pored lateral line or even absence (Weitzman, Vari, 1988; Marinho, 2017). This is a common process in small characids, not exclusive to miniaturized species *sensu* Weitzman, Vari (1988), *i.e.*, species reaching a maximum of 26 mm SL. In view of that, distinct levels of trunk lateral line reductions observed in the family (*i.e.*, discontinuous, incomplete

or absence of lateral line) are likely associated to a distinct degree of loss of terminal stages of development. It can be observed as a process occurring at species level (e.g., *Hemigrammus ataktos* Marinho, Dagosta & Birindelli, 2014, *M. sanctaefilomenae*, *P. rivularis*), or affecting specific populations (e.g., *Astyanax* aff. *rupestris*, *Moenkhausia celibela* Marinho & Langeani, 2010, and *Moenkhausia bonita* Benine, Castro & Sabino, 2004) or even at individual level (see below). Absence of lateral line was only observed in miniaturized species, in which developmental truncation is extreme [e.g., individuals of *Oxybrycon parvulus* Géry, 1964 and *Tyttobrycon hamatus* Géry, 1973; all individuals of *Priocharax* spp., according to Weitzman, Vari (1987) and Toledo-Piza *et al.* (2014)] (references for these observations are listed in Tab. 2).

Increased morphological variability of late-forming structures is also associated with developmental truncation (Hanken, Wake, 1993). Intraspecific variations at the lateral line development have been continuously documented for small characids (Tab. 2) and distinct states can be observed even in the same individual (bilateral asymmetry) (e.g., *H. barrigonae*, *P. rivularis*). Thus, the use of such labile character in systematics, such as in species delimitation or phylogenetic analysis, needs to be made with caution. In the search for a phylogenetic classification in the family, Weitzman (1962) stated “loss of various parts of the laterosensory system, or parts of the skeleton (...), must be used with extremely care in the studies of phyletic relationships of small fishes, since parallel loss is probably the rule rather than exception”. It is wise to look at “reductive” characters very closely (Weitzman, Fink, 1983; Mattox *et al.*, 2016). In depth investigation on the ontogeny, patterns of formation and morphology of trunk lateral line are decisive in helping to establish homology for phylogenetic analysis.

TABLE 2 | Species of Characidae with intraspecific variation in the lateral line trunk morphology. Classification of genera and subfamilies follows Miranda (2018). Burger *et al.* (2019) reported variation in the completeness of the lateral line in *Astyanax epiagos* Zanata & Camelier, 2008, *Deuterodon hastatus* (Myers, 1928) and *D. ribeirae* (Eigenmann, 1911), but specific condition were not mentioned by the authors. LL = lateral line, c = complete, d = discontinuous, i = incomplete, a = absent.

Species	cLL	dLL	iLL	aLL	References
Stethaprioninae					
<i>Astyanax brachypterygium</i> Bertaco & Malabarba, 2001	x	x	x		Oliveira (2006)
<i>Astyanax cremnobates</i> Bertaco & Malabarba, 2001	x	x	x		Oliveira (2006)
<i>Astyanax lorien</i> Zanata, Burger & Camelier, 2018	x	x			Zanata <i>et al.</i> (2018)
<i>Astyanax</i> sp.	x	x	x		MZUSP 110406
<i>Astyanax sincora</i> Burger, Carvalho & Zanata, 2019	x	x	x		Burger <i>et al.</i> (2019)
<i>Ctenobrycon spilurus</i> (Valenciennes, 1850)	x	x			Eigenmann (1927)
<i>Deuterodon luetkenii</i> (Boulenger, 1887)	x	x	x		Carvalho (2011); Carvalho, Malabarba (2015)
<i>Gymnocorymbus thayeri</i> Eigenmann, 1908	x	x	x		Benine <i>et al.</i> (2015)
<i>Hemigrammus ataktos</i> Marinho, Dagosta & Birindelli, 2014	x	x	x		Marinho <i>et al.</i> (2014)
<i>Hemigrammus barrigonae</i> Eigenmann & Henn, 1914	x	x	x		Eigenmann, Henn (1914); Soares, Bürnheim (2016); MZUSP 65681, 81312, 85018
<i>Hyphessobrycon auca</i> Almirón, Casciotta, Bechara & Ruíz Dias, 2004	x		x		Almirón <i>et al.</i> (2004)
<i>Hyphessobrycon balbus</i> Myers, 1927	x	x	x		Myers (1927); Carvalho (2011)
<i>Hyphessobrycon inconstans</i> (Eigenmann & Ogle, 1907)	x	x	x		Eigenmann, Ogle (1907); Carvalho (2011)
<i>Hyphessobrycon cachimbensis</i> Travassos, 1964		x	x		MZUSP 101377



