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A NEW SPECIES OF *CHAETOSTOMA* TSCHUDI (SILURIFORMES: LORICARIIDAE) FROM COLOMBIA WITH A DEFINITION OF THE *C. ANALE* SPECIES GROUP

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ABSTRACT

Chaetostoma formosae sp. nov. is described from piedmont tributaries of the upper río Meta on the Cordillera Oriental in Colombia. The new species is distinguished from its congeners by the presence of an elongate unbranched anal-fin ray with two posterior dermal ridges in mature males, the presence of strongly recurved cheek odontodes, the presence of a parieto-supraoccipital dermal keel, the posterior margin of the pelvic-fin strongly projected and angulate in shape in mature males, and by details of coloration. The new species belongs to an informal monophyletic group herein called the *Chaetostoma anale* species group, along with two additional species, *C. anale* and *C. jegui*, from Colombia and Brazil respectively, based on an apomorphic modification of the anal fin in mature males.

KEY-WORDS: Systematics; Ancistrini; Andes; Sexual dimorphism; Taxonomy.

INTRODUCTION

The catfish genus *Chaetostoma* Tschudi currently comprises 48 valid species (Salcedo, 2006) geographically distributed in regions both east and west of Andes and in the Guyana Shield. Representatives of the genus are common in swift water with high oxygen concentration in highland or piedmont creeks and rivers, as well as in white-water rivers, particularly west of Andes. So far, there are no records of *Chaetostoma* representatives from water bodies in the Orinoco savannas or Amazonian rivers far from Andean versants, therefore representing an almost entirely Andean distribution (Fisch-Muller, 2003). The only exceptions to this distribution pattern are *Chaetostoma jegui* and *Chaetostoma vasquezzi*, both species described from Guyana Shield rivers (Rapp Py-Daniel, 1991; Lasso & Provenzano, 1997).

The taxonomic status of most of the species of *Chaetostoma* has been largely unquestioned and there are but few local works in the recent literature concerning some species (e.g., Ceas & Page, 1996; Salcedo, 2006). For Colombian species there are just mentions in checklists without any taxonomic revision even at a local scale, and some general works for trans-Andean fish faunas (Miles, 1947; Dahl, 1971). The most recent citations of Colombian *Chaetostoma* species with a distribution east of Andes were in the context of comparisons with Venezuelan species (Ceas & Page, 1996).

Few hypotheses are available for the evolutionary history of *Chaetostoma* and related taxa (Salcedo, 2003; Armbruster, 2004, 2008) and it is still under debate whether the genus is monophyletic (particularly with respect to *Cordylancistrus*). There are two proposals available to date (Armbruster, 2004, 2008),

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but both focus on main interrelationships within the Loricariidae and therefore include few species of *Chaetostoma* in the analyses.

The main goal of this paper is to describe a new species of *Chaetostoma* from the upper río Meta basin in Colombia and to propose a monophyletic assemblage within the genus.

MATERIALS AND METHODS

Counts and measurements follow Armbruster (2003a) except for the inclusion of the second anal-fin ray length, not measured in the referred work. Measurements from the tip of snout were taken from the tip of the mesethmoid because species of *Chaetostoma* present extensive development of the skin and adipose tissue underneath the epidermis, therefore affecting repeatable measurements from the unlabeled snout.

Museum acronyms for material examined in this study follow Sabaj (2010) with the following clarifications whenever two or more collections present the same acronym: Muséum National d'Histoire Naturelle (MNHN) and Museo La Salle Bogotá (MLS). Material examined is reported using the following sequence: Catalog number, number of specimens, SL range, locality, collector and date. Given the lack of original information about exact coordinates for most of the material examined, the distribution map was prepared using detailed cartography in order to locate points and then scaling the resulting map. However, coordinates throughout the paper are approximate and should not be understood as original information from collectors but as approximate locations based on cartography and localities.

Comparative material examined is reported in the Appendix. Data from species unavailable for direct examination were obtained through photographs at the "All Catfish Species Inventory" web site (<http://acsi.acnatsci.org/base/index.html>) for primary type specimens and reported under Material Examined with indication that the types were examined by photographic means. Data for *Chaetostoma machiquense* and *C. nudirostre* were obtained from Ceas & Page (1996).

Abbreviations in the text are SL (standard length), c&ts (cleared and stained specimens prepared following the method of Taylor & van Dyke, 1985), and xray for radiographed specimens. Osteological nomenclature follows Geerinckx & Adriaens (2006) and Geerinckx *et al.* (2007) with exception of "cheek spines", called instead "cheek odontodes" herein in order to be consistent with the histology of

these structures. Position of fleshy ridges on pelvic and anal-fin rays are reported following the insertion plane of the fin; for instance, pelvic fins show dorsal and ventral planes, whereas anal fin shows anterior and posterior planes. Terminology of lateral plate series follows Schaefer (1997).

Statistics were performed with the program R v. 2.10.0 (R Development Core Team, 2009) and the R-Commander package v. 1.4-5 (Fox, 2009), both available at www.r-project.org.

RESULTS

Chaetostoma formosae sp. nov. (Figs. 1-3)

Holotype: ICNMHN 17114, male, 97.4 mm SL, Colombia: Departamento de Boyacá, San Luis de Gaceno, caño Chuy affluent of río Upía, Boyacá – Casanare border, upper río Meta basin, Orinoco drainage, coll. Y. Lopez-Pinto, 1-Jan-2009.

Paratypes: All from Colombia. CZUT-IC 7280, 14, 64.2-92.4 mm SL, Meta, San Carlos de Guaroa, río Orotoy below the Chichimene bridge, at the confluence with the quebrada San Francisco, 03°53'00"N, 73°40'40.7"W, coll. A. Ortega-Lara, 25-Mar-2010; ICNMHN 1172, 29, 43.7-41.9 mm SL, Meta, Acacías, río Acacías affluent of río Metica, 3°58'N, 73°42'W, coll. J. Castro & G. Castaño, 26-Feb-1987; ICNMHN 1479, 26, 50.0-90.2 mm SL, Meta, Acacías, Manzanares, quebrada La Candelaria affluent of río Guayuriba, 4°07'N, 73°47'W, coll. P. Cala, 10-Jan-1988; ICNMHN 2182, 1, 84.0 mm SL, Casanare, Yopal, quebrada Cuyandera affluent of río Cusiana, 5°21'N, 72°26'W, coll. J.I. Mojica, 1-Jan-1992; ICNMHN 5593, 3, 55.0-80.9 mm SL, Meta, Restrepo, between Restrepo and Cumaral, río Guatiquía basin, 4°15'N, 73°27'W, coll. J. Arroyabe, 1-Jan-1998; ICNMHN 7966, 10, 38.9-71.3 mm SL, Meta, San Martín, Hacienda Guaduales, 3°37'N, 73°39'W, coll. unknown, 5-Jun-1975; ICNMHN 8018, 3, 54.8-79.7 mm SL, Meta, Restrepo, río Caney, 4°17'N, 73°32'W, coll. G. Galvis & G. Briceño, 1-May-1993; ICNMHN 8024, 5, 57.8-72.3 mm SL, Meta, Restrepo, caño Caibe, 4°12'N, 73°26'W, coll. G. Galvis & G. Briceño, 1-May-1993; ICNMHN 16364, 4, 72.1-103.1 mm SL, Meta, San Martín, Finca El Caduceo, río Camoa (= caño Camoa), 3°38'N, 73°38'W, coll. G. Galvis *et al.*, 20-May-2006; ICNMHN 17594, 3, 58.1-89.2 mm SL, Meta, Parque Nacional Natural La Macarena, río Guejar,

