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Increasing the species diversity of the monotypic genus *Pariolius* Cope 1872 (Siluriformes: Heptapteridae) after more than 150 years

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Abstract

Pariolius is a heptapterid genus represented by *P. armillatus* that is distributed along the upper Amazon River basin. A taxonomic integrative revision of *Pariolius* from Colombian Rivers revealed two new species. Several approaches as morphological, morphometric, meristic, osteology and molecular data were used to distinguish between *Pariolius* species. The two new species are distinguished from congeners by the caudal-fin shape and numbers of rays, colorations patterns and several morphometric characters. The two new species of *Pariolius* are restricted to tributaries of the Upper Orinoco and Upper Negro rivers in Colombia.

Key words: endemic, freshwater, morphology, species delimitations, taxonomy

Introduction

Pariolius is a monotypic genus represented by *Pariolius armillatus* Cope 1872. This species was described within the current Trichomycteridae, but reassigned to Pimelodidae by Gosline (1940). Mees (1974) considered *Pariolius* Cope 1872 as junior synonym of *Heptapterus* Bleeker 1858 and listed it as *Heptapterus armillatus* by Ortega & Vari (1986) and Burgess (1989). After some studies, *Pariolius* was considered as a valid genus by several authors (Stewart, 1986; Ferraris, 1988; Lundberg *et al.*, 1988; Lundberg *et al.*, 1991; Bockmann, 1994; Bockmann & Guazzelli, 2003; Bockmann & Ferraris, 2005; Ferraris, 2007; Bockmann & Miquelarena, 2008; Bockmann & Castro, 2010; Bockmann & Slobodian, 2017) and placed within the *Nemuroglanis* subclade (Ferraris, 1988; Lundberg *et al.*, 1991; Bockmann, 1994; Bockmann & Ferraris, 2005, Bockmann & Castro, 2010). Currently, *Pariolius armillatus* is included in Heptapterini (Silva *et al.*, 2021 and Faustino-Fuster *et al.*, 2021) and mostly restricted to the upper of the Amazon River basin in Brazil, Ecuador, Colombia, and Peru (Fricke *et al.*, 2023).

Previous studies on *Pariolius* since the original description by Cope (1872) were just to compare it with others heptapterids (Bockmann & Ferraris, 2005; Bockmann & Miquelarena, 2008; Bockmann & Castro, 2010; Silva et al, 2021). Among heptapterids *Pariolius* Cope 1872 is characterized by the following features: upper mouth, posterior portion of the head with unpigmented collar, region anterior to dorsal fin with unpigmented mark, dorsal lobe of caudal fin slightly longer than ventral lobe, (Bockmann & Slobodian, 2017). An ongoing taxonomic study of *Pariolius* from the Orinoco and Amazon River basin in Colombia, revealed two species new to science that are described herein.

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Materials and Methods

Morphology

Measurements were taken with digital calipers (to 0.1 mm) on the left side of specimens following landmarks proposed by Faustino-Fuster *et al.* (2019, fig. 1), adding length of dorsal and ventral lobes of caudal fin. Standard length (SL) is given in mm and other measurements were expressed as percentages of standard (SL) or head length (HL) for subunits of the head.

Pectoral, pelvic, dorsal, anal, and caudal fin rays were counted in preserved specimens. Seven paratypes were clear and stained (c&s) following Taylor & van Dyke (1985) using ethanol with the alizarin red as were proposed by Springer & Johnson (2000). Pterygiophores, branchiostegal rays, branchial rakers, ribs, and vertebrae were counted in c&s specimens, as well as the insertion of the first fins elements related to vertebral number. Vertebral counts include the five vertebrae of the Weber apparatus and the caudal compound centrum (PU1+U1) counted as one element. Osteological nomenclature and laterosensory canals system follows Bockmann & Miquelarena, 2008 and Bockmann & Castro (2010), Carvalho *et al.* 2013. Institutional codes followed Sabaj (2020).

DNA sequencing

We sequenced the mitochondrial gene cytochrome oxidase subunit I (*coI*). Whole genomic DNA was extracted from fin or muscle tissues following a standard salt extraction protocol (Lujan *et al.*, 2020). The gene was amplified via standard polymerase chain reaction (PCR) using an Eppendorf Mastercycler pro S thermocycler (Eppendorf Ltd., Hamburg, Germany). A COI gene was amplified with an initial denaturation step of 1 min at 94°C followed by 35 cycles of 94°C for 30 s, annealing at 52°C for 40 s, extension at 72°C for 1 min, and final extension at 72°C for 10 min. Products of each amplification were visualized by running 2 µL of amplicon on a 1% agarose gel. Remaining PCR product was purified using exonuclease I and shrimp alkaline phosphatase (EXOSAP). Successful amplifications were bidirectionally sequenced using the dye termination method of Sanger *et al.* (1977).

Sequence editing, alignments, and phylogeny inference

Bidirectional sequences were assembled into contigs and manually edited using the software Geneious v6.1.7 (Biomatters Ltd., Auckland, New Zealand). Sequences for contigs having many ambiguities were reamplified and sequenced. Contigs for each gene region were aligned using the MUSCLE algorithm (Edgar, 2004), with the alignments being manually edited and evaluated based on amino acid translations of consensus sequences. Genetic distances between *Pariolius* species were calculated using the Kimura 2-parameter algorithm performed in MEGA11 (Tamura, *et al.*, 2021).

Molecular analysis included all available sequences of *coI* for Heptapteridae species in Faustino-Fuster *et al.* (2021). A species delimitation analysis was performed using an arbitrarily ultrametric *coI* gene tree for a general mixed Yule coalescent model (GMYC; Pons *et al.*, 2006) and Poisson Tree Processes (PTP, Zhang *et al.*, 2013) on the webserver for GMYC and PTP (Zhang *et al.*, 2013). The optimal model of molecular evolution for each partition was determined using the software Partition Finder v1.1.1 (Lanfear *et al.*, 2012). The ultrametric gene tree was constructed using the optimal model of molecular evolution with a relaxed molecular clock using a lognormal time distribution and birth–death prior implemented in the BEAST v1.7.5. program (Drummond *et al.*, 2012). BEAST was programmed to run for a total of 100,000,000 generations, sampling every 5000 trees, conducted on the CIPRES supercomputing cluster (Miller *et al.*, 2010). For the MCMC analysis each parameter fluctuating within a stable range, the effective sample size (ESS) for all metrics exceeding 100 was checked using the program Tracer 1.6 (Rambaut *et al.*, 2013). The first 10% of trees were discarded as burn in using TreeAnnotator 1.7.5 program (Rambaut and Drummond, 2013). The Bayesian topology of *coI* is presented showing the Bayesian posterior probability values for each node, support values is described along the text as strong (BI = 0.95–1) and moderate (BI = 0.94–0.8), and *Pimelodus ornatus* Kner 1858 was designated as the outgroup based on previous molecular studies finding Heptapteridae related to Pimelodidae (Sullivan *et al.*, 2013; Faustino *et al.*, 2021).

Results

Morphological result

Pariolius pax **new species**
urn:lsid:zoobank.org:act:DBC8415C-88B5-4EAE-BAC9-62CDE8E2FAE2
(Figs. 1 a–c, Tables 1–2)

Holotype. MHNU-I, 3258, 38.8 mm SL, Colombia, Meta, Mapiripán Municipality, vereda San Jorge, Caño Ovejas, tributary of the Guaviare River, 03°5'26.82''N; 72°42'33.14''W, 28 February 2021, J. M. Vásquez-Ramos, M. A. Cortés-Hernández, J. M. Quiñones-Montiel, Y. A. Rojas-Molina, J. A. López-Castaño.