TABLE 2 | (Continued)

Species	cLL	dLL	iLL	aLL	References
<i>Hyphessobrycon proteus</i> Eigenmann, 1913	x	x	x		Carvalho (2011); Burger <i>et al.</i> (2019)
<i>Hyphessobrycon santae</i> (Eigenmann, 1907)	x		x		Eigenmann in Eigenmann, Ogle (1907)
<i>Hyphessobrycon</i> sp.		x	x		MZUSP 96823
<i>Moenkhausia bonita</i> Benine, Castro & Sabino, 2004	x	x	x		Mota <i>et al.</i> (2018)
<i>Moenkhausia celibela</i> Marinho & Langeani, 2010	x	x	x		Marinho, Langeani (2010)
<i>Moenkhausia cotinho</i> Eigenmann, 1908	x	x	x		Eigenmann (1908); Mathubara, Toledo-Piza (2020)
<i>Moenkhausia lineomaculata</i> Dagosta, Marinho & Benine, 2015	x	x	x		Dagosta <i>et al.</i> (2015)
<i>Moenkhausia melogramma</i> Eigenmann, 1908	x	x			Soares <i>et al.</i> (2020)
<i>Moenkhausia phaeonota</i> Fink, 1979	x	x	x		MZUSP 91403; present study
<i>Moenkhausia sanctaefilomenae</i> (Steindachner, 1907)	x	x	x		Eigenmann (1917)
<i>Poptella compressa</i> (Günther, 1864)	x		x		Benine <i>et al.</i> (2015)
<i>Psalidodon anisitsi</i> (Eigenmann, 1907)	x		x		Carvalho, Malabarba (2015)
<i>Psalidodon rivularis</i> (Lütken, 1875)	x	x	x		Lütken (1875); Lütken (2001); Oliveira (2006)
<i>Astyanax</i> aff. <i>rupestres</i> Zanata, Burger & Camelier, 2018	x	x	x		Zanata <i>et al.</i> (2018)
<i>Psellogrammus kennedyi</i> (Eigenmann, 1903)	x		x		Britski <i>et al.</i> (2007)
Stevardiinae					
<i>Boehlkea fredcochui</i> Géry, 1966	x	x			Soares <i>et al.</i> (2017)
<i>Diapoma obi</i> (Casciotta, Almirón, Piálek & Řičan, 2012)		x	x		Casciotta <i>et al.</i> (2012)
<i>Gephyrocharax torresi</i> Vanegas-Ríos, Azpelicueta, Mirande & García Gonzales, 2013	x	x			Vanegas-Ríos <i>et al.</i> (2013)
<i>Glandulocauda melanopleura</i> (Ellis, 1911)	x	x	x		Camelier <i>et al.</i> (2018)
Cheirodontinae					
<i>Odontostilbe dialeptura</i> (Fink & Weitzman, 1974)	x		x		Fink, Weitzman (1974)
<i>Serrapinnus sterbai</i> Zarske, 2012	x		x		Malabarba, Jerep (2014)
<i>Serrapinnus tocantinenses</i> Malabarba & Jerep, 2014	x		x		Malabarba, Jerep (2014)
Incertae sedis					
<i>Oxybrycon parvulus</i> Géry, 1964			x	x	Géry (1964)
<i>Tyttobrycon hamatus</i> Géry, 1973			x	x	Géry (1973)

Comparative material examined. All from Brazil. Material examined are the same listed at Ohara, Marinho (2016), with the addition of *Astyanax* sp.: MZUSP 110406, 11, paratypes, 23.8–30.0 mm SL; MZUSP 118302, 164, 11.9–27.0 mm SL, 3 CS. *Hyphessobrycon cachimbensis*: MZUSP 97586, 64, 19.9–45.0 mm SL. *Hyphessobrycon* sp.: MZUSP 96823, 571, 16.2–48.5 mm SL. *Moenkhausia lineomaculata*: MZUSP 105953, three, paratypes, 14.8–36.6 mm SL. *Moenkhausia pittieri*: MZUSP 120441, 129, 2.8 mm NL to 15.4 mm SL. *Paracheiroidon innesi*: MZUSP 120442, 134, 2.4 mm NL to 13.8 mm SL.

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AUTHOR'S CONTRIBUTION 

Manoela Maria Ferreira Marinho: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Writing–original draft, Writing–review and editing.

Willian Massaharu Ohara: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Software, Writing–original draft, Writing–review and editing.

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

Neotropical Ichthyology

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The authors declare no competing interests.

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