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Source: Ichthyology & Herpetology, 112(3) : 429-443

Published By: The American Society of Ichthyologists and Herpetologists

URL: https://doi.org/10.1643/i2023091

Ichthyology & Herpetology 112, No. 3, 2024, 429–443

Two New Species of *Rineloricaria* (Siluriformes: Loricariidae) from Trans-Andean Rivers of Colombia, Unveiled through Iterative Taxonomy

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Two new species of *Rineloricaria* are described from the trans-Andean region of Colombia. *Rineloricaria atratoensis*, new species, is distributed in the Atrato River and is distinguished by the absence of the mid-dorsal plate series and by having three rows of median abdominal plates, first (unbranched) ray of dorsal, pectoral, and pelvic fins extended as a short filament, and breeding males with hypertrophied odontodes on sides of head and dorsum of pectoral fin. *Rineloricaria giua*, new species, is found in the Magdalena and Ranchería Rivers and is distinguished by absence of mid-dorsal plate series and by having four or five rows of median abdominal plates, four plates along sides of dorsal-fin base, lateral margins of snout straight, and breeding males with hypertrophied odontodes on sides of head and dorsum of pectoral fin. Phylogenetic analyses of COI sequences of species of *Rineloricaria* from trans-Andean and Central American river basins revealed the different phylogenetic positions of the new species. Likewise, species delimitation analyses corroborated their status as independent lineages. An identification key for the trans-Andean and Central American species of *Rineloricaria* is provided.

Se describen dos especies nuevas de *Rineloricaria* de la región transandina de Colombia. *Rineloricaria atratoensis*, especie nueva, se distribuye en el río Atrato y se distingue por no tener la serie de placas dorsales medias, y por poseer tres series de placas abdominales medias, el primer radio (no ramificado) de las aletas dorsal, pectoral y pélvica extendido como un filamento corto, y machos reproductores con odontodes hipertrofiados en los lados de la cabeza y el dorso de la aleta pectoral. *Rineloricaria giua*, especie nueva, se encuentra en los ríos Magdalena y Ranchería y se distingue por la ausencia de la serie de placas dorsales medias, y por tener cuatro o cinco series de placas abdominales medias, cuatro placas a los lados de la base de la aleta dorsal, márgenes laterales del hocico rectos y machos reproductores con odontodes hipertrofiados en los lados de la cabeza y el dorso de la aleta pectoral. Los análisis filogenéticos de las secuencias COI de especies de *Rineloricaria* de las cuencas transandinas y centroamericanas, revelaron la diferente posición filogenética de las especies nuevas. Asimismo, los análisis de delimitación de especies corroboraron su condición de linajes independientes. Se proporciona una clave de identificación para las especies transandinas y centroamericanas de *Rineloricaria*.

THE genus *Rineloricaria* is the most species-rich genus of the loricariid subfamily Loricariinae, with 72 valid species (Fricke et al., 2024). Species of *Rineloricaria* are widely distributed in Central and South America, extending from Costa Rica to Argentina, typically inhabiting small streams or shallow areas of large rivers and are associated with submerged vegetation or rocky and sandy bottoms (Chamon and Fichberg, 2022; Costa-Silva et al., 2022).

Rineloricaria lacks exclusive diagnostic characters and is currently distinguished by a unique combination of characters (Fichberg and Chamon, 2008): postorbital notch present; 7–15 teeth on each premaxilla; dentary teeth bicuspid and larger than premaxillary teeth; lower lip with short, rounded papillae; dorsal region of the body with dark brown bars or blotches; and conspicuous polygonal preanal plate (except *R. setepovos*; Ghazzi, 2008). However, species of *Rineloricaria* are not always easily differentiated, due to high levels of intraspecific variation, which makes it difficult to define species boundaries (Costa-Silva et al., 2015). In addition, several species are only known from their types (some are lost) or from their old original descriptions, which are generally short and vague, in some cases preventing the names from being properly applied to extant specimens (Reis and Cardoso, 2001; Costa-Silva et al., 2015).

DoNascimiento et al. (2024) listed 11 species of *Rineloricaria* originally described or otherwise recorded from Colombia, with four species distributed in trans-Andean basins. *Rineloricaria magdalenae* was the first species described from Colombia, from the Magdalena River basin (Steindachner, 1879). This species has also been recorded from the Atrato River (Eigenmann, 1922) and from the Lake Maracaibo basin (Schultz, 1944). *Rineloricaria jubata* was originally described from the Durango River in northwestern Ecuador (Boulenger, 1902) and was later recorded from the Condoto

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Submitted: 3 November 2023. Accepted: 1 July 2024. Associate Editor: R. E. Reis.

DOI: 10.1643/i2023091

River in the Colombian Pacific (Regan, 1914) and from the Atrato River in the Caribbean versant (Eigenmann, 1922). *Rineloricaria sneiderni* was described from the Jurubidá River, on the Pacific coast of Colombia (Fowler, 1944). Finally, *R. rupestris* was originally described from the Lake Maracaibo basin in Venezuela (Schultz, 1944), and it was also recorded from the Catatumbo River in Colombia (Galvis et al., 1997).

However, a revision of the trans-Andean species of *Rineloricaria* is unavailable, hence the uncertainty about their actual diversity and geographic distribution. As trans-Andean Colombian freshwater ecosystems are being increasingly disturbed by anthropogenic interference, this knowledge gap turns into a conservation challenge. In this scenario, species delimitation becomes crucial to the establishment of well-informed, effective strategies for protecting these populations from decline (Jiménez-Segura and Lasso, 2020).

In the context of an ongoing, comprehensive systematic revision of Colombian *Rineloricaria*, two species from trans-Andean basins were recognized as different from the above accounted species and were distinguished both by morphological and molecular data using an iterative taxonomic approach (Yeates et al., 2011). Consequently, these species are described herein as new.

MATERIALS AND METHODS

Morphological data.—Measurements were taken as point-to-point linear distances with digital calipers on the left side of specimens whenever possible and recorded to the nearest 0.1 mm. Most measurements and counts followed Armbruster (2003) and Isbrücker and Nijssen (1978). Orbital diameter was measured according to Isbrücker (1973). Identification and counts of dermal plates follow the terminology proposed by Schaefer (1997: fig. 2). Counts of coalesced keels and lateral abdominal plates were made according to Reis and Pereira (2000). Data on dorsal series of plates and sexual dimorphism of species not distributed in Colombia were obtained from Vera-Alcaraz et al. (2012). Standard length (SL) was expressed in millimeters, while all other measurements are given as percent of SL or head length (HL). Institutional abbreviations follow Sabaj (2020).

Morphometric analyses.—A total of 92 specimens were used in the morphological analyses as follows: *Rineloricaria atratoensis*, new species (10), *R. giua*, new species (13), *R. jubata* (27), *R. magdalenae* (33), *R. rupestris* (9). Due to the low number of specimens of *R. sneiderni* (1), this species was not included in morphometric analyses, but its measurements were taken into account for the diagnoses of the new species. We used morphometric data from these specimens to perform principal component analysis (PCA) and linear discriminant analysis (LDA), using MASS package (Venables and Ripley, 2002) in R (R Core Team, 2023). Size effect was corrected using the ratio technique, i.e., each size variable was expressed as percent of SL and subsequently log-transformed. Then, we executed a variance inflation factor to remove variables with values below a threshold of 5 to reduce collinearity (Zuur et al., 2010). The classification model quality was evaluated with the use of the “leave-one-out cross-validation” (LOOCV) procedure (Hastie et al., 2009).

Molecular procedures.—Total DNA was extracted from either skin clips of right-side paired fins or muscle tissue samples from the caudal region, using Qiagen DNeasy kit, following the manufacturer’s protocol (Supplemental Table A; see Data Accessibility). A region of the mitochondrial gene cytochrome oxidase gene subunit I (COI) was amplified using the primers FishF1 and FishR1 (Ward et al., 2005). PCR conditions followed the protocols described in Cortés-Hernández et al. (2023). A sample of 5 μl of PCR products plus 2 μl of BlueJuice (Invitrogen) diluted in nuclease-free water and mixed with 0.8 μl of GelRed (Invitrogen) was visualized on 1% agarose gel and sent to Macrogen (https://www.macrogen.com) for sequencing. Chromatographs were checked and manually edited using Geneious Prime v. 2023.1.2 (https://www.geneious.com). Substitution saturation was evaluated by the Iss index in DAMBE 7 (Xia, 2018), as described by Xia et al. (2003) and Xia and Lemey (2009). COI sequences obtained in this study were deposited in GenBank (accession numbers PP409420–PP409470; Supplemental Table A; see Data Accessibility).

Phylogenetic analysis.—We complemented our molecular dataset with nine sequences retrieved from GenBank and Bold Systems of *Rineloricaria*, *Farlowella*, *Lamontichthys*, and *Sturisomatichthys* (Supplemental Material A; see Data Accessibility) that were used as outgroups. Sequences were aligned using the G-INS-i plugin in MAFFT v.7, under default parameters in Geneious (Katoh and Standley, 2013). The best partition scheme and model of evolution were estimated using ModelFinder (Kalyaanamoorthy et al., 2017), implemented in IQTREE 2 (Minh et al., 2020). A maximum-likelihood tree was inferred, and nodal support was obtained using the ultrafast bootstrap method on 5,000 pseudoreplicates, as implemented in IQTREE 2 (Hoang et al., 2018; Minh et al., 2020). Finally, uncorrected genetic distances were calculated using MEGA v. 11 (Tamura et al., 2021).

Species delimitation analyses.—Two methods for species delimitation were implemented. First, we used assemble species by automatic partitioning (ASAP; Puillandre et al., 2021), through its website (https://bioinfo.mnhn.fr/abi/public/asap), to divide the group into hypothetical species, based on the substitution model Kimura K80. We chose this specific model because ASAP offers only two model options (JC and K80); thus, we first used MEGA v. 11 (Tamura et al., 2021) to evaluate which model fit best to our data, that in this case was the seventh best ranked model (AICc = 5630.159). The second species delimitation method was Bayesian Poisson tree process (bPTP; Zhang et al., 2013), through its website (https://species.h-its.org/), to estimate the number of mutations between two branching events by the branch length information of the input phylogeny. We ran PTP analyses using a tree of ML inference as input, 500,000 MCMC generations with a thinning of 500 and a burn-in of 0.1. Outgroups were pruned before conducting PTP analyses to avoid bias that may arise if some of the outgroup taxa were too distantly related to the ingroup taxa.

Rineloricaria atratoensis, new species

urn:lsid:zoobank.org:act:82E4A522-A6C0-473A-839A-50CAF3A3BD86
Figures 1A, 2; Table 1

Rineloricaria magdalenae (not Steindachner). Maldonado-Ocampo et al., 2006: 148 (in part: IAvH-P 6760).