Paratypes. Thirty-one specimens, all from Colombia, Orinoco basin, IavH-P 11228, 4, 25.8–27.3 mm SL (1C&S), Puerto Gaitán municipality, vereda Alto Neblinas, Finca Unillanos, Caño La Insula, 4°18'59.8" N; 72°03'57.6" W, 5 March 2008, E. Aya-Baquero, Rincón M. Meta: MPUJ 10047, 5 (2 C&S), 26.9–36.7 mm SL, Mapiripán Municipality, Caño Claro, tributary of the Guaviare River, 03°7'5.1''N; 72°30'14.8''W, 16 September 2013, J. E. Zamudio. MPUJ 10048, 3 (1 C&S), 24.5–29.1 mm SL, Mapiripán Municipality, Caño La División, 3°7'26.60" N; 72°32'18.50" W, 17 September 2013, J. E. Zamudio. MPUJ 10790, 2, 36.1–37.0 mm SL, Vista Hermosa municipality, Sardinata River, 3°1'7.10" N; 73°50'27.40" W, 25 January 2014, J. E. Zamudio. MPUJ 11256, 2, 31.8–32.6 mm SL, Mapiripán Municipality, 3°5'19.86" N; 72°35'2.31" W, 6 June 2011, J. E. Zamudio. MHNU-I 3256, 6, 27.2–33.4 mm SL, same data as holotype. MHNU-I 3337, 5, 17.2–34.8 mm SL, Puerto Gaitán municipality, 11 March 2021. MHNU-I 3325, 4, 20.8–25.6 mm SL, Puerto Gaitán Municipality, 24 March 2021. MUSM 71201, 2, 27.–33.1mm SL, same data as holotype.

Genseq-2 coI. GenBank accession number. Obtained from paratypes MUSM 71201 (PP057713 and PP057714).

Diagnosis. *Pariolius pax* is distinguished from all congeners by having very faint cream bar (collar) or homogeneus coloration of the nuchal region (vs. well-defined white nuchal collar present), six branched caudal-fin rays on dorsal lobe (vs. 4–5 in *P. maldonadoi* **sp. nov.** and five in *P. armillatus*) and light brown in life (vs. 4–5 in *P. maldonadoi* **sp. nov.** and five in *P. armillatus*) and light rosy in life (vs. dark grey in life). Additionally, it is further distinguished from *P. maldonadoi* vs. by having deeper body (13.3–17.0% SL vs. 9.5–13.2% SL), deeper head at supraoccipital (48.0–51.5% SL *vs.* 35.7–41.6% SL) and deeper head at interorbital (34.5–43.5% SL *vs.* 26.3–29.9% SL). It is further distinguished from *P. armillatus* by having shorter preadipose distance (70.2–73.3% SL *vs.* 74.0–76.7% SL), deeper adipose fin (3.1–4.6% SL *vs.* 2.1–2.2% SL), larger eye (8.5–11.5% SL *vs.* 6.8–7.3% SL), and wider internostril distance (9.5–11.5% SL *vs.* 6.3–9.0% SL).

Description. Morphometric data present in Table 1. Body cylindrical, moderately elongated. Oval in cross section at dorsal-fin origin and compressed on caudal peduncle. Dorsal body profile nearly straight from snout tip to supraoccipital, slightly convex from supraoccipital to dorsal-fin origin, straight from dorsal-fin origin to adipose-fin origin, slightly convex from adipose-fin origin to posterior base of adipose-fin, straight from posterior adipose-fin base to caudal-fin origin. Ventral profile of head slightly convex from snout tip to pectoral-fin origin, nearly convex from pectoral-fin origin to pelvic-fin origin, straight descending from pelvic-fin to anal-fin origin, and slightly convex from anal-fin origin to caudal-fin origin. Anus pore located at level of one third of pelvic fin length; urogenital papilla close to anus pore (approximately eye diameter).

Head small, depressed ascending to supraoccipital, and trapezoidal in dorsal view (Figure 1). Mouth wide and subterminal. Snout short and rounded in dorsal view. Barbels shorts, slender, flatted. Maxillary barbel longest; inserted dorsal to upper lip, lateral and nearly posterior to anterior nostrils; anterior portion extending in superficial groove under anterior- and posterior-nostril region; tip of maxillary barbel surpassing pectoral-fin origin (one third pectoral-fin length). Mental barbels inserted midway between the anterior border of lower jaw and gular fold. Inner mental barbel shorter than outer barbel, inserted approximately posterior to third pore of preoperculomandibular laterosensory canal (pm3); tip of inner mental barbel surpassing the inner margin of branchiostegal membrane. Outer mental barbel inserted posterior to fourth pore of preoperculomandibular laterosensory canal (pm4); tip of outer mental barbel surpassing the pectoral-fin origin. Eye small, elliptical horizontally, slightly dorsal, and anterior to midpoint of head length. Orbital margin not free and pupil rounded. Nostrils arranged as in vertices of squared, anterior internostril distance similar to posterior internostril distance. Anterior nostril tubular, closer to upper lip than posterior nostril. Posterior nostril closer to anterior margin of eye than anterior nostril, anterior margin with flap.

TABLE 1. Morphometric data of *Pariolius* species. H (Holotype); Min (minimum); Max (maximum); SD (standard deviation); N= individuals.

	Pariolius armillatus Cope 1872					***Pariolius pax*** **New species**						***Pariolius maldonadoi*** **New species**					
	N	Min	Max	Mean	SD	N	H	Min	Max	Mean	SD	N	H	Min	Max	Mean	SD
Standard length (mm)	12	21.4	37.6	28.5	-	19	38.8	25.5	39.7	31.7	-	16	29.9	17.8	38.8	27.8	-
Percents of Standard Length																	
Predorsal distance	11	44.7	49.8	47.5	1.7	19	45.4	44.1	49.6	46.3	1.4	16	43.9	42.2	46.0	44.2	1.0
Preadipose distance	11	74.0	79.6	76.7	1.5	19	71.8	70.2	76.6	71.8	1.5	16	72.2	70.8	74.4	72.7	0.8
Prepectoral distance	11	21.2	26.4	23.6	1.6	19	21.4	19.2	24.8	23.1	1.3	16	23.6	19.6	26.2	23.0	1.6
Prepelvic distance	11	39.8	46.0	43.3	2.1	19	41.0	40.7	44.8	42.8	1.2	16	42.3	36.7	42.4	40.5	1.5
Preanal distance	11	66.6	74.3	70.1	2.2	19	69.1	64.1	69.1	67.5	1.1	16	69.1	61.8	70.1	67.2	1.8
Body depth	11	8.8	14.7	12.4	1.7	19	13.5	13.3	17.0	14.4	0.9	16	11.2	9.5	13.2	11.6	0.9
Caudal peduncle depth	11	7.3	9.2	8.5	0.6	19	9.8	8.5	10.4	9.5	0.5	16	8.9	7.6	9.0	8.4	0.4
Caudal peduncle length	11	11.7	15.3	13.3	1.1	19	15.6	13.2	16.5	15.0	0.9	16	14.7	14.3	17.2	15.6	0.8
Body width	6	14.3	18.5	17.0	1.6	19	17.1	15.9	18.9	17.6	0.8	16	16.2	13.7	17.9	16.3	1.0
Dorsal-fin base length	11	9.5	12.7	11.6	1.0	19	10.6	10.3	12.8	11.4	0.6	16	11.4	11.0	12.4	11.6	0.4
Anal-fin base length	11	16.4	20.1	17.6	1.2	19	18.1	16.9	18.7	18.0	0.4	16	18.1	14.7	20.8	18.1	1.3
Unbranched dorsal-fin ray length	11	10.8	19.6	14.1	2.7	19	9.9	9.3	13.6	12.4	1.3	16	12.9	9.2	14.1	12.8	1.2
Dorsal-fin length	11	11.0	19.4	15.0	2.5	19	15.6	14.3	16.8	15.4	0.8	16	16.3	11.8	18.0	15.3	1.3
Adipose-fin depth	11	2.0	3.6	2.6	0.5	19	3.1	3.1	4.6	3.8	0.4	16	2.9	1.9	4.7	3.2	0.8
Adipose-fin base length	11	17.1	21.0	19.2	1.5	19	23.6	20.8	25.1	23.6	1.0	15	23.3	22.7	25.1	22.5	0.7
Interdorsal distance	11	15.6	19.4	17.4	1.3	19	17.1	12.4	18.0	15.8	1.4	16	17.8	16.7	18.5	17.4	0.5
Unbranched pectoral-fin ray length	11	9.9	17.5	12.6	2.6	19	11.9	10.3	14.0	12.2	1.0	16	13.3	9.8	13.8	12.9	0.9
Pectoral-fin length	11	11.5	15.6	13.7	1.5	19	15.6	13.0	16.0	14.8	0.8	16	14.9	11.4	16.5	15.2	1.2
Pelvic-fin length	11	10.8	16.9	13.5	2.2	19	13.4	12.5	16.2	14.2	1.1	16	14.5	13.9	17.0	15.1	1.0
Pectoral-pelvic fins distance	11	18.4	23.6	21.3	1.6	19	20.6	20.6	24.6	22.1	1.1	16	20.0	17.3	23.0	20.0	1.2
Pelvic-anal fins distance	11	25.3	28.8	26.5	1.0	19	25.5	24.3	26.3	25.3	0.5	16	27.6	26.0	28.1	27.1	0.7
Dorsal-fin insertion-hypural plate	6	52.7	55.8	53.7	1.1	19	55.8	53.5	58.3	55.6	1.0	16	56.8	55.1	58.9	56.7	1.0

