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A new species of *Chrysobrycon* Weitzman & Menezes, 1998 (Characiformes, Characidae, Stevardiinae) with remarkable sexually dimorphic pigmentation from the upper Río Vaupés basin, Colombian Amazon, with taxonomic key

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Abstract

This study describes *Chrysobrycon calamar*, a new stevardiine fish from the upper Río Vaupés basin in Colombia. The new species differs from its congeners by the following combined characters: adult males have a dark vertical blotch on the abdominal flanks that is confined to a small area immediately dorsal to the urogenital region and anterior to the third anal-fin ray; adult males with a well-developed vertically humeral blotch, numerous tiny bony hooks on nearly all the upper lobe caudal-fin rays (except *C. guahibo*, *C. hesperus*, and *C. mojicai*), and bony hooks on nearly all branched anal-fin rays (except *C. hesperus*); the number of vertebrae (43 *vs.* 38–42); an elongated maxillary anterior process, representing 40% or more of the total length of the bone (*vs.* with a shorter maxillary anterior process, representing less than 40% of that length); and the posterior portion of the maxilla not reaching the vertical through the anterior border of the eye when the mouth is closed (except from *C. yoliae*). Additionally, *C. calamar* differs from *C. mojicai* by the number of maxillary teeth (2–4 *vs.* 9–17) and shape of the distal tips of most maxillary teeth (straight along their lengths *vs.* lateroventrally curved). Remarks on the interspecific color variation associated with sexual dimorphism and other characteristics of the genus are provided. A key to the species of *Chrysobrycon* is presented. The discovery of *C. calamar* is a key advance in the understanding of fish biodiversity associated with endemism-rich regions that could be explored after the guerrilla demobilized in Colombia.

Key Words

Chiribiquete National Natural Park, cis-Andean basins, Neotropical freshwater fishes, sexual dimorphism, Stevardiini

* These authors contributed equally to this work.

Introduction

The Neotropical genus *Chrysobrycon* Weitzman & Menezes, 1998, is currently classified phylogenetically within Stevardiinae as a member of the tribe Stevardiini (Thomaz et al. 2017; Vanegas-Ríos 2018; Mirande 2019; Vanegas-Ríos et al. 2020). This genus was traditionally recognized by having hypertrophied scales that form a laterally open pocket on the lower caudal-fin lobe in adult males (Weitzman and Menezes 1998; Vanegas-Ríos et al. 2011, 2014). This pocket consists of a pouch scale (small in comparison with other stevardiines presenting pouch scale) that is characterized by being somewhat elongate, curved, confined to the dorsal region of the pouch opening, and horizontally folded so that its lateral face is laterally concave (Weitzman and Menezes 1998). More recently, Vanegas-Ríos and Urbano-Bonilla (2017) proposed an additional diagnostic character for *Chrysobrycon*: the extensive contact of the frontals along the midline in adults. Based on an extensive phylogenetic dataset including these variations in the frontals and hypertrophied caudal-fin squamation, the monophyly of most species of *Chrysobrycon* was corroborated by Vanegas-Ríos (2018) and Vanegas-Ríos et al. (2020).

Chrysobrycon is composed of six cis-Andean species distributed in the Orinoco and Amazon basins in Colombia, Ecuador, and Peru (Vanegas-Ríos et al. 2011; Vanegas-Ríos et al. 2013b; Vanegas-Ríos et al. 2014; Vanegas-Ríos et al. 2015; Vanegas-Ríos and Urbano-Bonilla 2017). The type species of the genus, *Chrysobrycon hesperus* (Böhlke, 1958), is known from the Río Marañon, Río Napo, and Río Putumayo basins (Böhlke 1958; Vanegas-Ríos et al. 2013b; Valdiviezo-Rivera et al. 2018; Toledo-Piza et al. 2024). *Chrysobrycon myersi* (Weitzman & Thomerson, 1970) occurs in the Río Pachitea and Río Ucayali basins (Weitzman and Thomerson 1970; Vanegas-Ríos et al. 2013b). *Chrysobrycon eliasi* Vanegas-Ríos, Azpelicueta & Ortega, 2011 is distributed in the Río Acre, Río Madre de Dios, and Río Manuripe basins (Vanegas-Ríos et al. 2011; Claro-García et al. 2013). *Chrysobrycon yoliae* Vanegas-Ríos, Azpelicueta & Ortega, 2014 occurs in the Río Yucamia system (Río Ucayali basin) (Vanegas-Ríos et al. 2014). *Chrysobrycon mojicai* Vanegas-Ríos & Urbano-Bonilla, 2017, the last described species of the genus from the Amazon basin, is known from several streams in Leticia, Colombia (Vanegas-Ríos and Urbano-Bonilla 2017). The only *Chrysobrycon* species known from the Orinoco basin is *C. guahibo* Vanegas-Ríos, Urbano-Bonilla & Azpelicueta, 2015, which is distributed along the upper Río Guaviare basin in Colombia (Vanegas-Ríos et al. 2015).

The Colombian Amazon exhibits some basins that remain unexplored (Jézéquel et al. 2020a), such as areas occupied by the Guerrilla (FARC-EP) that, after the signing of the peace agreements, have been studied, which has led to the discovery of new species (Irwin 2023). In fact, within these areas, some fish species have been described from the Río Vaupés basin (Londoño-Burbano and Urbano-Bonilla 2018; Lima et al. 2020; Urbano-Bonilla et al. 2023), a drainage with high values of richness and endemism (Jézéquel et al. 2020b). Furthermore, this basin is characterized by having its origin in the foothills of the Colombian eastern mountain range and running through outcrops of the Guiana Shield and the sandy soils of the Amazonian lowlands (Hernández-Camacho et al. 1992), in a series of numerous rapids that can act as natural ecological barriers limiting fish dispersal (Lima et al. 2005; Torrente-Vilara et al. 2011; Urbano-Bonilla et al. 2024 (in press)).

In expanding the area of the Serranía de Chiribiquete National Natural Park, explorations were carried out in the headwaters of the Vaupés basin, that is, the rapids of the Río Itilla, Río Unilla basin, and some associated streams and lagoons. As part of an ongoing revision of *Chrysobrycon*, we detected numerous specimens from these sampling efforts presenting a striking sexually dimorphic pigmentation in adult males, which diverges from what is known for the genus. Therefore, these specimens are described herein as a new species based on a comprehensive morphological comparison. We found several specimens collected in the upper Río Putumayo basin in Colombia that resemble the specimens from the Río Vaupes basin. These former specimens are analyzed comparatively to understand their taxonomic status with respect to the new species presented here. Additionally, a key to the species of *Chrysobrycon* is provided.

Materials and methods

The specimens are deposited in the following collections (acronyms according to Sabaj 2020): ANSP, CI-FML, FMNH, IAvH-P, ICN-MHN, LACM, MUSM, MLP-Ict (formerly MLP), MPUJ, ROM, and USNM. Counts of the pectoral-, pelvic-, and dorsal-fin rays follow Böhlke (1958). Measurements and other counts were taken according to Fink and Weitzman (1974), adding the following measurements: the dorsal-fin base length, anal-fin base length, and anal-fin lobe length by Menezes and Weitzman (1990), and the dorsal fin to pectoral fin distance, dorsal fin to adipose fin distance, pectoral fin to pelvic fin distance, pelvic fin to anal fin distance, and postorbital head length by Vanegas-Ríos et al. (2013a). Measurements were taken point-to-point with digital calipers under a stereomicroscope and are expressed as percent of standard length (SL) or head length (HL) for units of the head. Specimens that were analyzed from digitized photos using tpsDig 2.26 (Rohlf 2015) are indicated by an asterisk. The frequency of a particular meristic character is reported in parentheses, and the holotype values are indicated by an asterisk. Specimens were cleared and counterstained (c&s), according to Taylor and Van Dyke (1985). The total number of vertebrae was counted in c&s specimens. Those counts included the first preural centrum plus the first ural centrum (PU1+U1), counted as one element, and all four vertebrae of the Weberian apparatus.

To explore the morphometric variation between the specimens examined from the Río Vaupés and Río Putumayo basins, we conducted a morphometric comparison using a size-corrected principal component analysis (PCA), based on the "allometric *vs.* standard" procedure (Elliott et al. 1995). PCA was computed using the covariance matrix. The number of significant principal components (PCs) was decided by the broken-stick model (Frontier 1976) and the scree plot method (Cattel 1966). Statistical procedures were carried out in PAST 4.16 (Hammer et al. 2001) and GraphPad Prism 9.4.1 (GraphPad Software, San Diego, CA, USA). Coordinates were rounded off to the nearest second. Altitudes were rounded off to the nearest meter (expressed as above sea level = a.s.l.).

Results

Chrysobrycon calamar sp. nov.

