Journal of FISH BIOLOGY

fsbi An International Society for Fish Biology

Journal of Fish Biology (2017)
doi:10.1111/jfb.13317, available online at wileyonlinelibrary.com

A new species of *Chrysobrycon* (Characiformes, Characidae, Stevardiinae) from the Amazon River basin in Colombia, with a new diagnostic characteristic for the genus

J. A. Vanegas-Ríos*† and A. Urbano-Bonilla‡

**División Zoología de Vertebrados, Facultad de Ciencias Naturales y Museo, CONICET, UNLP, Paseo del Bosque S/N° B1900FWA, La Plata, Buenos Aires, Argentina and ‡Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH), Departamento de Biología, Facultad de Ciencias, Pontificia Universidad Javeriana, Carrera 7 N° 43-82, Bogotá D. C., Colombia*

(Received 4 May 2016, Accepted 9 March 2017, Published online 17 April 2017)

Chrysobrycon mojicai sp. nov. is described from forest streams that are part of the Amazon River basin in Colombia. It is distinguished from all congeners by having most of the maxillary teeth with distal tips lateroventrally curved (*v.* teeth straight along their lengths) and a greater number of dentary teeth (20–27 *v.* 11–19, except in *Chrysobrycon yoliae*). The posterior margin of the ventral process of the quadrate does not reach the vertical through the posterior margin of the symplectic and these features differentiate *C. mojicai* from *Chrysobrycon myersi* and *C. yoliae* (*v.* posterior margin of ventral process of quadrate reaching vertical through posterior margin of symplectic). In species of *Chrysobrycon*, the frontals are extensively contacting each other along the midline, resulting in an absent frontal fontanel and a reduced parietal fontanel. This extensive contact between the frontals modifying the fontanels is a condition rarely found within the Stevardiinae and hence is proposed as an additional diagnostic characteristic for the genus. An updated identification key for all *Chrysobrycon* species is provided.

Key words: Amacayacu National Natural Park; identification key; Leticia; Neotropical freshwater fishes; Stevardiini.

INTRODUCTION

The freshwater fish genus *Chrysobrycon* Weitzman & Menezes 1998 is part of the Stevardiinae, recognised by a group of hypertrophied scales that form a laterally open pocket on the lower caudal-fin lobe in adult males (Weitzman & Menezes, 1998; Vanegas-Ríos *et al.*, 2011, 2014). According to Weitzman & Menezes (1998), the pocket is mainly constituted by a pouch scale, which is relatively small (compared with other related stevardiines), somewhat elongate, curved, confined to the dorsal region of the pouch opening and horizontally folded so that its lateral face is laterally concave. Other distinctive characteristics of the genus are a superior mouth, dorsal fin situated posterior to the anal-fin origin, insemination and numerous pelvic, anal and caudal-fin

†Author to whom correspondence should be addressed. Tel.: +54 221 4228451 ext. 104; email: anyelovr@fcnym.unlp.edu.ar

bony hooks in adult males (Weitzman & Menezes, 1998; Burns & Weitzman, 2005; Vanegas-Ríos *et al.*, 2015). In a recent DNA-based phylogeny of the Stevardiinae (Thomaz *et al.*, 2015), *Chrysobrycon* was reclassified from the Xenurobryconini *sensu* Weitzman & Menezes (1998) to the Stevardiini.

Chrysobrycon was erected by Weitzman & Menezes (1998) to include two species that had already been placed in *Hysteronotus* Eigenmann 1911, *Chrysobrycon hesperus* (Böhlke 1958) and *Chrysobrycon myersi* (Weitzman & Thomerson 1970) (Böhlke, 1958; Weitzman & Thomerson, 1970). Subsequent studies have revealed that *Chrysobrycon* is more species rich than previously thought and consequently, three more species were described (Vanegas-Ríos *et al.*, 2011, 2014, 2015): *Chrysobrycon eliasi* Vanegas-Ríos, Azpelicueta & Ortega 2011; *Chrysobrycon guahibo* Vanegas-Ríos, Urbano-Bonilla & Azpelicueta 2015; *Chrysobrycon yoliae* Vanegas-Ríos, Azpelicueta & Ortega 2014.

In Colombia, Ecuador and Peru, four species of *Chrysobrycon* are recognised as valid for the Amazon River basin: *C. hesperus*, *C. eliasi*, *C. myersi* and *C. yoliae* (Weitzman & Menezes, 1998; Vanegas-Ríos *et al.*, 2011, 2014). During the examination of several characid species from the southern Amazon River basin in Colombia, some populations with a distinctive maxillary dentition were identified as *Chrysobrycon*. Further comparisons confirmed that these populations constitute a new species that is described here.

MATERIALS AND METHODS

The specimens examined are deposited in the collections of the Academy of Natural Sciences of Drexel University, Philadelphia (ANSP), U.S.A.; California Academy of Sciences, San Francisco (CAS), U.S.A.; Fundación Miguel Lillo, San Miguel de Tucumán (CI-FML), Argentina; Field Museum of Natural History, Chicago (FMNH), U.S.A.; Instituto Alexander von Humboldt, Villa de Leyva (IAvH-P), Colombia; Ictiología, INCIVA-Museo de Ciencias Naturales Federico Carlos Lehmann V., Cali (IMCN), Colombia; Laboratório de Biologia e Genética de Peixes, Departamento de Morfologia, Universidade Estadual Paulista "Júlio de Mesquita Filho", campus de Botucatu (LBP), Brazil; Natural History Museum of Los Angeles County, Los Angeles (LACM), U.S.A.; Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP), Brazil; Museum of Comparative Zoology, Harvard University, Cambridge (MCZ), U.S.A.; Museo de Historia Natural, Escuela Politécnica Nacional, Quito (MEPN), Ecuador; Museo de Historia Natural Javier Prado de la Universidad Nacional Mayor de San Marcos, Lima (MUSM), Peru; Museo de La Plata, La Plata (MLP), Argentina; Museo Javeriano de Historia Natural Lorenzo Uribe, S. J., Bogotá D. C. (MPUJ), Colombia; Royal Ontario Museum, Toronto (ROM), Canada; University of Florida, Florida Museum of Natural History, Gainesville (UF), U.S.A.; and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), U.S.A.

Counts of the pectoral, pelvic and dorsal-fin rays follow Böhlke (1958). Measurements and other counts were taken according to Fink & Weitzman (1974), with the addition of eight measurements: the lengths of the dorsal-fin base, anal-fin base and anal-fin lobe, following Menezes & Weitzman (1990) and the distances between dorsal and pectoral-fin origins, dorsal and adipose-fin origins, pectoral and pelvic-fin insertions, pelvic and anal-fin origins and postorbital head length, following Vanegas-Ríos *et al.* (2013*a*). Measurements were taken point to point with digital callipers under a stereomicroscope and are expressed as percentages of standard length (L_S) or head length (L_H) for units of the head. In the section on *Comparative material examined* (below), some specimens were analysed from digitised photographs using tpsDig 2.26 (Rohlf, 2015), which are indicated by an asterisk. Frequency of a particular meristic characteristic is presented in parentheses and the holotype values are represented by an asterisk. Specimens were cleared and counterstained (c&s) following Taylor & Dyke (1985). Total number of vertebrae were counted in c&s specimens. Those counts included the first preural

centrum plus first ural centrum (PU1 + U1) counted as one element and all four vertebrae of the Weberian apparatus. Linear least-square regressions implemented in PAST 3.06 (Hammer *et al.*, 2001) were carried out to identify sex-based differences in the morphometric data. For those analyses, normality was tested using a Shapiro–Wilk statistic (W) in each case ($\alpha < 0{\cdot}05$).

RESULTS

CHRYSOBRYCON MOJICAI, N. SP.

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Holotype

IAvH-P 13932, male, 50·6 mm L_S, Colombia, Amazonas Department, Leticia, Amacayacu National Natural Park, Amazon River basin, unnamed forest stream tributary of Matamatá River, 3° 48′ 23″ S; 70° 15′ 58″ W, 86 m a.s.l., 25 March 2006, F. Arbeláez & unknown collectors (Fig. 1).

Paratypes

All from Colombia, Amazonas Department: IAvH-P 8291, five specimens, 25·0–50·4 mm L_S (one c&s specimen, 50·4 mm L_S), collected with holotype. IAvH-P 8295, nine specimens, 29·0–47·7 mm L_S, Leticia, Amacayacu National Natural Park, Amazon River basin, unnamed forest stream tributary of Purité River headwaters, 3° 41′ 54″ S; 70° 12′ 24″ W, 127 m a.s.l., 25 March 2006, F. Arbeláez & unknown collectors. IAvH-P 8300, two specimens, 33·5–40·8 mm L_S, Leticia, Amacayacu National Natural Park, Amazon River basin, unnamed forest stream tributary of Purité River headwaters, 3° 41′ 37·5″ S; 70° 12′ 26·5″ W, F. Arbeláez & unknown collectors, 26 March 2006. IAvH-P 8917, 14 specimens, 17·1–47·5 mm L_S, Leticia, Amazon River basin, Sufragio stream in front of Zafire Biological Station, 4° 0′ 19·2″ S; 69° 53′ 55·5″ W, 118 m a.s.l., 8 December 2005, F. Arbeláez. IAvH-P 8951, nine specimens, 17·9–50·5 mm L_S, Sufragio stream in front of Zafire Biological Station, 9 December 2005, F. Arbeláez. IAvH-P 9022, six specimens, 43·8–50·8 mm L_S, Leticia, Amazon River basin, Sufragio stream in front of Zafire Biological Station, 14 December 2005, F. Arbeláez. IAvH-P 9070, four specimens, 48·6–55·0 mm L_S, Leticia, Amazon River basin, unnamed forest stream tributary of Calderon River, 45 min north-east of Zafire Biological Station, 3° 58′ 40·14″ S; 69° 53′ 31·8″ W, 130 m a.s.l., 12 December 2005, F. Arbeláez. IAvH-P 9093, four specimens, 23·7–47·8 mm L_S, Leticia, Amazon River basin, unnamed stream, tributary of Calderon River, 45 min north-east of Zafire Biological Station, 13 December 2005, F. Arbeláez. MPUJ 8058, one specimen, 49·5 mm L_S, collected with holotype. MPUJ 8059, one c&s specimen, 50·3 mm L_S, Leticia, Amazon River basin, unnamed forest stream tributary of Calderon River, 45 min north-east of Zafire Biological Station, 12 December 2005, F. Arbeláez.