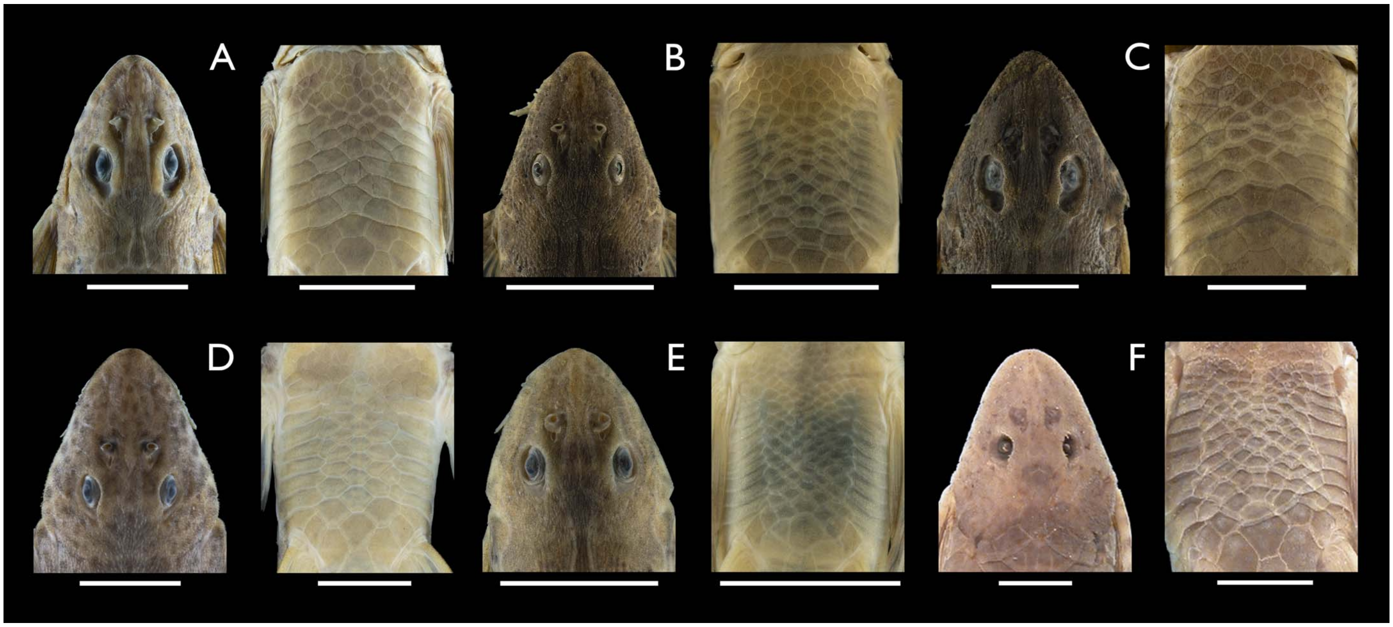

Fig. 1. Head and abdominal area showing ventral plates in (A) *Rineloricaria atratoensis*, CIUA 4629, holotype, 113.8 mm SL; (B) *R. giua*, CIUA 8370, paratype, 78.9 mm SL; (C) *R. magdalenae*, CIUA 7549, 114.6 mm SL; (D) *R. jubata*, IMCN 4015, 110.3 mm SL; (E) *R. rupestris*, CZUT-IC 19074, 99.1 mm SL; (F) *R. sneiderni*, ANSP 71433, holotype, 122 mm SL. Photographs in A–E by José Luis Londoño-López, copyright Colección de Ictiología de la Universidad de Antioquia; used with permission. Photographs in F by Kyle Luckenbill, copyright Ichthyology Department, Academy of Natural Sciences; used with permission. Scale bar 1 cm.

Rineloricaria sp. Maldonado-Ocampo et al., 2006: 148 (in part: IAvH-P 7403).

Holotype.—CIUA 4629, female, 113.8 mm SL, Colombia, Antioquia, Murindó, caño Chageradó, Atrato River basin, 06°49′56″N, 76°48′31″W, 8 m a.s.l., A. Loaiza, 15 March 2016.

Paratypes.—Colombia: Atrato River basin: Antioquia: CIUA 4767, 3, 88.4–108.9 mm SL, Murindó, caño Chageradó, 6°49′56″N, 76°48′31″W, 8 m a.s.l., A. Loaiza, 13 May 2015; CIUA 4770, 16, 61.9–118.4 mm SL, Vigía del Fuerte, caño El Chorro, 6°23′42″N, 76°44′36″W, 21 m a.s.l., A. Loaiza, 8 May 2015; CIUA 8683, 4, 108.8–117.1 mm SL, same locality and collector as CIUA 4767, 15 March 2016. Chocó: IAvH-P 614, 1, 132.7 mm SL, Atrato River, approx. 5°42′N, 76°37′W, 84 m a.s.l., P. A. Silverstone, 10 August 1971; IAvH-P 6760, 1, 126.3 mm SL, Atrato River, approx. 8°17′N, 76°58′W, 2 m a.s.l., Chaverra and Cuesta, 19 August 2004; IAvH-P 7279, 1, 100.6 mm SL, Atrato River, 7°52′44″N, 77°02′26″W, 3 m a.s.l., J. A. Maldonado-Ocampo, 17 July 2005; IAvH-P 7403, 1, 106.8 mm SL, Unguía River, 8°03′36″N, 77°07′21″W, 77 m a.s.l., J. A. Maldonado-Ocampo, 24 July 2005.

Diagnosis.—*Rineloricaria atratoensis* is distinguished from all trans-Andean and Central American congeners by having the first (unbranched) ray of dorsal, pectoral, and pelvic fins extended as a short filament (vs. coterminous with branched rays in *R. altipinnis*, *R. giua*, new species, *R. jubata*, *R. magdalenae*, *R. rupestris*, *R. sneiderni*, and *R. uracantha*). *Rineloricaria atratoensis* can also be distinguished from this group of species (except *R. magdalenae*) by having a paired deep depression between the nostrils and the interorbital region (vs. absent in *R. altipinnis*, *R. giua*, new species, *R. jubata*, *R. rupestris*, *R. sneiderni*, and *R. uracantha*). *Rineloricaria atratoensis* differs from *R. altipinnis*, *R. giua*, new species, *R. magdalenae*, *R. sneiderni*, and *R. uracantha* by having five plates along sides of dorsal-fin base (vs. four). *Rineloricaria atratoensis* differs from *R. altipinnis*, *R. giua*, new species, *R. rupestris*, *R. sneiderni*, and *R. uracantha* by having three rows of median abdominal plates (vs. four or more). The new species differs from *R. rupestris*, *R. sneiderni*, and *R. uracantha* by having six dark brown transverse bars on dorsal surface of body (vs. four or six). The new species is further distinguished from most of its congeners (except *R. aurata*, *R. beni*, *R. cadeae*, *R. castroi*, *R. catamarcensis*, *R. felipponei*, *R. giua*, new species, *R. lanceolata*, *R. langei*, *R. longicauda*, *R. magdalenae*, *R. misionera*, *R. nigricauda*, *R. pareiacantha*, *R. parva*, *R. quadrensis*, *R. sanga*, *R. setepovos*, *R. sneiderni*, *R. stellata*, *R. strigilata*, *R. thrissoceps*, *R. uracantha*, and *R. wolfei*) by absence of the mid-dorsal plate series (vs. present in *R. aequalicuspis*, *R. altipinnis*, *R. anhaguapitan*, *R. anitae*, *R. baliola*, *R. cacerensis*, *R. cachivera*, *R. capitonia*, *R. caracasensis*, *R. daraha*, *R. eigenmanni*, *R. fallax*, *R. formosa*, *R. hasemani*, *R. heteroptera*, *R. isaaci*, *R. jaraguensis*, *R. jubata*, *R. konopickyi*, *R. kronei*, *R. latirostris*, *R. maacki*, *R. malabarbai*, *R. maquinensis*, *R. melini*, *R. microlepidogaster*, *R. morrowi*, *R. nudipectoris*, *R. osvaldoi*, *R. pentamaculata*, *R. phoxocephala*, *R. platyura*, *R. reisi*, *R. rodriquezae*, *R. rupestris*, *R. steindachneri*, *R. stewarti*, *R. teffeana*, *R. tropeira*, and *R. zaina*). The new species differs from *R. cadeae*, *R. castroi*, *R. catamarcensis*, *R. langei*, *R. lima*, *R. longicauda*, *R. misionera*, *R. nigricauda*, *R. pareiacantha*, *R. parva*, *R. quadrensis*, *R. sanga*, *R. setepovos*, *R. stellata*, *R. strigilata*, and *R. uracantha* by breeding males with dimorphic odontodes on sides of head and on dorsum of pectoral fin (vs. breeding males lacking dimorphic odontodes). It is distinguished from *R. aequalicuspis*, *R. anhaguapitan*, *R. anitae*, *R. aurata*, *R. baliola*, *R. capitonia*, *R. isaaci*, *R. jaraguensis*, *R. kronei*, *R. latirostris*, *R. maacki*, *R. malabarbai*, *R. maquinensis*, *R.*

Fig. 2. Holotype of *Rineloricaria atratoensis*, CIUA 4629, 113.8 mm SL, female, caño Chageradó, Atrato River basin, Murindó, Antioquia, Colombia, 6°49′56″N, 76°48′31″W. Photograph by José Luis Londoño-López, copyright Colección de Ictiología de la Universidad de Antioquia; used with permission. Scale bar 1 cm.

microlepidogaster, *R. pentamaculata*, *R. reisi*, *R. rupestris*, and *R. tropeira* by having slender post-pectoral naked area (vs. wide).

Description.—Morphometric data in Table 1. Head and body depressed. Dorsal profile of head triangular. Snout elongated and tip rounded in dorsal view and straight (not raised) in lateral view (Fig. 1A). Naked area of snout tip transversally elliptical, not reaching first pore of infraorbital sensory canal. Dorsal profile convex from tip of snout to dorsal-fin origin, and straight to caudal-fin origin. Ventral profile straight from tip of snout to caudal-fin origin. Greatest body depth at posterior border of parieto-supraoccipital; lowest body depth along caudal peduncle (Fig. 2).

Hypertrophied odontodes of head small to moderate size, forming conspicuous ridges between nostrils, on posterior nasal plates to posterior margin of parieto-supraoccipital and compound pterotic. Five plates in infraorbital series, with sensory pores exposed ventrally. Predorsal plates and first three lateral plates of dorsal series slightly keeled, covered with small odontodes. Eye elliptical with large and deep postorbital notch, equal to half horizontal diameter of orbit (Fig. 1A).

Upper lip short and separated from naked area of snout by thin row of plates covered by tiny odontodes. Margin of upper lip with long, rugged, and regular papillae. Anteroventral border of upper lip separated from anterior border of premaxillary ramus by one row of papillae. Lower lip covered by irregular sized papillae, unorganized and distributed around oral cavity. Edge of lower lip with elongated, triangular fringes. Maxillary barbel long, with minute papillae. Teeth bicuspid and cusps rounded or slightly pointed; dentary teeth larger than premaxillary teeth. Premaxilla with 8(1), 10(1), 11(2)*, or 12(1) teeth; dentary with 9(1), 10(3)*, 11(2), or 12(1) teeth; accessory cusp almost of same size as main one.