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Figs 1–6, Table 1, Suppl. material 1: F–G

Type material. ***Holotype.*** MPUJ 18618, male, 39.3 mm SL, COLOMBIA, Guaviare department, San José del Guaviare, upper Río Vaupés, Calamar, Río Unilla, Caño Toño; 2°09'50"N, 72°50'16"W, c. 250 m a.s.l., Maldonado-Ocampo JA, Prada-Pedreros S, Moreno-Arias C, Zamudio JE, Cubides F, & Urbano-Bonilla A leg.; 5 Jan. 2017.

Paratypes. All from COLOMBIA, Guaviare department, San José del Guaviare, upper Río Vaupés: ICN-MHN 24743, 3, 31.4–37.7 mm SL; Calamar, Chiribiquete National Natural Park, Río Unilla, Caño Salado; 1°59'20"N, 72°53'22"W, c. 270 m a.s.l.; Maldonado-Ocampo JA, Prada-Pedreros S, Moreno-Arias C, Zamudio JE, Cubides F, & Urbano-Bonilla A leg.; 7 Jan. 2017. MLP-Ict 11733, 2, 34.6–36.5 mm SL; El Retorno, Río Unilla; 2°11'51"N, 72°44'59"W, c. 250 m a.s.l.; Maldonado-Ocampo JA, Prada-Pedreros S, Moreno-Arias C, Zamudio JE, Cubides F. & Urbano-Bonilla A leg.; 3 Jan. 2017. MPUJ 12850, 3, 32.9–36.9 mm SL, Calamar, Chiribiquete National Natural Park, Raudal del Río Itilla; 1°59'30"N, 72°53'15"W, c. 260 m a.s.l.; Maldonado-Ocampo JA, Prada-Pedreros S, Moreno-Arias C, Zamudio JE, Cubides F, & Urbano-Bonilla A leg.; 7 Jan. 2017. MPUJ 12965, 3, 34.8–41.2 mm SL; Calamar, Chiribiquete National Natural Park, Río Unilla, Caño Salado; 1°59'20"N, 72°53'22"W, c. 270 m a.s.l.; Maldonado-Ocampo JA, Prada-Pedreros S, Moreno-Arias C, Zamudio JE, Cubides F, & Urbano-Bonilla A leg.; 7 Jan. 2017. MPUJ 12966, 8 (2 c&s, 35.7–35.8 mm SL), 33.2–40.9 mm SL; same data as for holotype. MPUJ 12967, 7, 31.1–39.4 mm SL; Calamar, Río Unilla, Caño La Tigra; 2°10'57"N, 72°50'16"W; c. 250 m a.s.l., Maldonado-Ocampo JA, Prada-Pedreros S, Moreno-Arias C, Zamudio JE, Cubides F, & Urbano-Bonilla A leg.; 4 Jun. 2017. MPUJ 12969, 3, 33.2–37.2 mm SL, El Retorno, Río Unilla; 2°11'51"N, 72°44'59"W, c. 250 m a.s.l.; Maldonado-Ocampo JA, Prada-Pedreros S, Moreno-Arias C, Zamudio JE, Cubides F, & Urbano-Bonilla A leg.; 3 Jan 2017.

Diagnosis. *Chrysobrycon calamar* differs from its congeners by the following combined characters: a distinctive dark vertical blotch placed laterally on the abdominal flanks in adult males, just immediately dorsal to the urogenital region (*vs.* this pigmentation weak, diffuse, poorly

Figure 1. *Chrysobrycon calamar*: **A.** MPUJ 18618, male, holotype, 39.3 mm SL, Colombia, Guaviare department, San José del Guaviare, upper Río Vaupés, Calamar, Río Unilla, Caño Toño; **B.** MPUJ 12966, female, paratype, 34.1 mm SL, same data as holotype.

developed, or if well-defined, more developed longitudinally than vertically, never forming a distinctive vertical blotch); a well-developed vertically humeral blotch in adult males (almost rectangular-shaped, see additional details in sexual dimorphism section *vs.* scarcely expanded vertically, somewhat irregular, or circular-shaped mark); the possession of numerous (two to 12) tiny bony hooks on nearly all the upper lobe caudal-fin rays in adult males (*vs.* hooks confined to the lower lobe caudal-fin rays, except in *C. guahibo*, *C. hesperus*, and *C. mojicai*, with hooks arranged in a set of one to three hooks on a single ray), the number of vertebrae (43 *vs.* 38–42); the posterior portion of the maxilla not reaching the vertical through the anterior border of the eye when the mouth is closed, except from *C. yoliae* (*vs.* this portion reaching or surpassing the vertical through the anterior border of eye); an elongated maxillary anterior process, representing proportionally 40% or more of the total length of the bone (*vs.* with a shorter maxillary anterior process, representing less than 40% of its length); and the presence of bony hooks in adult males on nearly all the branched anal-fin rays, except *C. hesperus* (*vs.* bony hooks restricted up to the anterior half of fin or not extending to the posteriormost rays).

The presence of a simple terminal lateral-line tube between the caudal-fin rays 11 and 12 (*v.* tube absent) distinguishes *C. calamar* from *C. hesperus* and *C. myersi*. Additionally, *C. calamar* is also distinguished from *C. myersi* by the number of circumpeduncular scales (13–14 *vs.* 17–19), distance between dorsal- and adipose-fin origins (20.4–24.4% SL *vs.* 28.2–33.5% SL), dorsal-fin to caudal-fin base (33.0–39.6% SL *vs.* 40.1–47.4% SL), eye to dorsal-fin origin (51.9–57.2% SL *vs.* 45.8–49.2% SL), and upper jaw length (38.1–45.5% HL *vs.* 48.9–54.9% HL), and from *C. hesperus* by the maximum number of cusps on the maxillary teeth (tricuspid *vs.* pentacuspid) and number of supraneurals (11 *vs.* 12–14). The number of dentary teeth differentiates *C. calamar* from *C. mojicai* and *C. yoliae* (13–17 *vs.* 20–27). Furthermore, *C. calamar* is also distinguished from *C. mojicai* by the number of radii on the lateral-line scales (5–9 *vs.* 11–18), number of maxillary teeth (2–4 *vs.* 9–17), and shape of the distal tips of most maxillary teeth (straight along their lengths *vs.* lateroventrally curved), and from *C. yoliae* by the body depth at dorsal-fin origin (27.5–33.5% SL *vs.* 34.4–42.2% SL), and distance between dorsal- and adipose-fin origins (20.4–24.4% SL *vs.* 26.8–28.8% SL).

Description. Morphometric data in Table 1. Largest male 41.2 mm SL, largest female 35.8 mm SL. Body laterally compressed, maximum depth at vertical through area immediately anterior to anal-fin origins (Fig. 1).

Table 1. Morphometric data of *Chrysobrycon calamar*. Males were sexed by presence of bony hooks on fins and pouch scale on lower caudal-fin lobe. Range and mean of males include values of holotype. SD: standard deviation. Data of specimens treated as *C.* aff. *calamar* from the Putumayo basin are provided.