Non-type specimens

IAvH-P 9022, three c&s specimens (badly preserved, disarticulated skeletons), 47·0–50·0 mm L_S, Colombia, Amazonas Department, Leticia, Amazon River basin, Sufragio stream in front of Zafire Biological Station.

FIG. 1. *Chrysobrycon mojicai*, (a) IAvH-P 13932, male, holotype, 50·6 mm standard length (L_S), Colombia, Amazonas Department, Leticia, Amacayacu National Natural Park, Amazon River basin, unnamed forest stream tributary of Matamatá River; (b) MPUJ 8058, female, paratype, 49·5 mm L_S, collected with holotype.

Diagnosis

Chrysobrycon mojicai differs from all congeners by having most maxillary teeth with distal tips lateroventrally curved (*v*. teeth straight along their lengths) and the number of dentary teeth (20–27 *v*. 11–19, except in *C*. *yoliae*). The presence of a terminal lateral-line tube between the caudal-fin rays 11 and 12 (*v*. tube absent) distinguishes *C*. *mojicai* from *C*. *hesperus* and *C*. *myersi*. From *C*. *yoliae*, *C*. *myersi* and *C*. *guahibo*, *C*. *mojicai* is differentiated in the number of vertebrae (42 *v*. 38–41). *Chrysobrycon mojicai* can also be distinguished from *C*. *guahibo* and *C*. *hesperus* by the bony hooks on the 11 anterior branched anal-fin rays with continuous arrangement, forming a single series along the rays' length in adult males (*v*. bony hooks on three to seven anterior branched anal-fin rays with discontinuous arrangement, forming two separate series on each ray). *Chrysobrycon mojicai* is differentiated from *C*. *eliasi* and *C*. *myersi* by the snout length (32·0–35·9% L_H *v*. 27·0–31·5% L_H). Furthermore, *Chrysobrycon mojicai* is distinguished from *C*. *guahibo* by the number of maxillary teeth (9–17 *v*. 1–3) and the nasal as long as the antorbital (*v*. nasal bone longer than antorbital). *Chrysobrycon mojicai* is also distinguished from *C*. *myersi* by the distance between the snout and dorsal-fin origin (62·9–70·5% L_S *v*. 56·6–63·0% L_S), distance between the dorsal and adipose-fin origins (23·5–27·5% L_S *v*. 28·2–33·5% L_S), distance between the eye and dorsal-fin origin (50·3– 57·2% L_S *v*. 45·8–49·2% L_S) and number of circumpeduncular scales (14–15 *v*. 17–19). The posterior margin of the ventral process of the quadrate not reaching the vertical through posterior margin of symplectic also differentiates *C*. *mojicai* from *C*. *myersi* and *C*. *yoliae* (*v*. posterior margin of the ventral process of symplectic reaching vertical through posterior margin of symplectic).

Description

Morphometric data are given in Table I. Largest male is 50·6 mm L_S, largest female is 55·0 mm L_S. Body laterally compressed, maximum depth at vertical through area between pelvic and anal-fin origins (Fig. 1). Dorsal profile of body straight over head; convex, straight or slightly convex (specimens from IAvH-P 9022) from posterior end of supraoccipital area to dorsal-fin origin; straight and slanting ventrally from first dorsal-fin ray to caudal peduncle. Dorsal profile of caudal peduncle straight. Ventral profile of body convex from tip of snout to pelvic-fin origin, straight or slightly convex between pelvic and anal-fin origins, straight or slightly convex and slanting dorsally from this point to caudal peduncle. Ventral profile of caudal peduncle straight or slightly concave. Head with anterior region acute. Frontal fontanel absent. Epiphyseal branch of supraorbital canal absent. Anterior nostril rounded, separated by skin fold from posterior nostril; posterior nostril opening larger. Two pit organs developed in grooves of head; anterior groove rounded, between nasal bone and nostril; posterior groove extended along frontal, covered with rows of neuromasts. Few additional neuromasts located over anteroventral portion of nostrils.

Mouth superior, lower jaw projecting slightly anterior to upper jaw. Premaxilla with two rows of teeth [Fig. 2(a)]. Outer row with three (2), four (8) or five* (27) teeth; usually tricuspid, rarely conical. Inner row with four (35) or five* (2) teeth, symphyseal tooth tetracuspid, remaining teeth pentacuspid (rarely posteriormost tooth tricuspid). Maxilla almost entirely toothed, with nine (1), 10 (2), 11 (4), 12 (1), 13 (8), 14*(5), 15 (5), 16 (9) or 17(1) teeth [Fig. 2(a)]; anteriormost first, second and third teeth tricuspid (rarely conical or bicuspid), remaining teeth conical or bicuspid (rarely tricuspid). Most maxillary teeth conspicuously projected laterally, with their distal portion curved lateroventrally [Fig. 2(b)]. Maxilla surpassing vertical through anterior margin of eye, sometimes reaching anterior border of pupil. Dentary extensively toothed, with 20 (1), 21 (11), 22 (3), 23 (2), 24* (6), 25 (8) or 27 (4) teeth; three anteriormost teeth large, pentacuspid (rarely tri or tetracuspid); one median-sized tooth tri to pentacuspid followed by 16 (1), 17 (11), 18 (3), 19 (2), 20* (6), 21 (8) or 23 (4) smaller conical posterior teeth [Fig. 2(a)].

Dorsal-fin rays ii (37), 7 (1) or 8* (36). Nine proximal pterygiophores in dorsal fin (two c&s). Dorsal-fin origin at vertical between anal-fin rays seven to 10. Adipose-fin origin at vertical crossing posteriormost anal fin ray or scale posterior to this point. Anal-fin rays iv* (31) or v (6), 25 (4), 26 (5), 27 (13), 28 (5), 29 (7) or 30* (3). Twenty-eight to 29 proximal pterygiophores in anal fin (two c&s). Anal-fin origin at posterior half of body, always anterior to vertical through dorsal-fin origin. Pectoral-fin rays i (36), nine (16), 10* (19) or 11 (1). Pectoral-fin distal tip reaching one-quarter to one-half of pelvic-fin length (Fig. 1). Pelvic-fin rays i (36), six (1) or seven* (35). Pelvic-fin origin slightly anterior to half of body. Caudal fin forked with 10/9 principal rays in all specimens.

Scales cycloid, with seven to 15 radii along posterior region. Lateral line completely pored: 41 (1), 42 (9), 43 (10), 44 (12) or 45* (4) scales. Terminal lateral-line tube present on caudal-fin interradial membrane. Predorsal scales 20 (2), 21* (18), 22 (11), 23 (4) or 24 (1), forming continuous row (three specimens with anteriormost scales misaligned). Scale rows between dorsal fin and lateral line five (4), six (30) or seven* (2). Four (1), five* (26) or six (9) scale rows between lateral line and anal fin. Four (2), five* (32) or six (29) scale rows between lateral line and pelvic fin. Circumpeduncular scales 14 (26) or 15*(7). Two rows of scales forming sheath along anal-fin base, dorsal

TABLE I. Morphometric data of *Chrysobrycon mojicai*. Identification of males based on presence of bony hooks on fins and pouch scale on lower caudal-fin lobe. Range and mean of males include values of holotype