...Continued on the next page

TABLE 2. (Continued)

	Pariolius armillatus Cope 1872					**Pariolius pax** **New species**						**Pariolius maldonadoi** **New species**					
	N	Min	Max	Mean	SD	N	H	Min	Max	Mean	SD	N	H	Min	Max	Mean	SD
Pelvic-fin insertion-hypural plate	6	56.7	59.7	57.8	1.2	19	60.2	57.4	60.2	58.8	0.8	16	60.9	58.1	62.6	60.8	1.1
Anal-fin insertion-hypural plate	11	30.5	34.9	31.9	1.6	19	33.2	32.7	35.0	33.7	0.7	16	33.4	31.9	36.1	33.5	1.2
Ventral caudal-fin lobe length	11	16.3	24.0	20.4	2.2	19	18.3	17.4	21.2	19.8	0.9	15	21.5	18.0	25.8	22.5	1.8
Dorsal caudal-fin lobe length	11	18.5	25.5	22.9	2.0	19	21.9	20.7	25.7	23.3	1.2	14	29.7	24.4	42.6	29.6	4.2
Percents of Head Length																	
Head length	11	20.7	26.8	23.3	1.5	19	22.5	22.5	26.1	25.0	0.9	16	23.4	21.7	26.7	24.0	1.2
Snout length	11	30.2	40.2	34.8	2.5	19	33.2	32.9	37.2	35.2	1.2	16	35.9	31.4	37.8	35.3	2.1
Orbital diameter	11	6.8	15.0	11.1	2.8	19	10.0	8.5	11.5	10.0	0.7	16	11.6	3.7	12.0	10.6	1.9
Head width	11	68.3	94.2	82.3	10.0	19	72.0	69.0	73.0	71.7	0.9	16	66.3	64.3	68.3	66.3	1.2
Mouth width	11	41.5	58.8	49.5	6.5	19	46.0	42.8	50.9	46.6	1.6	16	46.2	44.3	47.7	46.0	1.1
Maxillary barbel length	11	99.3	137.3	122.2	11.6	19	93.7	83.5	104.9	95.3	7.2	16	109.8	91.9	119.4	107.8	6.5
External mandibular barbel length	11	62.8	102.4	86.3	11.7	19	74.9	66.4	79.6	74.6	3.3	16	78.5	77.5	88.2	82.7	3.4
Internal mandibular barbel length	11	51.4	71.3	57.5	5.3	19	59.5	55.7	67.5	59.9	2.7	16	60.2	55.4	66.3	59.3	3.4
Postorbital distance	6	47.7	63.4	55.4	6.6	19	57.8	56.0	60.4	58.3	1.2	16	56.1	55.3	59.7	56.9	1.2
Interorbital width	11	22.0	29.4	26.8	2.4	19	25.9	23.4	26.3	24.9	0.8	16	23.1	20.1	27.7	24.0	1.8
Snout-anterior nostril distance	6	11.5	13.7	12.8	0.8	19	11.0	8.9	12.9	10.5	1.0	16	10.7	7.7	12.9	10.7	1.3
Internostril distance	11	6.3	20.9	14.9	4.8	19	11.1	9.3	11.5	10.3	0.7	16	9.1	6.6	10.7	9.1	1.0
Posterior nostril-orbit distance	11	4.9	21.2	13.0	7.1	19	5.8	4.3	7.0	6.0	0.6	16	8.0	4.4	9.6	7.5	1.5
Head depth at supra occipital	11	37.7	57.0	49.4	6.6	19	49.9	48.0	51.5	49.5	1.1	16	38.2	35.7	41.6	38.9	1.7
Head depth at interorbital	6	23.7	38.2	32.1	5.6	19	38.1	34.5	43.5	37.5	1.9	16	28.0	26.3	29.9	28.2	1.1
Head width at posterior nostril	6	53.3	60.3	56.6	2.4	19	61.9	58.6	64.7	62.1	1.2	16	56.2	54.2	59.4	57.5	1.4
Dorsal head length	6	84.0	91.9	88.7	3.1	19	86.0	81.8	87.9	85.2	1.3	16	88.6	85.4	90.9	87.7	1.4

TABLE 2. Pairwise genetic distances for the cytochrome oxidase c subunit 1 (*coI*) gene using the Kimura 2 parameter.

	1	2	3
1. *Pariolius armillatus* (Nanay River)	**0**		
2. *Pariolius* sp. (Itaya River)	**15.4**		
3. *Pariolius pax* (Orinoco River)	**12.7**	**14.8**	
5. *Pariolius maldonadoi* (Orinoco/Amazonas River)	**15.4**	**13.2**	**10.5**

Pectoral fin rays i + 7 (14), distal margin rounded; unbranched pectoral-fin ray soft and short (0.8–0.9 times length of pectoral-fin length); second pectoral-fin ray (first branched rays) as long as third ray (second branched ray); last branched rays short and decreasing gradually; tip of pectoral fin not reaching pelvic-fin origin. Pelvic fin rays i + 5 (14), distal margin rounded; unbranched pelvic-fin rays soft and shorter than branched pelvic-fin rays; second pelvic-fin ray (first unbranched ray) shorter than third ray (second branched rays); third pelvic-fin ray (second branched ray) as long as and fourth ray (third branched ray); last two branched rays short and decreasing gradually; pelvic-fin origin anterior to midpoint body (excluding caudal fin), anterior to vertical through dorsal-fin origin; tip of pelvic fin surpassing the urogenital papilla (one half its length). Insertion of first pelvic-fin ray on basipterygium at vertical through between centra 13–14.