	Holotype	Paratypes						Putumayo basin		
		Males			Females			both sexes		
		n	Range	Mean+± SD	n	Range	Mean+± SD	n	Range	Mean+± SD
Standard length (mm)	39.3	15	33.2–41.2	37.5±2.3	15	31.1–35.8	33.5±1.5	7	34.2–44.4	41.4±3.6
Percent of standard length:										
Depth at dorsal-fin origin	31.9	15	27.5–33.5	30.6±1.8	15	27.7–31.4	29.0±1.1	7	29.5–33.8	32.1±1.3
Snout to dorsal-fin origin	66.1	15	61.1–69.8	65.4±2.2	15	64.7–68.7	67.0±1.2	7	65.2–68.3	66.4±1.0
Snout to pectoral-fin origin	28.7	15	26.3–29.6	27.9±0.9	15	26.4–29.3	27.7±0.8	7	26.3–28.9	27.4±0.9
Snout to pelvic-fin origin	44.3	15	42.6–48.6	45.7±1.6	15	44.2–48.2	45.7±1.1	7	45.9–48.4	47.7±0.9
Snout to anal-fin origin	59.2	15	57.2–63.9	59.6±1.5	15	58.4–62.2	60.4±1.1	7	59.1–62.8	61.5±1.3
Distance between dorsal- and pectoral-fin origins	48.6	15	45.8–49.9	48.2±1.1	15	44.8–50.6	47.3±1.5	7	44.4–50.0	48.5±1.8
Distance between dorsal- and adipose-fin origins	22.1	15	20.9–24.4	22.4±1.2	15	20.4–24.2	22.1±1.0	7	22.1–25.2	23.6±1.0
Dorsal fin to caudal-fin base	37.4	15	33.0–39.6	36.5±1.6	15	34.7–38.9	36.0±1.2	7	33.4–38.0	35.9±1.7
Eye to dorsal-fin origin	55.5	15	52.1–57.2	54.2±1.4	15	51.9–56.4	54.5±1.2	7	52.3–57.1	54.7±1.5
Distance between pectoral- and pelvic-fin insertions	17.9	15	17.0–19.7	18.2±0.8	15	17.1–20.4	18.8±1.0	7	18.9–22.8	20.7±1.3
Distance between pelvic- and anal-fin origins	15.8	15	14.3–16.3	15.4±0.6	15	12.1–15.5	14.7±0.8	7	14.6–17.1	15.6±0.9
Dorsal-fin length	17.3	15	14.5–20.7	18.2±1.6	15	15.9–21.2	18.2±1.8	7	17.7–23.2	19.4±1.9
Dorsal-fin base length	8.1	15	8.1–11.4	9.6±0.9	15	8.4–10.5	9.3±0.7	7	8.9–10.8	10.0±0.6
Pectoral-fin length	25.1	15	23.5–30.5	27.1±1.7	15	24.2–28.7	26.8±1.3	7	24.0–28.4	26.7±1.7
Pelvic-fin length	18.0	15	12.7–18.0	16.5±1.3	15	13.6–16.8	15.0±0.9	7	13.7–15.9	14.7±0.8
Anal-fin lobe length	16.1	15	16.1–21.6	18.6±1.6	15	16.0–19.7	18.3±0.9	7	16.3–19.6	17.7±1.1
Anal-fin base length	31.2	15	29.8–34.1	31.5±1.1	15	29.6–32.8	31.4±0.9	7	28.9–32.7	31.3±1.6
Caudal peduncle depth	10.8	15	9.3–11.6	10.8±0.5	15	8.3–10.6	9.6±0.6	7	8.5–11.3	10.0±1.1
Caudal peduncle length	13.9	15	11.5–14.0	12.9±0.8	15	9.3–13.3	11.7±1.0	7	11.1–13.5	12.6±0.9
Head length	23.5	15	23.5–25.5	24.4±0.5	15	22.5–25.2	24.2±0.7	7	22.9–25.9	24.3±1.2
Percent of head length:										
Snout length	32.6	15	24.5–33.7	29.9±2.3	15	26.6–31.4	28.5±1.6	7	30.1–33.8	31.5±1.4
Horizontal eye length	30.7	15	28.5–36.3	32.4±2.2	15	32.2–38.2	34.8±1.6	7	30.3–33.7	32.0±1.5
Postorbital head length	43.2	15	35.6–43.5	40.7±2.2	15	35.6–41.0	38.5±1.7	7	35.5–45.8	40.0±3.1
Least interorbital width	36.7	15	34.4–37.1	35.9±0.8	15	32.3–37.2	36.1±1.2	7	34.7–37.1	36.2±0.8
Upper jaw length	45.5	15	39.8–45.5	42.3±1.6	15	38.1–43.2	40.7±1.6	7	40.8–43.4	42.4±1.0

Dorsal profile of body: straight from tip of premaxilla to posterior region of head; slightly convex 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, slightly convex between pelvic- and anal-fin origins, straight and slanting dorsally from this point to caudal peduncle. Belly with like keel-shaped area between pelvic-fin origin and urogenital pore, consisting of one row of four to six scales forming sharp edge. Ventral profile of caudal peduncle straight. Head with anterior region acute. Frontal fontanel absent. Epiphyseal branch of supraorbital canal absent. Anterior nostril round, separated by skin fold from posterior nostril; posterior nostril opening considerably larger than anterior one. Two well-developed pit organs along grooves in head; anterior groove round, between nasal bone and nostril; posterior groove larger, extended along entire frontal, and covered with rows of neuromasts.

Mouth superior, lower jaw projecting slightly anterior to upper jaw. Premaxillary teeth arranged in two rows (Fig. 2). Outer row with four (5), five (22), or six* (3) tricuspid teeth. Inner row with four (1) or five* (29) teeth; symphyseal tooth tetracuspid; contiguous teeth pentacuspid; and posteriormost tooth conical to pentacuspid. Maxilla not fully toothed, with two (1), three* (23), or four (6) teeth tricuspid, sometimes conical. Maxillary teeth straight along their lengths, not distally curved lateroventrally. Maxilla short, with elongated anterior process, and extending on point at vertical between nostrils and anterior margin of orbit, but never reaching anterior margin of eye when mouth closed and body horizontally straight.

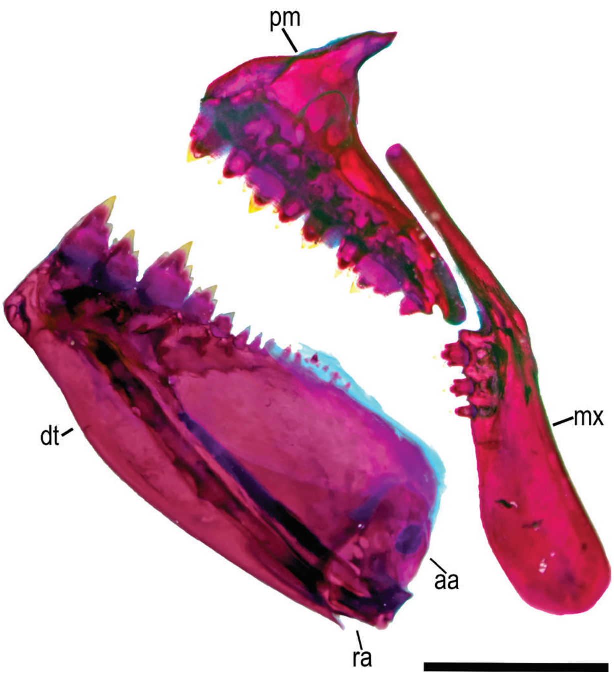

Figure 2. Jaws and dentition of *Chrysobrycon calamar*. MPUJ 12966, paratype, 35.8 mm SL. Premaxilla: pm; maxilla: mx; dentary: dt; anguloarticular: aa; retroarticular: ra. Bones reflecting an upper mouth. Scale bar: 1 mm.

Dentary moderately toothed, with 13 (3), 14 (12), 15* (6), 16 (5), or 17 (4) teeth; three anteriormost teeth large, pentacuspid (rarely tetracuspid); one median-sized tooth tri to pentacuspid, followed by 9 (3), 10 (12), 11* (6), 12 (5), or 13 (4) smaller conical or biscupid posterior teeth (Fig. 2).

Dorsal-fin rays ii (30), 8*(28), or 9 (2). Nine proximal dorsal-fin pterygiophores (2 c&s). Dorsal-fin origin at vertical between anal-fin rays 10 and 13. Adipose-fin origin at vertical crossing the second scale posterior to anal-fin termination. Anal-fin rays iv (6) or v* (24), 24 (1), 25 (1), 26 (8), 27* (6), 28 (8), or 29 (6). Twenty-seven to 29 proximal pterygiophores in anal fin (2 c&s). Anal-fin origin at posterior half of body, always anterior to vertical through dorsal-fin origin. Pectoral-fin rays i,9 (17), or 10* (13), last ray usually simple but counted as branched. Pectoral-fin distal tip reaching or surpassing one-half of pelvic-fin length (Fig. 1). Pelvic-fin rays i,7* in all specimens; last ray simple but counted as branched. Pelvic-fin origin slightly anterior to half of body. Caudal fin forked with 10/9 principal rays in all specimens.

Scales cycloid, with six to nine radii along posterior field, circuli on anterior, dorsal, and ventral fields, surpassing one-half scale length. Lateral line completely pored: 42 (8), 43* (8), 44 (11), 45 (2), or 46 (1). Terminal lateral-line tube present on caudal-fin interradial membrane. Predorsal scales 21 (1), 22* (13), 23 (14), or 24 (2) forming nearly continuous row. Scale rows between dorsal fin and lateral line five (24) or six* (6). Five* (28) or six (2) scale rows between lateral line and anal fin. Four (1) or five* (29) scale rows between lateral line and pelvic fin. Circumpeduncular scales 13 (1) or 14* (29). One row of 13 (1), 14 (1), 15 (4), 16 (5), 17 (9), 18* (7), or 19 (3) scales forming sheath along anal-fin base. Total number of vertebrae 43 (2 c&s), 17 precaudal, and 26 caudal. Six* (27), or seven (3) gill rakers on upper arm of first branchial arch; lower arm with 11 (11), 12*(14), or 13 (5).