	Males				Females and unsexed juveniles		
	n	Holotype	Range	Mean ± S.D.	*n*	Range	Mean ± S.D.
Standard length (L_S, mm)	9	37·0	37·0–50·6	45·9 ± 5·0	47	17·1–55·0	35·1 ± 13·9
Percentages of L_S							
Depth at dorsal-fin origin	9	34·2	30·8–36·7	33·2 ± 2·2	29	25·9–35·1	31·3 ± 2·5
Snout to dorsal-fin origin	9	67·3	63·6–68·8	66·1 ± 1·5	26	62·9–70·5	67·3 ± 1·7
Snout to pectoral-fin origin	9	30·3	26·9–30·3	28·6 ± 1·1	26	25·1–29·3	27·2 ± 1·0
Snout to pelvic-fin origin	9	46·3	45·2–48·0	46·3 ± 0·9	26	45·8–50·2	48·1 ± 1·2
Snout to anal-fin origin	9	58·5	58·5–62·3	60·1 ± 1·5	26	59·9–66·0	62·9 ± 1·6
Distance between dorsal and pectoral-fin origins	9	50·5	46·5–51·8	48·7 ± 1·9	26	44·2–51·7	49·7 ± 1·7
Distance between dorsal and adipose-fin origins	9	24·4	23·5–27·7	25·6 ± 1·3	26	23·5–27·6	25·3 ± 1·0
Dorsal fin to caudal-fin base	9	34·8	34·8–37·5	36·7 ± 0·8	26	34·0–42·1	36·5 ± 1·9
Eye to dorsal-fin origin	9	55·9	51·3–55·9	53·7 ± 1·4	26	50·3–57·2	54·5 ± 1·5
Distance between pectoral and pelvic-fin insertions	9	17·4	17·4–22·7	19·5 ± 1·5	26	19·6–23·2	21·2 ± 1·0
Distance between pelvic- and anal-fin origins	9	13·6	13·4–16·0	14·6 ± 0·9	26	14·8–17·8	16·7 ± 0·8
Dorsal-fin length	8	19·2	18·4–20·9	19·7 ± 0·8	26	15·3–20·2	18·2 ± 1·3
Dorsal-fin base length	9	11·4	8·7–12·1	11·2 ± 1·0	26	8·7–12·4	10·5 ± 0·9
Pectoral-fin length	9	25·5	25·2–27·3	26·2 ± 0·7	26	21·1–28·4	26·0 ± 1·6
Pelvic-fin length	9	16·9	13·7–17·4	15·7 ± 1·3	26	11·9–16·6	14·4 ± 1·1
Anal-fin lobe length	8	17·5	15·8–18·8	17·4 ± 1·1	24	15·6–19·1	17·8 ± 0·8
Anal-fin base length	9	34·7	30·5–35·2	33·4 ± 1·4	26	29·2–34·8	32·0 ± 1·4
Caudal peduncle depth	9	12·3	9·4–12·3	11·2 ± 1·0	26	7·3–10·0	9·1 ± 0·5
Caudal peduncle length	9	11·4	11·1–12·5	11·8 ± 0·4	26	8·7–13·6	11·5 ± 1·4
Head length (L_H)	9	26·4	23·6–26·4	25·0 ± 0·9	26	23·0–27·0	24·2 ± 0·8
Percentages of L_H							
Snout length	9	3·0	32·1–35·2	33·6 ± 1·2	22	32·0–35·9	33·9 ± 1·0
Horizontal eye length	9	3·0	28·3–35·4	31·7 ± 2·4	22	30·0–35·4	32·2 ± 1·5
Postorbital head length	9	3·4	37·0–42·1	39·9 ± 1·6	26	34·0–43·9	38·8 ± 2·2
Least inter orbital width	9	3·0	32·5–37·1	34·7 ± 1·5	26	31·3–39·4	35·1 ± 2·1
Upper jaw length	9	4·0	43·1–49·2	45·3 ± 1·9	22	43·1–49·8	45·5 ± 1·7

n, number of specimens measured.

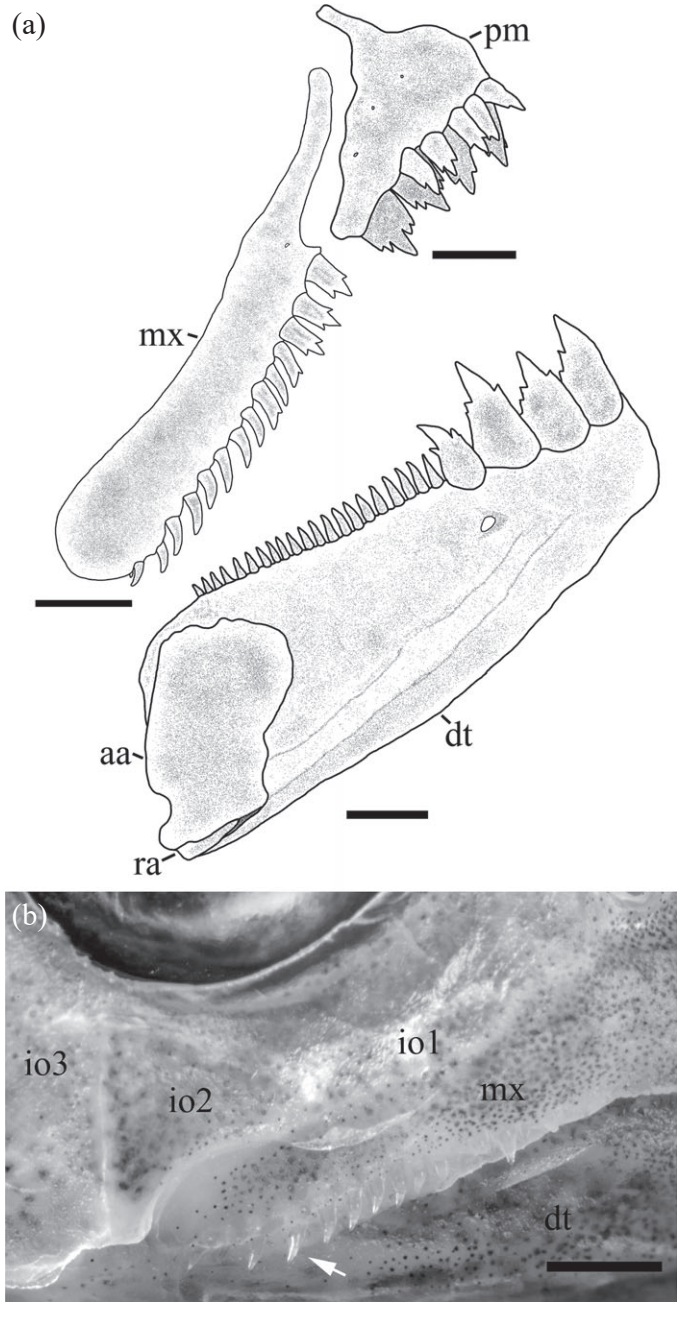

FIG. 2. Jaws and dentition of *Chrysobrycon mojicai*. (a) Upper and lower jaws, IAvH-P 8291, female, paratype, standard length (L_S) 50·4 mm (maxilla) and MPUJ 8059, male, paratype, 50·3 mm L_S (dentary and premaxilla). (b) Detail of lateral right-side view of the maxillary teeth (▭) in an alcohol-preserved specimen, IAvH-P 13932, male, holotype, 50·6 mm L_S. aa, anguloarticular; dt, dentary; io, infraorbital; pm, premaxilla; mx, maxilla; ra, retro-articular. Scale bar: 1 mm.

row partially covering rays, ventral row with 14 (1), 16 (1), 17 (1), 18 (2), 19 (1), 20 (5), 21 (5), 22 (5), 23 (5), 26* (1), 27 (1) or 28 (1) scales. Total number of vertebrae 42 (two c&s), 16 precaudal and 26 caudal. Five (1), six (30) or seven* (4) gill rakers on dorsal arm of first branchial arch; ventral arm with 11(27) or 12*(8).

Colour in alcohol

Ground colour pale yellowish in preserved males and females, slightly darker dorsally. Dark chromatophores on all body, in minor proportion on ventral region, forming narrow line along mid-dorsal region, often diffuse. Humeral blotch dark, usually more developed vertically than longitudinally, sometimes rounded (specimens from IAvH-P 8295). Dark midlateral stripe faint, extending from posterior region of humeral blotch to caudal peduncle. Caudal-peduncle blotch often diffuse, more expanded and intense posteriorly than anteriorly, extending onto middle caudal-fin rays. Few dark chromatophores forming stripes between myomeres on posterior ventral one-third of body. Dorsal fin mostly hyaline, with dark chromatophores more concentrated on interradial membranes than on rays. Adipose fin mostly hyaline, with few dark chromatophores. Anal fin somewhat dusky, with dark chromatophores extending over interradial membranes, being more concentrated on distal portion of fin. Caudal fin mostly hyaline, anterior region of lobes whitish, with dark chromatophores more concentrated on rays than on interradial membranes; outermost caudal-fin rays more intensely pigmented with dark chromatophores. Pectoral and pelvic fins mostly hyaline with scarce dark chromatophores on rays. Head darker dorsally and yellowish ventrally except anterior region of isthmus with intense dark pigmentation. Dark chromatophores concentrated on premaxilla, maxilla and lower jaw. Opercle somewhat dusky, chromatophores more intensely concentrated posteriorly. Infraorbitals yellowish, with scattered dark chromatophores.