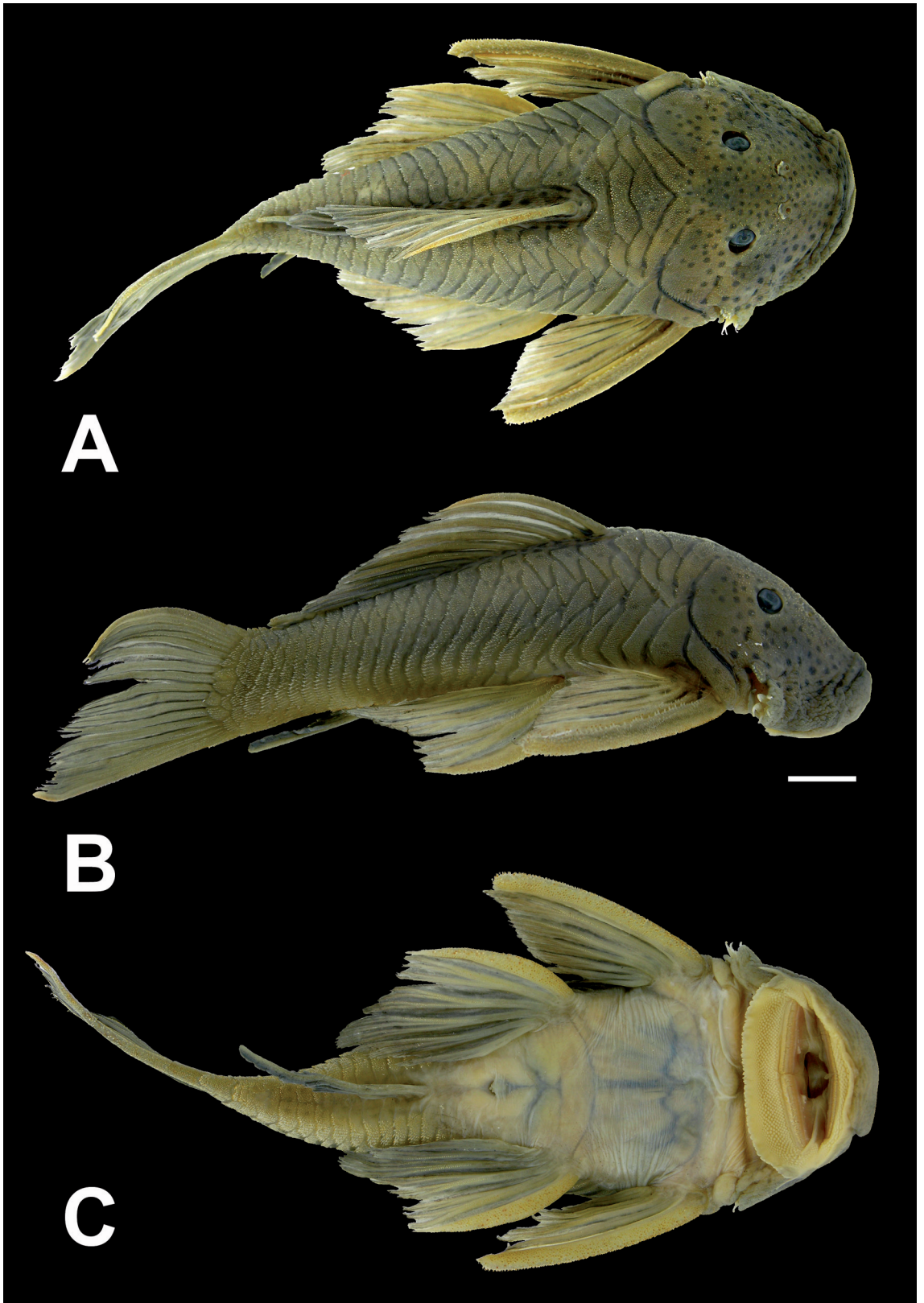


FIGURE 1: *Chaetostoma formosae* sp. nov., holotype, ICNMHN 17114, adult male, 97.4 mm SL. **A)** Dorsal view; **B)** Lateral view; **C)** Ventral view. Note the enlarged anal fin in B and C. Scale bar equals 10 mm.

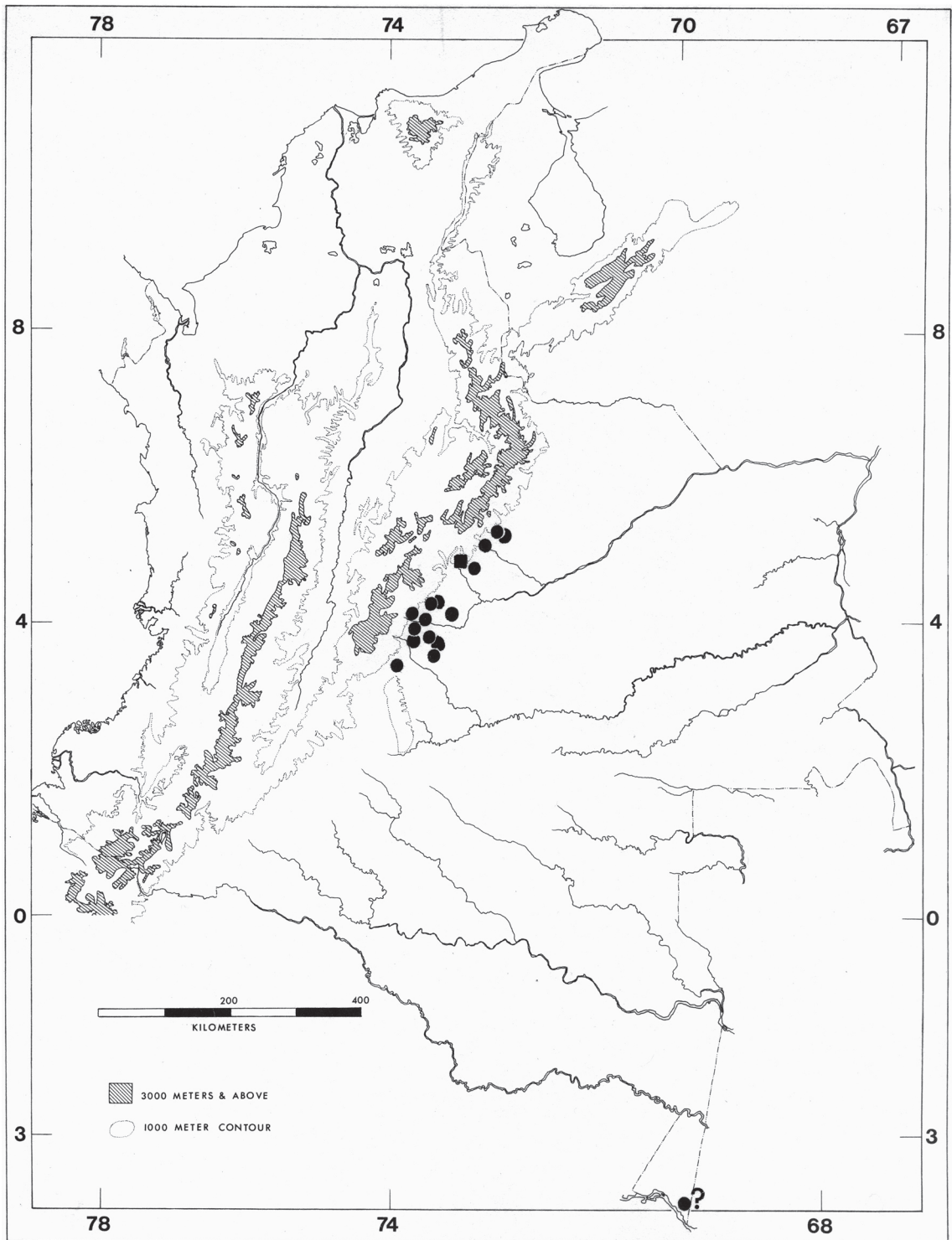


FIGURE 2: Distribution of *Chaetostoma formosae* sp. nov. Square = type locality; Circles = remaining localities. One symbol may represent either more than one locality or lot of specimens. Dashed areas represent the 3000 masl contour, dotted areas represent the 1000 masl contour. Southernmost symbol with a question mark represents an erroneous record for Leticia, Amazonas, Colombia. Base map provided by John D. Lynch.

3°21'N, 73°57'W, coll. G. Galvis, 1-Sep-1987; MLS 1242, 3, 80.4-93.0 mm SL, Casanare, Villanueva, Finca La Victoria, 4°36'N, 72°55'W, coll. Brother R. Casallas, 12-Dec-2007.

Non-type specimens: All collections from Colombia. ICNMHN 1150, 63, 51.8-80.7 mm SL, Meta, Acacías, Hacienda Cisneros, río Acacías, affluent of río Metica, 03°58'N, 73°44'W, coll. P. Cala, 1-Apr-1985; ICNMHN 1156, 3, 48.1-69.5 mm SL, Casanare, Yopal, small creek 3 km on the road to Guacavía, 05°17'N, 72°27'W, coll. P. Cala, 25-Nov-1971; ICNMHN 11966, 2, 47.3-76.7 mm SL, Meta,

Acacías, Vereda La Esmeralda, 04°01'N, 73°44'W, coll. J.I. Mojica *et al.*, 22-Apr-2004; ICNMHN 1476, 2, 53.5-71.1 mm SL, Meta, Villavicencio, Villavicencio-Acacías road, río Ocoa, 04°06'N, 73°32'W, coll. A. Silfvergrip, 6-Jan-1988; ICNMHN 1477, 6, 35.5-52.4 mm SL, Meta, Villavicencio, caño Quenane at the río Negro, coll. A. Silfvergrip, 13-Jan-1988; ICNMHN 2526, 5, 57.6-95.9 mm SL, Meta, Parque Nacional Natural La Macarena, La Curia Station of INDERENA, caño La Curia, affluent of río Guejar, 03°19'N, 73°59'W, coll. G. Galvis, 19-Sep-1987; ICNMHN 3435, 2, 59.2-63.4 mm SL, Meta, Acacías, caño Orotoy, affluent of río Acacías, 03°58'N,