Color in alcohol. Ground color pale yellow in preserved males and females, moderately darker dorsally. Dark chromatophores on all body, in minor proportion in ventral region, forming dark brown narrow band along mid-dorsal line, often diffuse. Humeral blotch dark, widely developed vertically, forming a rectangular-shaped pattern in most specimens (Fig. 1); frequently less developed vertically or somewhat rounded in female specimens. Dark black midlateral stripe extending from vertical through pelvic-fin origin to caudal peduncle. Wider lateral band of dark brown chromatophores located dorsal and ventral to this black stripe, less intense but more dorsoventrally developed, especially toward lateral line, and usually forming somewhat oval-shaped blotch from last portion of caudal peduncle, crossing interradialis muscles, to middle caudal-fin rays. Dark chromatophores forming stripes between myomeres ventrally located to midlateral stripe on posterior half of body. Dorsal fin mostly hyaline, with dark chromatophores mainly distributed on interradial membranes. Adipose fin mostly hyaline, with few dark chromatophores. Anal fin somewhat dusky, with dark chromatophores extending over interradial membranes, more concentrated on base and distal portions of fin.

Figure 3. Coloration in life of *Chrysobrycon calamar* from the upper Río Vaupes basin, Amazon basin, Colombia. **A.** MPUJ 12966, 40.9 mm SL (type locality: Caño Toño), paratype; **B.** MPUJ 12967, 39.4 mm SL, paratype.

Caudal fin mostly hyaline, with dark chromatophores extending mainly on interracial membranes and borders of rays; middle caudal-fin rays slightly pigmented with dark chromatophores. Pectoral and pelvic fins mostly hyaline with scarce dark chromatophores, but pectoral fins slightly more pigmented by having chromatophores on borders of rays. Head darker dorsally and light yellow ventrally, except for intense dark pigmentation on anterior region to isthmus. Dark chromatophores concentrated on premaxilla, maxilla, and lower jaw. Opercle dusky, with dark chromatophores intensely concentrated, especially on posterior region. Infraorbitals light yellow with scattered dark chromatophores (first infraorbital usually less pigmented).

Color in life. Based on adult male specimens photographed (Fig. 3). Ground color pale yellow dorsally and white or whitish yellow ventrally, being darker on midflanks. Dark chromatophores on all body, with abdominal region lighter below lateral line. Head yellowish orange dorsally but silvery laterally, with scattered dark chromatophores. Well-defined dark humeral blotch expanded vertically. Dark black midlateral stripe extending from vertical through pelvic-fin origin to caudal peduncle. Red half-moon shaped spot situated dorsally on pupil. Snout slightly bright yellow anteriorly. Wider lateral band of dark chromatophores located dorsal and ventral to this black stripe, usually forming somewhat oval-shaped blotch from last portion of caudal peduncle, crossing interradialis muscles, to middle caudal-fin rays. Dark blotch vertically expanded on abdominal flanks, located dorsally to urogenital region and anterior to first anal-fin rays. Pectoral and pelvic fins somewhat hyaline. Dorsal fin somewhat dusky. Orange adipose fin. Anal fin somewhat dusky, especially on base and distal tips of rays, but with yellowish-orange pigmentation in middle region of first anterior rays. Caudal fin somewhat yellowish orange on outer rays.

Sexual dimorphism. Adult males differ from females by the presence of bony hooks on the caudal-, pelvic-, and anal-fin rays. The caudal fin of males has four to 32 short, slender antrorse hooks that are usually paired (one or two pairs per segment) and placed on the dorsal margin of the lower caudal-fin rays 11 to 17. Additionally, two to 12 unpaired (sometimes paired) tiny antrorse hooks are placed on the ventral margin of the caudal-fin rays 2 to 10. All pelvic-fin rays of males bear slender antrorse hooks positioned lateroventrally along most rays length (on their margins) and are much more numerous and longer on the segmented and branched portions of each one (usually grouped in two pairs per segment). The anal fin of males has four to 30 variable-sized hooks distributed in one or two pairs per segment along the posteriormost simple ray and on all the branched rays; from the fifth to 10th branched anal-fin rays, the bony hooks are discontinuously arranged along the rays' length, clearly forming two separated groups of hooks (one closer to the

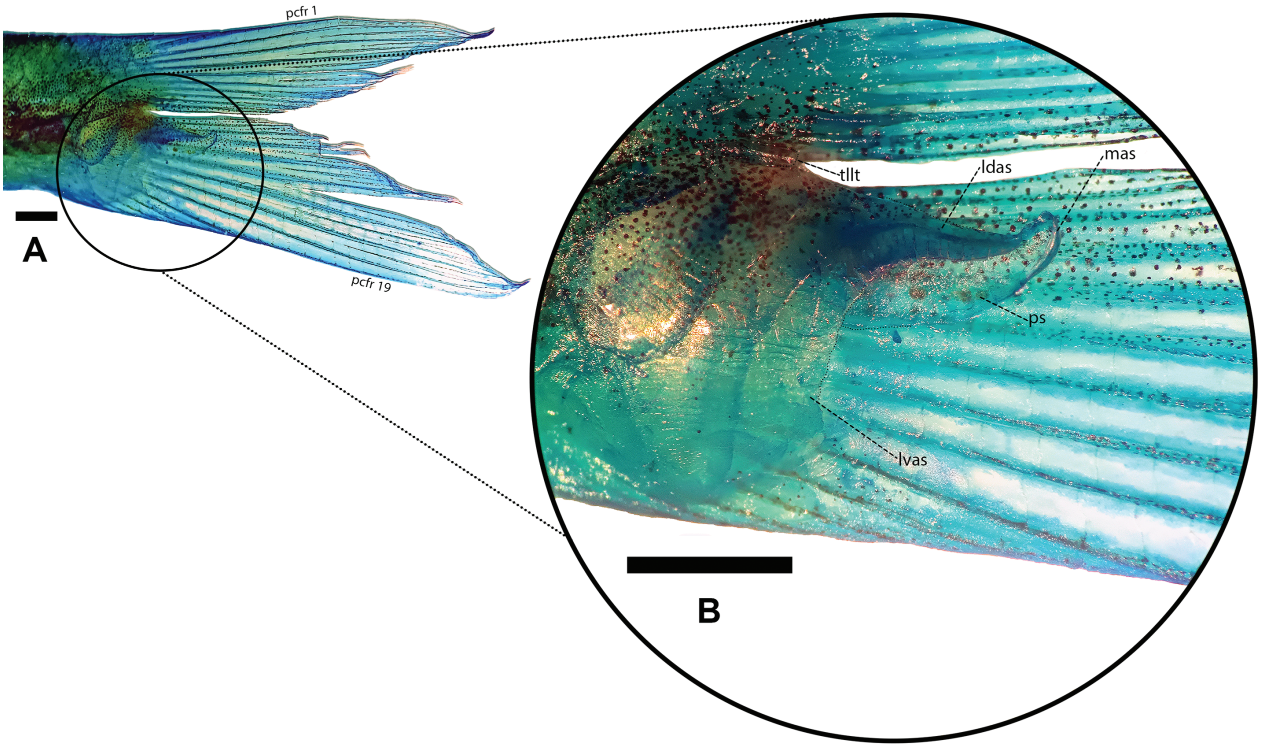

Figure 4. Caudal fin of *Chrysobrycon calamar* (**A**), with details of the hypertrophied caudal-fin squamation on the lower caudal-fin lobe (**B**). MLP-Ict 11733, male, 35.6 mm SL. Laterodorsal accessory scale: ldas; lateroventral accessory scale: lvas; medial accessory scale: mas; pouch scale: ps; principal caudal-fin ray: pcfr; terminal lateral-line tube: tllt. Specimen stained with Alcian Blue solution. Scale bar: 1 mm.

base and another nearer the distal portion). The anal-fin bony hooks placed closer to the base are more lateroventrally oriented in comparison with the hooks distributed on the distal portion. From the eighth or ninth anal-fin ray, the bony hooks are much more restricted to the distal portions, gradually decreasing in size anteroposteriorly.

The lower caudal-fin lobe of adult males has a broadly open pocket consisting of a single pouch scale and at least three accessory scales (Fig. 4). The pouch scale is relatively small, elongate, curved, and slightly folded laterally on its posterior portion; its hypertrophied radii are ventrally arranged at an obtuse angle, almost perpendicular to the caudal-fin rays. Underneath the pouch scale is located a medial accessory scale of similar shape, which is usually indistinguishable in lateral view. Lateral to the pouch scale, there are two accessory scales that largely outline the outermost margin of the pocket opening. One of them is curved and elongated, forming mainly the laterodorsal face of the pocket (its border with radii is almost completely concave). This laterodorsal accessory scale is independent from the pouch scale, but both are strongly attached to each other dorsally through a well-developed medial mass of connective tissue. The other accessory scale is extended between the previous ones but is not displaced posteroventrally, and for this reason, its radii are almost parallel to the horizontal axis of the body. The posterior border of this accessory scale delineates almost the entire lateroventral region of the pocket opening. A small scale laterally placed on the lateroventral accessory scale often closes the ventral margin of the pocket over the caudal-fin ray 19.