Sexual dimorphism

Males differ from females by the presence of bony hooks on the caudal, pelvic and anal-fin rays. The caudal fin of males has 10–37 short slender hooks that are usually paired (one or two pairs per segment), anterodorsally oriented and placed on the dorsal margin of the lower rays 13–17. All pelvic-fin rays of males bear short slender hooks, positioned anteroventrally along most ray lengths and on both the main branches of each ray. The pelvic-fin bony hooks of males are grouped in two pairs per segment, being more numerous on the middle pelvic-fin rays. The anal fin of males has two to 12 variable-sized hooks distributed in one or, rarely, two pairs per segment and oriented anterodorsally mainly on the lateral or dorsal surface of the posteriormost unbranched ray and up to the first 11 anterior branched rays. The anal-fin bony hooks are more numerous, robust, larger on the middle rays of this range and form continuous rows along the ray length. The tiny anal-fin hooks usually are located more dorsally than laterally on the rays. The lower caudal-fin lobe of males has a single pouch scale plus at least two accessory scales forming a broadly open pocket [Fig. 3(a)]. The pouch scale is relatively small, somewhat elongated, curved and weakly horizontally folded so that its lateral face forms a laterally concave, open pouch. The accessory scales are differently located regarding the pouch position. A medial accessory scale is curved, elongated and located under the lateral face of the pouch scale (sometimes partially visible posteriorly in lateral view) and a lateral accessory scale is large and

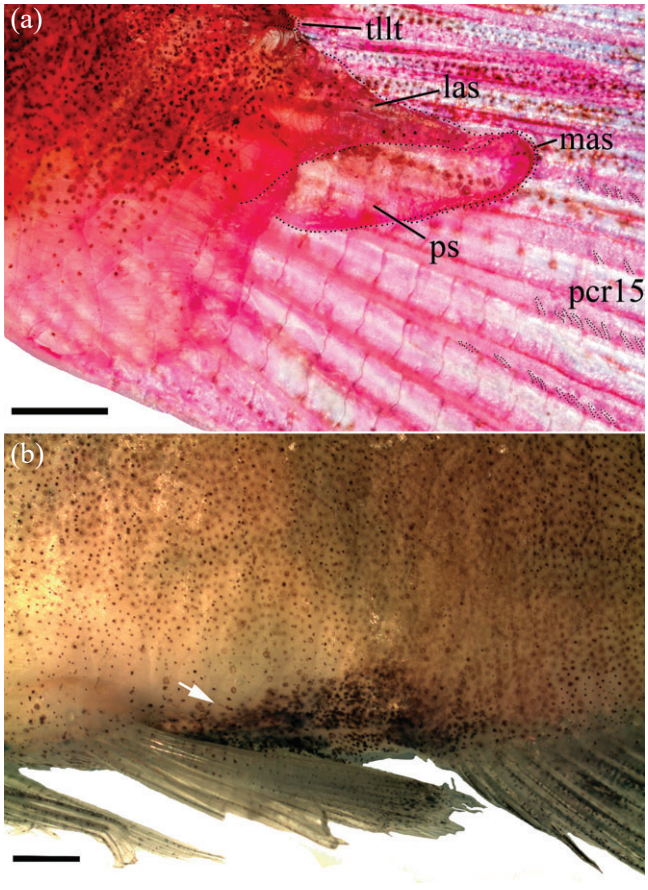

FIG. 3. Major sexually dimorphic characteristics of *Chrysobrycon mojicai*, MPUJ 8059, male, paratype, standard length (L_S) 50·3 mm. (a) Hypertrophied squamation on lower caudal-fin lobe (......, site of bony hooks). (b) Left-side view of distinctive pigmentation (▭) around urogenital region in adult males. las, Lateral accessory scale; mas, medial accessory scale; ps, pouch scale; pcr, principal caudal-fin ray; tllt, terminal lateral-line tube. Scale bar: 1 mm.

somewhat elongated posterodorsally, forming part of the laterodorsal region of the pouch. The pouch scale and lateral accessory scale are independent but in contact, both scales are strongly attached to each other dorsally through a well-developed medial mass of connective tissue. An additional scale is vertically elongated, located between the lateral accessory scale and pouch scale. The caudal-fin rays 15–17 (sometimes 18) and the lateral surface of the pouch scale have some aggregations of apparent glandular tissue.

Males have a dark pigmentation located between the pelvic- and anal-fin origins, being more intense ventrally around the urogenital pore [Fig. 3(b)]. The anal-fin chromatophores are more concentrated in males than in females, resulting in darker anal-fin interradial membranes. Males have the anal fin slightly straight or convex, whereas in females it is slightly concave anteriorly. The gill gland of males is relatively long, formed by the fusion of the anterior 13 (2), 14 (1), 15 (1), 16* (2) or 17 (1)

TABLE II. Results of comparative regressions performed between females ($n = 25$) and males ($n = 9$) of *Chrysobrycon mojicai*, using the morphometric variables as function of L_S. Only those measures that were observed partially sexually dimorphic are presented

Measures	Sex	W	P	r	r^2	α	95% C.I.(α)	β	95% C.I. (β)
Distance between pectoral- and pelvic-fin insertions	Females	1·0	>0·05	0·9	0·8	0·2	0·2, 0·3	−1·7	−5·1, 1·4
	Males	0·9	>0·05	0·8	0·7	0·2	0·1, 0·3	−1·1	−5·2, 4·8
Distance between pelvic- and anal-fin origins	Females	1·0	>0·05	0·9	0·8	0·2	0·1, 0·2	−1·3	−3·4, 0·7
	Males	0·9	>0·05	0·8	0·7	0·1	0·1, 0·2	1·6	−3·1, 3·8
Caudal peduncle depth	Females	1·0	>0·05	0·9	0·8	0·1	0·1, 0·1	−0·4	1·2, 1·4
	Males	0·9	>0·05	0·9	0·9	0·2	0·1, 0·2	−3·3	−4·5, −0·9
Standard length (L_S)	Females	1·0	>0·05	–	–	–	–	–	–
	Males	0·9	>0·05	–	–	–	–	–	–

α, slope; β, intercept; r, correlation coefficient, r^2, determination coefficient; W, Shapiro–Wilk statistic.

gill filaments of the ventral arm of the first gill arch. The total number of ventral arm gill filaments is 26 (1), 28* (3), 29 (1), 30 (2) or 33 (1). The gill-gland length ranges between 5·1 and 6·8% L_S (mean = 5·8% L_S), 5·9% L_S*. The gill gland was not observed in adult females (gill filaments are not fused). The morphometric comparisons between sexes revealed that the distance between the pectoral and pelvic-fin insertions, distance between the pelvic and anal-fin origins, and the caudal peduncle depth (all as function of L_S) are partially sexually dimorphic along the regression lines, especially in larger specimens (Table II). Since an overlapping was found between several female specimens and the 95% confidence lines of the males in the regressions and *vice versa*, the plots are not presented (Table II).

Distribution

Chrysobrycon mojicai is known from upland forest streams that are part of the Amazon basin in Colombia (Fig. 4).

Etymology

The species name, *mojicai*, is a patronym in honour to José Iván Mojica, who has contributed to the knowledge of the Amazonian freshwater fishes in Colombia.

Ecological notes

The specimens used here to describe *C. mojicai* were collected by F. Arbeláez between 2005 and 2006, who posteriorly published an ecological study about the freshwater fish communities from the southern Amazonian drainages of Colombia based on these collecting events (Arbeláez *et al.*, 2008). According to that study, the streams in which *C. mojicai* occurs are characterised by the following physicochemical variables (mean values): Matamatá (pH = 5·7–5·9; dissolved oxygen = 3·7–4·0 mg l^{-1}), Zafire (pH = 6·8–6·9; dissolved oxygen = 5·3–5·4 mg l^{-1}) and Purité (pH = 5·0–5·1; dissolved oxygen = 3·7–4·4 mg l^{-1}).

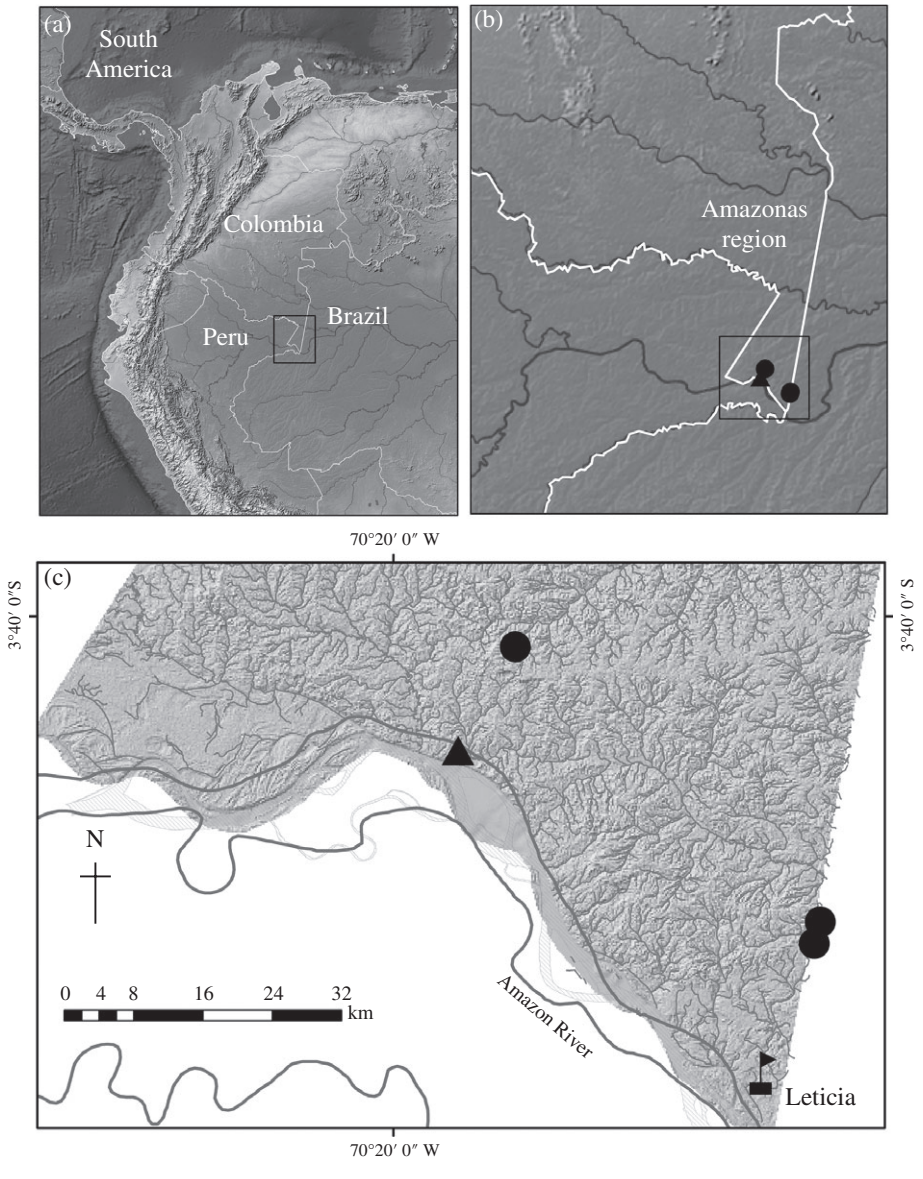

FIG. 4. (a) Geographical distribution of *Chrysobrycon mojicai* along southern Amazon River basin in Colombia, South America; (b) and (c) collection points (●) and type locality (▲).