Plates on median series 29(2), 30(6), or 31(2)*; coalesced plates 13(1), 14(3), or 15(6)*, lateral abdominal plates 5(1), 6(3), or 7(6)*; median abdominal plate rows 3(10)* (Fig. 1A). Lateral line complete. Mid-dorsal series absent. Lateral plates keeled with odontodes along lateral line. Abdomen totally covered by plates, including cleithral region (Fig. 1A). Abdominal plates organized in three sections: anterior abdominal plates small, quadrangular, covering pectoral girdle; median abdominal plates large and trapezoidal, between pectoral and pelvic girdles; posterior abdominal plates with preanal shield formed by three large plates surrounding polygonal preanal plate. Two plates along sides of anal-fin base.

Dorsal-fin rays i,7 (10), dorsal-fin spinelet present, locking mechanism not functional. Five plates along sides of dorsal-fin base. Pectoral-fin rays i,6 (10), adpressed unbranched ray slightly surpassing pelvic-fin origin. Pelvic-fin rays i,5 (10), adpressed unbranched ray reaching anal-fin origin. Anal-fin rays i,5 (10). Caudal-fin rays i,5 + 5,i (10); margin of fin emarginated, with long and thin filament on upper caudal-fin ray; lower caudal-fin ray filament absent.

Color in alcohol.—Background coloration of dorsal surface light brown. Pores of sensory system on head and lateral medial plates dark. Dorsal surface of body with six dark

Table 1. Morphometric data of *Rineloricaria atratoensis* and *R. giua*; *n* = number of specimens; Min = minimum; Max = maximum; SD = standard deviation. Holotype measurements are included in ranges.

	Rineloricaria atratoensis						*Rineloricaria giua*					
Measurements	Holotype	*n*	Min	Max	Mean	SD	Holotype	*n*	Min	Max	Mean	SD
Standard length (mm) (SL)	113.74	10	100.6	132.7	113.1		79.5	13	52.1	95.0	74.8	12.1
Percent of SL												
Head length (HL)	13.7	10	13.2	15.2	14.4	0.7	15.3	13	14.1	17.0	16.0	0.7
Predorsal length	29.8	10	29.7	32.9	31.2	1.2	34.2	13	30.1	34.7	33.0	1.3
Head-dorsal length	15.5	10	14.8	19	16.6	1.2	16.6	13	15.1	19.2	16.9	1.1
Head-pectoral length	14	10	14	16.4	15.2	0.8	18.5	13	14.3	19.2	17.7	1.4
Dorsal-spine length	21.5	10	21.5	24	22.5	0.8	19.8	13	18.9	22.5	20.2	1.1
Anal-spine length	17.1	10	16.2	19.9	17.6	1.2	17.0	13	15.4	19.0	17.3	1.0
Pectoral-spine length	16.1	10	15.5	18.8	16.9	1.1	16.3	13	15.6	19.1	16.7	1.0
Pelvic-spine length	16.7	10	14.3	19.6	17.1	1.6	15.2	13	13.5	16.2	15.1	0.8
Thoracic length	14.6	10	14.6	16.8	15.9	0.9	16.3	13	13.1	16.9	14.9	1.2
Abdominal length	15.1	10	13.7	16.9	14.8	0.9	14.6	13	13.5	15.5	14.6	0.7
Dorsal–pectoral distance	19.4	10	18.7	21.9	19.7	0.9	20.6	13	17.3	20.7	19.3	1.0
Dorsal–pelvic distance	10.6	10	10	12.9	10.9	0.9	10.5	13	9.0	11.8	10.6	0.9
Dorsal–anal distance	8.6	10	7.6	9.8	8.4	0.6	8.2	13	7.3	9.7	8.5	0.6
Dorsal-fin base length	8.7	10	8.1	10.6	9.3	0.7	9.4	13	7.5	10.2	8.9	0.8
Cleithral width	14	10	13.3	16.7	14.8	0.9	16.5	13	13.9	16.9	15.5	0.9
Caudal-peduncle depth	1.3	10	1.3	3	2.1	0.7	2.6	13	2.2	2.7	2.5	0.1
Postanal length	60.2	10	55.5	60.2	57.8	1.4	55.2	13	51.6	58.5	54.4	1.9
Percent of HL												
Snout length	64.5	10	60.1	67.3	64.3	1.9	74.0	13	63.8	74.0	69.4	3.1
Orbital diameter with notch	38.4	10	33.1	38.8	36.2	2.1	29.9	13	27.7	35.8	30.5	2.3
Interorbital width	35.6	10	31.3	35.7	33.8	1.4	41.2	13	33.8	43.8	38.8	2.9
Internare width	11.5	10	10.3	13.6	11.8	1	15.1	13	9.3	15.1	11.9	1.7
Head depth	67.1	10	60.9	68.6	64.1	2.4	66.4	13	54.5	66.4	60.7	4.0
Mouth length	48.6	10	48.6	61.9	55.1	5	70.9	13	55.0	76.6	65.3	6.7
Free maxillary barbel	17.2	10	14.5	27	20.3	4	15.8	13	10.6	20.8	15.0	3.0
Premaxillary ramus	7.7	10	7.7	12.2	9.2	1.4	8.9	13	8.7	11.5	10.0	0.9
Counts												
Premaxillary teeth	11	5	8	12			9.0	11	7.0	9.0		
Dentary teeth	10	7	9	12			8.0	11	8.0	9.0		
Median lateral plates	16	10	15	16			15.0	13	13.0	16.0		
Coalescent plates	15	10	13	15			14.0	13	12.0	15.0		
Lateral abdominal plates	6	10	5	7			6.0	13	6.0	7.0		
Caudal peduncle plates rows	16	10	16	17			17.0	13	16.0	17.0		
Median abdominal plates rows	3	10	3	3			5.0	13	4.0	5.0		
Transverse bars	6	10	6	6			5.0	13	5.0	6.0		
Dorsal-fin rays	i,7	10	i,7	i,7			i,7	13	i,7	i,7		
Pectoral-fin rays	i,6	10	i,6	i,6			i,6	13	i,6	i,6		
Pelvic-fin rays	i,5	10	i,5	i,5			i,5	13	i,5	i,5		
Anal-fin rays	i,5	10	i,5	i,5			i,5	13	i,5	i,5		
Caudal-fin rays	i,10,i	10	i,10,i	i,10,i			i,10,i	13	i,10,i	i,10,i		

brown transverse bars; first at dorsal-fin origin, second at level of tip of adpressed dorsal fin, following posterior bars on caudal peduncle. All fins covered by dark dots on fin rays. Ventral surface pale yellow (Fig. 2).

Distribution.—*Rineloricaria atratoensis* is only known from the Atrato River basin, draining directly to the Caribbean Sea, in northwestern Colombia (Fig. 3).

Sexual dimorphism.—Adult males with hypertrophied odontodes on sides of head and on dorsum of pectoral fin.

Etymology.—The species name *atratoensis* is in reference to its type locality, the Atrato River.

Remarks.—*Rineloricaria jubata* and *R. magdalenae* were originally recorded from the Atrato River by Eigenmann (1922), and subsequent authors (Mojica et al., 2004; Maldonado-Ocampo et al., 2006, 2012) have also listed these two species from the Atrato basin. Maldonado-Ocampo et al. (2006) recognized for the first time a third species of *Rineloricaria* from this basin, which was positively confirmed by us as *R. atratoensis* (IAvH-P 7403). However, another record listed by Maldonado-Ocampo et al. (2006) as *R. magdalenae* (IAvH-P 6760) turned out to be *R. atratoensis*, thus the presence of *R. magdalenae* as well as *R. jubata* in the Atrato River is the subject for confirmation in our ongoing systematic revision of *Rineloricaria* in Colombia.

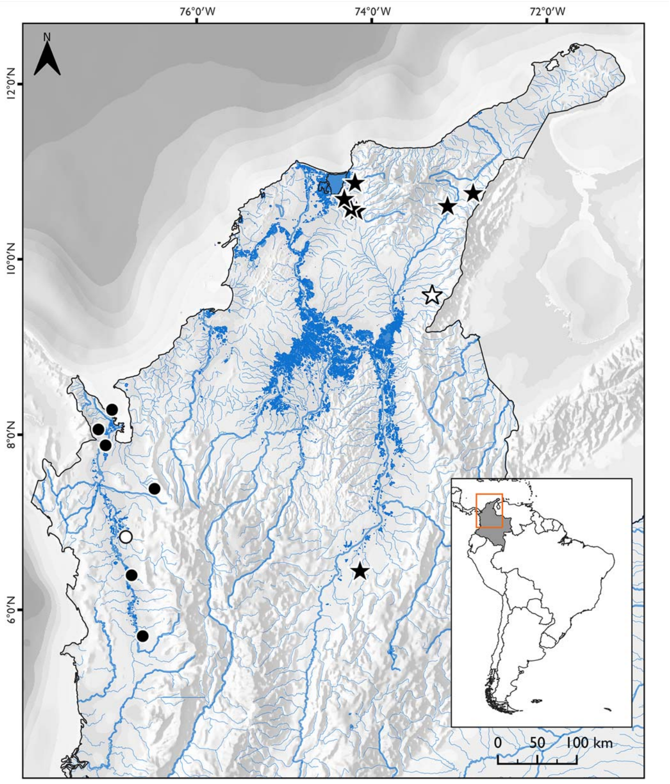

Fig. 3. Map of north region of Colombia showing distribution of *Rineloricaria atratoensis* (dots) and *R. giua* (stars). White symbols: type localities.

Rineloricaria giua, new species

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Figures 1B, 4, 5; Table 1

Holotype.—CIUA 8680, male, 79.5 mm SL, Colombia, Cesar, La Jagua de Ibirico, Tucuy River, Magdalena River Basin, 9°35′13″N, 73°18′34.9″W, 122 m a.s.l., V. M. Medina, J. G. Ospina, and D. Restrepo, 9 September 2023.

Paratypes.—Colombia: Magdalena River basin: Cesar: CIUA 8370, 8, 44.9–80.7 mm SL, La Jagua de Ibirico, Tucuy River, 9°35′13″N, 73°18′34.9″W, 122 m a.s.l., V. M. Medina, J. G. Ospina, and D. Restrepo, 9 September 2023; CIUA 8371, 1, 52.1 mm SL, Badillo, Badillo River, 10°36′12″N, 73°8′4″W, 195 m a.s.l., V. M. Medina, J. G. Ospina, and D. Restrepo, 9 September 2023. Magdalena: CZUT-IC 14919, 1, 81.0 mm SL, Aracataca, Aracataca River, 10°34′18″N, 74°14′18″W, 46 m a.s.l., J. G. Albornoz and G. Beltran, 14 October 2015; UARC-IC 1079, 3, 44.5–54.5 mm SL, Zona Bananera, Frío River, 10°52′06″N, 74°11′29″W. Santander: IAvH-P 20904, 1, 74.8 mm SL, Cimitarra, Carare River Basin, 6°26′23″N, 74°08′04″W, 121 m a.s.l., J. G. Albornoz, A. Méndez, and M. Arias, 13 July 2018. Ranchería River basin: La Guajira: CZUT-IC 17447, 2, 82.1–82.4 mm SL, San Juan del Cesar, Manantial Cañaverales, 10°45′01″N, 72°50′30″W, 281 m a.s.l., C. Conde, 2 March 2017.