The gill gland of males is relatively long, formed by the fusion of the anterior 17 (3), 18 (4), 19* (5), 20 (2), or 22 (2) gill filaments of the ventral arm of the first gill arch. The gill-gland length ranged between 7.8 and 10.4% SL (mean = 9.0% ± 0.7, n = 15). Adult males have the anal-fin distal margin slightly straight or convex, whereas in females it is slightly concave.

The scale rows forming a sharp region between the pelvic-fin origin and urogenital pore are covered by dark chromatophores in both sexes, but the area is more intensely pigmented in adult males. The anal-fin distal margin of adult males is convex, whereas in females it is straight. Additionally, adult males are distinguished from females by possessing an irregular dark blotch vertically extended on the dorsal region between the anus and third anal-fin ray, reaching up to three or four scale rows of height and expanding up to three or four scales longitudinally (Fig. 1; Suppl. material 1: fig. S1F–G). Both types of pigmentations were observed to be dark or black in live or alcohol-preserved specimens (Figs 1, 2). In adult males, the oval-shaped caudal peduncle blotch is incompletely developed horizontally by the presence of a less intense or clearer area on the region associated with the hypertrophied caudal-fin squamation. The humeral mark was observed to be more greatly developed vertically in adult males, but it was less developed vertically in most females, being somewhat rounded.

Distribution. *Chrysobrycon calamar* is known from several streams flowing into the upper portion of the Vaupés basin in Colombia (Fig. 5; Suppl. materials 2, 3).

Etymology. The species is named "*calamar*" in reference to Calamar, a municipality in the department of Guaviare, which is part of its type locality. This is treated as a noun in apposition. Despite the fact that the municipality was the epicenter of slavery for the Carijona and Witoto indigenous people in the rubber era (1879 and 1912) and the Second World War (1942 and 1945), in addition to processes of colonization, extraction of natural resources, introduction of illicit crops, subversion, and paramilitarism (Arcila et al. 1999), it is currently a peaceful territory.

Ecological notes. *Chrysobrycon calamar* inhabits the main tributaries of the upper Vaupés (Río Itilla and Río Unilla basins) and associated drainages (Fig. 5; Suppl. materials 2, 3) between 250 and 270 m of altitude. It is generally found in shallow, clear, black water (< 1 m) with moderate flow over sand, pebbles, and rocks. In the rapids of the Río Itilla, the water has a temperature of 25.7 °C with high concentrations of dissolved oxygen (7.99 mg/l), a slightly acidic pH (6.5), and a low conductivity of 14.0 µS/cm. The gastrointestinal content of two samples examined (MPUJ 12966) mainly evidences a high consumption of aquatic and terrestrial invertebrates (remains of Diptera, Lepidoptera, Formicidae). The new species was collected in syntopy with other characids such as *Aphyocharax pusillus* (Günther, 1869), *Charax tectifer* (Cope, 1870), *Moenkhausia oligolepis* (Günther, 1864), *M. comma* Eigenmann, 1908, *Brachychalcinus copei* (Steindachner, 1882), *Jupiaba abramoides* (Eigenmann, 1909), *Hyphessobrycon agulha* Fowler, 1913, and *Hemigrammus yinyang* Lima & Sousa, 2009, *Tyttocharax* sp. and *Phenacogaster* sp.

Remarks. Comparing the morphometric and meristic data between the specimens from the Río Vaupés and Río Putumayo basins, no discrete differences were observed between the ranges obtained. However, the specimens from the Río Putumayo basin are slightly larger than those from the Río Vaupés basin (34.2–44.4% SL, mean = 41.4% SL vs. 33.2–41.2% SL, mean = 35.5% SL). Across the PCA comparing the specimens of both basins, the first four components (which accounted for 64.4% of the total variance) were chosen as consensus between the scree plot method and broken-stick model (Suppl. materials 4, 5). In the plots obtained (Fig. 6A, B), the individuals of both basins did not separate in shape. In fact, we observed that the females and males from the Vaupés and Putumayo basins also overlapped each other slightly in the plots. The measures that most influenced the first four components were the snout to dorsal-fin origin (PC1: -0.6), dorsal fin to caudal-fin base (PC2: 0.4), dorsal-fin length (PC2: 0.4), pelvic-fin length (PC3: -0.3), and pectoral-fin length (PC4: -0.3) (Suppl. material 6). The specimens from the Río Putumayo basin shared almost completely the diagnostic characteristics of the new species. However, we observed that the dark

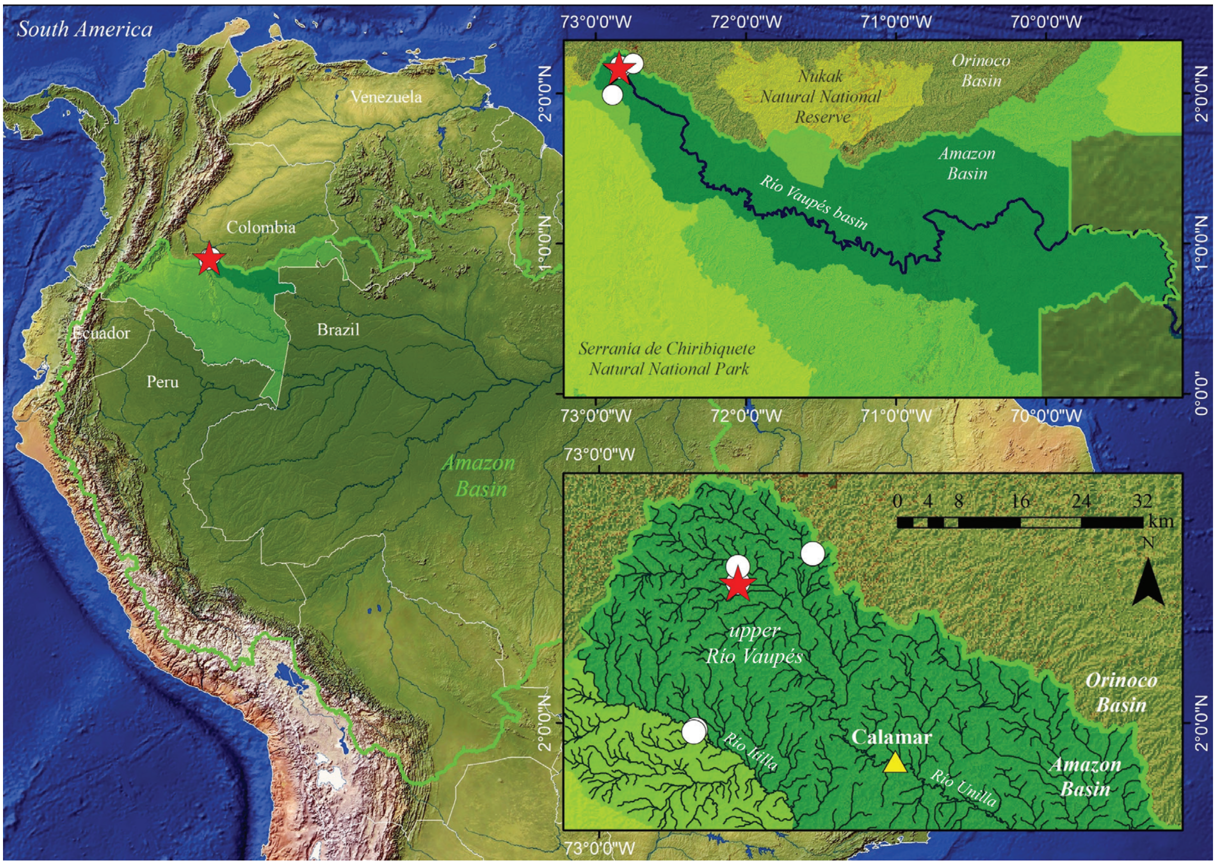

Figure 5. Geographical distribution of *Chrysobrycon calamar* along the upper Río Vaupés basin in Colombia, South America. Red star: type locality; white circle: paratype localities.