KEY TO THE SPECIES OF *CHRYSOBRYCON*

1a. 33–39 branched anal-fin rays; 17–19 circumpeduncular scales; adult males with longer and expanded anal fin and with series of spinelets developed on pelvic, anal and caudal-fin rays; pelvic-fin rays i,6 (rarely i,7); outer premaxillary row teeth with 2–4 teeth (mode = 3) . . . . . *C. myersi*

1b. 24–32 branched anal-fin rays; 14–16 circumpeduncular scales; adult males with shorter and unexpanded anal fin and lacking spinelets on pelvic, anal and caudal-fin rays; pelvic-fin rays i,7 (rarely i,6 or i,8 in *C. eliasi* or *C. guahibo*); outer premaxillary row teeth with 4–6 (mode = 5 in *C. eliasi*; 5 in *C. guahibo*; 5 in *C. hesperus*; 4 in *C. yoliae*) 2

2a. Anal-fin bony hooks located on nearly all branched anal-fin rays in adult males (>80% of total number of rays); larger specimens (usually > 50 mm L_S) with anteriormost maxillary tooth usually pentacuspid (rarely tetracuspid); terminal lateral-line tube on middle caudal-fin rays absent . . . . . *C. hesperus*

2b. Anal-fin bony hooks distributed on anterior branched anal-fin rays 1–12 in adult males (≤50% of total number of rays); larger specimens (usually > 30 mm L_S in *C. eliasi*; >28 mm L_S in *C. guahibo*; >30 mm L_S in *C. mojicai*; and >35 mm L_S in *C. yoliae*) with anteriormost maxillary tooth usually tricuspid (rarely conical, bicuspid or tetracuspid); terminal lateral-line tube on middle caudal-fin rays present 3

3a. Maxillary teeth 1–3 (occasionally absent in juvenile specimens); anal-fin bony hooks on third to seventh branched rays forming two separate series along each ray in mature males . . . . . *C. guahibo*

3b. Maxillary teeth 6–16; anal-fin bony hooks on third to seventh branched anal-fin rays forming single, continuous series along each ray in mature males 4

4a. Distal tips of most maxillary teeth lateroventrally curved . . . . . *C. mojicai*

4b. All maxillary teeth straight 5

5a. Dentary teeth 20–26; body depth at dorsal-fin origin 34·4–42·2% L_S; distance between dorsal- and adipose-fin origins 26·8–28·8% L_S; dorsal-fin origin situated at vertical between anal-fin rays 5–7 . . . . . *C. yoliae*

5b. Dentary teeth 12–19; body depth at dorsal-fin origin 24·1–34·5% L_S; distance between dorsal and adipose-fin origins 23·9–26·8% L_S; dorsal-fin origin situated at vertical between anal-fin rays 8–10 . . . . . *C. eliasi*

DISCUSSION

The occurrence of *Chrysobrycon* in the Orinoco Basin remained unknown until the description of *C. guahibo* (Vanegas-Ríos *et al.*, 2015). The genus includes five valid species (including *C. mojicai*) and is more widespread in the Amazon Basin than in the Orinoco Basin. The Amazonian species of *Chrysobrycon* are mainly known from the geographical records of their descriptions (Böhlke, 1958; Weitzman & Thomerson, 1970; Vanegas-Ríos *et al.*, 2011, 2014) as well as from additional records provided by Vanegas-Ríos *et al.* (2013*b*) for *C. hesperus* and *C. myersi*. Although *C. hesperus* seems to be the most widespread species of the genus, occurring widely in the Amazon River basin of Colombia, Ecuador and Peru, the precise extent of its geographical distribution is yet to be determined.

Chrysobrycon mojicai is easily distinguished from its congeners, as well as from other stevardiines, by the presence of most maxillary teeth with distal tips lateroventrally curved [Fig. 2(b)]. The adult males of most species of *Chrysobrycon* have a variously developed dark pigmentation extending lateroventrally between the pelvic- and anal-fin origins [Fig. 3(b)]. *Chrysobrycon mojicai* is the only species with that pigmentation well developed lateroventrally around the urogenital region. In one adult male of *C. yoliae*, the dark pigmentation resembles that of *C. mojicai*, but

with the chromatophores less concentrated laterally on the urogenital region. In *C. eliasi*, *C. guahibo* and *C. hesperus*, the dark pigmentation is exclusively located ventrally between the pelvic- and anal-fin origins being comparatively less intense than those of *C. mojicai* and *C. yoliae*. In *C. myersi*, the absence or presence of the dark pigmentation could not be reliably ascertained due to the faded condition of the examined mature males. Further comparisons should be made to confirm if the dimorphic pigmentation may distinguish *C. mojicai* from its congeners.

Chrysobrycon is diagnosed by the combined presence in adult males of a small elongated pouch scale plus one medial accessory scale (Weitzman & Menezes, 1998). After examining many specimens of the genus, it was observed that all species of *Chrysobrycon* have the frontals, rarely the parietals, extensively contacting each other along the midline in adult specimens (even frequently in juveniles). As result of this contact, the frontal fontanel is absent, whilst the parietal fontanel is confined to a narrow opening limited posteriorly by the supraoccipital and anterolaterally by the frontal and parietal bones. The contact of the frontals is a feature rarely found within the Stevardiinae and especially when it is posterior to the epiphyseal bar (Mirande, 2010; Mirande *et al.*, 2013). In some specimens of *Pterobrycon myrnae* Bussing 1974, the frontals are extensively contacting each other (in other specimens the contact is partial) and the parietal fontanel resembles that of the species of *Chrysobrycon*. A variably developed reduction of the parietal fontanel was found in *Gephyrocharax chocoensis* Eigenmann 1912 and *Gephyrocharax major* Myers 1929. According to Eigenmann (1911), *Hysteronotus megalostomus* Eigenmann 1911 has the frontal fontanel like a slit, with the parietal fontanel forming a narrow rhomboidal opening. In one examined specimen of *H. megalostomus*, the frontal fontanel is only partially closed anterior to the epiphyseal bar, which seems to be in agreement with the Eigenmann's (1911) description. Despite the observed variations in the anterior fontanel of these stevardiins, *Chrysobrycon* is differentiated from *Gephyrocharax* Eigenmann 1912, *Hysteronotus* Eigenmann 1911 and *Pterobrycon* Eigenmann 1913 by the combination of the following features: the possession of the aforementioned pouch scale, the lack of paddle-shaped scales on the body flanks in adult males, the absence of pouch-scale lobes and by not having the second and third ventral procurrent rays forming a spur-shaped structure in adult males (Menezes *et al.*, 2016; Vanegas-Ríos, 2016). Therefore, the extensive contact of the frontals is proposed as a new diagnostic characteristic for the genus, which also might constitute a putative synapomorphy supporting its monophyly.

COMPARATIVE MATERIAL EXAMINED

Acrobrycon ipanquianus (Cope 1877), CI-FML 3890, seven specimens, 48·8–58·1 mm L_S (four c&s specimens, 49·0–54·7 mm L_S), Argentina, Tucumán, Monteros, Capitán Cáceres, Mandolo River. *Argopleura magdalenensis* (Eigenmann 1913), Colombia: CI-FML 5016, 2, 49·4–52·5 mm L_S (one c&s specimen, 49·4 mm L_S), Quindío, Quimbaya, Alejandría, La Vieja River. CI-FML 5879, two specimens, 36·3–41·0 mm L_S (one c&s specimen, 41·0 mm L_S), Colombia, Tolima, Magdalena River system, Tuluní creek. *Attonitus ephimeros* Vari & Ortega 2000, CI-FML 3895, 3, 45·0–51·4 mm L_S (one c&s specimen, 51·4 mm L_S), Peru, Cuzco, Coribeni River, near Kiteni. *Aulixidens eugeniae* Böhlke 1952, Venezuela: ANSP 134797, two c&s specimens, 39·7–41·7 mm L_S, Matepalma Beach, Orinoco River. ANSP 150127, two specimens, 34·8–35·2 mm L_S, Orinoco River, in Matepalma Beach, below of