Diagnosis.—*Rineloricaria giua* is distinguished from most trans-Andean and Central American congeners (except *R. jubata* and *R. uracantha*) by having four or five rows of median abdominal plates (vs. three in *R. atratoensis* and *R. magdalenae*, more than six in *R. altipinnis*, *R. rupestris*, and *R. sneiderni*). *Rineloricaria giua* is also distinguished from this group of species (except *R. magdalenae*) by having lateral margins of the snout straight (vs. convex in *R. altipinnis*, *R. atratoensis*, *R. jubata*, *R. rupestris*, *R. uracantha*, and *R. sneiderni*). *Rineloricaria giua* differs from *R. atratoensis*, *R. jubata* and *R. rupestris* by having four plates along sides of dorsal-fin base (vs. five). Also, *R. giua* is distinguished from *R. atratoensis* and *R. magdalenae* by absence of a paired deep depression between the nostrils and the interorbital region (vs. present) and postorbital notch small and shallow (vs. large and deep). The new species is further distinguished from most of its congeners (except *R. atratoensis*, *R. aurata*, *R. beni*, *R. cadeae*, *R. castroi*, *R. catamarcensis*, *R. felipponei*, *R. lanceolata*, *R. langei*, *R. longicauda*, *R. magdalenae*, *R. misionera*, *R. nigricauda*, *R. pareiacantha*, *R. parva*, *R. quadrensis*, *R. sanga*, *R. setepovos*, *R. sneiderni*, *R. stellata*, *R. strigilata*, *R. thrissoceps*, *R. uracantha*, and *R. wolfei*) by lacking the mid-dorsal plate series (vs. present in *R. aequalicuspis*, *R. altipinnis*, *R. anhaguapitan*, *R. anitae*, *R. baliola*, *R. cacerensis*, *R. cachivera*, *R. capitonia*, *R. caracasensis*, *R. daraha*, *R. eigenmanni*, *R. fallax*, *R. formosa*, *R. hasemani*, *R. heteroptera*, *R. isaaci*, *R. jaraguensis*, *R. jubata*, *R. konopickyi*, *R. kronei*, *R. latirostris*, *R. maacki*, *R. malabarbai*, *R. maquinensis*, *R. melini*, *R. microlepidogaster*, *R. morrowi*, *R. nudipectoris*, *R. osvaldoi*, *R. pentamaculata*, *R. phoxocephala*, *R. platyura*, *R. reisi*, *R. rodriquezae*, *R. rupestris*, *R. steindachneri*, *R. stewarti*, *R. teffeana*, *R. tropeira*, and *R. zaina*). The new species can be separated from *R. cadeae*, *R. castroi*, *R. catamarcensis*, *R. langei*, *R. lima*, *R. longicauda*, *R. misionera*, *R. nigricauda*, *R. pareiacantha*, *R. parva*, *R. quadrensis*, *R. sanga*, *R. setepovos*, *R. stellata*, *R. strigilata*, and *R. uracantha* by breeding males with dimorphic odontodes on sides of head and on dorsum of pectoral fin (vs. breeding males lacking dimorphic odontodes). Finally, the new species differs from *R. aequalicuspis*, *R. anhaguapitan*, *R. anitae*, *R. aurata*, *R. baliola*, *R. capitonia*, *R. isaaci*, *R. jaraguensis*, *R. kronei*, *R. latirostris*, *R. maacki*, *R. malabarbai*, *R. maquinensis*, *R. microlepidogaster*, *R. pentamaculata*, *R. reisi*, *R. rupestris*, and *R. tropeira* by having a slender post-pectoral naked area (vs. wide).

Description.—Morphometric data in Table 1. Head and body depressed. Dorsal profile of head triangular. Snout tip acutely pointed in dorsal view and straight (not raised) in lateral view (Fig. 1B). Naked area of snout tip transversally elliptical, not reaching first pore of infraorbital sensory canal. Dorsal profile convex from tip of snout to dorsal-fin origin, and straight to caudal-fin origin. Ventral profile straight from tip of snout to caudal-fin origin. Greatest body depth at posterior border of parieto-supraoccipital; lowest body depth along caudal peduncle (Fig. 4).

Hypertrophied odontodes of head small to moderate size, forming conspicuous ridges between nostrils, on posterior nasal plates to posterior margin of parieto-supraoccipital and compound pterotic. Five plates in infraorbital series, with sensory pores exposed ventrally. Predorsal plates and first three lateral plates of dorsal series slightly keeled, covered with small odontodes. Eye elliptical with small and shallow postorbital notch, slightly shorter than half of horizontal diameter of orbit (Fig. 1B).

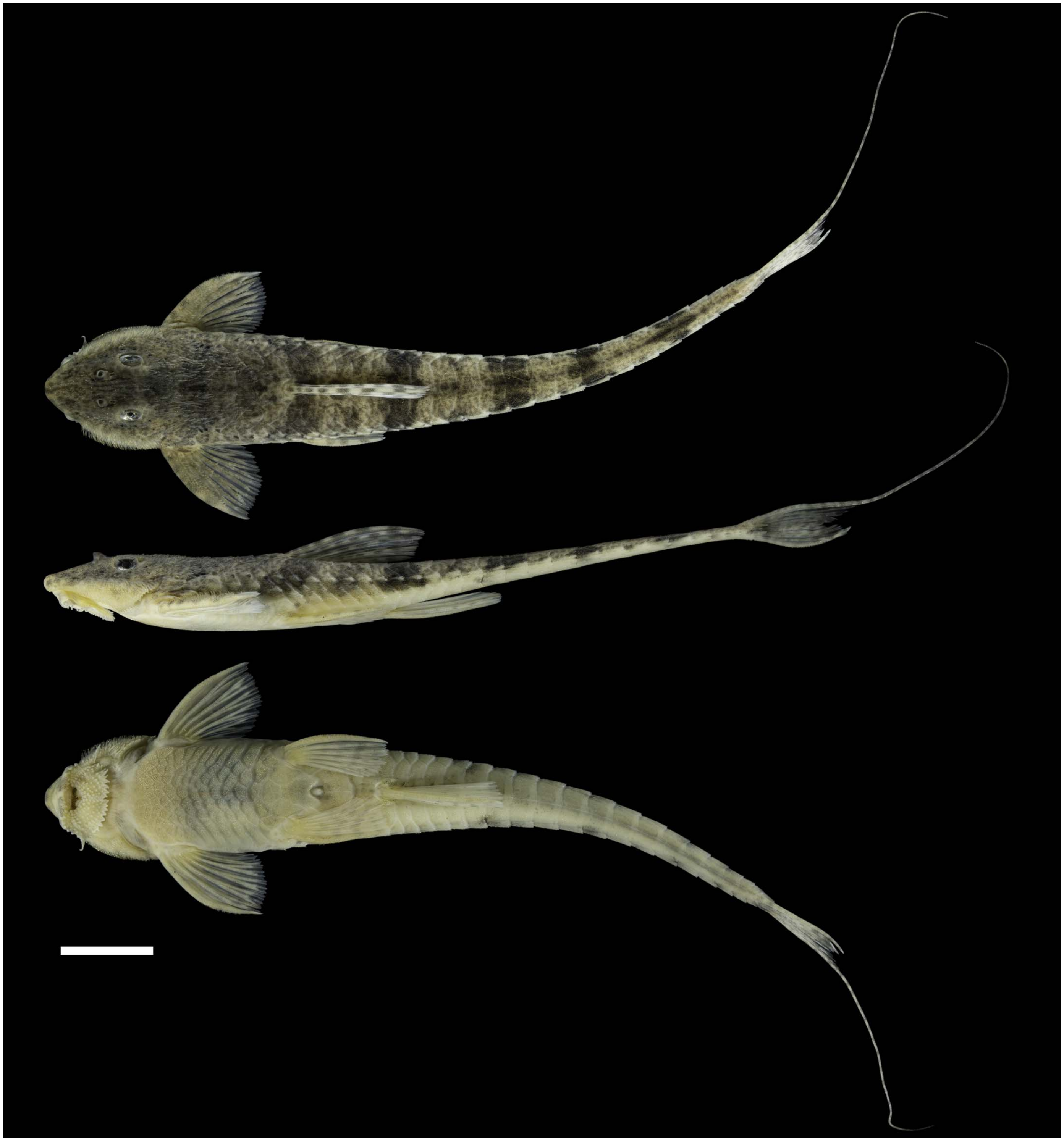

Fig. 4. Holotype of *Rineloricaria giua*, CIUA 8680, 79.5 mm SL, male, Tucuy River, Magdalena River basin, La Jagua de Ibirico, Cesar, Colombia, 9°35′13″N, 73°18′34.9″W. Photographs by José Luis Londoño-López, copyright Colección de Ictiología de la Universidad de Antioquia; used with permission. Scale bar 1 cm.

Upper lip short and separated from naked area of snout by thin row of plates covered by tiny odontodes. Margin of upper lip with long, rugged, and regular papillae. Anteroventral border of upper lip separated from anterior border of premaxillary ramus by one row of papillae. Lower lip covered by irregular sized papillae, unorganized and distributed around oral cavity. Edge of lower lip with elongated, triangular fringes. Maxillary barbel long, with minute papillae. Teeth bicuspid and cusps rounded or slightly pointed; dentary teeth larger than premaxillary teeth. Premaxilla with 7(3), 8(6), or 9(2)* teeth; dentary with 8(9)* or 9(2) teeth; accessory cusp almost of same size as main one.