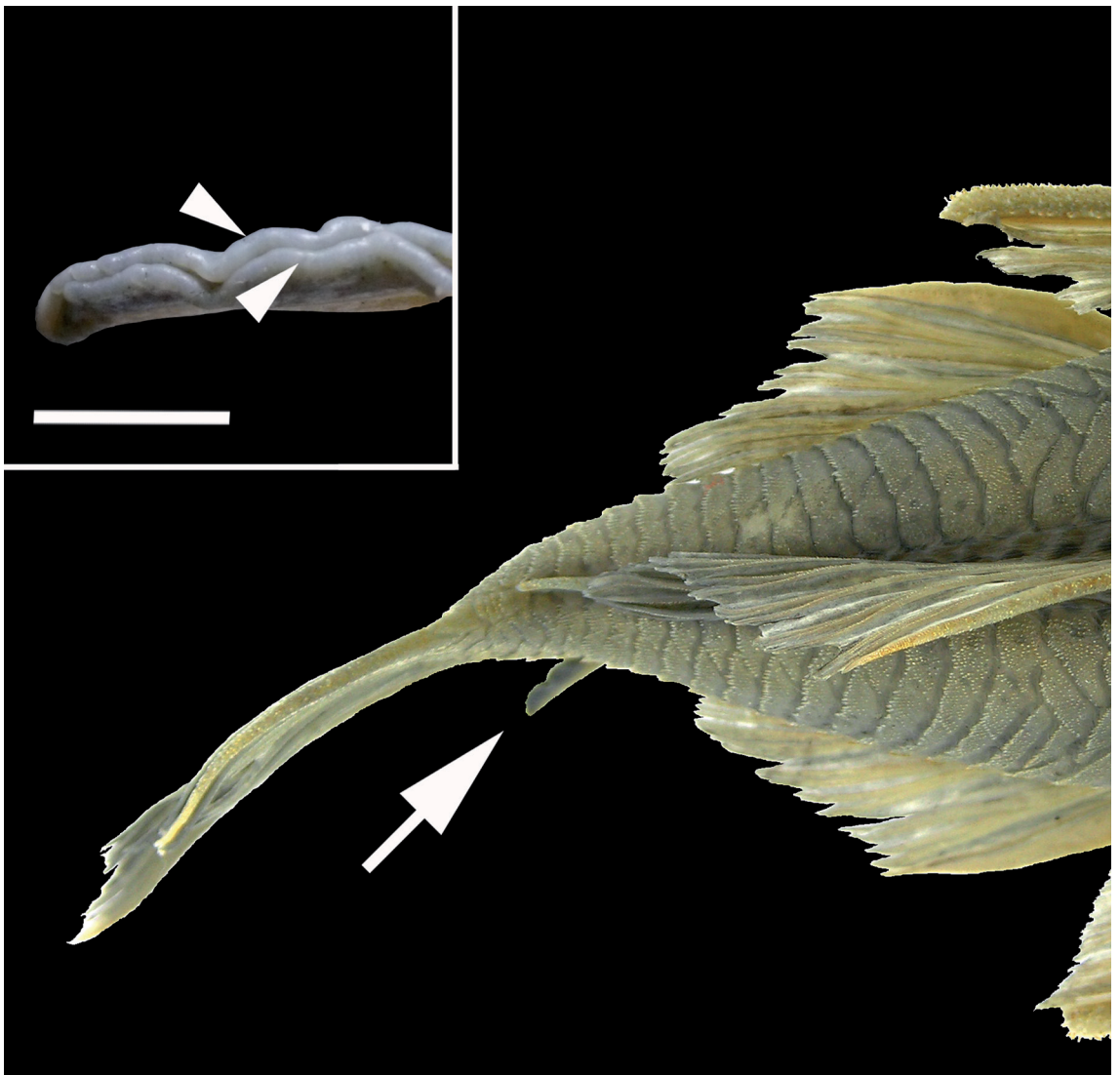


FIGURE 3: Posterior portion of the body in dorsal view of *Chaetostoma formosae* sp. nov., holotype, ICNMHN 17114, adult male, 97.4 mm SL. The square detail shows the distal portion of the anal fin in posterior view; small arrows indicate the posterior dermal folds reaching the tip of the enlarged anal-fin ray in mature males. The large arrow indicates the distal portion of the anal fin for which the detail is provided. Scale bar in the square detail equals 3.3 mm.

73°47'W, coll. G. Galvis *et al.*, 29-Apr-1989; ICNMHN 3455, 1, 84.5 mm SL, Meta, Acacías, caño Orotoy, affluent of río Acacías, 03°58'N, 73°47'W, coll. G. Galvis *et al.*, 29-Apr-1989; ICNMHN 6761, 13, 58.2-64.4 mm SL, Meta, Villavicencio, Estación Apiay, río Ocoa, 04°05'N, 73°34'W, coll. Daphnia Consulting Company, 1-Oct-2001; ICNMHN 6762, 13, 56.7-72.1 mm SL, Meta, Villavicencio, Estación Apiay, río Ocoa, 04°05'N, 73°34'W, coll. Daphnia Consulting Company, 1-Oct-2001; ICNMHN 7357, 1, 65.2 mm SL, Meta, Villavicencio, Estación Apiay, río Ocoa, 04°05'N, 73°34'W, coll. Daphnia Consulting Company, date unknown; ICNMHN 7962, 5, 53.7-60.2 mm SL, Meta, Villavicencio, Villavicencio-Puerto López road, caño Quenane, 04°05'N, 73°12'W, coll. P. Cala, 1-Feb-1971; ICNMHN 7963, 13, 38.3-73.7 mm SL, Meta, San Martín, río Humadea, 03°46'N, 73°31'W, coll. P. Cala, 1-Jun-1976; ICNMHN 7977, 3, 54.0-77.9 mm SL, Meta, Cumaral, quebrada Piedras Negras, 04°14'N, 73°19'W, coll. G. Galvis, 1-Oct-1990; ICNMHN 7987, 2, 81.6-90.2 mm SL, Amazonas, Leticia, Parque Nacional Natural Amacayacu, Quebrada Mata-Mata, affluent of río Amazonas, 03°49'N, 69°58'W, coll. J. Ramirez, 1-Apr-1985; ICNMHN 8001, 1, 70.4 mm SL, Amazonas, Leticia, Parque Nacional Natural Amacayacu, Quebrada Mata-Mata, affluent of río Amazonas, 03°49'N, 69°58'W, coll. J. Ramirez, 1-Apr-1985; ICNMHN 8010, 4, 52.5-59.0 mm SL, Meta, Restrepo, caño Caibe, 04°15'N, 73°29'W, coll. G. Galvis, 1-Jun-1989; ICNMHN 8015, 3, 44.9-52.4 mm SL, Meta, Cumaral, río Caney, 04°13'N, 73°32'W, coll. G. Galvis & G. Briceño, 1-Oct-1993; ICNMHN 8022, 2, 72.0-77.2 mm SL, Meta, Guamal, Caño Orotoy, affluent of río Acacías, coll. G. Galvis *et al.*, 7-Dec-1985; ICNMHN 8038, 3 c&s, 69.0-96.1 mm SL, Amazonas, Leticia, Parque Nacional Natural Amacayacu, Quebrada Mata-Mata, affluent of río Amazonas, 03°49'N, 69°58'W, coll. J. Ramirez, 1-Apr-1985; ICNMHN 11970, 10, 54.8-66.3 mm SL, Meta, Acacías, caño Orotoy, affluent of río Acacías, 03°58'N, 73°47'W, coll. J.I. Mojica *et al.*, 21-Apr-2004; ICNMHN 11971, 2, 46.7-48.5 mm SL, Meta, Guamal, Vereda El Carmen, quebrada Guamal, affluent of río Humadea, 03°53'N, 73°46'W, coll. Proyecto Ornamentales Orinoco, 21-Apr-2004; ICNMHN 12775, 9, 48.4-75.1 mm SL, Meta, Restrepo, caño Mateguadua affluent of río Upía, 04°14'N, 73°33'W, coll. Proyecto Ornamentales Orinoco, 5-Oct-2004; ICNMHN 12776, 43.4-75.9 mm SL, Meta, Acacías, Vereda La Loma, caño Chichimene affluent of río Acacías, 03°59'N, 73°48'W, coll. Proyecto Ornamentales Orinoco, 2-Oct-2004; ICNMHN 12777,

1, 63.2 mm SL, Meta, Acacías, Vereda La Loma, caño Chichimene affluent of río Acacías, 03°59'N, 73°48'W, coll. Proyecto Ornamentales Orinoco, 3-Oct-2004; ICNMHN 13141, 2, 47.8-58.6 mm SL, Meta, Acacías, Estación Corveica, río Acacías, 03°59'N, 73°42'W, coll. Proyecto Ornamentales Orinoco, 18-Apr-2004; ICNMHN 13208, 1, 55.1 mm SL, Meta, Cubarral, río Ariari, 03°47'N, 73°50'W, coll. G. Galvis, date unknown; ICNMHN 17595, 18, 52.6-84.0 mm SL, Casanare, río Cusiana basin, exact locality unknown, coll. V. Ortiz, 1-Jul-1997; ICNMHN 17596, 4, 36.6-66.1 mm SL, Meta, Cumaral, caño Caibe, 04°16'N, 73°32'W, coll. Biology Students (Universidad Nacional de Colombia), 23-Apr-2005.

Diagnosis: *Chaetostoma formosae* sp. nov. differs from all the species currently in *Chaetostoma* with the exception of *Chaetostoma anale* and *Chaetostoma jegui* by the presence in mature males of an enlarged second unbranched anal-fin ray bearing two distinct posterior dermal folds, and reaching the base of the caudal fin when fully developed (Figs. 1B, 3). *Chaetostoma formosae* differs from *C. anale* in having an angular distal pelvic-fin margin in mature males (vs. W-shaped distal margin in mature *C. anale* males, Figs. 1C, 4B), and the leading pelvic-fin ray neither elongate nor filamentous, not reaching beyond the adjacent branched ray in mature males (vs. leading pelvic-fin ray both enlarged and filamentous, longer than the remaining rays in mature males of *C. anale*). *Chaetostoma formosae* differs from *C. jegui* in having dark spots restricted to the head and the dorsal region surrounding the dorsal-fin base, and with compound pterotic and lateral plates bordered by dark pigment (vs. dark background with light blotches in *C. jegui*); and by the shape of the distal margin of the pelvic fin strongly projected and angular in mature males, vs. distal margin straight and with leading-fin ray sometimes surpassing the distal margin of the fin as evident in photographs).