Yapacama. CAS 16940*, holotype, 36·1 mm L_S (radiograph), Amazonas, Orinoco River basin, Casiquiare River, mouth of Curamuni River. FMNH 103417*, one specimen, 38·6 mm L_S, Orinoco River, beach on Cuao River. *Bryconamericus agna* Azpelicueta & Almirón 2001, CI-FML 3896, two c&s specimens, 42·1–48·9 mm L_S, Argentina, Misiones, Aristóbulo del Valle, Cuñá-Pirú. *Bryconamericus exodon* Eigenmann 1907, CI-FML 3897, 11 specimens, 24·1–43·9 mm L_S (two c&s specimens, 39·0–41·1 mm L_S), Paraguay, upper Paraguay, Bahía Negra, Paraguay River. *Bryconamericus indefessus* (Mirande, Aguilera & Azpelicueta 2004), Argentina: CI-FML 3940, one c&s specimen, 41·6 mm L_S, Salta, Orán, Estancia Anta Muerta, Pescado River. CI-FML 3941, one c&s specimen, 35·2 mm L_S, Jujuy, Pozo de los Sauces, between Purmamarca and Tilcara, Grande River. *Carlastyanax aurocaudatus* (Eigenmann 1913), CI-FML 5015, 15 specimens, 31·3–48·1 mm L_S (two c&s specimens, 39·4–40·1 mm L_S), Colombia, upper Cauca, La Vieja River basin, La Siria creek. *Creagrutus anary* Fowler 1913, CI-FML 3905, one c&s specimen, 47·1 mm L_S, Peru, Loreto, Maynas, Napo River, near town of Mazan. *Creagrutus atrisignum* Myers 1927, Brazil, Goiás: CAS 41339*, holotype, 44·6 mm L_S, Tocantins River basin, Maranhão River in Tocantins River. MCP 15929, six c&s specimens, L_S not taken, Niquelândia, Ribeirão do Engenho, on route between Niquelândia and Codemin, 29 km South of Codemin. *Chrysobrycon eliasi*, all from Peru, Madre de Dios Department, Tambopata: MUSM 39970, holotype, 34·3 mm L_S, Madre de Dios basin, Loboyoc creek, 12° 27′ 07″ S; 69° 7′ 43″ W, 210 m a.s.l. MLP 10831, three paratypes, 33·0–43·5 mm L_S (two c&s specimens 33·0–39·9 mm L_S), Manuripe River basin, creek at km 50, 12° 11′ 21″ S; 69° 6′ 57″ W, 248 m a.s.l. CI-FML 6153, two paratypes, 37·3–37·6 mm L_S, Manuripe River basin, Yarinal creek, 12° 3′ 06″ S; 69° 4′ 50″ W, 250 m a.s.l. MUSM 39971, 14 paratypes, 26·1–40·8 mm L_S, collected with holotype. MUSM 39972, eight paratypes, 28·0–43·2 mm L_S, Manuripe basin, creek at km 50, 12° 11′ 21″ S; 69° 6′ 57″ W, 248 m a.s.l. MUSM 39973, two paratypes, 36·11–37·63 mm L_S, Madre de Dios River basin, Loboyoc creek, 12° 27′ 21″ S; 69° 7′ 42″ W, 225 m a.s.l. MUSM 39974, three paratypes, 29·3–41·2 mm L_S, San Antonio, Heath River basin, San Antonio creek, 12° 41′ 03″ S; 68° 43′ 09″ W, 193 m a.s.l. ROM 66378, four specimens, 27·6–31·6 mm L_S, Peru, Madre de Dios, Tambopata, La Colpa, lodge, río Tambopata, stream at left bank at 2·1 km. *Chrysobrycon guahibo*, all from Colombia, Meta Department, Orinoco River basin, Guaviare River basin, Ariari River basin: MPUJ 7160, holotype, 31·9 mm L_S, Colombia, Fuente de Oro municipality, Caño Abrote, 3° 17′ 39″ N; 73° 32′ 02″ W, 258 m a.s.l. CI-FML 6152, six paratypes, 26·5–33·6 mm L_S. MLP 10829, two c&s specimens, 30·4–31·3 mm L_S. MPUJ 7162, 11 paratypes, 26·7–29·0 mm L_S, Puerto Lleras municipality: Caño Cunimia, 3° 11′ 24″ N; 73° 39′ 39″ W, 268 m a.s.l. MLP 10830, four paratypes, 28·9–31·3 mm L_S. MPUJ 7161, 10 paratypes, 23·0–29·6 mm L_S, collected with holotype. MPUJ 7163, one paratype, 31·0 mm L_S, Puerto Lleras municipality, Caño Cunimia, 3° 11′ 24″ N; 73° 39′ 39″ W, 268 m a.s.l. MPUJ 7164, three specimens, 31·0–34·8 mm L_S, Puerto Lleras municipality, Caño Cunimia, 3° 11′ 24″ N; 73° 39′ 39″ W, 268 m a.s.l. MPUJ 7165, six paratypes, 28·7–35·3 mm L_S, San Juan de Arama municipality, Caño Casa Roja; 3° 22′ 25″ N; 73° 52′ 13″ W, 448 m a.s.l. MPUJ 7166, eight, 31·3–36·6 mm L_S; Vista Hermosa municipality, Caño Uricacha, 3° 16′ 56″ N; 73° 36′ 45″ W, 270 m a.s.l. MPUJ 7167, 10 paratypes, 29·0–35·2 mm L_S, Fuente de Oro municipality, Caño Abrote, 3° 17′ 39″ N; 73° 32′ 02″ W, 258 m a.s.l. MPUJ 7168, two paratypes, 43·5–44·6 mm L_S; Vista Hermosa municipality, Caño Guapaya, 3° 2′ 59″ N; 73° 49′ 17″ W, 285 m a.s.l.

Chrysobrycon hesperus, all from Ecuador: ANSP 75912, one paratype, 77·4 mm L_S, upper Villano River near Villano, upper Napo River basin, 1° 30′ 00″ S; 77° 28′ 00″ W. ANSP 79513, one paratype, 67·4 mm L_S, upper Villano River, near Villano, upper Napo River system, 1° 30′ 00″ S; 77° 28′ 00″ W. ANSP 75914, one paratype, 63·2 mm L_S, Suno River near mouth, tributary upper Napo River, 0° 42′ S; 77° 8′ W, 300–320 m a.s.l. ANSP 79159, two paratypes, 60·3–76·0 mm L_S, Pucuno River, a tributary of Suno River, upper Napo River system, *c*. 350 m a.s.l. USNM 164042, one paratype, 70·5 mm L_S, Napo-Pastaza provinces, Villano River, upper Curaray, near Villano, 1° 30′ S; 77° 28′ W, *c*. 375 m a.s.l. USNM 164056, holotype, 72·3 mm L_S (radiograph), Napo-Pastaza provinces, Pucuno River, tributary of Suno River, Pucuno, enters of Suno, 0° 46′ 00″ S; 77° 12′ 00″ W, *c*. 300–350 m a.s.l. USNM 175124, one paratype, 59·1 mm L_S (radiograph), Napo-Pastaza provinces, Pucuno River, tributary of Suno River, Pucuno, enters of Suno, 3° 46′ 00″ S; 17° 12′ 00″ W. All from Peru: MUSM 26607, 2, 59·9–66·1 mm L_S, Loreto Department, Andoas District: upper Amazon Basin, Corrientes River basin, Caballo creek, 2° 33′ 41″ S; 76° 13′ 45″ W, 209 m a.s.l. MUSM 26617, 2, 29·8–33·1 mm L_S, Loreto Department, upper Amazon Basin, Corrientes River, drainage flowing into Huayuri Creek, 2° 35′ 51″ S; 76° 13′ 53″ W, 208 m a.s.l. MUSM 28640, two specimens, 25·5–27·0 mm L_S, Forestal Creek, Corrientes River basin, 2° 19′ 14″ S; 76° 10′ 31″ W, 215 m a.s.l. MUSM 28665, three specimens, 36·2–54·6 mm L_S (one c&s specimen, 54·6 mm L_S), Loreto Department, Andoas District, upper Amazon basin, Corrientes River basin, Forestal Creek, 2° 21′ 28″ S; 76° 9′ 25″ W, 237 m a.s.l. MUSM 28682, three specimens, 41·6–46·1 mm L_S, Loreto Department, Andoas District, upper Amazon basin, San Carlos Creek, flowing into Manchari River, 2° 24′ 35″ S; 76° 6′ 36″ W, 196 m a.s.l. MUSM 32124, one specimen, 27·1 mm L_S, Loreto Department, Andoas District, upper Amazon basin, Corrientes River basin, Platanoyacu River, 3° 08′ 27″ S; 75° 45′ 09″ W, 153 m a.s.l. MUSM 33159, two specimens, 29·3–43·9 mm L_S, Loreto Department, Andoas District, upper Amazon basin, Pastaza River, Carmen Creek, 2° 22′ 44″ S; 76° 09′ 44″ W, 216 m a.s.l. *Chrysobrycon myersi*, all from Peru: ANSP 112325, two paratypes, 30·1–46·1 mm L_S, Huanuco Department, small creek at north-eastern outskirts of Tournavista, tributary of Pachitea River. ANSP 112326, three paratypes, 28·3–32·0 mm L_S, Huanuco Department, small creek at north-eastern outskirts of Tournavista, tributary of Pachitea River. LACM 37720.4, three specimens, 34·3–63·8 mm L_S, Pasco Department, Iscozacin Valley, Pan de Azúcar, stream *c*. 100 yards above entrance into Iscozacin River. MUSM 12040, one specimen, 29·7 mm L_S, Cusco Department, La Convención Province, Echarate District, Urubamba Basin, Picha River, Cocha Kamariampiveni, *c*. 11° 36′ 00″ S; 73° 05′ 00″ W, 380 m a.s.l. MUSM 18908, two specimens, 42·4–48·6 mm L_S, Pasco Department, Oxapampa province, Puerto Bermudez District, Pachitea River basin, Atas Creek, *c*. 10° 17′ 47″ S; 74° 56′ 11″ W, 259 m a.s.l. MUSM 36068, one specimen, 31·6 mm L_S, Cusco Department, La Convención Province, Echarate District, Urubamba River basin, Parotori River system, Poyiriari River, 12° 10′ 44″ S; 73° 05′ 06″ W, 544 m a.s.l. MUSM 36084, three specimens, 37·1–58·7 mm L_S, Cusco Department, La Convención province, Echarate District, Urubamba basin, Parotori River system, Poyiriari River, 12° 10′ 45″ S; 73° 05′ 18″ W, 585 m a.s.l. MUSM 36109, two specimens, 32·8–36·3 mm L_S, Cusco Department, La Convención province, Echarate District, Urubamba River, Parotori River, Poyiriari River, Piriabindeni creek, 12° 01′ 13″ S; 73° 00′ 24″ W, 585 m a.s.l. MUSM 36125, 3, 29·2–38·6 mm L_S, Cusco Department, La Convención