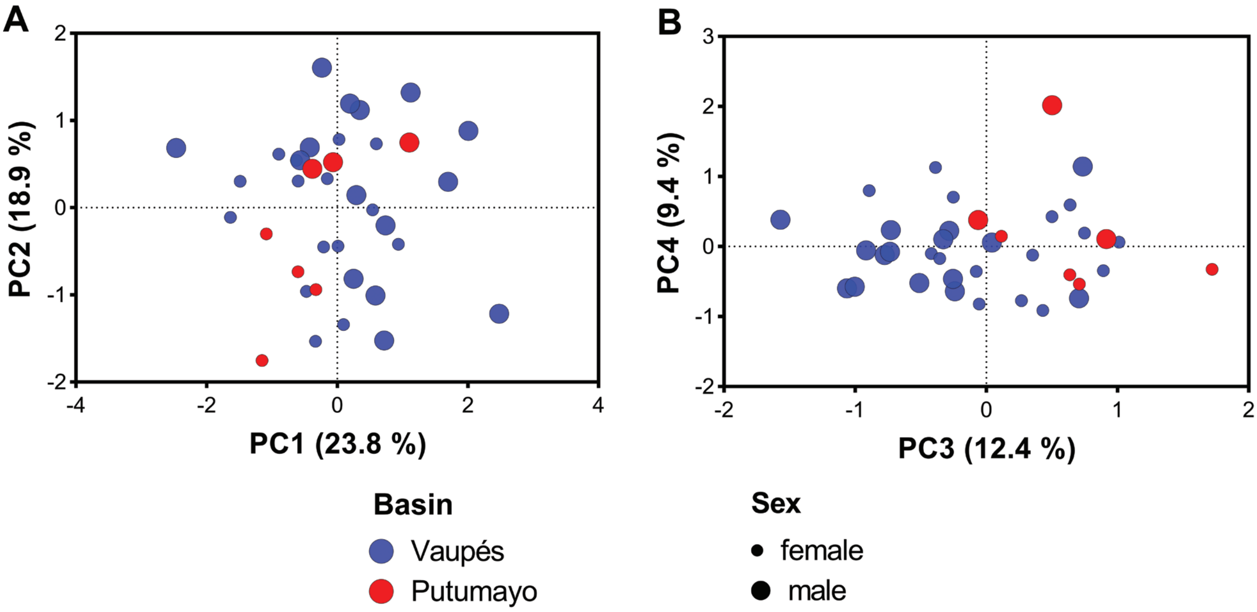

Figure 6. Size-corrected PCA performed comparing the morphometric data of *Chrysobrycon calamar* (blue circle) and the specimens examined from the Río Putumayo basin (red circle). **A.** PC1 *vs.* PC2 plot; **B.** PC3 *vs.* PC4 plot.

blotch on the abdominal flanks is slightly more developed laterally to the urogenital region than dorsally, and the number of maxillary teeth is slightly greater (3–7, mode = 6 *vs.* 2–4, mode = 3). In addition, we did not have enough well-preserved adult males to observe in more detail the variation associated with this pigmentation. For these reasons, we treat this population as *C.* aff. *calamar* and are cautious in this regard, pending further specimens or DNA samples that can become available to conduct additional comparisons. We hope this population can be reanalyzed in the future as part of the ongoing revision of the genus that the first author performs in the Amazon basin.

Key to the species of *Chrysobrycon* (modified from Vanegas-Ríos and Urbano-Bonilla, 2017)

1 Distal tips of maxillary teeth straight along their lengths 2
– Distal tips of most maxillary teeth lateroventrally curved .... *C. mojicai*
2 Irregular, or circular-shaped humeral mark, always scarcely developed vertically; adult males with subtle or weak dark pigmentation on lateroventral portion of body between the pelvic- and anal-fin origins or slightly developed dorsally on first eight anal-fin rays, but never widely developed dorsally to anus on abdominal flanks; caudal-fin bony hooks of adult males restricted to lower lobe rays or, if present on upper lobe rays, with 1–3 hooks restricted to single ray; posterior portion of maxilla reaching or surpassing vertical through anterior margin of eye when mouth closed (intraspecifically variable in *C. yoliae*, not reaching such vertical in some specimens) 3
– Dark humeral mark intensely developed vertically in adult males (and some females); dark vertical blotch on abdominal flanks in adult males on small area between pelvic- and first two anal-fin rays, being widely expanded dorsally up to 3 or 4 scale rows; caudal-fin bony kooks of adult males present and numerous (4–10) on nearly all rays; posterior portion of maxilla not reaching vertical through anterior margin of eye when mouth closed .... *C. calamar*
3 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*; and 4 in *C. yoliae*) 4
– 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*
4 Anal-fin bony hooks distributed on anterior branched anal-fin rays 1–12 in adult males (≤ 60% of total number of rays); larger adult specimens (usually > 30 mm SL in *C. eliasi*; > 28 mm SL in *C. guahibo*; and > 35 mm SL in *C. yoliae*) with anteriormost maxillary tooth usually tricuspid (rarely conical, bicuspid, or tetracuspid); terminal lateral-line tube on middle caudal-fin rays present; irregular or rounded humeral mark usually overlapped by pored lateral line 5
– Anal-fin bony hooks located on nearly all branched anal-fin rays in adult males (> 80% of total number of rays); larger adult specimens (usually > 50 mm SL) with anteriormost maxillary tooth usually pentacuspid (rarely tri- or tetracuspid); terminal lateral-line tube on middle caudal-fin rays absent; circular-shaped humeral mark usually not overlapping with pored lateral line .... *C. hesperus*

5 Maxillary teeth 6–16; anal-fin bony hooks on third to seventh branched anal-fin rays forming single, continuous series along each ray in adult males 6
– 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 adult males .... *C. guahibo*
6 Dentary teeth 20–26; body depth at dorsal-fin origin 34.4–42.2% SL (mean = 36.7% SL); dorsal fin to adipose fin distance 26.8–28.8% SL (mean = 27.9% SL); dorsal-fin origin situated at vertical between anal-fin rays 5–7 .... *C. yoliae*
– Dentary teeth 12–19; body depth at dorsal-fin origin 24.1–34.5% SL (mean = 29.8% SL); dorsal fin to adipose fin distance 23.9–26.8% SL (mean = 25.4% SL); dorsal-fin origin situated at vertical between anal-fin rays 8–10 .... *C. eliasi*