Dorsal fin rays i + 6 (14), distally rounded in lateral profile, unbranched dorsal fin soft and short (0.7–0.8 times length of longest dorsal-fin rays) followed by six branched rays decreasing gradually in length; dorsal fin origin anterior to vertical through pelvic-fin origin. First dorsal-fin pterygiophore inserted on bifid neural spine of vertebra 13 (2). Last dorsal-fin pterygiophore inserted between space of neural spine of vertebrae 15–16 (1) or 16–17 (1). Anal-fin rays iv + 8 (1), v + 7 (4), iii + 8 (3), iii +9 (5), v + 9 (1). Anal fin convex and short (0.2 times its standard length). Anal-fin origin anterior to vertical through adipose-fin origin, last anal-fin ray slightly posterior to half adipose-fin base length. First anal-fin pterygiophore inserted between hemal spines of vertebrae 22–23 (2); last anal-fin pterygiophore inserted between hemal spines of vertebrae 29–30(1) or 30–31 (1); anal fin with 11 (1) or 12 (1) pterygiophores. Adipose fin short (0.2–0.3 times of standard length), rectangular and gently convex in lateral profile (Figure 1a); adipose-fin base longer than dorsal to adipose fin distance (1.2–1.9 times its length) and anal-fin base (1.2–1.5 times its length). Adipose-fin origin posterior of anal-fin origin and posteriorly not continuous with dorsal procurrent caudal-fin rays. Insertion of adipose fin at vertical through vertebrae centra 27–28; terminus of adipose fin at vertebrae 38–39.

Caudal fin gently emarginate with rounded border, dorsal lobe slightly longer than ventral lobe; dorsal caudal lobe with six (14) branched rays; ventral lobe with five (8) or six (6) branched rays. Total caudal-fin rays 40 (2) or 42 (1); with 20 (1) or 21(2) rays on the dorsal lobe and 19 (1), 20 (1) or 21(1) rays on ventral lobe. Five hypural series: hi1, hi2, hi3, hi4, and hi5. Ventral caudal plate (hi1 and hi2) free from parhypural, dorsal caudal plate hi3, hi4 separated from hi5 or fused (Figure 2A).

Canals of laterosensory system with simple pores and arrangement according to figure 3. Supraorbital canal with four branches: s1, s2, s3 and s8; each supraorbital laterosensory opening into a single pore, except branch s2 fused with antorbital branch (s2+i2). Infraorbital canals with six branches: i1, i2, i3, i4, i5 and i6; all opening into its own, except branch i2 fused with s2 opening into a single pore (s2+i2). Preoperculomandibular canal with 11 branches: pm1, pm2, pm3, pm4, pm5, pm6, pm7, pm8, pm9, pm10 and pm11; all opening into its own pore except branch pm11, fused with branch po1 (pm11+po1). Postotic canal with three branches: po1, po2 and po3; all opening into its own pore except branch po1 fused with pm11 opening into a single pore (pm11+po1). Lateral line incomplete, last pore approximately at vertical through the end of anal-fin base.

Total vertebrae 40 (1) or 41 (2). 14 (2) or 15 (1) vertebrae with incomplete hemal spine on vertebrae. 26 (2) or 27 (1) vertebrae with complete hemal spine. Six (3) pair ribs.

Osteology. Cranial skeleton (Figure 4) not ornamented; dorsal surface straight or slightly convex without crests; orbital region well defined dorsally; slightly concave, limited by lateral ethmoid anteriorly, frontal laterally, and sphenotic posteriorly; interorbital approximately half its length; two cranial fontanels separated by epiphyseal bar; posterior and anterior fontanels similar width; posterior fontanel longer than anterior in length; anterior and posterior region of anterior fontanel rounded; anterior region of posterior fontanel triangular and posterior region rounded; epiphyseal bar located to midpoint of frontal length. Mesethmoid with dorsal and ventral horizontal plane; anterolateral mesethmoid in dorsal horizontal plane, anterolateral mesethmoid ramus shorter, thicker, and more blunt-tipped than posterolateral mesethmoid, and anterolaterally directed; posterolateral mesethmoid anterolaterally projected forming a conspicuous cornu; region between posterior border of posterolateral mesethmoid and anterior border of lateral ethmoid filled by ethmoidean cartilage. Vomer arrow-shaped, posterior portion longer than lateral arms, anterior margin of vomer anterior of posterolateral mesethmoid cornu. Lateral ethmoid slightly quadrangular; posterior and anterior face straight and lateral face concave; posterior portion longer than anterior portion; posterolateral angle more pointed than anterolateral angle. Premaxilla rectangular, size three times its width, anterior margin continuous and without process, posterolateral angle not pronounced; six or seven irregular rows of villiform teeth. Maxilla small and trapezoidal (distal margin longer than proximal margin), distal region forming bony tubule attached to maxillary barbel. Autopalatine rod-like, shorter than orbital region; small cartilages at extremities, anterior cartilage longer than posterior one. Nasal bone poorly ossified, shorter and narrower than autopalatine. Antorbital poorly ossified triangular, and shorter than autopalatine. Frontal smooth and lacking any process; anteriorly limited by lateral ethmoid, posterolaterally limited by sphenotic and posteriorly limited by supraoccipital; posterior portion slightly wider than anterior portion; orbital face straight. Sphenotic longer and gently narrower than pterotic length; anterior portion with anterior and lateral process. Pterotic shorter and wider than sphenotic; anterior and posterior portion with similar width. Supraoccipital limited laterally by posterior portion of sphenoid and the pterotic; supraoccipital process thin and not reaching the anterior region of complex *centra* (in dorsal view).

Complex anterior vertebra (Figure 5A). Composed of first five vertebrae; vertebra 1 disc-like element and attached to complex vertebra with tissues ventrally; complex vertebra (vertebrae 2 to 4) attached to vertebra 5 with suture ventrally; neural spine of vertebra 4 not covering neural spine of vertebra 5. Transverse process of vertebra 4 divided in anterior and posterior branches. Anterior branch of transverse process of vertebra 4 wide, laminar, and expanded laterally; proximal portion wider than distal portion. Posterior branch of transverse process of vertebra 4 arborescent; proximal region wider than distal region; distal region divided in anterior and posterior portion; anterior portion laminar, rectangular, notched and joined to distal region of the posterior portion; posterior portion triangular. Transverse process of vertebra 5 is expanded and not branched.

Suspensory (Figure 6A). Entopterygoid small and slightly triangular; posterior edge concave and attached to anterior margin of metapterygoid. Metapterygoid quadrangular, smooth, and approximately three times entopterygoid size; dorsal margin convex; posteroventral and medial margin of metapterygoid attached with dentate suture and cartilaginous bar to dorsal margin of quadrate; and ventral margin joint with anterodorsal process of quadrate. Quadrate approximately quadrangular and slightly shorter than hyomandibula; anterior and posterior portion separates; anterior margin of quadrate with long anterodorsal process covering ventrolateral margin of metapterygoid; dorsal margin gently concaves along its free dorsal margin; posterior and ventral margin join to hyomandibula with denticulate suture and cartilaginous bar; anteroventral portion of quadrate with robust quadrangular process to articulate to angulo- retroarticular. Hyomandibula quadrangular; mostly smooth; anterodorsal margin slightly concave; posterodorsal hyomandibular process slightly rectangular with posterior margin gently pointed. Opercle triangular and two times interopercle length; anterior and posterior margins convex, ventral-posterior margin slightly convex, and dorsal margin straight; Interopercle triangular; anterior, posterior, and dorsal margin pointed; ventral margin slightly convex, anterodorsal and posterodorsal region concave.