Chaetostoma formosae further differs from *Chaetostoma anomalum*, *C. breve*, *C. carrioni*, *C. dorsale*, *C. lobarhynchus*, *C. machiquense*, *C. microps*, *C. nudirostre*, *C. platyrhynchus*, and *C. sovichthys* by having a parieto-supraoccipital dermal keel (vs. skin on the parieto-supraoccipital unmodified in the form of a dermal keel in the cited species) and by the presence of strongly recurved cheek odontodes (vs. cheek odontodes straight in the same species cited above, Figs. 5 and 6). In addition, *C. formosae* differs from *C. platyrhynchus* by having an unplated snout (vs. snout plated in *C. platyrhynchus*).

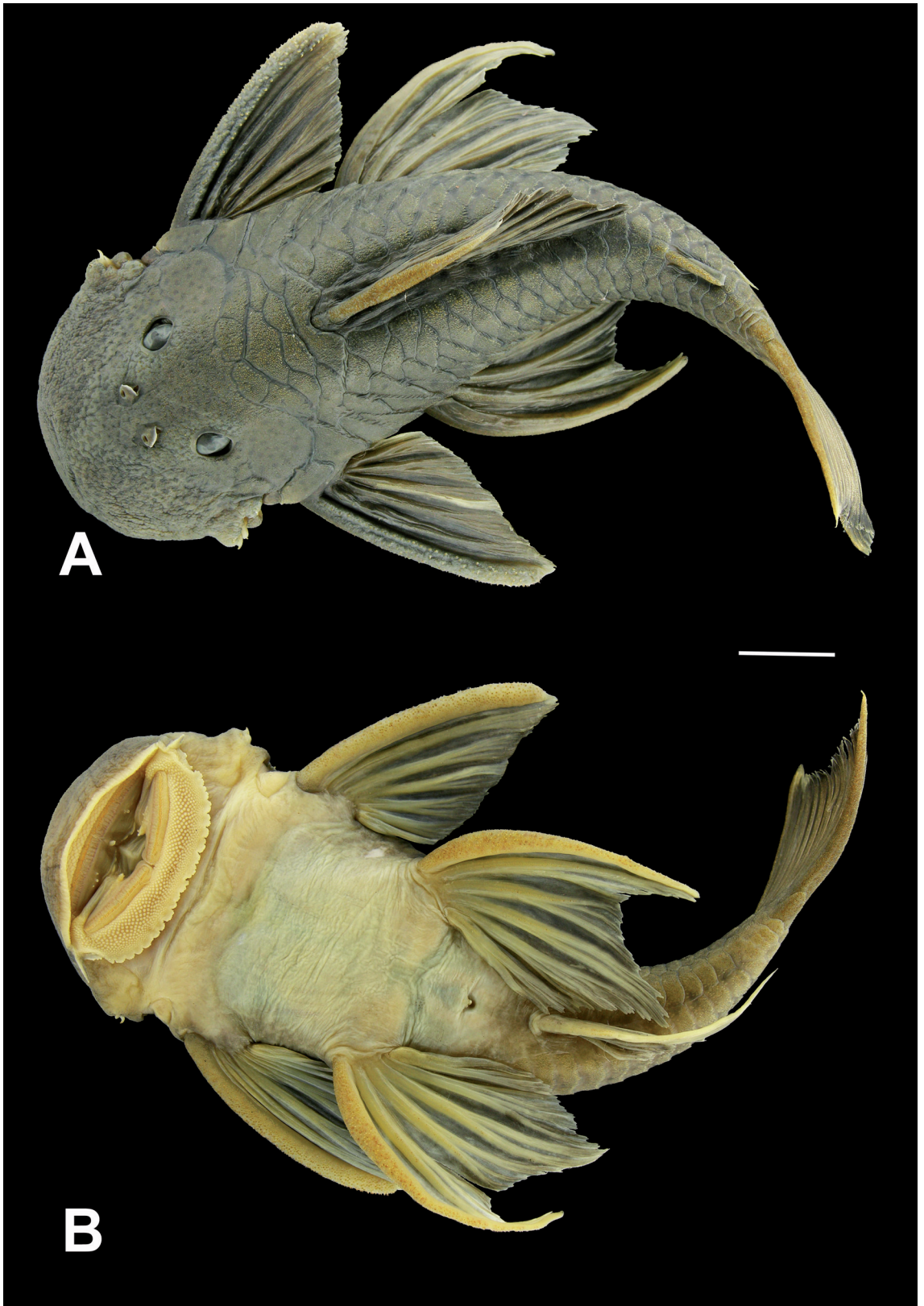


FIGURE 4: *Chaetostoma anale*, ICNMHN 17634, adult male, 188.0 mm SL. **A)** Dorsal view; **B)** Ventral view. Note the enlarged anal fin and the W-shaped distal margin of the pelvic fins in B. Scale bar equals 20 mm.

Description: Measurements presented in Table 1. Small-sized *Chaetostoma*, with largest examined specimen 103.1 mm SL (paratype male, ICNMHN 16364). Head and body slightly depressed and wide. Dorsal profile of anterior portion of head in lateral view convex from unplated region of snout to vertical through posterior nares, then moderately convex toward dorsal-fin insertion. Dorsal profile of body straight to slightly convex and slightly concave from dorsal-fin insertion to caudal-fin origin. Ventral profile of head and body straight from snout tip to insertion of ventral leading caudal-fin ray.

Interorbital area ranging from slightly flat to convex. Dorsal surface of snout region convex. Head in dorsal view roundish or oval with irregular margin due to development of integument and underlying fatty tissues. Snout naked, covered by epithelial papillae and ridges apparently being formed by fusion of papillae. Anterior margin of plated portion of snout roughly V- or U-shaped, starting on snout midline

and then extending further posteriorly to dorsal margin of exposed portion of opercle forming ventral margin nearly parallel or slightly transverse to ventral head margin. Unplated snout region more extensive in mature males than in females. Parieto-supraoccipital dermal keel present, less evident or even apparently lost in faded specimens due to dehydration or inadequate preservation.

All lateral plate series other than ventral series complete from compound pterotic to caudal peduncle; ventral series incomplete anteriorly and beginning just anterior to pelvic-fin insertion. Abdomen completely naked. First anal-fin pterygiophore not exposed. Median series with 23-25 plates (mode 24), showing individual and intraindividual variation.

Cheek apparatus with five protruding hypertrophied cheek odontodes supported by internal bony ossicles and basally covered with skin. Some individuals with six cheek odontodes. Despite apparent variation in number, inner ossicles present only five