Comparative material examined

Chrysobrycon eliasi. All from PERU, Madre de Dios department, Tambopata: MUSM 39970, holotype, 34.3 mm SL; Madre de Dios basin, Loboyoc creek; 12°27'07"S, 69°7'43"W, c. 210 m a.s.l. MLP-Ict 10831, 3 paratypes, 33.0–43.5 mm SL (2 c&s specimens 33.0–39.9 mm SL); Río Manuripe basin, creek at km 50; 12°11'21"S, 69°6'57"W, c. 250 m a.s.l.; CI-FML 6153, 2 paratypes, 37.3–37.6 mm SL, Río Manuripe basin, Yarinal creek; 12°3'06"S, 69°4'50"W, c. 250 m a.s.l.; MUSM 39971, 14 paratypes, 26.1–40.8 mm SL; same data as for holotype. MUSM 39972, 8 paratypes, 28.0–43.2 mm SL; Manuripe basin, creek at km 50; 12°11'21"S, 69°6'5"W; c. 250 m a.s.l.; MUSM 39973, 2 paratypes, 36.11–37.63 mm SL; Río Madre de Dios basin, Loboyoc creek; 12°27'21"S, 69°7'42"W, c. 230 m a.s.l.; MUSM 39974, 3 paratypes, 29.3–41.2 mm SL, San Antonio, Río Heath basin, San Antonio creek; 12°41'03"S, 68°43'09"W, c. 190 m a.s.l. ROM 66378, 4, 27.6–31.6 mm SL; Tambopata, La Colpa, lodge, Río Tambopata, stream at left bank at 2.1 km. *Chrysobrycon* aff. *calamar*. All from COLOMBIA, Río Putumayo basin: MLP-Ict 11734, 5, 34.1–44.4 mm SL; Valle del Guamuez municipality, Río Cohembí. MLP-Ict 11735, 2, 42.4–43.9 mm SL; Puerto Asís municipality, Quebrada Tuayá. MPUJ 18619, 1, male. 34.2 mm SL; Putumayo, Puerto Asís municipality, Quebrada NN4. *Chrysobrycon guahibo*. All from COLOMBIA, Meta department, Río Orinoco basin, Río Guaviare basin, Río Ariari basin: MPUJ 7160, holotype, 31.9 mm SL; Fuente de Oro municipality, Caño Abrote; 3°17'39"N, 73°32'02"W, 260 m a.s.l. All are paratypes, Puerto Lleras municipality, Caño Cunimia; 3°11'24"N, 73°39'39"W, c. 270 m: CI-FML 6152, 6, 26.5–33.6 mm SL; MLP-Ict 10829, 2 c&s specimens, 30.4–31.3 mm SL; MPUJ 7162, 11, 26.7–29.0 mm SL; MLP-Ict 10830, 4, 28.9–31.3 mm SL. All are paratypes: MPUJ 7161, 10, 23.0–29.6 mm SL, same data as for holotype. MPUJ 7163, 1, 31.0 mm SL; Puerto Lleras municipality, Caño Cunimia; 3°11'24"N, 73°39'39"W, c. 270 m a.s.l. MPUJ 7164, 3, 31.0–34.8 mm SL, Puerto Lleras municipality, Caño Cunimia; 3°11'24"N, 73°39'39"W, c. 270 m a.s.l. MPUJ 7165, 6, 28.7–35.3 mm SL, San Juan de Arama municipality, Caño Casa Roja; 3°22'25"N, 73°52'13"W, c. 450 m a.s.l. MPUJ 7166, 8, 31.3–36.6 mm SL; Vista Hermosa municipality, Caño Uricacha; 3°16'56"N, 73°36'45"W, c. 270 m a.s.l. MPUJ 7167, 10, 29.0–35.2 mm SL; Fuente de Oro municipality, Caño Abrote; 3°17'39"N, 73°32'02"W, c. 250 m a.s.l. MPUJ 7168, 2, 43.5–44.6 mm SL; Vista Hermosa municipality, Caño Guapaya, 3°2'59"N, 73°49'17"W, c. 290 m a.s.l. *Chrysobrycon hesperus*. All from ECUADOR: All from Napo-Pastaza provinces, upper Río Villano near Villano, Río Napo system: ANSP 75912, 1 paratype, 77.4 mm SL; ANSP 79513, 1 paratype, 67.4 mm SL. All from Napo-Pastaza provinces, Río Pucuno, tributary of Río Suno, Pucuno enters of Suno: USNM 164056, holotype of *Hysteronotus hesperus*, 72.3 mm SL (radiographed); USNM 175124, 1 paratype, 59.1 mm SL (radiographed). ANSP 75914, 1 paratype, 63.2 mm SL; Napo-Pastaza provinces, Río Suno near mouth, tributary upper Río Napo. ANSP 79159, 2 paratypes, 60.3–76.0 mm SL; Río Pucuno, a tributary of Río Suno, upper Río Napo system. USNM 164042, 1 paratype, 70.5 mm SL; Napo-Pastaza provinces, Río Villano, upper Río Curaray, near Villano. FMNH 94557, 2*, 49.3–68.4; Napo, Río Arajuno, Quebrada to Río Gusano [Cusano], joins Río Gusano [Cusano] about 100 m upstream from mouth; [c. 1°05'25"S, 77°32'46"W, 420 m a.s.l.]. All from PERU, Loreto department: MUSM 26607, 2, 59.9–66.1 mm SL; Andoas, upper Amazon basin, Río Corrientes basin, Caballo creek, 2°33'41"S, 76°13'45"W, c. 210 m a.s.l. MUSM 26617, 2, 29.8–33.1 mm SL, upper Amazon basin, Río Corrientes, drainage flowing into Huayuri creek; 2°35'51"S, 76°13'53"W, c. 210 m a.s.l. MUSM 28640, 2, 25.5–27.0 mm SL; Forestal creek, Río Corrientes basin, 2°19'14"S, 76°10'31"W, c. 220 m a.s.l. MUSM 28665, 3, 36.2–54.6 mm SL (1 c&s specimen, 54.6 mm SL); Andoas, upper Amazon basin, Río Corrientes basin, Forestal creek; 2°21'28"S, 76°9'25"W, c. 240 m a.s.l. MUSM 28682, 3, 41.6–46.1 mm SL, Andoas, upper Amazon basin, San Carlos creek, flowing into Río Manchari; 2°24'35"S, 76°6'36"W, c. 200 m a.s.l. MUSM 32124, 1, 27.1 mm SL, Andoas, upper Amazon basin, Río Corrientes basin, Río Platanoyacu; 3°8'27"S, 75°45'09"W; c. 150 m a.s.l. MUSM 33159, 2, 29.3–43.9 mm SL, Andoas, upper Amazon basin, Río Pastaza, Carmen creek; 2°22'44"S, 76°9'44"W, c. 220 m a.s.l. *Chrysobrycon myersi*. All from PERU: Huanuco department, small creek directly tributary to Río Pachitea (itself tributary to Río Ucayali) at the northeastern outskirts of Tournavista; ANSP 112325, 2 paratypes, 30.1–46.1 mm SL; ANSP 112326, 3 paratypes, 28.3–32.0 mm SL; USNM 203697, holotype of *Hysteronotus myersi*, 46.5 mm SL; USNM 203698, 6 paratypes, 24.9–31.3 mm SL (1 radiographed, 31.3 mm SL). LACM 37720.4, 3, 34.3–63.8 mm SL, Pasco department, Iscozacin Valley, Pan de Azúcar, stream about 100 yards above entrance into Río Iscozacin. MUSM 12040, 1, 29.7 mm SL, Cusco department, La Convención province, Echarate, Urubamba basin, Río Picha, Cocha Kamariampiveni; c. 11°36'00"S, 73°05'00"W, 380 m a.s.l. MUSM 18908, 2, 42.4–48.6 mm SL; Pasco department, Oxapampa province, Puerto Bermudez, Río Pachitea basin, Atas creek; c. 10°17'47"S, 74°56'11"W, 260 m a.s.l. MUSM 36068, 1, 31.6 mm SL, Curso department, La Convencion province, Echarate, Río Urubamba basin, Río Parotori system, Río Poyiriari; 12°10'44"S, 73°5'06"W, c. 540 m a.s.l. MUSM 36084, 3, 37.1–58.7 mm SL, Cusco department, La Convención province, Echarate, Urubamba basin, Río Parotori system, Río Poyriari; 12°10'45"S, 73°5'18"W, c. 590 m a.s.l. MUSM 36109, 2, 32.8–36.3 mm SL, Cusco department, La Convención province, Echarate, Río Urubamba, Río Parotori, Río Poyiriari, Piriabindeni creek; 12°1'13"S, 73°0'24"W, c. 590 m a.s.l. MUSM 36125, 3, 29.2–38.6 mm SL, Cusco department, La Convención province, Echarate, Río Parotori basin, Piriabindeni creek; 12°1'19"S, 73°4'15"W, c. 550 m a.s.l. MUSM 37889, 2, 45.1–51.0 mm SL, Junin department, Satipo province, Mashira, Río Tambo basin, Capirosankari creek; 11°1'25"S, 73°33'36"W, c. 420 m a.s.l. MUSM 37933, 3, 58.0–60.8 mm SL, Cusco department, La Convención province, Echarate, Kinterani, Naca-naca creek; 11°28'09"S, 73°18'02"W, c. 420 m a.s.l. MUSM 38671, 3, 50.9–60.7 mm SL (1 c&s specimen, 58.6 mm SL), Junin department, Satipo province, Río Tambo basin, Pukakunga creek; 73°28'02"W, 11°24'37"S, c. 590 m a.s.l. *Chrysobrycon mojicai*. All from COLOMBIA, Amazonas department, Río Amazon basin, Leticia: IAvH-P 13932, holotype, 50.6 mm SL; Amacayacu National Natural Park, unnamed forest stream tributary of Río Mata-Matá; 3°48'23"S, 70°15'58"W, c. 90 m a.s.l. All are paratypes: IAvH-P 8291, 5, 25.0–50.4 mm SL (one c&s specimen, 50.4 mm SL), same data as for the holotype. IAvH-P 8295, 9, 29.0–47.7 mm SL; Amacayacu National Natural Park, unnamed forest stream, tributary of Río Pureté headwaters, 3°41'54"S, 70°12'24"W, c. 130 m a.s.l. IAvH-P 8300, 2, 33.5–40.8 mm SL; Amacayacu National Natural Park, unnamed forest stream tributary of Río Pureté headwaters; 3°41'38"S, 70°12'27"W. IAvH-P 8917, 14, 17.1–47.5 mm SL; Sufragio stream in front of Zafire Biological Station, 4°0'19"S, 69°53'56"W, c. 120 m a.s.l. IAvH-P 8951, 9, 17.9–50.5 mm SL, Sufragio stream in front of Zafire Biological Station; 4°0'20"S, 69°53'56"W, c. 120 m a.s.l. IAvH-P 9022, 6, 43.8–50.8 mm SL (including 3 c&s specimens fully disarticulated as non-types), Sufragio stream in front of Zafire Biological Station; 4°0'19"S, 69°53'56"W, c. 120 m a.s.l. IAvH-P 9070, 4, 48.6–55.0 mm SL, unnamed forest stream tributary of Río Calderon, 45 min. NE of Zafire Biological Station; 3°58'40"S, 69°53'32"W, c. 130 m a.s.l. IAvH-P 9093, 4, 23.7–47.8 mm SL; unnamed stream, tributary of Río Calderon, 45 min. NE of Zafire Biological Station; 3°58'40.14"S, 69°53'31.8"W, 130 m a.s.l. MPUJ 8058, 1, 49.5 mm SL, same data as for the holotype. MPUJ 8059, 1 c&s, 50.3 mm SL; unnamed forest stream tributary of Río Calderon, 45 min. NE of Zafire Biological Station; 3°58'40"S, 69°53'32"W, c. 130 m a.s.l. *Chrysobrycon yoliae*. All from PERU, Ucayali department, Coronel Portillo province, Abujao, Río Yucamia subsystem, unnamed creek, 8°39'14"S, 73°21'17"W, c. 273 m: MUSM 46140, holotype, 51.6 mm SL; CI-FML 5882, 3 paratypes, 44.8–52.3 mm SL (one c&s specimen, 44.8 mm SL); MLP-Ict 10517, 1 paratype, 48.4 mm SL; MUSM 46141, 8 paratypes, 38.2–51.5 mm SL.