Branchial arches (Figure 7A). Three basibranchial series: bb2, bb3, and bb4 (basibranchial 1 absent). Basibranchial 2 anteroposteriorly elongate, largely ossified, size is three times bb3 length, anterior portion wider than posterior portion. Basibranchial 4 completely cartilaginous, quadrangular shape; bordered by cartilaginous heads of hb3 anteriorly, cb5 posteriorly and cb4 laterally. Three hypobranchial series: hb1, hb2, hb3. Hypobranchial 1 laterally elongate, largely ossified, size more than three times its greatest width, cartilage in extremities, anterior portion with uncinate process. Hypobranchial 2 slightly elongate, *L*-shape, anterior portion ossified and posterior portion cartilaginous with similar size. Hypobranchial 3 completely cartilaginous, rectangular, elongate anterolaterally. Five ceratobranchial series: cb1, cb2, cb3, cb4, cb5; fully ossified with cartilage only at their distal and proximal extremities; ceratobranchial 1, 2 and 3 similar size and longer than ceratobranchial 4 and 5. Ceratobranchial 1 to 4 with similar width along its length. Ceratobranchial 5 expanded anteromedially to support patch of conical teeth, teeth with similar size and covering more than two-thirds of cb5 length. Four epibranchial series plus accessory element of ceratobranchial 4: eb1, eb2, eb3, eb4, and aecb4; first four rod-shaped, anteromedial narrower than posterolateral portion; eb1, eb2, eb3 and eb4 mostly ossified; aecb4 cartilaginous; epibranchial 1 and 2 similar size and longer than epibranchial 3 and 4. Epibranchial 3 with triangular posterior uncinate process close to epibranchial 4. Epibranchial

4 expanded at anterior and posterior portion. Two pharyngobranchial series: pb3 and pb4; pharyngobranchial 1 and 2 absent. Pharyngobranchial 3 rod-like, ossified, anterior portion narrower than posterior portion; posterior margin mostly expanded. Pharyngobranchial 4 ossified; quadrangular and anteroposteriorly elongate.

Color. Dorsal and lateral surface of body cream covered by brown marbled melanophores in preserved specimens and light rosy in life (Figure 8A). Ventral surface of head cream. Upper portion of head covered by brown pigment; cheeks with brown scattered melanophores fading ventrally. Dorsal surface of head between eyes and supraoccipital with dark brown quadrate spot. Very faint cream bar (collar) above pectoral fins contacting each other dorsally. Region between posterior margin of eye and maxillary barbel insertion with dark brown bar. Maxillary barbel pigmented with dark brown dorsally (until one half its length) and ventrally unpigmented. Outer mental barbel pigmented with dark brown dorsally (until one half its length) and ventrally unpigmented. Inner mental barbel unpigmented (some brown melanophores at base). At least seventeen brown chevron-shape lines marking the myosepta, progressively narrower, more angled, and intense posteriorly. Dorsal, anal, caudal, pectoral, and pelvic fins with dispersal brown melanophores along rays and inter-radial membranes devoid of melanophores. Base of caudal fin with dark brown semilunar spot. Base of dorsal and anal fins with concentration of dark brown melanophores. Adipose fin with concentration of brown melanophores (half its height) and distal region unpigmented. Lateral line with dark brown and narrow stripe, nearly convex above pectoral fin and straight along midbody from that point to caudal-fin base and more intense anteriorly (Figure 2), lateral stripe more intense in life (Figure 8A).

Geographic distribution. *Pariolius pax* is distributed in small tributaries to the Guaviare River and Meta River in the Orinoco River basin, Meta State, Colombia (Figure 9).

Etymology. The specific epithet is the Latin noun *pax*, which means peace and is in honor of the Colombian peace process signed in 2012. Peace allowed for access to territories that were previously not possible due to the armed conflict, such as Mapiripán, Meta; this species was recorded in this place, and it was a municipality where a massacre occurred in 1997. Treated as a noun in apposition.

Pariolius maldonadoi new species

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(Figs. 10 a–c, Tables 1, 2)

Holotype. MHNU-I 3257, 29.9 mm SL, Colombia, Guaviare State, Retorno Municipality, Caño Potosí, tributary of the Inírida River, Orinoco River basin, 2°10'50.8"N; 72°38'48.8"W, 27 February 2021, J. M. Vásquez-Ramos, M. A. Cortés-Hernández, J. M. Quiñones-Montiel, Y. A. Rojas-Molina, J. A. López-Castaño.

Paratype. Thirty specimens, **all from Colombia: Amazon River basin:** Guaviare State: MPUJ 13074, 11, 19.3–38.8 mm SL, Calamar Municipality, Caño Bálsamo, tributary of the Unilla River, Upper Negro River, 1°57'59.0"N; 72°37'16.5"W, 11 January 2017, C. Moreno-Arias. **Orinoco River basin:** Meta State: IAvH-P-16263, 1, 22.5 mm SL, La Macarena Municipality, unnamed creek tributary to El Silencio Lake, Guayabero River, 02°14'57.5"N; 73°45'33.8"W, 28 October 2016, L. Mesa Salazar, C. A. Lasso, P. Herrera. IAvH-P-16293, 1, 26.6 mm SL, La Macarena Municipality, Canoas creek, tributary to Guayabero River, 02°28'29.8"N; 73°44'33.2"W, 31 October 2016, C. A. Lasso, M. Morales-Betancourt, P. Herrera. Guaviare State: MPUJ 13075, 1, 33.5 mm SL, El Retorno Municipality, Caño Platanales, tributary of Inírida River, 2°10'50.81"N; 72°38'48.80"W, 11 January 2011, C. Moreno-Arias. MPUJ 13076, 5, 23.2–35.4 mm SL, El Retorno Municipality, Caño Blanco, tributary of the Inírida River, 2°11'1.72"N; 72°41'26.99"W, 12 January 2017, C. Moreno-Arias. MPUJ 13077, 5, 17.8–27.3 mm SL, El Retorno Municipality, Caño Potosí, tributary of the Inírida River, 2°12'18.40"N; 72°38'14.71"W, 12 January 2017, C. Moreno-Arias. MHNU-I 3250, 6, 20.7–32.6 mm SL, same data as holotype. MUSM 71200, 2, 20.5–28.5 mm SL, same data as holotype.

Genseq-2 coI. GenBank accession number. Obtained from paratypes MUSM 71200 (PP057715).

Diagnosis. *Pariolius maldonadoi* is distinguished from all congeners by having six branched pectoral-fin rays (vs. seven branched rays) and narrower head (64.3–68.3 % SL vs. 69.0–73.0% in *P. pax* and 68.3–94.2% SL in *P. armillatus*). It is further distinguished from *P. pax* by having well-defined white nuchal collar (vs. very faint or undistinguishable white nuchal collar), five branched caudal-fin rays on dorsal lobe (vs. six branched rays), deeper body (9.5–13.2% SL *vs.* 13.3–17.0% SL), deeper head at supraoccipital (35.7–41.6% SL *vs.* 48.0–51.5% SL), deeper head at interorbital (26.3–29.9% SL *vs.* 34.5–43.5% SL). Additionally, *Pariolius maldonadoi* can be distinguished from *P. armillatus* by having longer adipose fin *vs.* 17.1–21.0% SL).