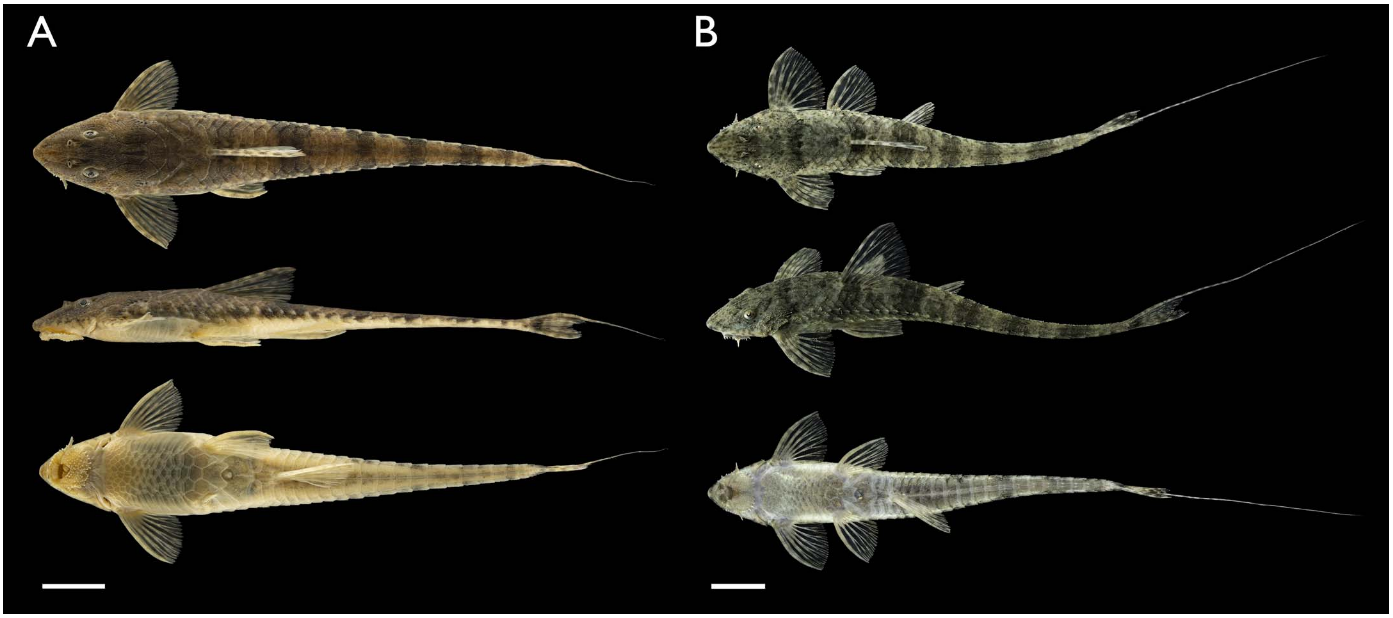

Fig. 5. Paratypes of *Rineloricaria giua*, CIUA 8370, 79.5 mm SL, female, Tucuy River, Magdalena River basin, La Jagua de Ibirico, Cesar, Colombia, 9°35′13″N, 73°18′34.9″W. (A) Preserved specimen; (B) live specimen. Photographs by José Luis Londoño-López, copyright Colección de Ictiología de la Universidad de Antioquia; used with permission. Scale bar 1 cm.

Plates on median series 28(1), 29(6)*, or 30(5), coalesced plates 12(1), 13(2), 14(6)*, or 15(4), lateral abdominal plates 6(9) or 7(4); median abdominal plate rows 4(11) or 5(2)* (Fig. 1B). Lateral line complete. Mid-dorsal series absent. Lateral plates keeled with odontodes along lateral line. Abdomen totally covered by plates, including cleithral region (Fig. 1B). Abdominal plates organized in three sections: anterior abdominal plates small, quadrangular, covering pectoral girdle; median abdominal plates large and trapezoidal, between pectoral and pelvic girdles; posterior abdominal plates with preanal shield formed by three large plates surrounding polygonal preanal plate. Two plates along sides of anal-fin base.

Dorsal-fin rays i,7 (12), dorsal-fin spinelet present, locking mechanism not functional. Four plates along sides of dorsal-fin base. Pectoral-fin rays i,6 (13), adpressed unbranched ray slightly surpassing pelvic-fin origin. Pelvic-fin rays i,5 (13), adpressed unbranched ray reaching anal-fin origin. Anal-fin rays i,5 (13). Caudal-fin rays i,5 + 5,i (13); margin of fin emarginated, with long and thin filament on upper caudal-fin ray; lower caudal-fin ray filament absent.

Color in alcohol.—Background coloration of dorsal surface light brown. Pores of sensory system on head and lateral medial plates dark. Dorsal surface of body with five or six dark brown transverse bars; first at dorsal-fin origin, second at level of tip of adpressed dorsal fin, following posterior bars on caudal peduncle. All fins covered by dark spots on fin rays. Ventral surface pale yellow (Fig. 4). Coloration in life similar to that in preserved specimens (Fig. 5B).

Distribution.—*Rineloricaria giua* is currently known from the Aracataca River in the lower section of the Magdalena River basin, from the Carare River in the middle section of the Magdalena River, and from the arroyo Manantiales, a tributary of the Caribbean Ranchería River (Fig. 3).

Sexual dimorphism.—Adult males with hypertrophied odontodes on sides of head and on dorsum of pectoral fin (Fig. 4), absent in females of similar size (Fig. 5A).

Etymology.—In honor of the Grupo de Ictiología of Universidad de Antioquia (acronym GIUA). Used as a noun in apposition.

Remarks.—*Rineloricaria giua* is widely distributed across the middle and lower sections of the Magdalena River, being sympatric and even syntopic with *R. magdalenae*. However, scarce records of the new species in ichthyological collections in Colombia suggest that populations of *R. giua* are less abundant when compared to the ubiquitous specimens of *R. magdalenae*.

Morphometric analysis.—The PCA analysis shows broad overlap of all species, with the first two axes accounting for 41.2% of the variance between groups (Fig. 6A). In turn, LDA analysis shows a clear separation of specimens corresponding to *Rineloricaria giua* (Fig. 6B), indicating that morphometric variables used in this study allow morphometric recognition of this species. Contrarily, *R. atratoensis* overlaps with *R. magdalenae*.

The first two LDA axes explain 79.7% of the variance (Fig. 6B), and the overall precision of the classification in the correct group was 75.3%. Variables with higher scores on the positive LD1 axis were postanal length, orbital diameter with notch, and abdominal length, while those on the negative side were mouth length, pectoral-spine length, and interorbital width. Higher positive scores for LD2 were accounted by abdominal length, interorbital width, and orbital diameter with notch; and for the negative axis, postanal length, dorsal-spine length, dorsal-fin base length, and internare width.

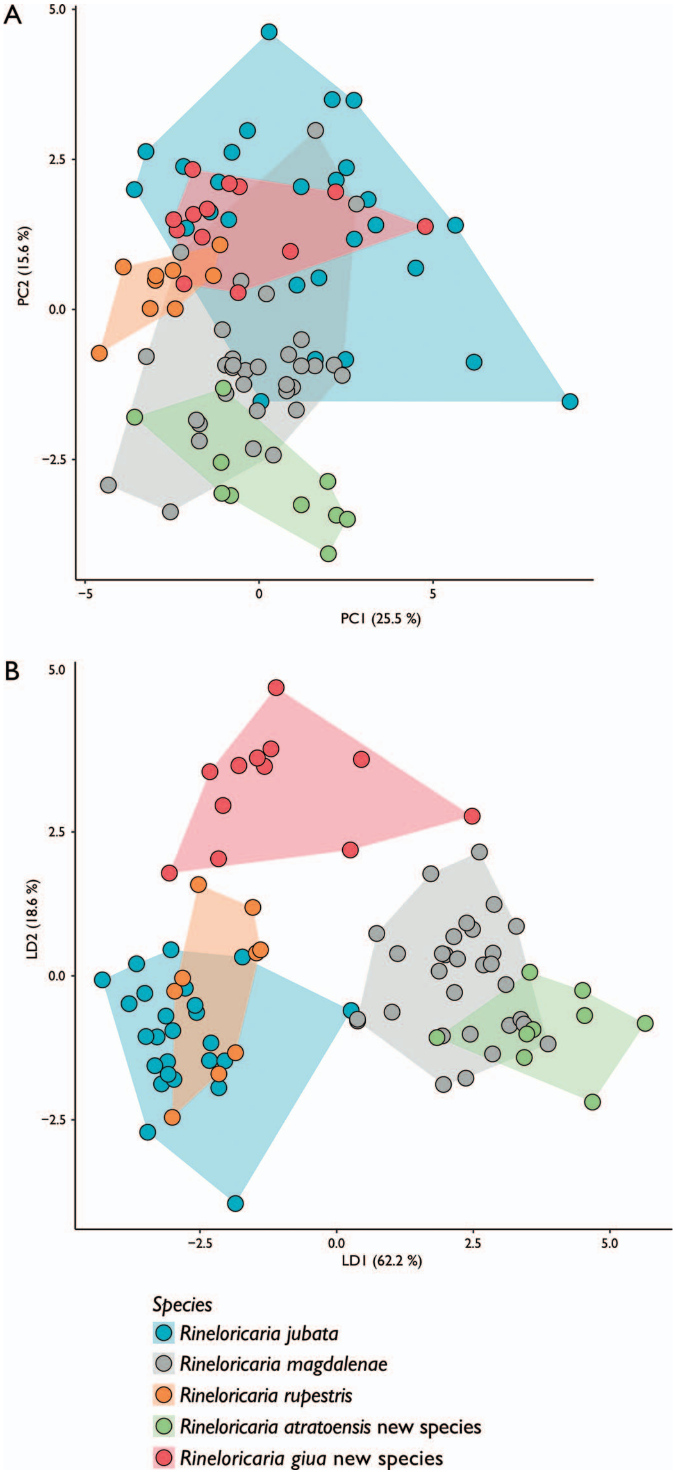

Fig. 6. Scatter plots of (A) principal component analysis (PC1 and PC2) and (B) linear discriminant analysis (LD1 and LD2), based on body measurements of trans-Andean species of *Rineloricaria* from Colombia.

Phylogenetic relationships.—The molecular dataset included 60 non-saturated COI sequences (Iss.c > Iss; 606 bp). The gene tree recovered *Rineloricaria* as monophyletic with node support above 95% (Fig. 7). Under this hypothesis, trans-Andean species are not grouped as a single clade. *Rineloricaria atratoensis* was recovered sister to *R. magdalenae* (node support: 98%). *Rineloricaria giua*, which was consistently found to be different from *R. magdalenae* in morphometric analyses (see above), was recovered as sister to a clade comprising *R. altipinnis*, *R. jubata*, *R. rupestris*, and *R. uracantha* (node support: 72%).

Genetic distances.—Distribution of paired genetic distances of sequences from the trans-Andean species in our analysis shows a variation range between 3.1% and 15.9%. The minimum interspecific genetic distance value found for *R. atratoensis* and *R. magdalenae* was 3.1%, while the maximum scores recorded between *R. atratoensis* and remaining species were 14.1–15.9%. For *R. giua*, genetic distances varied from 10.3% to 15.1% (Table 2).

Delimitation analyses.—Both ASAP and PTP analysis yielded the same 11 putative species, eight of them from the trans-Andean region (Fig. 7). In the ASAP analysis, the second partition was selected, since it agrees with our morphology-based species delimitation (score = 5.00). In the PTP analysis, support values for trans-Andean species were below 50%, except for *Rineloricaria giua*, which was 86.7% (Fig. 7).