Province, Echarate District, Parotori River basin, Piriabindeni creek, 12° 01′ 19″ S; 73° 4′ 15″ W, 545 m a.s.l. MUSM 37889, two specimens, 45·1–51·0 mm L_S, Junin Department, Satipo Province, Mashira District, Tambo River basin, Capirosankari creek, 11° 01′ 25″ S; 73° 33′ 36″ W, 420 m a.s.l. MUSM 37933, three specimens, 58·0–60·8 mm L_S, Cusco Department, La Convención Province, Echarate District, Kinterani, Naca-naca Creek, 11° 28′ 09″ S; 73° 18′ 02″ W, 420 m a.s.l. MUSM 38671, three specimens, 50·9–60·7 mm L_S (one c&s specimen, 58·6 mm L_S), Junin Department, Satipo Province, Tambo River basin, Pukakunga creek, 11° 24′ 37 ″S; 73° 28′ 02″ W, 587 m a.s.l. USNM 203697, holotype, 46·5 mm L_S, Huanuco Department, small stream directly tributary to Pachitea River (itself tributary to Ucayali River) at north-eastern outskirt of Tournavista. USNM 203698, six paratypes, 24·9–31·3 mm L_S (one radiograph, 31·3 mm L_S), collected with holotype. *Chrysobrycon yoliae*, all from Peru, Ucayali Department, Coronel Portillo Province, Abujao, Yucamia River subsystem, unnamed creek, 8° 39′ 14″ S; 73° 21′ 17″ W, *c*. 273 m a.s.l.: MUSM 46140, holotype, 51·6 mm L_S. CI-FML 5882, three paratypes, 44·8–52·3 mm L_S (one c&s specimen, 44·8 mm L_S). MLP 10517, one paratype, 48·4 mm L_S. MUSM 46141, eight paratypes, 38·2–51·5 mm L_S. *Diapoma alburnus* (Hensel 1870), CI-FML 3906, two specimens, 37·5–46·4 mm L_S; MCP 7054, nine specimens, 30·6–57·1 mm L_S, Brazil, Rio Grande do Sul, Porto Alegre, Praia das Pombas. *Diapoma obi* (Cascciota, Almirón, Piálek & Říčan 2012), CI-FML 3892, three c&s specimens, 31·2–57·3 mm L_S, Argentina, Misiones, Aristóbulo del Valle, Moreno creek. *Diapoma speculiferum* Cope 1894, Brazil, Rio Grande do Sul, Barra do Ribeiro: CI-FML 3891, one c&s specimen, 33·1 mm L_S, BR-116 km 56, Açude dos García. MCP 7979, four specimens, 31·3–43·3 mm L_S, drainage Guaíba, açude dos Garcia, beside BR-116 route, km 56. *Eretmobrycon emperador* (Eigenmann & Ogle 1907), Colombia: CI-FML 4011, four specimens, 27·0–39·8 mm L_S (one c&s specimen, 39·8 mm L_S), Chocó, Chintado River, tributary of Atrato River. CI-FML 4012, two specimens, 54·6–83·0 mm L_S, Ladrilleros-Buenaventura, Bahía Málaga. *Eretmobrycon scleroparius* (Regan 1908), ANSP 163169, five specimens, 32·8–75·0 mm L_S (two c&s specimens, 58·0–65·3 mm L_S), Costa Rica, Limón, river on the road between Sixaola and Limón, 7 km north-east from Bribri. *Gephyrocharax chocoensis*, IMCN 4830, 12 specimens, 29·9–42·6 mm L_S (two c&s specimens, 38·9–39·4 mm L_S), Valle del Cauca, Calima, lower San Juan River basin, *c*. 3° 59′ 59·89″ N; 76° 59′ 0·13″ W 28 m a.s.l. *Gephyrocharax major*, UF 38194, seven specimens, 41·4–46·8 mm L_S (two c&s specimens 45·4–46·5 mm L_S), Bolivia, Cochabamba, Chapare, creek 7 km north-west of Villa Tunari, *c*. 16° 56′ 51·3″ S; 65° 22′ 19·1″ W 268 m a.s.l. *Gephyrocharax melanocheir* Eigenmann 1912, IMCN 3425, five specimens, 23·3–29·1 mm L_S, Colombia, Tolima, Honda, Magdalena River basin, Bernal creek, *c*. 5° 12′ 19·7″ N; 74° 45′ 46·1″W 284 m a.s.l. *Gephyrocharax venezuelae* Schultz 1944, IAvH-P 9788, nine specimens, 32·1–41·4 mm L_S, Norte de Santander, middle Catatumbo Basin, river before El Aserrío-Divisó, *c*. 8° 31′ 28·9″ N; 73° 15′ 29·2″ W 410 m a.s.l. *Hemibrycon dariensis* Meek & Hildebrand 1916, ANSP 104426, two c&s specimens, 36·6–43·4 mm L_S, Panamá, Coclé, creek of Coclé River *c*. 5 miles north of Penonomé on road to La Pintada. *Hysteronotus megalostomus*, USNM 236399*, one specimen, 30·1 mm L_S, Brazil, Minas Gerais, a little stream in District of Contendas, 3–4 km north-west of Lagoa Santa. *Knodus meridae* Eigenmann 1911, MCP 44038, two c&s specimens, L_S not taken, Venezuela, Amazonas, Culebra, near Puerto Ayacucho. USNM 221933, four c&s specimens, 39·7–58·1 mm L_S, Venezuela, Maracaibo, Motatán River, 4 km above

Motatán. *Knodus tanaothoros* (Weitzman, Menezes, Evers & Burns 2005), MCP 30516, five c&s specimens, 16·0–32·1 mm L_S, Brazil, Mato Grosso, Cláudia, Corrego Tatú, MT-423 *c*. 14 km West of Cláudia. *Landonia latidens* Eigenmann & Henn 1914, Ecuador, Los Ríos: CAS 55297*, holotype, 42·0 mm L_S (radiograph), Guayas River basin, Vinces River at Vinces. MEPN RBS89.12, 57 specimens, 20·0–39·4 mm L_S, Vinces River, 5 km upstream of Vinces city. *Markiana nigripinnis* (Perugia 1891), CI-FML 3936, two c&s specimens, 75·3–78·6 mm L_S, Paraguay, upper Paraguay, Defensores del Chaco National Park. *Microgenys minuta* Eigenmann 1913, CI-FML 5021, two specimens, 24·7–31·4 mm L_S (one c&s specimen, 31·4 mm L_S), Colombia, Quindío, Quimbaya, Alejandría, La Vieja River. *Mimagoniates rheocharis* Menezes & Weitzman 1990, MCP 29273, three c&s specimens, 38·6–53·1 mm L_S, Brazil, Santa Catarina, Praia Grande, Mampituba River basin, Molha Coco Stream in Vila Rosa. *Planaltina glandipedis* Menezes, Weitzman & Burns 2003, LBP 14618, two c&s specimens, 27·5–29·1 mm L_S, Brazil, Botucataru, SP, Paraná River, Araquá River, 22° 44′ 50·2″ S; 48° 28′ 30·5″ W. *Phenacobrycon henni* (Eigenmann 1914), Ecuador, Los Ríos: MCZ 48660, 11 specimens, 22·1–29·6 mm L_S (one c&s specimen, 29·8 mm L_S), Vinces River in Vinces. MCZ 48661, three c&s specimens, 25·6–27·7 mm L_S, Ecuador, Nuevo River site where flows on left side of Vinces River in Vinces. *Piabarchus analis* (Eigenmann 1914), MCP 15571, three c&s specimens, L_S not taken, Brazil, Mato Grosso, Cáceres, stream near Barra do Bugres road. *Piabina argentea* Reinhardt 1867, ANSP 171965, three specimens, 38·8–44·2 mm L_S; CI-FML 3907, one c&s specimen, 41·2 mm L_S: Brazil, Minas Gerais, Riacho dos Poções, tributary of Coxá-Carinhanha rivers. CI-FML 5899, 18 specimens, 32·8–68·3 mm L_S, Brazil, Paraná, Paraíso do Norte, Ribeirão 19, tributary of Juai River, 23° 15′ 57″ S; 52° 32′ 38″ W. *Pseudocorynopoma doriae* Perugia 1891, CI-FML 3893, one c&s specimen, 57·5 mm L_S, not locality data. *Pterobrycon landoni* Eigenmann 1913, Colombia, Chocó: FMNH 56250*, holotype of *Microbryon minutus* Eigenmann & Wilson in Eigenmann, Henn & Wilson 1914, 20·98 mm L_S (radiograph), tributary of Atrato River near Boca de Raspadura. FMNH 56606*, holotype, 22·9 mm L_S (radiograph), Truandó River, tributary of Atrato River. USNM 367131*, four specimen, 15·8–20·0 mm L_S (four radiographs), Colombia, aquarium specimens. *Pterobrycon myrnae*, Costa Rica, Punta Arenas: ANSP 164243, 20 specimens, 20·6–29·2 mm L_S (two c&s specimens, 29·1–29·2 mm L_S), Culvert pool on the Inter-American Highway near 20 km south of Palmar Norte. LACM 33861.001, 10 paratypes, 24·2–34·7 mm L_S (two c&s specimens, 30·6–32·9 mm L_S), Banegas Creek (10 m) 0·8 km upstream from Pacific road 3 south-west of Rinco. *Scopaeocharax rhinodus* (Böhlke 1958), MUSM 8441, four specimens, 25·7–29·0 mm L_S (two c&s specimens, 25·7–28·0 mm L_S), Peru, San Martín, Tarapoto, Morales, San Antonio, Cumbaza River. *Tyttocharax* sp., MUSM 36130, five specimens, 17·5–20·6 mm L_S (two c&s specimens, 17·5–19·9 mm L_S), Peru, Cuzco, La Convención, Echarate, Urubamba River basin, Parotori River, Piriabindeni Creek. *Xenurobrycon macropus* Myers & Miranda Ribeiro 1945, MUSM 16974, five specimens, 11·6–12·6 mm L_S (two c&s specimens, 12·3–12·5 mm L_S), Brazil, Aquidauana, Taboco River.