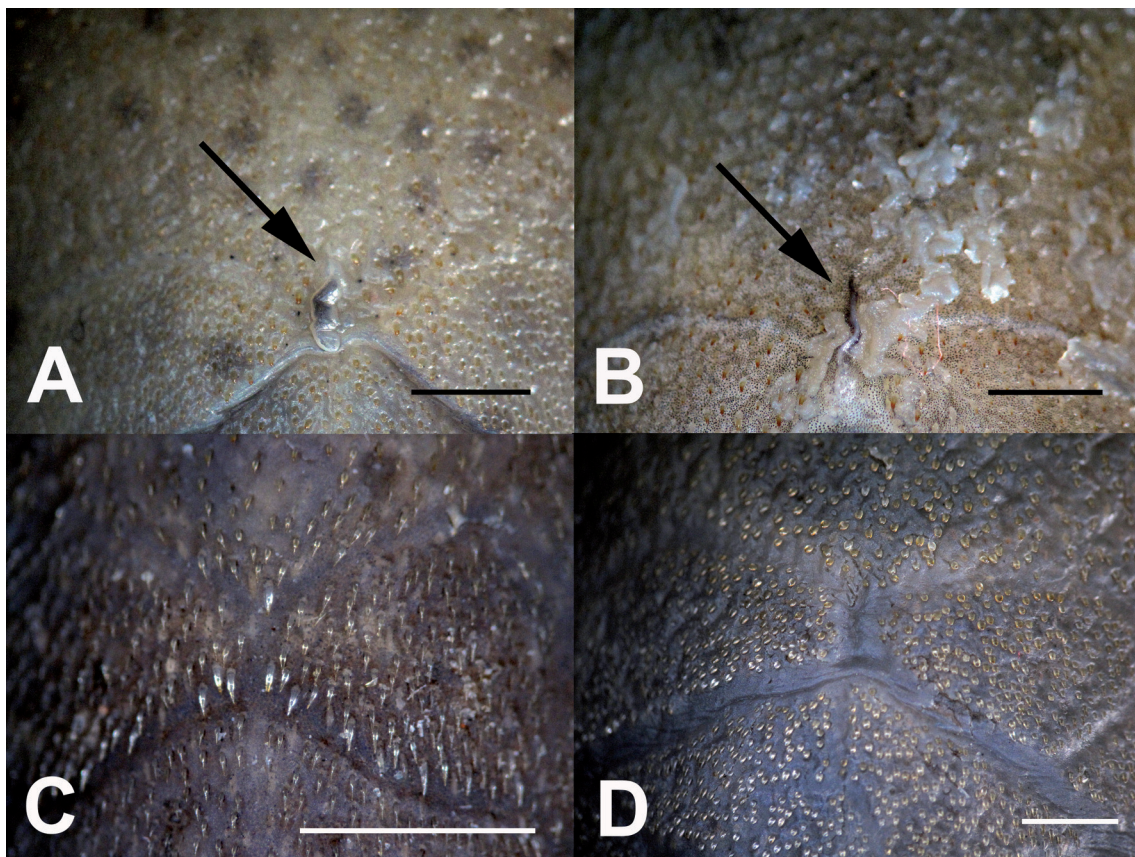


FIGURE 5: Supraoccipital region in species of *Chaetostoma* in dorsal view, anterior portion of body upward; arrows indicate the parieto-supraoccipital keel when present. A-B, species showing fleshy supraoccipital ridge; C-D, species with skin on supraoccipital region unmodified. **A)** *Chaetostoma milesi*, ICNMHN 16923, subadult male, 122.6 mm SL; **B)** *Chaetostoma formosae* sp. nov., ICNMHN 16364, paratype, adult female, 74.7 mm SL; **C)** *Chaetostoma platyrhynchus*, ICNMHN 5492, subadult male, 48.4 mm SL; **D)** *Chaetostoma sovichthys*, ICNMHN 16221, adult male, 96.4 mm SL. Scale bars equal 3 mm.

sockets as evident in c&s specimens. Hypertrophied cheek odontodes distally and strongly recurved, usually not surpassing posterior margin of exposed opercle when adpressed. Some specimens with supernumerary odontodes on fleshy ridge posterior to hypertrophied cheek odontodes and ventral to exposed opercle. Exposed portion of opercle roughly triangular in shape, weak mesial indentation evident externally where *musculus dilatator operculi* complex

inserts onto opercle. Cheek plates not exposed, but located anterior to margin of opercle as evident in c&s specimens. Fleshy ridge posterior to cheek odontodes present, sometimes reaching ventral margin of exposed opercle dorsally when cheek odontodes adpressed. Frontal, infraorbital, nasal, exposed opercle, compound pterotic, sphenotic, and parieto-supraoccipital bones supporting odontodes. Odontodes present on exposed portion of opercle, those on lateral

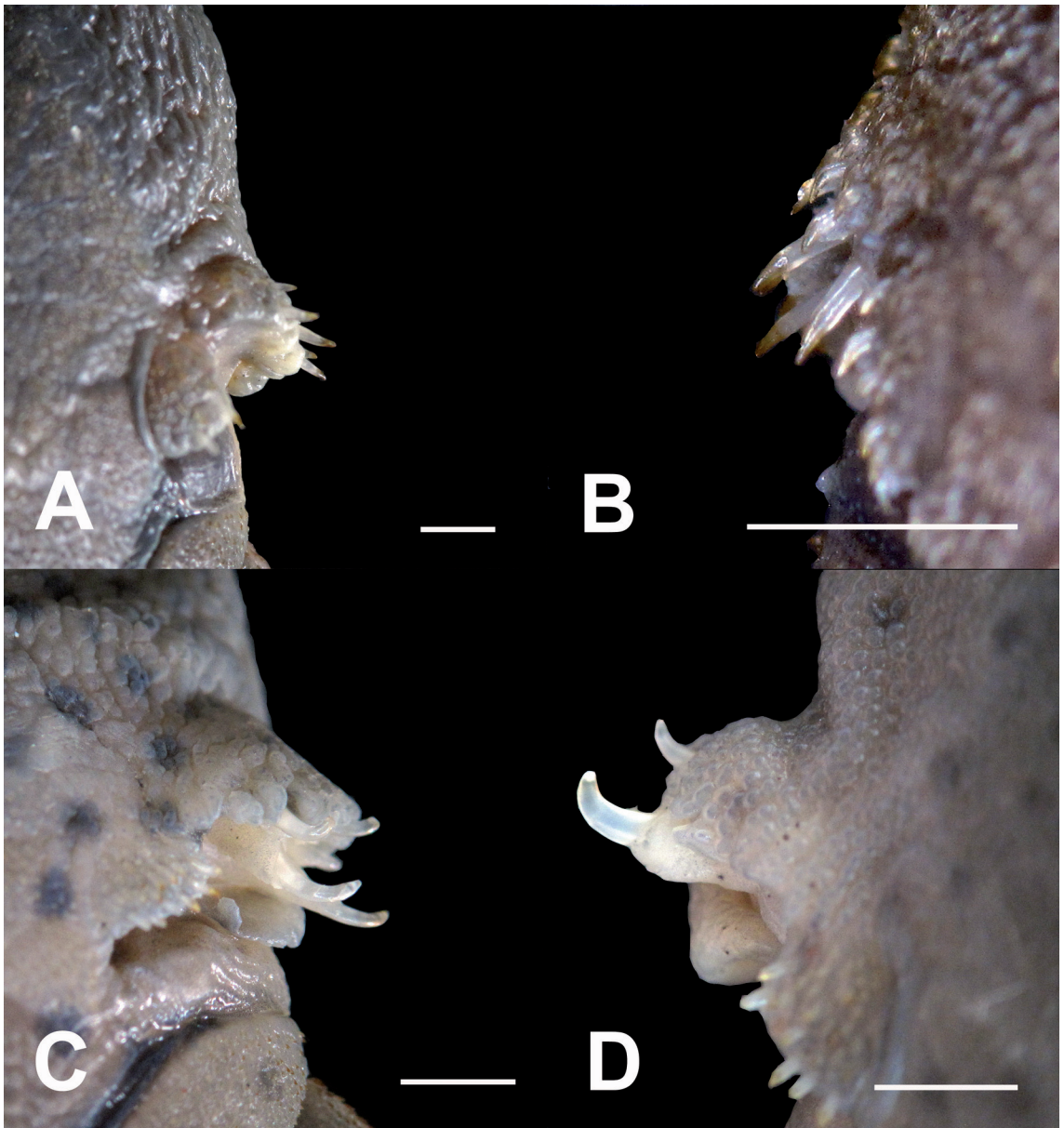


FIGURE 6: Cheek odontodes in species of *Chaetostoma* in dorsal view, anterior portion of body upward; A and C from right side of the head; B and D from left side of the head. A-B, species showing straight cheek odontodes; C-D, species showing recurved cheek odontodes. A) *Chaetostoma sovichthys*, ICNMHN 16221, adult male, 96.4 mm SL; B) *Chaetostoma platyrhynchus*, ICNMHN 5492, subadult male, 48.4 mm SL; C) *Chaetostoma formosae* sp. nov., holotype, ICNMHN 17114, adult male, 97.4 mm SL; D) *Chaetostoma milesi*, ICNMHN 16923, subadult male, 122.6 mm SL. Scale bars equal 3 mm.

TABLE 1: Measurements for *Chaetostoma formosae* sp. nov. Landmarks and measurements follow Armbruster (2003b) except for Anal-fin second ray L., not measured in that work. Predorsal L. through Pelvic-dorsal D. are percentages of SL; Head-eye L. through Premax.tooth.cup L are percentages of Head L. Standard Deviation = SD.