Discussion

Based on morphological data, Vanegas-Ríos et al. (2020) found nine synapomorphies supporting the monophyly of five species of *Chrysobrycon* analyzed as part of a phylogenetic hypothesis of Stevardiinae. The synapomorphies proposed in that study (some not exclusive, with varied degrees of homoplasy in Stevardiinae) are: 1) the absence of the frontal fontanel (Character 26); the absence or reduced parietal fontanel (character 40); the dorsolateral process of the anguloarticular with greatest vertical dimension as large as that of the posterior region of the horizontal process of the anguloarticular (character 128); the posterior margin of the hypural 2 as large as vertical distance between the bases of the caudal-fin rays 11 to 13 (character 341); bony hooks on the base of the pelvic-fin rays in small number compared to the segmented portion of rays (character 456); interradialis muscle fibers not exceeding the posterodorsal border of the pouch scale (character 475); pouch scale horizontally folded, forming a laterally concave pocket (character 494); 35 or fewer pouch-scale radii (character 499); and the presence of a medial accessory pouch scale (character 517). *Chrysobrycon calamar* shares the traditional characteristics used by Weitzman and Menezes (1998) and Vanegas-Ríos and Urbano-Bonilla (2017) to define the genus, as well as the synapomorphies found in Vanegas-Ríos et al. (2020) (character 128 is polymorphic).

In all *Chrysobrycon* species, the accessory lateral membranes located on all the dorsal-fin rays have lamellae that are extended from the ventral surface of rays, covering partially the interradial membranes, being slightly more developed in males than in females. Comparatively, these lamellae are less developed laterally in *C. calamar*, *C. eliasi*, and *C. guahibo*. The distinctive dark blotch on the abdominal flanks along the urogenital region in adult males of *C. calamar* is a remarkable characteristic that seems to be rare in Characidae. However, the presence of dark pigmentation on the belly is also found in related members of Stevardiini, for instance, in *Gephyrocharax caucanus* Eigenmann, 1912 (Vanegas-Ríos 2016), which possesses a urogenital pigmentation in adult males that partially resembles that of *C. calamar* or *C. mojicai*. This pigmentation in Stevardiini seems to be associated with courtship behavior, so that is exclusive to adult males with bony hooks. We observed in adult males of the *Chrysobrycon* species several sexually dimorphic patterns of color variation associated with the region between the pelvic and anal fins (Suppl. material 1): (1) region poorly pigmented ventrally or laterally, not forming a detectable blotch (*e.g. C. eliasi*); (2) area with scattered dark chromatophores extending dorsally between the anus and anal-fin origin, being weak or diffuse lateroventrally (*e.g. C. guahibo*); (3) region slightly darkened by scattered chromatophores lateroventrally, being a little more developed laterally between the pelvic- and anal-fin origins (*e.g. C. hesperus*); (4) urogenital region without distinguishable blotch or pigmentation, but with dark longitudinal pigmentation extended dorsally on the first anal-fin rays (*e.g. C. myersi*); (5) area moderately darkened ventrally, but forming a dark vertical blotch that reaches dorsally up to three or four scales between the urogenital pore and first two anal-fin rays (*C. calamar*); and 6) area strongly darkened lateroventrally but confined to the region between the scale rows covering the urogenital pore and those rows located immediately dorsal to that area (*e.g. C. mojicai*). This sexually dimorphic pigmentation is present in life and most well-preserved adult male specimens, but in some species where it is found to be less developed, it could be erroneously estimated if the body color is not well preserved. In further contributions, we expect to continue analyzing the morphological variations associated with this pigmentation in a phylogenetic context and using additional male specimens to explore its potential significance within the genus and/or Stevardiini.

In *Chrysobrycon* species (except *C. myersi*), we also observed that the urogenital region in both sexes is modified as follows (but more noticeably developed in adult males): the urogenital pore is completely covered by one row of four to six scales in each flank, which face each other, forming a sharp edge between the anal- and pelvic-fin origins (Suppl. material 7). These scales are also slightly projected ventrally beyond the ventral profile of the belly, like a keel. This characteristic was not extensively described before for the species of the genus, but it was partly observed by Böhlke (1958) as some preventral scales forming a distinctive edge in *C. hesperus*. These scale rows forming a sharp edge ventrally are also observed in other members of Stevardiini (*e.g.*, *G. caucanus* or *Pseudocorynopoma doriae* Perugia, 1891). In *C. myersi*, no sharp keel between the pelvic-fin base and urogenital pore was observed, in agreement with Weitzman and Thomerson (1970); the preanal scales are not projected ventrally beyond the skin. In fact, in some females, a small triangular urogenital papilla was observed to be developed externally.

Currently, Brazilian colleagues (C. Silva-Oliveira, A. L. C. Canto, and F. R. V. Ribeiro) and the first author are studying some specimens from the Amazon basin in Brazil that could represent a new species for the genus. *Chrysobrycon calamar* can be distinguished from that morphotype by the dark pigmentation between the urogenital region and anal fin (vertically developed, reaching up to the first two anal-fin rays *vs.* longitudinally developed, reaching up to the first ten anal rays). It is worth mentioning that, although four species have been described within *Chrysobrycon* in the last 15 years, we still continue to reveal the hidden richness of this outstanding group of Stevardiinae.

It is important to recognize that the demobilization of FARC-EP troops between 2016 and 2018 had a strong impact on Colombia´s biodiversity. Many regions with previously scarce information were now the target of a series of biological expeditions by different universities and institutions throughout the country (Restrepo-Santamaria et al. 2023; Bogotá-Gregory et al. 2024). As a result of these studies in previously unexplored areas, from 2017 to date, 13 new fish species have been described just for the Colombian Amazon (DoNascimiento et al. 2024). Thus, the present description of *C. calamar* constitutes a priceless result of the achievement of having regained access in this type of area to understand their biodiversity and, at the same time, exemplifies the potential associated with such regions to have hidden diversity. In both cases, there are positive impacts not only on scientific progress but also on the increase of the country's biological heritage.

Conclusions

We concluded that the specimens analyzed from the Río Vaupés basin are a new species based on the exhaustive morphological comparison using morphometric, meristic, and osteological data. The specimens examined from the upper Río Putumayo are considered *C.* aff. *calamar* based on the inconsistency observed in the urogenital pigmentation and the few adult males available to better assess this variation. It is important to emphasize that the urogenital pigmentation associated with sexual dimorphism has begun to play a prominent role in resolving the alpha taxonomy within the genus and can be very useful for identifying the species of *Chrysobrycon* in the field. The discovery of *C. calamar* is really significant because this is one of several new species that have been found in endemism-rich regions that could be explored after the guerrilla demobilized in Colombia.

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Supplementary material 1

Interspecific variation of the dark pigmentation on the urogenital region in adult males of *Chrysobrycon* species

Authors: James Anyelo Vanegas-Ríos, Alexander Urbano-Bonilla, Gian Carlo Sánchez-Garcés

Data type: pdf

Link: https://doi.org/10.3897/zse.100.121499.suppl1

Supplementary material 2

Photographs of the typical localities where *Chrysobrycon calamar* was collected in Colombia

Authors: James Anyelo Vanegas-Ríos, Alexander Urbano-Bonilla, Gian Carlo Sánchez-Garcés
Data type: pdf

Link: https://doi.org/10.3897/zse.100.121499.suppl2

Supplementary material 3

Coordinates used

Authors: James Anyelo Vanegas-Ríos, Alexander Urbano-Bonilla, Gian Carlo Sánchez-Garcés
Data type: xlsx

Link: https://doi.org/10.3897/zse.100.121499.suppl3

Supplementary material 4

Total variance accounted for the size-corrected PCA performed for the morphometric data

Authors: James Anyelo Vanegas-Ríos, Alexander Urbano-Bonilla, Gian Carlo Sánchez-Garcés
Data type: pdf

Link: https://doi.org/10.3897/zse.100.121499.suppl4

Supplementary material 5

Scree plot obtained from the morphometric data analyzed

Authors: James Anyelo Vanegas-Ríos, Alexander Urbano-Bonilla, Gian Carlo Sánchez-Garcés
Data type: pdf

Link: https://doi.org/10.3897/zse.100.121499.suppl5

Supplementary material 6

Loadings obtained from the size-corrected PCA comparison using the morphometric data

Authors: James Anyelo Vanegas-Ríos, Alexander Urbano-Bonilla, Gian Carlo Sánchez-Garcés
Data type: pdf

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Supplementary material 7

Ventral view of preanal scales

Authors: James Anyelo Vanegas-Ríos, Alexander Urbano-Bonilla, Gian Carlo Sánchez-Garcés
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