We thank the following individuals and institutions for the assistance and support: J. Lundberg, M. Sabaj Pérez, M. Arce and K. Luckenbill (ANSP); J. Fong and D. Catania (CAS); M. Rogers, K. Swagel and S. Mochel (FMNH); C. Donascimiento and C. Medina-Uribe (IAvH-P); G. Aguilera and J. Mirande (CI-FML); C. Oliveira and R. Britzke (LBP); R. Feeny (LACM); M. Azpelicueta and D. Nadalin (MLP); J. Maldonado-Ocampo and S. Prada (MPUJ); H. Ortega

(MUSM); H. López-Fernández (ROM); and R. Vari†, S. Weitzman†, S. Raredon, K. Murphy, J. Clayton, J. Williams and L. Palmer (USNM). J. G. Melo (MPUJ) helped with most photographs presented in this work. J.A.V.-R. is grateful for the postdoctoral grant and financial support received from the CONICET. We also thank F. Arbeláez for the collecting efforts made in the Colombian Amazonia. This work was improved by helpful comments from J. Mirande, J. Arroyave, I. Harrison and an anonymous reviewer.

References

Arbeláez, F., Duivenvoorden, J. F. & Maldonado-Ocampo, J. A. (2008). Geological differentiation explains diversity and composition of fish communities in upland streams in the southern Amazon of Colombia. *Journal of Tropical Ecology* **24,** 505–515. https://doi.org/10.1017/S0266467408005294

Böhlke, J. (1958). Studies on fishes of the family Characidae.: no. 14. A report on several extensive recent collections from Ecuador. *Proceedings of the Academy of Natural Sciences of Philadelphia* **110,** 1–121. https://doi.org/10.2307/4064529

Burns, J. R. & Weitzman, S. H. (2005). Insemination in ostariophysan fishes. In *Viviparous Fishes* (Uribe, M. C. & Grier, H. J., eds), pp. 107–134. Homestead, FL: New Life Publications.

Eigenmann, C. H. (1911). New characins in the collection of the Carnegie museum. *Annals of Carnegie Museum* **8,** 164–181. https://doi.org/10.5962/bhl.part.14707

Fink, W. L. & Weitzman, S. H. (1974). The so-called Cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae). *Smithsonian Contributions to Zoology* **172,** 1–45. https://doi.org/10.5479/si.00810282.172

Hammer, Ø., Harper, D. A. T. & Ryan, P. D. (2001). PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4,** 1–9.

Menezes, N. A. & Weitzman, S. H. (1990). Two new species of *Mimagoniates* (Teleostei: Characidae: Glandulocaudinae), their phylogeny and biogeography and a key to the glandulocaudin fishes of Brazil and Paraguay. *Proceedings of the Biological Society of Washington* **103,** 380–426.

Menezes, N. A., Weitzman, S. H. & Teixeira, T. F. (2016). Redescription of *Hysteronotus megalostomus* (Characiformes: Characidae: Stevardiinae), a poorly known characid from tributaries of the Rio São Fancisco, Brazil with comments on the conservation of the species. *Journal of Fish Biology* **89,** 495–509. https://doi.org/10.1111/jfb.13000

Mirande, J. M. (2010). Phylogeny of the family Characidae (Teleostei: Characiformes): from characters to taxonomy. *Neotropical Ichthyology* **8,** 385–568. https://doi.org/10.1590/S1679-62252010000300001

Mirande, J. M., Jerep, F. C. & Vanegas-Ríos, J. A. (2013). Phylogenetic relationships of the enigmatic *Carlastyanax aurocaudatu*s (Eigenmann) with remarks on the phylogeny of the Stevardiinae (Teleostei: Characidae). *Neotropical Ichthyology* **11,** 747–766. https://doi.org/10.1590/S1679-62252013000400003

Rohlf, F. J. (2015). The tps series of software. *Hystrix* **26,** 9–12. https://doi.org/10.4404/hystrix-26.1-11264

Taylor, W. R. & Dyke, G. C. V. (1985). Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium* **9,** 107–119.

Thomaz, A. T., Arcila, D., Ortí, G. & Malabarba, L. R. (2015). Molecular phylogeny of the subfamily Stevardiinae Gill, 1858 (Characiformes: Characidae): classification and the evolution of reproductive traits. *BMC Evolutionary Biology* **15,** 146. https://doi.org/10.1186/s12862-015-0403-4

Vanegas-Ríos, J. A. (2016). Taxonomic review of the Neotropical genus *Gephyrocharax* Eigenmann, 1912 (Characiformes, Characidae, Stevardiinae). *Zootaxa* **4100,** 1–92. https://doi.org/10.11646/zootaxa.4100.1.1

Vanegas-Ríos, J. A., Azpelicueta, M. M. & Ortega, H. (2011). *Chrysobrycon eliasi*, new species of stevardiine fish (Characiformes: Characidae) from the Río Madre de Dios and upper Río Manuripe basins, Peru. *Neotropical Ichthyology* **9,** 731–740. https://doi.org/10.1590/S1679-62252011000400004

Vanegas-Ríos, J. A., Azpelicueta, M. M., Mirande, J. M. & Gonzales, M. D. G. (2013*a*). *Gephyrocharax torresi* (Characiformes: Characidae: Stevardiinae), a new species from the río Cascajales basin, río Magdalena system, Colombia. *Neotropical Ichthyology* **11,** 275–284. https://doi.org/10.1590/S1679-62252013000200005

Vanegas-Ríos, J. A., Meza-Vargas, V. & Azpelicueta, M. M. (2013*b*). Extension of geographic distribution of *Chrysobrycon hesperus* and *C. myersi* (Characiformes, Characidae, Stevardiinae) for several drainages flowing into the Amazon River basin in Peru and Colombia. *Revista Mexicana de Biodiversidad* **84,** 384–387. https://doi.org/10.7550/rmb.29591

Vanegas-Ríos, J. A., Azpelicueta, M. M. & Ortega, H. (2014). *Chrysobrycon yoliae*, a new species of stevardiin (Characiformes: Characidae) from the Ucayali basin, Peru. *Neotropical Ichthyology* **12,** 291–300. https://doi.org/10.1590/1982-0224-20130123

Vanegas-Ríos, J. A., Urbano-Bonilla, A. & Azpelicueta, M. M. (2015). *Chrysobrycon guahibo*, a new species from the Orinoco River basin, with a distribution expansion of the genus (Teleostei: Characidae). *Ichthyological Exploration of Freshwaters* **26,** 171–182.

Weitzman, S. H. & Menezes, N. A. (1998). Relationships of the tribes and genera of Glandulocaudinae (Ostariophysi: Characiformes: Characidae) with a description of a new genus, *Chrysobrycon*. In *Phylogeny and Classification of Neotropical Fishes* (Malabarba, L. R., Reis, R. E., Vari, R. P., Lucena, Z. M. S. d. & Lucena, C. A., eds), pp. 171–192. Porto Alegre: EDIPUCRS.

Weitzman, S. H. & Thomerson, J. E. (1970). A new species of glandulocaudine characid fish, *Hysteronotus myersi*, from Peru. *Proceedings of the California Academy of Sciences* **38,** 139–156.