KEY TO THE SPECIES OF RINELORICARIA FROM TRANS-ANDEAN AND CENTRAL AMERICAN RIVERS

1a. Mid-dorsal plate series absent 2
1b. Mid-dorsal plate series present 6
2a. Five plates along sides of dorsal-fin base, first (unbranched) ray of dorsal, pectoral, and pelvic fins extended as a short filament .... ***Rineloricaria atratoensis*, new species** (Fig. 2)
2b. Four plates along sides of dorsal-fin base, first (unbranched) ray coterminous with remaining branched rays 3
3a. 7–10 rows of median abdominal plates (Fig. 1F) .... ***Rineloricaria sneiderni*** (Fig. 8D)
3b. 3–5 rows of median abdominal plates 4
4a. Three rows of median abdominal plates, paired deep depression between nostrils and interorbital region, postorbital notch large and deep (Fig. 1C) .... ***Rineloricaria magdalenae*** (Fig. 8B)
4b. Four or five rows of median abdominal plates, absence of paired deep depression between nostrils and interorbital region, postorbital notch small and shallow 5
5a. Lateral margins of snout convex, four rows of median abdominal plates, five dark brown transverse bars on dorsal surface of body, breeding males lacking dimorphic odontodes on sides of head and on dorsum of pectoral fin .... ***Rineloricaria uracantha***
5b. Lateral margins of snout straight, four or five rows of median abdominal plates, five or six dark brown transverse bars on dorsal surface of body, breeding males with dimorphic odontodes on sides of head and on dorsum of pectoral fin (Fig. 4) .... ***Rineloricaria giua*, new species** (Fig. 4)
6a. Four plates along sides of dorsal-fin base .... ***Rineloricaria altipinnis***
6b. Five plates along sides of dorsal-fin base 7
7a. 3–5 rows of median abdominal plates, 5–6 dark brown transverse bars on dorsal surface

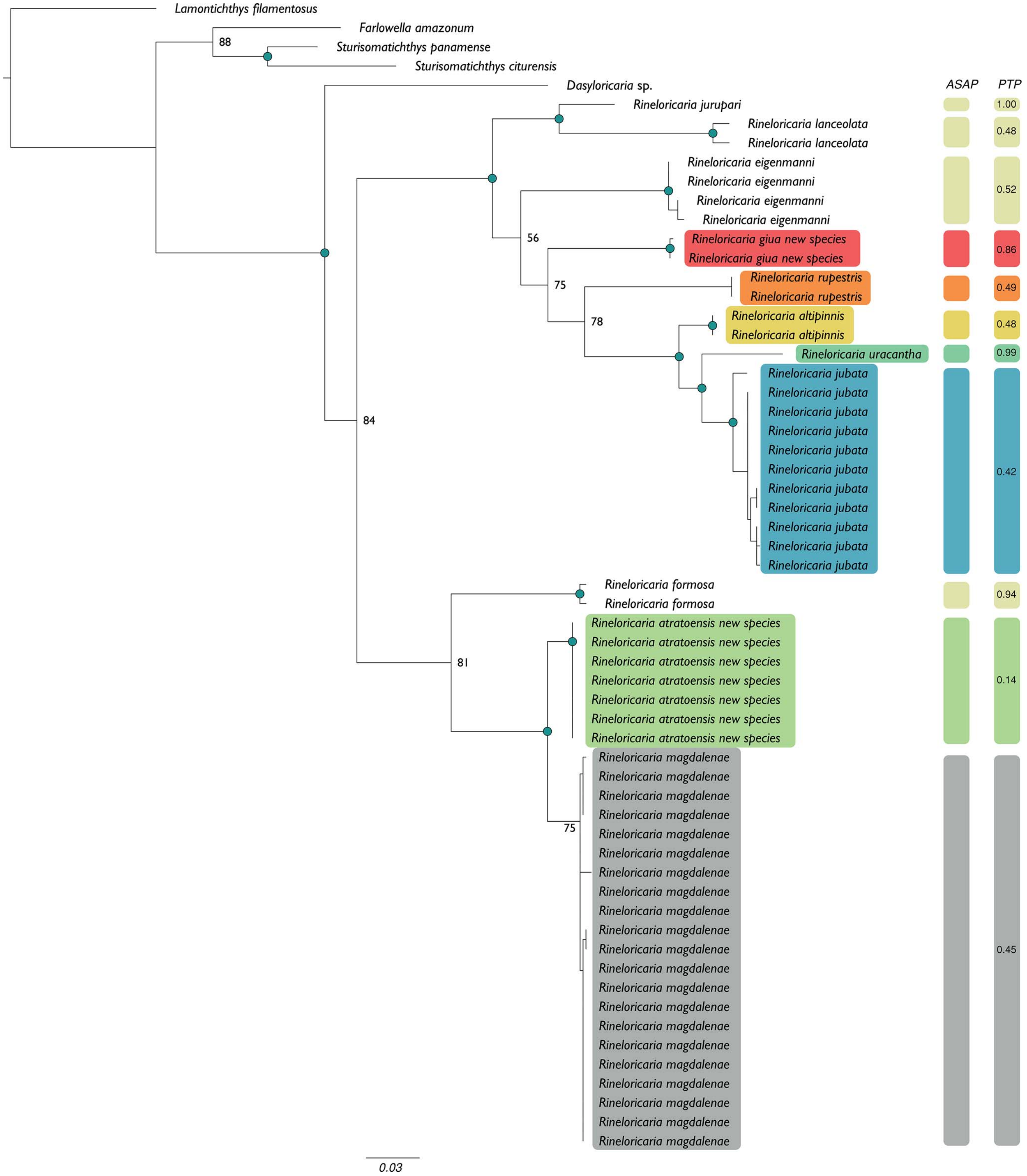

Fig. 7. Maximum likelihood phylogenetic tree of *Rineloricaria* obtained with COI data. Dots indicate nodal support ≥95%. See Supplemental Material A (see Data Accessibility) for detailed tree with individual sequences as terminal nodes.

of body, post-pectoral naked area slender (Fig. 1D) .... ***Rineloricaria jubata*** (Fig. 8A)

7b. 6–9 rows of median abdominal plates, 4–5 dark brown transverse bars on dorsal surface of body, post-pectoral naked area wide (Fig. 1E) .... ***Rineloricaria rupestris*** (Fig. 8C)

DISCUSSION

Previous taxonomic studies of *Rineloricaria* have shown that the diversity of species across its entire geographic distribution is incompletely documented. As a result, an iterative approach has proven to be an effective strategy to uncover and more accurately delineate previously unrecognized

Table 2. Average uncorrected genetic distances between species of *Rineloricaria* for the trans-Andean region.

Species	*R. altipinnis*	*R. jubata*	*R. uracantha*	*R. rupestris*	*R. giua*	*R. magdalenae*	*R. atratoensis*
R. altipinnis		0.048	0.061	0.097	0.103	0.150	0.149
R. jubata	0.048		0.060	0.105	0.111	0.137	0.144
R. uracantha	0.061	0.060		0.123	0.120	0.159	0.159
R. rupestris	0.097	0.105	0.123		0.114	0.134	0.141
R. giua	0.103	0.111	0.120	0.114		0.146	0.151
R. magdalenae	0.150	0.137	0.159	0.134	0.146		0.031
R. atratoensis	0.149	0.144	0.159	0.141	0.151	0.031	

species, possibly leading to the discovery of new ones (Costa-Silva et al., 2015). Our study incorporates such an iterative approach, bringing together multiple lines of evidence to assess the independent evolutionary history hypothesized for the species here recognized as new. Based on the taxonomic sampling selected for analyses presented herein, our results corroborate the monophyly of *Rineloricaria* as currently accepted (Covain et al., 2016; Londoño-Burbano and Reis, 2021) and also show that *R. atratoensis* and *R. giua* are members of different clades, with robust support values (>95%). This separate placement is further supported by high (>10% for *R. giua*) to moderate (>3% for *R. atratoensis*) estimated genetic distance values.

Although genetic distance between *Rineloricaria atratoensis* and *R. magdalenae* was lower (3.1%) than values found for remaining paired comparisons (≥4.8%, Table 1), this genetic distance value is still higher than minimum distances of 0.8% found by Costa-Silva et al. (2015) to recognize morphospecies in *Rineloricaria*. Likewise, distance between *R. atratoensis* and *R. magdalenae* is still above the 2% threshold proposed to delimit species in other teleostean groups (Ward et al., 2009; Gomes et al., 2015; Ribolli et al., 2017). Regarding delimitation methods implemented (ASAP and PTP), we chose two complementary approaches based on their different criteria (phenetic and phylogenetic), with their own inherent limitations (Puillandre et al., 2021). Both delimitation analyses agreed in finding *R. atratoensis* and *R. giua* as different lineages. Interestingly, our ASAP results are consistent with results obtained by Puillandre et al. (2021), who found that selection of the second-best score increases the precision of delimited partitions.

It is worth noting that trans-Andean species of *Rineloricaria* were not found to cluster as a single clade. These results are congruent with the findings of Costa-Silva et al. (2015; albeit trans-Andean species were represented only by *R. rupestris* and *R. uracantha*) and partially agree with those obtained by Covain et al. (2016), who also recovered two distinct clades. However, one of their groups was only composed of *R. altipinnis*, which in our analysis is grouped together with *R. uracantha*, *R. sneiderni*, and an unidentified species from Panama to form the second group identified by Covain et al. (2016). Such biogeographic pattern (i.e., consisting of more than a single trans-Andean clade) has been identified in other distantly related genera of fishes: *Apteronotus* (Bernt et al., 2019), *Astroblepus* (Ochoa et al., 2020a), *Brycon* (Abe et al., 2014), *Chaetostoma* (Lujan et al., 2015), *Characidium* (Agudelo-Zamora et al., 2020), *Gephyrocharax* (Vanegas-Ríos, 2018), *Hemibrycon* (García-Melo et al., 2019), *Pimelodus* (Martínez et al., 2022), *Pseudopimelodus* (Rangel-Medrano et al., 2020), *Trichomycterus* (Ochoa et al., 2020b). The fact that species of *Rineloricaria* show a complex pattern with more than one trans-Andean clade, variably related with different cis-Andean clades, hints at a heterogeneous biogeographic history of the trans-Andean basins (Abe et al., 2014; Musilová et al., 2015; Rangel-Medrano et al., 2020).

Morphological analyses corroborated distinctiveness of *Rineloricaria giua* by morphometrics and meristics, while *R. atratoensis* was also distinguished by morphometrics from most trans-Andean species from Colombia (except *R. magdalenae*), with these two species being distinguished by meristics (number of plates along sides of dorsal-fin base) and discrete characters (first ray of dorsal, pectoral, and pelvic fins extended as a short filament in *R. atratoensis*). Some morphological characters (e.g., number of transverse bars on dorsal surface of body, number of rows of median abdominal plates, number of longitudinal rows in lateral plates series, and number of plates along sides of dorsal-fin base) have shown a consistent pattern of interspecific variation based on our own observations in large series of specimens that are abundantly represented in ichthyological collections in Colombia (see Material Examined).

Future research must be oriented to expand taxonomic sampling (e.g., *Rineloricaria sneiderni*) and molecular markers (still predominantly restricted to COI) to have more robust hypotheses of the evolutionary history of *Rineloricaria*.

MATERIAL EXAMINED

Rineloricaria altipinnis: Panamá: Darién: AMNH 8404, holotype (photograph), 154.0 mm SL, Chico River.