Measurement	Combined sexes (n = 21)			Males (n = 11)			Females (n = 10)		
	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
SL	70,9	54.3-102.6	15,5	81,0	59.0-102.6	14,4	59,8	54.3-71.4	6,4
Predorsal L.	44,4	41.8-50.3	1,9	44,7	43.3-50.3	2,0	44,1	41.8-48.2	1,8
Head L.	33,8	30.9-40.8	2,0	34,4	32.1-40.8	2,3	33,1	30.9-35.0	1,3
Head-dorsal L.	11,1	9.1-13.3	1,3	11,1	9.2-12.8	1,1	11,1	9.1-13.3	1,4
Cleithral W.	35,8	32.5-39.8	2,1	36,8	34.8-39.8	1,8	34,7	32.5-38.8	1,8
Head-pectoral L.	28,5	21.9-31.1	2,0	29,2	26.3-31.1	1,4	27,8	21.9-30.2	2,5
Thorax L.	23,4	19.5-26.7	2,0	22,1	19.5-23.6	1,2	25,0	22.6-26.7	1,4
Pectoral-spine L.	31,7	28.5-35.4	1,8	32,9	30.3-35.4	1,5	30,4	28.5-31.9	1,1
Abdominal L.	25,6	22.8-28.3	1,3	26,0	24.4-27.7	1,0	25,1	22.8-28.3	1,5
Pelvic-spine L.	25,1	22.0-28.1	1,6	26,0	23.6-28.1	1,3	24,1	22.0-26.3	1,4
Postanal L.	29,7	27.6-33.9	1,4	30,6	28.7-33.9	1,3	28,8	27.6-29.7	0,8
Anal-fin spine L.	10,3	7.4-15.1	2,1	11,8	10.1-15.1	1,7	8,7	7.4-10.5	1,0
Anal-fin second ray L.	17,5	10.2-32.4	7,2	22,7	14.1-32.4	6,3	11,8	10.2-12.9	0,8
Dorsal-pectoral D.	30,5	28.4-33.1	1,5	30,6	28.7-32.7	1,4	30,4	28.4-33.1	1,7
Dorsal spine L.	27,9	24.8-31.8	1,7	28,4	26.4-31.8	1,8	27,4	24.8-30.5	1,4
Dorsal-pelvic D.	23,6	20.5-28.7	2,1	23,7	21.5-28.7	2,1	23,6	20.5-28.0	2,3
Dorsal-fin base L.	28,3	24.5-41.8	3,5	28,4	26.3-31.9	1,7	28,2	24.5-41.8	4,9
Dorsal-adipose D.	15,9	14.4-18.1	1,1	16,2	14.5-18.1	1,3	15,6	14.4-17.1	0,9
Adipose-spine L.	7,9	5.6-13.8	1,6	8,0	6.3-13.8	2,0	7,7	5.6-8.9	1,1
Adipose-up. Caudal D.	14,3	11.5-16.3	1,5	13,7	11.5-16.3	1,8	15,0	13.8-15.7	0,6
Caudal peduncle Dp.	13,1	10.9-20.1	1,9	14,2	12.4-20.1	2,1	12,0	10.9-13.0	0,8
Adipose-low. Caudal D.	21,1	19.6-23.5	1,1	21,4	20.3-22.4	0,7	20,7	19.6-23.5	1,3
Adipose-anal D.	18,6	16.1-20.9	1,3	18,8	17.4-20.7	1,1	18,3	16.1-20.9	1,6
Dorsal-anal D.	15,1	13.5-17.1	1,0	14,9	13.9-16.6	0,9	15,3	13.5-17.1	1,0
Pelvic-dorsal D.	29,7	27.0-34.9	2,1	30,1	27.0-32.8	1,7	29,4	27.0-34.9	2,6
Head-eye L.	36,1	18.9-40.1	4,2	34,6	18.9-37.6	5,3	37,8	36.0-40.1	1,5
Orbit dia.	16,2	13.2-18.3	1,6	15,2	13.2-18.1	1,6	17,2	15.0-18.3	1,0
Snout L.	65,0	54.4-69.3	3,0	64,6	54.4-69.3	4,0	65,4	63.2-67.5	1,5
Internares W.	22,3	15.9-43.7	5,3	20,6	15.9-25.0	2,4	24,2	20.4-43.7	7,0
Interorbital W.	47,4	37.5-52.6	3,3	46,6	37.5-52.6	4,0	48,4	45.7-51.8	2,1
Head Dp.	76,8	64.2-108.1	8,3	77,6	64.2-108.1	11,0	76,0	70.7-82.6	3,9
Mouth L.	53,3	42.2-59.5	4,1	52,9	42.2-58.9	5,3	53,7	50.0-59.5	2,8
Mouth W.	83,9	48.9-92.3	9,6	82,2	48.9-91.7	12,9	85,6	80.8-92.3	3,6
Barbel L.	10,0	6.0-12.4	1,9	10,3	6.0-12.4	1,9	9,7	6.1-12.3	2,0
Dentary tooth cup L.	30,7	26.7-34.1	1,6	30,6	26.7-34.1	1,9	30,7	27.7-33.1	1,4
Premax. tooth cup L.	26,2	21.4-29.0	1,7	25,7	21.4-29.0	2,0	26,8	24.7-28.5	1,2

and posterior margins longer and thicker than those on dorsal surface.

Odontodes flat and sharp on lateral plates but flat and spatulate on area between orbit and naris, mesethmoidal region and dorsal surface of snout. Odontodes flat and spatulate on dorsal surface of dorsal-fin leading ray and spinelet, adipose fin, and dorsal leading ray of caudal fin. Odontodes flat and spatulate on ventral and lateral surfaces of pectoral and pelvic fin, and on anterior surface of anal fin and ventral leading ray of caudal fin. Hypertrophied pectoral-spine odontodes basally surrounded by fleshy collar and frequently with small posterior papilla; fleshy papillae present when odontodes are not fully developed, as well as among developed odontodes

on pectoral-fin spine (as described for *Dekeyseria* by Sabaj *et al.*, 1999). Remaining odontodes developing directly on plates and rays without associated papillary soft tissues. All plates of lateral series with largest odontodes on posterior margin and shorter ones on plate surface.

Posterior tip of dorsal fin reaching or surpassing origin of adipose spine when adpressed. Dorsal-fin leading ray not elongate or extending beyond margin of remainder of fin. Dorsal-fin leading ray stiff basally but flexible distally. Distal margin of dorsal fin slightly convex. Margin of dorsal-fin spinelet moderately acute, covered in smaller individuals, yet visible through skin, bearing odontodes protruding through skin. Dorsal-fin spinelet exposed in mature

specimens, regardless of sexual condition. Dorsal-fin lock functional. Dorsal-fin ray formula ii,8. Adipose spine preceded by one unpaired plate, spine absent in one specimen examined. Dorsal procurent caudal-fin rays 5-7 (mode 6) and ventral procurent rays 3-5 (mode 4) as evident in c&s preparations and alcohol-preserved specimens. Caudal fin oblique with lower portion longer than upper portion; dorsal and ventral unbranched leading rays longer than branched rays. Distal margin straight or slightly emarginate. Caudal fin base covered by acute platelets variable in number. Caudal-fin ray formula i,14,i. Anal-fin base short; anal fin length variable and dependent on sexual condition; males with longer rays than females. Relative length of anal-fin rays generally ascending from posteriormost to anteriormost ray fin ($i < 4 < 3 < 2 < 1 \leq ii$). First branched ray in females usually largest as opposed to modal formula depicted above; variation present in relative length of anal-fin rays in some specimens showing first unbranched ray longer than fourth branched ray. Anal-fin ray formula ii,3-4 (mode ii,4). Pectoral-fin spine with short and thick hypertrophied odontodes on tip but with distinct dorsal row of odontodes throughout midline, showing sexual variation in odontode curvature. Tip of pectoral-fin spine when adpressed reaching to level of vent in mature specimens. Posterior margin of pectoral fin from straight to slightly convex. Tip of adpressed pectoral-fin spine reaching from one-third to middle of leading pelvic-fin ray length. Pectoral-fin ray formula i,6. Tip of pelvic-fin leading ray reaching posteriorly to, or beyond, anal-fin insertion when adpressed. Odontodes on dorsal surface of pelvic-fin rays presenting sexual dimorphism. Pelvic fin with variable distal margin from convex and round in females to strongly convex and angular in mature males (See below for comments on ontogenetic, sexual and individual variation). Pelvic-fin leading ray more than twice as thick as remaining rays. Pelvic-fin ray formula i,5.

Iris operculum present. Short, fleshy flap with round margin present between anterior and posterior nares, deeper mesially. Upper lip with multiple series of papillae, those proximate to mouth opening small and round, followed distally by larger and widely elongate ones. Lower lip with medium-sized round papillae anteriorly and smaller ones posteriorly, with smooth skin close to posterior margin of lip; border crenate. Maxillary barbels moderate in length, separate distally from lower lip. Lower lip basally fused up to one-third or even half of total barbel length in some individuals; fleshy ridge present dorsally almost over entire length of each barbel, also showing individual

variation. Buccal papilla present at symphysis of premaxillae. Premaxillary ornamentation usually consisting of individual small papillae arranged transversely. Dentary ornamentation consisting of mesial transverse papillary ridge and secondary single papillae arranged lateral to main ridge.

Jaws wide transversely. Posterior margin of premaxillae forming nearly straight line. Dentary wider than premaxilla. Both ramii with nearly straight cups only recurved on lateral margins. Tooth peduncle fairly long, narrow, and distally recurved. Cusps asymmetrically developed with lateral tooth cusp approximately one-half length of medial cusp. Dentary teeth 50-120, premaxillary teeth 35-79, showing ontogenetic variation increasing with age.

Coloration in alcohol: Overall body background from grayish-green to light brown with black marks on head, fins and body. Head and dorsum with black spots, more numerous on head than on dorsum; lateral plates bordered with black pigment always on anterior portion of body, and occasionally on posterior plates. Posterior head margin bordered by black pigment. Parieto-supraoccipital fleshy keel usually black, but sometimes less intensely pigmented. Pectoral, pelvic, dorsal, anal, and caudal fins with hyaline membranes and black longitudinal bands adjacent to each ray; branched rays unpigmented. Pectoral-fin spine with black longitudinal dorsal band along entire length. Dorsal fin with basal anterior black spot between leading ray and first branched ray. Anteriormost ray in anal fin sometimes pigmented longitudinally; longest unbranched ray and paired posterior ridges in mature males dark gray in coloration. Caudal fin with light reddish areas at least on upper and lower tips, sometimes along entire distal margin. Venter light without dark pigment, postanal ventral plates with some black transverse bars or spots in some individuals.

Etymology: This species is named *formosae*, an adjective in genitive case derived from the latin *formosa*. The name honours my sister, Laura María Ballen, in recognition of her unconditional love and support to me.