Description. Morphometric data present in Table 1. Body moderately elongated. Cylindrical in cross section at dorsal-fin origin and compressed on caudal peduncle. Dorsal body profile straight from snout tip to supraoccipital, nearly convex from supraoccipital to dorsal-fin origin, straight from dorsal-fin origin to adipose-fin origin, slightly convex from adipose-fin origin to caudal-fin origin. Ventral profile of head gently convex from snout tip to pectoral-fin origin, convex from pectoral-fin origin to pelvic-fin origin, straight from pelvic-fin to anal-fin origin, and from anal-fin origin to caudal-fin origin. Anus pore located at level of one third of pelvic fin length, urogenital papilla close to anus pore (separated approximately eye diameter).

Head small (0.2–0.3 times of SL), depressed (ascending to supraoccipital), and trapezoidal in dorsal view (Figure 10). Mouth wide and subterminal. Snout short and rounded in dorsal view. Barbels shorts, slender, flatted. Maxillary barbel longest; inserted dorsal to upper lip, lateral and gently posterior to anterior nostrils; anterior portion extending in superficial groove under anterior- and posterior-nostril region; tip of maxillary barbel surpassing pectoral-fin origin (one third pectoral-fin length). Mental barbels inserted midway between the anterior border of lower jaw and gular fold. Inner mental barbel shorter than outer barbel and inserted posterior to third pore of preoperculomandibular laterosensory canal (pm3); tip of inner mental barbel reaching pectoral-fin origin. Outer mental barbel inserted approximately posterior to midway between fourth and fifth pore of preoperculomandibular laterosensory canal; tip of outer mental barbel surpassing the pectoral-fin origin. Eye small, elliptical horizontally, slightly dorsal, and anterior to midpoint of head length. Orbital margin not free and pupil rounded. Nostrils arranged as in vertices of squared, anterior internostril distance similar than posterior internostril distance. Anterior nostril tubular, closer to upper lip than posterior nostril. Posterior nostril closer to anterior margin of eye than anterior nostril, anterior margin with flap.

Pectoral fin rays i +6 (16), distal margin rounded; unbranched pectoral-fin ray soft and short (0.8–0.9 times length of pectoral-fin ray); second pectoral-fin ray (first branched rays) as long as third ray (second branched ray); last branched rays short and decreasing gradually; tip of pectoral fin behind vertical through pelvic-fin origin. Pelvic fin rays i + 5 (16), distal margin rounded; unbranched pectoral -fin rays soft and short (0.7 times length of pelvic-fin ray); second pelvic-fin ray (first unbranched ray) shorter than third ray (second branched rays); third pelvic-fin ray (second branched ray) as long as and fourth ray (third branched ray); last two branched rays short and decreasing gradually; pelvic-fin origin anterior to midpoint body (excluding caudal fin) and anterior to vertical through dorsal-fin origin; tip of pelvic fin surpassing the urogenital papilla (one half its length). Insertion of first pelvic-fin ray on basipterygium at vertical through between centra 13–14.

Dorsal fin rays i + 6 (16), distally rounded in lateral profile, unbranched dorsal-fin soft and short (0.8–0.96 times length of longest dorsal-fin rays) followed by six branched rays; dorsal-fin origin anterior to vertical through pelvic-fin origin. First dorsal-fin pterygiophore inserted on bifid neural spine of vertebrae 13 (2). Last dorsal-fin pterygiophore inserted between space of neural spine of vertebrae 16–17 (2) or 17–18 (1). Anal fin rays iv + 7 (1), iii + 8 (2), iv +8 (12), v + 8 (1). Anal fin convex and short (0.1–0.2 times its standard). Anal-fin origin anterior to vertical through adipose-fin origin, and last anal-fin ray slightly anterior to half adipose-fin base length. First anal-fin pterygiophore inserted between hemal spines of vertebrae 24–25 (3). Last anal-fin pterygiophore inserted between hemal spines of vertebrae 31–32(3). Anal fin with 12 (2) pterygiophores. Adipose fin short (0.2–0.25 times its standard length), rectangular and slightly convex in lateral profile (Figure 1a); adipose-fin base longer than dorsal to adipose fin distance (1.1–1.5 times its length) and anal-fin base (1.2–1.6 times its length). Adipose-fin origin posterior of anal-fin origin and terminus not continuous with dorsal procurrent caudal-fin rays. Insertion of adipose fin at vertical through vertebrae centra 28–29 (2); and terminus of adipose fin at vertebrae 39–40 (2). Caudal fin gently emarginate, dorsal lobe longer and pointed than ventral lobe; dorsal caudal lobe with rarely four (2) or usually with five (13) branched rays; ventral lobe with rarely four (4) or usually five (11) branched rays. Total caudal-fin rays 36 (2) or 37 (1); with 18 (2) or 19 (1) rays on dorsal lobe and 18 (3) rays on ventral lobe (Figure 2B).

Canals of laterosensory system with simple pores and arrangement according to Figure 11. Supraorbital canal with four branches: s1, s2, s3 and s8; each supraorbital laterosensory opening into a single pore, except branch s2 fused with antorbital branch (s2+i2). Infraorbital canals with six branches: i1, i2, i3, i4, i5 and i6; all opening into its own, except branch i2 fused with s2 opening into a single pore (s2+i2). Preoperculomandibular canal with 11 branches: pm1, pm2, pm3, pm4, pm5, pm6, pm7, pm8, pm9, pm10 and pm11; all opening into its own pore except branch pm11, fused with branch po1 (pm11+po1). Postotic canal with three branches: po1, po2 and po3; all opening into its own pore except branch po1 fused with pm11 opening into a single pore (pm11+po1). Lateral line incomplete, last pore approximately at vertical through end of dorsal-fin base.

Total of vertebrae 41 (1) or 41 (2). 14 (1) or 15 (1) vertebrae with incomplete hemal spine. 27 (1) or 28 (2) vertebrae with complete hemal spine. Six (3) pair ribs.

Osteology. Cranial skeleton (Figure 12) not ornamented; dorsal surface straight or slightly convex and without crests; orbital region well defined dorsally; slightly concave and limited by lateral ethmoid anteriorly, frontal laterally, and sphenotic posteriorly; interorbital region similar its length; two cranial fontanels separated by epiphyseal bar; anterior fontanel wider than anterior one; posterior fontanel longer than anterior in length; anterior and posterior edge of anterior fontanel slightly rounded; anterior region of posterior fontanel triangular and posterior region rounded; epiphyseal bar located to anterior to midpoint of frontal length. Mesethmoid with dorsal and ventral horizontal plane; anterolateral mesethmoid in dorsal horizontal plane, anterolateral mesethmoid ramus shorter, narrower, and more blunt-tipped than posterolateral mesethmoid, and anterolaterally directed; posterolateral mesethmoid anterolaterally projected forming a conspicuous cornu. Vomer arrow-shape, posterior portion longer than lateral arms, anterior margin of vomer at same level of posterolateral mesethmoid cornu. Lateral ethmoid slightly quadrangular; posterior and anterior face straight and lateral face concave; posterior portion longer than anterior portion; posterolateral angle more pointed than anterolateral angle. Premaxilla rectangular, size three times its width, anterior margin continuous and without process, posterolateral angle not pronounced; five or six rows of villiform teeth on premaxilla. Maxilla small and trapezoidal (distal margin longer than proximal margin), distal region forming bony tubule attached to maxillary barbel. Autopalatine rod-like, shorter than orbital region. Nasal bone poorly ossified, and shorter and narrower than autopalatine. Antorbital poorly ossified triangular, and shorter than autopalatine. Frontal smooth and lacking any process; anteriorly limited by lateral ethmoid, posterolaterally limited by sphenotic and posteriorly limited by supraoccipital; posterior portion slightly wider than anterior portion; orbital face straight. Sphenotic longer and gently narrower than pterotic length; anterior portion with anterior and lateral process. Pterotic shorter and wider than sphenotic; anterior and posterior portion with similar width. Supraoccipital limited laterally by posterior portion of sphenoid and the pterotic; supraoccipital process thin and not reaching the anterior region of complex *centra* (in dorsal view).