Rineloricaria jubata: Ecuador: Esmeraldas: BMNH 1902.5.27.45, 1, lectotype, 179.8 mm SL, Durango River; BMNH 1901.3.29. 74-76, 3, paralectotypes, 165.9–188.1 mm SL, Durango River. Colombia: Cauca: CZUT-IC 12120, 1, 110.2 mm SL, Patía River; CZUT-IC 18368, 1, 77.2 mm SL, Patía River; IAvH-P 4737, 1, 104.3 mm SL, Guachicono River. Chocó: CZUT-IC 21302, 1, 87.1 mm SL, Baudó River; CZUT-IC 21387, 1, 76.6 mm SL, San Juan River; CZUT-IC 21404, 1, 96.0 mm SL, San Juan River; IMCN 1518, 1, 162.2 mm SL, San Juan River; IMCN 1982, 1, 132.4 mm SL, San Juan River. Nariño: ICN-MHN 19148, 1, 138.2 mm SL, Caunapí River; ICN-MHN 19283, 1, 146.3 mm SL, Rosario River; ICN-MHN 19289, 1, 86.6 mm SL, Caunapí River; ICN-MHN 19328, 1, 150.4 mm SL, Zapotal; ICN-MHN 19367, 1, 140.9 mm SL, Rosario River; IMCN 294, 1, 136.7 mm SL, Mayo River; IMCN 308, 1, 133.4 mm SL, Patía River. Valle del Cauca: CZUT-IC 18279, 1, 93.9 mm SL, Calima River; IAvH-P 21874, 1, 105.8 mm SL, quebrada La Brea, Calima River basin; IMCN 4753, 1, 140.7 mm SL, Anchicayá River; IMCN 9074, 3, 90.2–102.1 mm SL, San Cipriano River; IMCN 9075, 1, 120.2 mm SL, San Cipriano River.

Fig. 8. Species of *Rineloricaria* from the trans-Andean region of Colombia: (A) *R. jubata*, IMCN 4015, 110.3 mm SL; (B) *R. magdalenae*, CIUA 7549, 114.6 mm SL; (C) *R. rupestris*, CZUT-IC 19074, 99.1 mm SL; (D) *R. sneiderni*, ANSP 71433, holotype, 122 mm SL. Photographs in A–C by José Luis Londoño-López, copyright Colección de Ictiología de la Universidad de Antioquia; used with permission. Photographs in D by Kyle Luckenbill, copyright Ichthyology Department, Academy of Natural Sciences; used with permission. Scale bar 1 cm.

Rineloricaria magdalenae: Colombia: NMW 45080, lectotype (photograph), 125.3 mm SL, Magdalena River; NMW 45800, 1, paralectotype (photograph), 104 mm SL, Magdalena River. Antioquia: CIUA 6529, 1, 117.5 mm SL, ciénaga Nueva, Cauca River basin; CIUA 7445, 1, 110.0 mm SL, Man River, Cauca River basin; CIUA 7557, 1, 114.3 mm SL, ciénaga La Ilusión, Cauca River basin. Bolívar: CIUA 6529, 1, 117.5 mm SL, ciénaga Nueva, Cauca River basin; CIUA 7324, 1, 117.4 mm SL, ciénaga La Caimanera, Cauca River basin; CIUA 7393, 1, 120.1 mm SL, ciénaga El Floral, Cauca River basin; CIUA 7394, 1, 132.9 mm SL, ciénaga Piqué, Cauca River basin; CIUA 7424, 1, 122.5 mm SL, ciénaga La Caimanera, Cauca River basin; CIUA 7426, 1, 106.8 mm SL, Cauca River basin; CIUA 7548, 1, 88.5 mm SL, Cauca River; CIUA 7549, 3, 111.0–124.0 mm SL, ciénaga Grande, Cauca River basin; CIUA 7632, 2, 120.7–126.0 mm SL, ciénaga Culebras, Cauca River basin; CIUA 7633, 3, 118.7–138.2 mm SL, Cauca River basin. Magdalena: CZUT-IC 14040, 1, 107.5 mm SL, Frío River, Magdalena River basin; CZUT-IC 14959, 1, 93.9 mm SL, Aracataca River, Magdalena River basin; UARC-IC 866, 1, 64.6 mm SL, Frío River, Magdalena River basin. Norte de Santander: CZUT-IC 19125, 1, 113.7 mm SL, Zulia River, Catatumbo River drainage, Lake Maracaibo basin; CZUT-IC 19157, 2, 102.1–110.1 mm SL, Quebrada Agualasal, Catatumbo River drainage, Lake Maracaibo basin. Santander: IAvH-P 20848, 1, 60.0 mm SL, caño San Juan, Carare River drainage, Magdalena River basin; IAvH-P 23033, 2, 55.6–95.2 mm SL, quebrada La Lizama, Sogamoso River drainage, Magdalena River basin; IAvH-P 24529, 1, 94.5 mm SL, quebrada La Lizama, Sogamoso River drainage, Magdalena River basin. Sucre: CIUA 7419, 2, 93.3–118.9 mm SL, Cauca River basin; ICN-MHN 10933, 1, 112.4 mm SL, ciénaga Gamboa, San Jorge River drainage, Magdalena River basin.

Rineloricaria rupestris: Colombia: La Guajira: IAvH-P 11, 1, 91.8 mm SL, Ranchería River. Norte de Santander: CZUT-IC 19048, 2, 74. 8–83.0 mm SL, Peralonso River, Catatumbo River drainage, Lake Maracaibo basin; CZUT-IC 19074, 1, 99.1 mm SL, Zulia River, Catatumbo River drainage, Lake Maracaibo basin; IAvH-P 9817, 1, 90.9 mm SL, Catatumbo River drainage, Lake Maracaibo basin; IAvH-P 11804, 1, 83.0 mm SL, Zulia River, Catatumbo River drainage, Lake Maracaibo basin; IAvH-P 15875, 1, 70.0 mm SL, Zulia River, Catatumbo River drainage, Lake Maracaibo basin; IAvH-P 15897, 1, 85.2 mm SL, quebrada Agualasal, Catatumbo River drainage, Lake Maracaibo basin; ICN-MHN 2397, 1, 72.1 mm SL, Pamplonita River, Catatumbo River drainage, Lake Maracaibo basin.

Rineloricaria sneiderni: Colombia, Chocó: ANSP 71433, holotype (photograph), 122.0 mm SL, Jurubidá River, Nuquí; IAvH-P 10932, 1, 123.56 mm SL, Condoto River, Itsmina.

Rineloricaria uracantha: Panamá, Empire Station: USNM 16673, holotype of *Loricaria bransfordi* (photograph).

DATA ACCESSIBILITY

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ACKNOWLEDGMENTS

We want to thank the support of several people from the Grupo de Ictiología of Universidad de Antioquia: Luz Fernanda Jiménez-Segura, Daniel Restrepo-Santamaría, Juan Guillermo Ospina-Pabón, and Víctor Manuel Medina-Ríos for unconditional technical and logistic support; José Luis Londoño-López for photographs; Omer Campo-Nieto for processing of samples in the laboratory; Karen Lineke Álvarez-Álvarez and Miguel Ángel Cortés-Hernández for technical support at CIUA. We also thank Andrés Felipe Galeano (EPM) for technical support at EPM. We are indebted to curators and staff of ichthyological collections that provided support during visits or requests of information: James Maclaine (BMNH), Francisco Antonio Villa-Navarro (CZUT-IC), Ángela Gutiérrez (IAvH-P), Lauren Raz and Henry Agudelo-Zamora (ICN-MHN), Wilber Alfonso Triana and Carlos Caballero (IMCN), Saúl Prada-Pedreros and Tiago Pinto Carvalho (MPUJ), and Anja Palandačić (NMW). Thanks to Andrés Felipe Murillo for design of figures. This study was funded by Research Agreements CT-2021-000023-A3 and CW140036, between Universidad de Antioquia and Empresas Públicas de Medellín, and made part of the research line "Biblioteca de la vida de la biota acuática de la cuenca del Magdalena-Cauca" under the Project "Respuesta de la ictiofauna a la formación de embalses en los Andes colombianos."

LITERATURE CITED

Abe, K. T., T. C. Mariguela, G. S. Avelino, F. Foresti, and C. Oliveira. 2014. Systematic and historical biogeography of the Bryconidae (Ostariophysi: Characiformes) suggesting a new rearrangement of its genera and an old origin of Mesoamerican ichthyofauna. BMC Evolutionary Biology 14:152.

Agudelo-Zamora, H. D., J. Tavera, Y. D. Murillo, and A. Ortega-Lara. 2020. The unknown diversity of the genus *Characidium* (Characiformes: Crenuchidae) in the Chocó biogeographic region, Colombian Andes: two new species supported by morphological and molecular data. Journal of Fish Biology 97:1662–1675.

Armbruster, J. W. 2003. *Peckoltia sabaji*, a new species from the Guyana Shield (Siluriformes: Loricariidae). Zootaxa 344:1–12.

Bernt, M. J., V. A. Tagliacollo, and J. S. Albert. 2019. Molecular phylogeny of the ghost knifefishes (Gymnotiformes: Apteronotidae). Molecular Phylogenetics and Evolution 135:297–307.

Boulenger, G. A. 1902. Descriptions of two new fishes of the genus *Loricaria* from north-western Ecuador. Annals and Magazine of Natural History 9:69–71.

Chamon, C. C., and I. Fichberg. 2022. *Rineloricaria quilombola*: a new species of whiptail catfish (Siluriformes, Loricariidae, Loricariinae) from upper and middle Tocantins River basin, Brazil. Zootaxa 5194:58–70.

Cortés-Hernández, M. Á., J. A. López-Castaño, N. Milani, and C. DoNascimiento. 2023. A new cryptic species of *Imparfinis* (Siluriformes: Heptapteridae) from the Orinoco River basin, revealed by an iterative approach. Journal of Fish Biology 103:1015–1030.

Costa-Silva, G. J., M. S. Rodriguez, F. F. Roxo, F. Foresti, and C. Oliveira. 2015. Using different methods to access the difficult task of delimiting species in a complex Neotropical hyperdiverse group. PLoS ONE 10:e0135075.

Costa-Silva, G. J., G. S. C. Silva, and C. Oliveira. 2022. A new species of spiny *Rineloricaria* (Siluriformes: Loricariidae) from the Rio Paraba do Sul basin and coastal rivers from Rio de Janeiro State. Zootaxa 5175:285–292.

Covain, R., S. Fisch-Muller, C. Oliveira, J. H. Mol, J. I. Montoya-Burgos, and S. Dray. 2016. Molecular phylogeny of the highly diversified catfish subfamily Loricariinae (Siluriformes, Loricariidae) reveals incongruences with morphological classification. Molecular Phylogenetics and Evolution 94:492–517.

DoNascimiento, C., H. D. Agudelo-Zamora, J. D. Bogotá-Gregory, A. Méndez-López, A. Ortega-Lara, C. Lasso, M. A. Cortés-Hernández, J. G. Albornoz Garzón, F. A. Villa-Navarro, A. L. Netto-Ferreira, F. C. T. Lima, A. Thomaz, and M. Arce H. 2024. Lista de especies de peces de agua dulce de Colombia/Checklist of the freshwater fishes of Colombia. v. 2.16. Asociación Colombiana de Ictiólogos. Dataset/Checklist.