Sexual variation: Males of *Chaetostoma formosae* differ in several ways from females. The most conspicuous feature is the enlarged anal fin in mature males, where the second unbranched anal-fin ray elongates, also developing two posterior and longitudinal fleshy ridges and reaching the ventral caudal-fin base once the ray is totally developed (Fig. 3); in females such condition is absent, presenting the second unbranched anal-fin

ray comparable in length to the branched adjacent ones. Mature males develop a fleshy dorsal ridge on the pelvic-fin leading ray, from insertion of fin to near the tip of ray; in contrast, females lack such a condition as well as the coloration associated to the fleshy ridge. In addition, mature males show a more extensive unplated portion of snout, whereas mature females show a more plated snout. Development of odontodes on pectoral-fin spines is more pronounced in males than in females but both sexes show odontode development; in addition, the dorsal longitudinal single row presents acute recurved odontodes in mature males whereas mature females show straight odontodes. Distal margin of pelvic fin convex in both sexes, but males always show an angular margin whereas females usually show round margin; however, some larger females can approach the male condition. Males develop several rows of acute recurved hypertrophied odontodes protruding from skin on the dorsal surface of pelvic-fin rays, whereas mature females present odontodes visible through skin but not protruding as in males. Males present a pointed and discrete genital papilla, in contrast to females where the papilla is wide and pad-like. Both kinds of papilla show terminal aperture; however, once reaching maturity and when eggs are mature, females show a swollen posterior portion, what makes the papilla to give the impression of being directed proximal to the vent tube. Males are larger than females (largest male examined 103.1 mm SL vs. largest female examined 71.4 mm SL, both mature adults).

Ontogenetic variation: Some structures show ontogenetic variation. Pectoral-fin spines are longer in mature individuals. In addition, the parieto-supra-occipital fleshy ridge is always evident in immature individuals whereas in some large adults it might be less evident and hard to visualize either by preservation effects or due to a more extensive development of skin surrounding lateral plates occurring with age, therefore causing the ridge to be less evident. Teeth in premaxillary and dentary rami less numerous in immature individuals than in adult ones, probably due to growth of ramus cup with age allowing more teeth to develop, as reported for *Farlowella* (Retzer & Page, 1996). Distal margin of pelvic fin also shows ontogenetic variation with immature individuals showing a straight margin in contrast to adult males and females where margin is convex and either angular or round respectively as described above.

Distribution: *Chaetostoma formosae* is currently known from western piedmont tributaries of the upper río

Meta and Guaviare basins, in departments of Meta and Casanare, Eastern Colombia, Orinoco drainage (Fig. 2).

Some referred specimens were reported as collected in Colombian Amazonia (Fig. 2, southernmost record with a question mark). Such records are far outside the known range for the genus in Colombia and raise questions on the validity of their locality information. Further searches in the ICNMHN catalog database recovered some other Andean components supposedly collected in the Parque Nacional Natural Amacayacu by J. Ramírez. Those fishes include *Astroblepus* sp., *Dolichancistrus fuesslii* and *Eremophilus mutisii*, as well as some Amazonian species such as *Brachyplatystoma filamentosum*. Furthermore, *D. fuesslii* and *E. mutisii* are known to have allopatric distributions; the former along the Cordillera Oriental piedmont east of Andes and the latter over the Sabana de Bogotá, without known localities across the eastern watershed of the Cordillera Oriental. Even though some of the collections deposited by J. Ramírez at ICNMHN represent Amazonian taxa, some other specimens belong to strictly Andean species (e.g., *Astroblepus* spp., *D. fuesslii* and *E. mutisii*). Additionally, all of the collections by J. Ramírez were catalogued by the same people, increasing the possibility of an erroneous assignment of locality data for fishes apparently originating from several localities on the Cordillera Oriental in Colombia. Given the situation of such collections, those referred specimens (ICNMHN 7987, 8001 and 8038) are assigned to an unknown locality restricting their distribution to the Upper río Meta basin.

The distribution of *Chaetostoma formosae* is replicated by that of *Chaetostoma dorsale* (G.A. Ballen, unpubl. data) and *Dolichancistrus fuesslii* (Ballen & Vari, in prep.). However, both *C. dorsale* and *D. fuesslii* reach higher altitudes than do *C. formosae*, what could be an artifact of sampling effort from collectors working only eventually on the eastern flank of the Cordillera Oriental in Colombia. The same stands valid for *C. formosae*, for which the currently-known localities are concentrated in highly-sampled areas where most of the inventories were carried out in the last fifty years (e.g., around Villavicencio, Departamento de Meta) but with few records (and specimens) on the northernmost- and southernmost-known localities of this species. This coincidence in distributions might be interesting for deeper questions concerning vicariance biogeography, but to date, the distributions of these three species are not well understood in terms of northern, southern and altitudinal limits. On the other hand, the phylogenetic relationships within

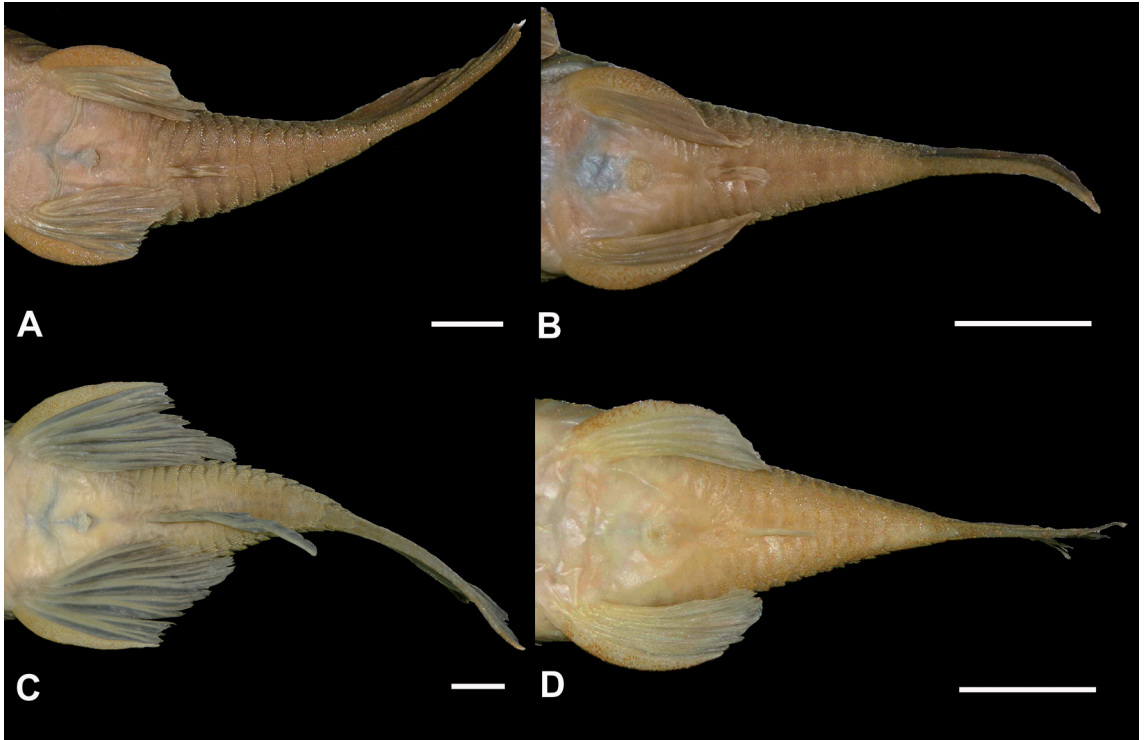


FIGURE 7: Sexual variation in the anal-fin length; ventral view, anterior to left. A-B represents the primitive condition (Condition A); C-D represents the derived condition (Condition B). **A)** *Chaetostoma dorsale*, ICNMHN 8011, adult male, 80.6 mm SL; **B)** *Chaetostoma dorsale*, ICNMHN 1183, adult female, 59.4 mm SL; **C)** *Chaetostoma formosae* sp. nov., holotype, ICNMHN 17114, adult male, 97.4 mm SL; **D)** *Chaetostoma formosae* sp. nov., paratype, ICNMHN 16364, adult female, 74.7 mm SL. Scale bars equal 10 mm.

both *Chaetostoma* and *Dolichancistrus* are not known, therefore precluding any attempt to use such data for a component analysis concerning potential endemism areas east and west of the Cordillera Oriental in Colombia.

DISCUSSION

The *Chaetostoma anale* species group

Content: Three species. *Chaetostoma anale* (Fowler), *C. formosae* Ballen, and *C. jegui* Rapp Py-Daniel.

The notable condition in the anal fin of mature males shared by *C. anale*, *C. formosae* and *C. jegui* is herein proposed as a synapomorphy for those species within *Chaetostoma*. All the remaining species from the genus have unmodified unbranched rays in the anal fin of mature males. Herein it is proposed that considering *Chaetostoma* (*sensu* Armbruster, 2004) as the ingroup and the remaining anastrins as the outgroup; and the character as having two conditions, namely, second unbranched anal-fin ray unmodified and comparable in length to branched rays in mature

males (Condition A; Loricariidae including most of *Chaetostoma* except *C. anale*, *C. formosae* and *C. jegui*, Fig. 7A, B) and second unbranched anal-fin ray in mature males enlarged and bearing two posterior fleshy ridges (Condition B; *C. anale*, *C. formosae* and *C. jegui*, Fig. 7C, D), then the derived character-state (B) in the transformation series A → B is evidence for a monophyletic group comprising those three species within *Chaetostoma*.