Complex anterior vertebra (Figure 5B). Composed by vertebrae 1, 2, 3, 4 and 5; vertebrae 1 disc-like element and attached to complex vertebra with tissues ventrally; complex vertebra (vertebrae 2 to 4) attached to vertebra 5 with suture ventrally; neural spine of vertebra 4 not covering neural spine of vertebra 5. Transverse process of vertebra 4 divided in anterior and posterior branches. Anterior branch of transverse process of vertebra 4 wide, laminar, and expanded laterally; proximal portion wider than distal portion. Posterior branch of transverse process of vertebrae 4 arborescent; proximal region wider than distal region; distal region divided in anterior and posterior portion; anterior portion laminar, rectangular, notched and joined to distal region of the posterior portion; posterior portion triangular. Transverse process of vertebra 5 is expanded and not branched.

Suspensory (Figure 6B). Entopterygoid small and rectangular; posterior edge concave and attached to anterior margin of metapterygoid. Metapterygoid rectangular, smooth, and approximately three times entopterygoid size; dorsal margin convex; posteroventral and medial margin of metapterygoid attached with dentate suture and cartilaginous bar to dorsal margin of quadrate; posterodorsal margin joint with dentate suture to anterodorsal margin of hyomandibula and ventral margin joint with anterodorsal process of quadrate. Quadrate approximately rectangular and similar size than hyomandibula; anterior and posterior portion separates; anterior margin of quadrate with long and strong anterodorsal process covering ventrolateral margin of metapterygoid; dorsal margin straight along its free dorsal margin; posterior and ventral margin join to hyomandibula with denticulate suture and cartilaginous bar; dorsal margin joint to posterodorsal margin of metapterygoid and anteroventral margin of hyomandibula; anteroventral portion of quadrate with rectangular process to articulate to angulo-retroarticular. Hyomandibula quadrangular; mostly smooth; anterodorsal margin slightly concave; posterodorsal hyomandibular process triangular with posterior margin very pointed. Opercle triangular and less than two times interopercle size; anterior and posterior margins rounded, ventral margin slightly convex, posterior and dorsal margin slightly concave. Interopercle triangular; anterior, posterior, and dorsal margin pointed; ventral margin convex, anterodorsal straight and posterodorsal margin concave.

Branchial arches (Figure 7B). Three basibranchial series: bb2, bb3, and bb4 (basibranchial 1 absent). Basibranchial 2 anteroposteriorly elongate, largely ossified, anterior portion wider than posterior, size is three times bigger than bb3 length, anterior portion wider than posterior portion. Basibranchial 3, completely cartilaginous, size two times its anterior width size, anterior portion wider than posterior region. Basibranchial 4 completely cartilaginous, rectangular shape; bordered by cartilaginous heads of hb3 anteriorly, cb5 posteriorly and cb4 laterally. Three hypobranchial series: hb1, hb2, hb3. Hypobranchial 1 laterally elongate, largely ossified, size three times its greatest width, cartilage just in proximal and distal extremities, anterior portion with uncinate process. Hypobranchial 2 slightly elongate, L-shape, anterior portion ossified and posterior portion cartilaginous with two times ossified size. Hypobranchial 3 completely cartilaginous, triangular, elongate laterally. Five ceratobranchial series: cb1, cb2, cb3, cb4, cb5; fully ossified with cartilage at their extremities; ceratobranchial 1, 2 and 3 similar size and longer than ceratobranchial 4 and 5. Ceratobranchial 1 to 4 with similar width along its length. Ceratobranchial 5 expanded anteromedially to support patch of conical teeth, teeth with similar size and covering one-half of cb5 length. Four epibranchial series plus accessory element of ceratobranchial 4: eb1, eb2, eb3, eb4, and plus accessory element of ceratobranchial 4; first four epibranchials rod-shaped, anteromedial narrower than posterolateral portion; eb1, eb2, eb3 and eb4 mostly ossified; aecb4 cartilaginous; epibranchial 1 and 2 similar size and longer than epibranchial 3 and 4. Epibranchial 3 with rectangular posterior uncinate process. Epibranchial 4 expanded at anterior and posterior portion. Two pharyngobranchial series: pb3 and pb4; pharyngobranchial 1 and 2 absent. Pharyngobranchial 3 rod-like, ossified, anterior portion narrower than posterior portion; posterior margin mostly expanded. Pharyngobranchial 4 ossified; rectangular and anteroposteriorly elongate.

Colour in alcohol. Dorsal and lateral surface of body dark brown (Figure 9) and dark grey in life (Figure 8B). Ventral body surface cream. Upper portion of head covered by brown pigment, surface between posterior eye margins and supraoccipital more intense; cheeks with brown scattered melanophores fading ventrally. Cream bar (collar) above pectoral fins contacting each other dorsally. Region between posterior margin of eye and maxillary barbel insertion with dark brown bar. Maxillary barbel pigmented with dark brown dorsally (one half its length) and ventrally unpigmented. Outer mental barbel pigmented with dark brown dorsally (until one third its length) and ventrally unpigmented. Inner mental barbel unpigmented (some brown melanophores at base). At least twenty-four brown chevron-shape lines marking the myosepta at the posterior region of the body, progressively narrower, more angled, and intense posteriorly. Dorsal-, anal-, pectoral-, and pelvic-fin with some dispersal brown (preserved) and grey (life) melanophores along rays and inter-radial membranes devoid of melanophores. Caudal- and adipose-fin with marbled. Caudal-fin base with triangular spot dark brown (preserved) and dark grey (life). Lateral line with dark brown and narrow stripe; nearly convex above pectoral fin and straight along midbody from that point to caudal-fin base and more intense anteriorly.

Geographic distribution. *Pariolius maldonadoi* is distributed is small tributaries to the Inírida and Guayabero rivers in the Orinoco River basin, Meta State and Vaupes River in the Rio Negro basin, Guaviare State, Colombia (Figure 9).

Etymology. The specific name is in honor of the authors' colleague and friend *in memoriam*; to Javier Maldonado-Ocampo, professor of the Pontificia Universidad Javeriana in Bogotá, Colombia for his great contribution and devotions to the Colombian and Neotropical Ichthyology. Treated as a noun in the genitive case.

Identification key of *Pariolius*

1 Body color light brown; caudal-fin base with a triangular dark brown spot; very faint or undistinguishable white nuchal collar. . . . . *P. pax* sp. nov. (Orinoco)
- Body color dark brown; caudal-fin base with a semilunar dark brown spot; well-defined white nuchal collar.
2 Six branched rays in pectoral fin; subterminal mouth, upper jaw longer than lower jaw; long adipose-fin base, 22.7–25.1 % of SL. . . . . *P. maldonadoi* sp. nov. (Orinoco/Amazonas)
- Seven branched rays in pectoral fin; upper mouth, lower jaw longer than upper jaw; short adipose-fin base, 17.1–21.0 % of SL. . . . . *P. armillatus* (Amazonas)

Molecular results

The cytochrome oxidase subunit I (*coI*) matrix comprising 567 pb x 79 individuals. The novel sequences were for *Pariolius armillatus* (PP057711), *Pariolius* sp. Nanay (PP057712), *P. maldonadoi* and *P. pax.* The nucleotide frequencies for *Pariolius armillatus* is 27. 5% (T), 29.3% (C), 24.7% (A) and 18.5% (G); *P. pax* is 30.2% (T), 27.0% (A), 25.7% (C) and 17.1% (G); *P. maldonadoi* has 29.1% (T), 27.3% (A), 26.6 (T) and 16.9 (G).