Eigenmann, C. H. 1922. The fishes of western South America, Part I. The fresh-water fishes of northwestern South America, including Colombia, Panama, and the Pacific slopes of Ecuador and Peru, together with an appendix upon the fishes of the Rio Meta in Colombia. Memoirs of the Carnegie Museum 9:1–346.

Fichberg, I., and C. C. Chamon. 2008. *Rineloricaria osvaldoi* (Siluriformes: Loricariidae): a new species of armored catfish from rio Vermelho, Araguaia basin, Brazil. Neotropical Ichthyology 6:347–354.

Fowler, H. W. 1944. Fresh-water fishes from northwestern Colombia. Proceedings of the Academy of Natural Sciences of Philadelphia 96:227–248.

Fricke, R., W. N. Eschmeyer, and R. Van der Laan. 2024. Eschmeyer's Catalog of Fishes: Genera, Species, References. https://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (accessed 6 February 2024).

Galvis, G., J. I. Mojica, and M. Camargo. 1997. Peces del Catatumbo. Asociación Cravo Norte, Santafé de Bogotá, D.C.

García-Melo, J. E., C. Oliveira, G. J. Da Costa Silva, L. E. Ochoa-Orrego, L. H. Garcia Pereira, and J. A. Maldonado-Ocampo. 2019. Species delimitation of Neotropical characins (Stevardiinae): implications for taxonomy of complex groups. PLoS ONE 14:e0216786.

Ghazzi, M. S. 2008. Nove espéces do gênero *Rineloricaria* (Siluriformes, Loricariidae) do rio Uruguai, do sul do Brasil. Iheringia, Série Zoologia 98:100–122.

Gomes, L. C., T. C. Pessali, N. G. Sales, P. S. Pompeu, and D. C. Carvalho. 2015. Integrative taxonomy detects cryptic and overlooked fish species in a Neotropical river basin. Genetica 143:581–588.

Hastie, T., R. Tibshirani, and J. H. Friedman. 2009. The Elements of Statistical Learning: Data Mining, Inference, and Prediction. Second edition. Springer, New York.

Hoang, D. T., O. Chernomor, A. von Haeseler, B. Q. Minh, and L. S. Vinh. 2018. UFBoot2: improving the ultrafast bootstrap approximation. Molecular Biology and Evolution 35:518–522.

Isbrücker, I. J. H. 1973. Redescription and figures of the South American mailed catfishes *Rineloricaria lanceolata* (Günther, 1868) (Pisces, Siluriformes, Loricariidae). Beaufortia 21:75–89.

Isbrücker, I. J. H., and H. Nijssen. 1978. Two new species and a new genus of Neotropical mailed catfishes of the subfamily Loricariinae Swainson, 1838 (Pisces, Siluriformes, Loricariidae). Beaufortia 339:177–206.

Jimenéz-Segura, L., and C. A. Lasso (Eds.). 2020. XIX. Peces de la cuenca del río Magdalena, Colombia: diversidad, conservación y uso sostenible. Serie Editorial Recursos Hidrobiológicos y Pesqueros Continentales de Colombia, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, D.C., Colombia.

Kalyaanamoorthy, S., B. Q. Minh, T. K. F. Wong, A. von Haeseler, and L. S. Jermiin. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods 14:587–589.

Katoh, K., and D. M. Standley. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30:772–780.

Londoño-Burbano, A., and R. E. Reis. 2021. A combined molecular and morphological phylogeny of the Loricariinae (Siluriformes: Loricariidae), with emphasis on the Harttiini and Farlowellini. PLoS ONE 16:e0247747.

Lujan, N. K., V. Meza-Vargas, V. Astudillo-Clavijo, R. Barriga-Salazar, and H. López-Fernández. 2015. A multilocus molecular phylogeny for *Chaetostoma* clade genera and species with a review of *Chaetostoma* (Siluriformes: Loricariidae) from the Central Andes. Copeia 103:664–701.

Maldonado-Ocampo, J. A., F. A. Villa-Navarro, A. Ortega-Lara, S. Prada-Pedreros, U. Jaramillo Villa, A. Claro, J. S. Usma, T. S. Rivas Lara, W. Chaverra Salazar, J. F. Cuesta Barrios, and J. E. García-Melo. 2006. Peces del río Atrato, zona hidrogeográfica del Caribe, Colombia. Biota Colombiana 7:143–154.

Maldonado-Ocampo, J. A., J. S. Usma Oviedo, F. A. Villa-Navarro, A. Ortega-Lara, S. Prada-Pedreros, L. F. Jiménez S., U. Jaramillo-Villa, A. Arango, T. S. Rivas, and G. C. Sánchez Garcés. 2012. Peces Dulceacuícolas del Chocó Biogeográfico de Colombia. WWF Colombia, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Universidad del Tolima, Autoridad Nacional de Acuicultura y Pesca, Pontificia Universidad Javeriana, Bogotá.

Martínez, J. G., J. D. Rangel-Medrano, A. J. Yepes-Acevedo, N. Restrepo-Escobar, and E. J. Márquez. 2022. Species limits and introgression in *Pimelodus* from the Magdalena-Cauca River basin. Molecular Phylogenetics and Evolution 173:107517.

Minh, B. Q., H. A. Schmidt, O. Chernomor, D. Schrempf, M. D. Woodhams, A. von Haeseler, and R. Lanfear. 2020. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution 37:1530–1534.

Mojica, J. I., S. Usma, and G. Galvis. 2004. Peces dulceacuícolas del Chocó Biogeográfico–Catálogo, p. 725–744. *In*: Colombia Diversidad Biótica IV: El Chocó Biogeográfico/Costa Pacífica. O. Rangel (ed.). Universidad Nacional de Colombia, Bogotá, D.C.

Musilová, Z., O. Říčan, Š. Říčanová, P. Janšta, O. Gahura, and J. Novák. 2015. Phylogeny and historical biogeography of trans-Andean cichlid fishes (Teleostei: Cichlidae). Vertebrate Zoology 65:333–350.

Ochoa, L. E., A. Datovo, C. DoNascimiento, F. F. Roxo, M. H. Sabaj, J. Chang, B. F. Melo, G. S. C. Silva, F. Foresti, M. Alfaro, and C. Oliveira. 2020b. Phylogenomic analysis of trichomycterid catfishes (Teleostei: Siluriformes) inferred from ultraconserved elements. Scientific Reports 10:2697.

Ochoa, L. E., B. F. Melo, J. E. García-Melo, J. A. Maldonado-Ocampo, C. S. Souza, J. G. Albornoz-Garzón, C. C. Conde-Saldaña, F. Villa-Navarro, A. Ortega-Lara, and C. Oliveira. 2020a. Species delimitation reveals an underestimated diversity of Andean catfishes of the family Astroblepidae

(Teleostei: Siluriformes). Neotropical Ichthyology 18: e200048.

Puillandre, N., S. Brouillet, and G. Achaz. 2021. ASAP: assemble species by automatic partitioning. Molecular Ecology Resources 21:609–620.

R Core Team. 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rangel-Medrano, J. D., A. Ortega-Lara, and E. J. Márquez. 2020. Ancient genetic divergence in bumblebee catfish of the genus *Pseudopimelodus* (Pseudopimelodidae: Siluriformes) from northwestern South America. PeerJ 8:e9028.

Regan, C. T. 1914. IV. Fishes from the Condoto River, Colombia, collected by Dr. H. G. F. Spurrell. Annals and Magazine of Natural History 14:31–33.

Reis, R. E., and A. Cardoso. 2001. Two new species of *Rineloricaria* from southern Santa Catarina and northeastern Rio Grande do Sul, Brazil (Teleostei: Loricariidae). Ichthyological Exploration of Freshwaters 12:319–32.

Reis, R. E., and E. H. L. Pereira. 2000. Three new species of the loricariid catfish genus *Loricariichthys* (Teleostei: Siluriformes) from southern South America. Copeia 2000:1029–1047.

Ribolli, J., B. M. S. Scaranto, O. A. Shibatta, R. A. Bombardelli, and E. Zaniboni-Filho. 2017. DNA barcoding confirms the occurrence of *Rhamdia branneri* and *Rhamdia voulezi* (Siluriformes: Heptapteridae) in the Iguaçu River Basin. Neotropical Ichthyology 15:e160147.

Sabaj, M. H. 2020. Codes for natural history collections in ichthyology and herpetology. Copeia 108:593–669.

Schaefer, S. A. 1997. The Neotropical cascudinhos: systematics and biogeography of the *Otocinclus* catfishes (Siluriformes: Loricariidae). Proceedings of the Academy of Natural Sciences of Philadelphia 148:1–120.

Schultz, L. P. 1944. The catfishes of Venezuela, with descriptions of thirty-eight new forms. Proceedings of the United States National Museum 94:173–338.

Steindachner, F. 1879. Zur Fisch-Fauna des Magdalenen-Stromes. Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien. Mathematisch-Naturwissenschaftliche Classe 39:19–78.

Tamura, K., G. Stecher, and S. Kumar. 2021. MEGA11: molecular evolutionary genetics analysis version 11. Molecular Biology and Evolution 38:3022–3027.

Vanegas-Ríos, J. A. 2018. Phylogeny of the Neotropical genus *Gephyrocharax* (Characiformes: Characidae: Stevardiinae), with remarks on the tribe Stevardiini. Zoological Journal of the Linnean Society 182:808–829.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth edition. Springer, New York.

Vera-Alcaraz, H. S., C. S. Pavanelli, and C. H. Zawadzki. 2012. Taxonomic revision of the *Rineloricaria* species (Siluriformes: Loricariidae) from the Paraguay River basin. Neotropical Ichthyology 10:285–311.

Ward, R. D., R. Hanner, and P. D. N. Hebert. 2009. The campaign to DNA barcode all fishes, FISH-BOL. Journal of Fish Biology 74:329–356.

Ward, R. D., T. S. Zemlak, B. H. Innes, P. R. Last, and P. D. N. Hebert. 2005. DNA barcoding Australia's fish species. Philosophical Transactions of the Royal Society B: Biological Sciences 360:1847–1857.

Xia, X. 2018. DAMBE7: new and improved tools for data analysis in molecular biology and evolution. Molecular Biology and Evolution 35:1550–1552.

Xia, X., and P. Lemey. 2009. Assessing substitution saturation with DAMBE, p. 615–630. *In*: The Phylogenetic Handbook: A Practical Approach to DNA and Protein Phylogeny. P. Lemey, M. Salemi, and A. M. Vandamme (eds.). Cambridge University Press, Cambridge.

Xia, X., Z. Xie, M. Salemi, L. Chen, and Y. Wang. 2003. An index of substitution saturation and its application. Molecular Phylogenetics and Evolution 26:1–7.

Yeates, D., A. Seago, L. Nelson, S. Cameron, L. Joseph, and J. Trueman. 2011. Integrative taxonomy, or iterative taxonomy? Systematic Entomology 36:209–217.

Zhang, J., P. Kapli, P. Pavlidis, and A. Stamatakis. 2013. A general species delimitation method with applications to phylogenetic placements. Bioinformatics 29:2869–2876.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.