The phylogenetic analysis (Fig. 13) strongly supports the monophyly of *Pariolius* (BI=1). Within *Pariolius, P. pax* and *P. maldonadoi* from the Orinoco River was strongly supported as sisters (BI = 1), both previous species were strongly supported (BI = 1) to be sister to *Pariolius armillatus* from the Nanay River in Peru, and all previous species strongly supported (BI = 1) to be sister to an undescribed *Pariolius* from the Itaya River in Peru. Genetic divergence among *Pariolius* species is generally high (10.5–16.2%, (Table 2), *Pariolius maldonadoi* diverges 10.5% from *Pariolius pax* moreover it diverges 15% from *Pariolius armillatus*, nevertheless *P. pax* specimens diverge 12.7 % from *Pariolius armillatus*.

The species delimitation GMYC model estimated using a birth–death branching rate prior showed a threshold time of –0.0125, which indicates the time before all nodes reflect diversification and after which all nodes reflect the coalescent events (Figure 13). The maximum likelihood for the null model was 395.996 and the maximum likelihood for the GMYC model was 430.901. Single threshold models from GMYC also supported the presence of 4 operational taxonomy units (OTUs) within *Pariolius* species (Figure 13). The PTP analysis using 100000 generation of Monte Carlo Markov Chain (MCMC) thinning 100, 0.1 burning within *Pariolius* showed acceptance rate 0.055, supporting the presence of 4 (OTUs) within the genus (Figure 13).

Discussion

Bockmann & Slobodian (2017) proposed some features to distinguished *Pariolius* from all Heptapteridae (see above). According to our analysis and inclusion of the new species we found most of them not exclusive to Pariolius. Posterior portions of the head with an unpigmented collar and region anterior to dorsal fin with an unpigmented mark are also present in most species of *Cetopsorhamdia*, and *Chasmocranus*. A dorsal lobe of the caudal fin slightly longer than the ventral lobe is present in most Heptapterinae. Mouth dorsal is present in *Phenacorhamdia*, but here we found *Pariolius* with subterminal mouth.

Based on previous studies and our results, *Pariolius* is distinguished from all Heptapterini genera by having the apomorphic character: distal region of anterior and the posterior portion of posterior branch of trp4 joined (Figure 5 A–B). Additionally, it can be distinguished from related genera, *Phenacorhamdia* and *Cetopsorhamdia,* by having the dorsal caudal-fin lobe longer than ventral lobe.

Pariolius armillatus is widely distributed along the Upper Amazon River basin in Brazil, Colombia, Ecuador, and Peru (Ortega & Vari, 1986; Bockmann & Guazzelli, 2003; Ferraris, 2007; Barriga, 2014; Donascimiento *et al.*, 2017). Despite several ichthyological expeditions being carried out along the main rivers of the Colombian River and well recorded Heptapteridae species in literature (Donascimiento *et al.*, 2017); *Pariolius pax* was found only in small creeks tributaries of the upper Orinoco River basin, while *P. maldonadoi* was found in small creeks tributaries of the Upper Orinoco and Negro Rivers. Here we increase two new species with specific distribution pattern, *P. maldonadoi* distributed within both basins (Amazon and Orinoco) and *P. pax* restricted to Orinoco River as found in the heptapterids *Nemuroglanis mariai* (Schultz 1944) and ‘*Chasmocranus*’ *rosae* Eigenmann 1922 and other fish groups (Crampton & Albert, 2003; Freeman *et al.*, 2007; Littmann, 2007; Willis *et al.*, 2007; Albert and Carvalho, 2011; Reis *et al.*, 2016; Van der Sleen & Albert, 2017). Thus, this geographical distribution shows us an interesting headwater capture scenario between the Amazon and Orinoco rivers to be investigated in future studies.

Genetic divergence result and species delimitation analyses based on GMYC and PTP are congruent to the morphological result, recognition the two new species of *Pariolius* as separate species (Figure 13 and Table 2). Furthermore, the previous molecular analysis based on UCEs dataset (Silva *et al.*, 2021) found *Pariolius armillatus* more related to *Phenacorhamdia* spp., we corroborated this hypothesis in this study based on *coI* gene. (Figure 13).

Comparative material examined

In addition to the comparative material listed by Faustino-Fuster *et al.* (2019), Faustino-Fuster & Ortega (2020), Faustino-Fuster *et al.* (2021) and Faustino-Fuster & de Souza (2022) the following lots were examined:

Pariolius armillatus: **All from Peru**: Loreto State: FMNH 139554, 1, 29.2 mm SL, Maynas. FMNH 140844, 1, 32.1 mm SL, Putumayo. FMNH 140850, 1, 27.8 mm SL, Putumayo. FMNH 142189, 2, 26.7–29.3 mm SL, Putumayo. FMNH 142297, 1, 30.2 mm SL, Putumayo. MCP 35607, 1, 21.7 mm SL, Parnayari creek, Jenaro Herrera. MCP 37408, 3, 12.3–27.2 mm SL, Chica creek, Jenaro Herrera. MCP 37496, 4, 14.2–28.9 mm SL, unnamed creek tributary to Parnayari creek, Jenaro Herrera. USNM 176001, 1, 31.3 mm SL, Peru, Mariscal Ramon Castilla, Pebas, Shansho Caño tributary to Río Amazon. **All from Colombia**: MPUJ 3460, 1, 24.5 mm SL, Leticia.

Pariolius cf. *armillatus*: All from Ecuador: All from Napo: FMNH 98303, 1, 26.5 mm SL, Sucumbios. FMNH 98304, 5, 14.9–39.6 mm SL, Sucumbios. FMNH 103238, 5, 27.1–36.5 mm SL, Sucumbios. FMNH 103237, 3, 13.1–20.5 mm SL, Sucumbios. FMNH 103239, 1, 19.4 mm SL, Palma Roja. FMNH 103240, 1, 24.1 mm SL, Palma Roja. FMNH 103241, 2, 25.2–26.7 mm SL, Orellana, San Sebastian del Coca. FMNH 103242, 9, 17.9–34.2 mm SL, Sucumbios, Palma Roja.

Pariolius sp: **All from Ecuador: Napo State:** ANSP 130595, 3, 24.1–34.2 mm SL, unnamed stream tributary to Conejo River, Santa Cecilia. ANSP 130596, 6, 16.0–35.8 mm SL, unnamed stream tributary to Aguarico River, Santa Cecilia. ANSP 130597, 3, 20.5–31.2 mm SL, unnamed stream tributary to Aguarico River, Santa Cecilia. ANSP 130598, 3, 33.5–35.1 mm SL, effluent to unnamed Lake, Santa Cecilia. ANSP 170611, 1, 34.4 mm SL, unnamed stream tributary to Aguarico River, Santa Cecilia. **All from Peru: Loreto:** FMNH 142750, 5, 28.5–44.4 mm SL, Contamana. FMNH 142855, 1, 32.8 mm SL, Yaquerana. FMNH 142905, 5, 31.2–37.1 mm SL, Contamana. FMNH 142912, 3, 30.7–40.2 mm SL, Contamana. FMNH 142916, 2, 36.8–38.2 mm SL, Contamana. FMNH 142925, 3, 37.1–41.1 mm SL, Contamana. FMNH 142986, 1, 39.2 mm SL, Contamana. FMNH 142988, 2, 36.0–37.7 mm SL, Contamana. FMNH 143087, 2, 19.4–24.9 mm SL, Contamana.

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