There is another particular structure present in those three species of *Chaetostoma*, namely, a parieto-supraoccipital dermal keel (Fig. 5A, B). However this structure is found in other species of *Chaetostoma* (e.g., *C. leucomelas*, *C. milesi*, *C. tachiraense* and *C. vagum*), and in some species of *Cordylancistrus* (G.A. Ballen, unpubl. data). Therefore both conditions are uninformative for the interrelationships among species of *Chaetostoma* given that both conditions (*i.e.*, skin on parieto-supraoccipital unmodified in the form of a darkly pigmented dermal keel, Fig. 5C, D; and skin on parieto-supraoccipital modified into a dermal keel) would be recovered as plesiomorphic given that both are present in both ingroup and outgroup. This would be enough to reject such a transformation series as a phylogenetic character pertinent as evidence for the

systematics of the species within *Chaetostoma*. Nevertheless, this character has shown to be informative under a more inclusive question on interrelationships of fishes from the *Chaetostoma* group (Ballen and Vari, in prep.). In addition, Salcedo (2006) noted its presence in eleven species of the genus including *C. anale* and *C. jegui*, arguing that they conform a monophyletic group within *Chaetostoma* as evidenced by this synapomorphy and noting some ontogenetic variation also documented for *C. formosae* in the present paper. However, such a monophyletic assemblage does not stand as valid by the presence of the presumed derived state because some species outside *Chaetostoma* as currently understood do show this state (i.e., "*Dolichancistrus*" *setosus* and an undescribed species of *Cordylancistrus* from northern Colombia).

Recognition of subgeneric arrangements in the Hypostominae is rare. Armbruster (2004, 2008) Proposed substantial changes to the generic composition of the Hypostominae (including the Ancistrini), and such modifications resulted in a striking and improved classification. The author provided diagnoses for most of his recognized genera, sometimes clumping together several monotypic or small genera traditionally believed to represent different units. One of the most interesting instances of such changes is the genus *Panaque*, now composed of three subgenera: *Panaque*, *Panaqolus* and *Scobinancistrus* (Armbruster, 2004; Lujan *et al.*, 2010). All three genera were considered different units under a non-phylogenetic framework (e.g., Isbrücker, 2001). However, Armbruster (2004) included *Panaqolus* and *Scobinancistrus* as subgenera of *Panaque*, making the genus diagnosable and allowing easy recognition of any species of *Panaque* as member of a particular subgenus, therefore allowing taxonomic arrangements that reflect evolutionary relationships and facilitate identification of species. This is one of the cases where formal subgeneric arrangements were made for hypostomine genera, but unfortunately it is not the rule in current taxonomy of this group of fishes. Although *Hypostomus* lacks an explicit and formal subgeneric arrangement, there are recognized species groups, as informal hierarchical categories. Although informal, such species groups facilitate identification. For instance, the recognition of the *Hypostomus cochliodon* species group (Armbruster, 2003b) makes it easier to identify a species of *Hypostomus* by restricting the necessary comparisons among species of the genus.

Chaetostoma, in contrast to other large or moderate genera of the Hypostominae, lacks to date explicit subgeneric arrangements, and the present recognition of the *Chaetostoma anale* species group is the first

attempt to organize the genus. Identification of *Chaetostoma* species is very difficult, and taxonomic decisions are often based on geographical distribution, a very questionable taxonomic strategy for groups with poorly-resolved taxonomies. It is anticipated that recognition of subgeneric units, either formal (i.e., subgenera) or informal (i.e., species groups) will improve our understanding of the taxonomy of *Chaetostoma*, one of the most speciose hypostomine genera. Despite its few included species, the recognition of the *C. anale* species group is a first step towards a more complete scheme of classification. Further work on some other subunits within *Chaetostoma* is in progress and hopefully will help to clarify the taxonomy of the genus.

RESUMEN

Se describe Chaetostoma formosae, sp. nov. de tributarios pedimontanos del alto río Meta sobre la Cordillera Oriental en Colombia. La nueva especie se distingue de sus congéneres por la presencia de un radio alargado no ramificado en la aleta anal con dos carnosidades longitudinales posteriores en machos maduros, presencia de odontoides cefálicos fuertemente recurvados, presencia de una quilla carnosa parieto-supraoccipital, margen posterior de las aletas pélvicas fuertemente proyectado y de forma angular en machos maduros, así como detalles de coloración. Se propone que la nueva especie pertenece a un grupo monofilético informal llamado en el presente trabajo el grupo de especies Chaetostoma anale, junto con dos especies adicionales, C. anale y C. jegui, de Colombia y Brasil respectivamente, con base en una apomorfía de la aleta anal en machos maduros.

PALABRAS-CLAVE: Sistemática; Ancistrini; Andes; Dimorfismo sexual; Taxonomía.

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APPENDIX

Comparative material examined

Chaetostoma group.

Chaetostoma: *C. alternifasciatum*, ANSP 71711 (holotype, photograph, xray); *C. anale*, ANSP 70525 (holotype), ICNMHN 13397, 17634; *C. anomalum*, USNM 133135 (syntype, photograph, xray); *C. brevilabiatum*, ICNMHN 6134 (holotype); *C. breve*, BMNH 1898.11.4.33-36 (syntypes, photograph); *C. carrioni*, BMNH 1933.5.29.1 (holotype, photograph); *C. dorsale*, ICNMHN 1183, 3372, 3535, 7997, 8011, 8013, 8027, 8031, 17499, 17646, MLS 588, 747, 604; *C. jegui*, INPA Uncatalogued (photograph); *C. lobarhynchus*, MUSM 20291 (photograph), CZUT-IC 5551, 5552; *C. microps*, BMNH 1860.6.16.137-143 (syntypes, photograph); *C. milesi*, ANSP 69330 (holotype), ICNMHN 10420, 15528, 16123, 16268, 16291, 16923, MLS 562; *C. pearsei*, ICNMHN 10361; *C. platyrhynchus*, ICNMHN 5488, 5492, 7971, 9417, 17624, 17625, 17626, 17628, 17629, 17630, 17631; *C. sovichthys*, ICNMHN 2381, 16221, 16223, MLS 568, 590, 600, USNM 121053 (holotype, photograph, xray); *C. tachiraense*, MLS 797, 799, 805, USNM 121052 (holotype, photograph, xray); sp. "Perú", AUM 45597, 45634; *C. vagum*, ANSP 70521 (holotype, photograph). *Cordylancistrus*: *C. daguae*, ICNMHN 3515, 17643, 17644, 17645; *C. perijae*, ANSP 168917 (paratype), ICNMHN 17502 (ex CAR 270, ex MBUCV-V 21745, paratype); *C. platycephalus*, BMNH 1898.11.4:42 (holotype, photograph); *C. sp1*. "Ranchería", ICNMHN 17503 (ex CAR 370), MLS 541; *C. sp2*. "Pacífico", BMNH 1908.5.29.70-79; *C. sp3*. "Magdalena", CP-UCO 1060, 1062; *C. sp4*. FMNH 76213 (c&s); *C. torbesensis*, USNM 121001 (holotype, xray). *Dolichancistrus*: *D. atratoensis*, CIUA 768, 769, 771, 772, IAvH-P 6630, ICNMHN 51 (holotype), 46 (paratypes), 74 (paratype), 3460; *D. carnegiei*, ICNMHN 591, 1822, 3235, 3571, 5445, 16016, 16017, 16018, 17498, 17500, 17501, MLS 522, 542, 543, 550; *D. cobrensis*, AUM 30377, 46306, MCNG 541, USNM 121036 (holotype), 121037 (paratypes); *D. fuesslii*, IAvH-P 7931, 11381, 3939, 3940, 9230, 9605, ICNMHN 2638, 2817, 2839, 3212, 3641, 14582, 16811, NMW 48026. *Leptoancistrus*: *L. canensis*, USNM 78300 (paratypes, xray); *L. cf. cordobensis*, CIUA 774, 775, 776, 777, 778, 779, 780, 781.

Remaining Ancistrini.

Ancistrus: *A. centrolepis*, IAvH-P 10473, ICNMHN 104, 189, 1632, 3153; *A. martini*, ICNMHN 1206, 17647, 17648, 17649; *A. triradiatus*, ICNMHN 17650. *Baryancistrus*: *B. niveatus*, MNRJ 19344. *Dekeyseria*: *D. niveata*, ANSP 185259; *D. pulcher*, ANSP 185298; *D. scaphirhyncha*, ICNMHN 12787, 12788. *Hemiancistrus*: *H. guahiborum*, ICNMHN 5323, 11915; *H. punctulatus*, ANSP 170168; *H. sabaji*, ANSP 185153. *Hopliancistrus*: *H. tricornis*, AUM 39853. *Hypancistrus*: *H. contradens*, ICNMHN 11917, 11918; *H. debilitera*, ICNMHN 10691. *Lasiancistrus*: *L. caucanus*, ICNMHN 8763; *L. guacharote*, ICNMHN 16916. *Leporacanthicus*: *L. galaxias*, AUM 42144; *L. triactis*, ZMA 120774. *Lithoxus*: *L. jantjae*, ANSP 182809 (paratypes); *L. lithoides*, ANSP 39121 (paratype). *Megalancistrus*: *M. aculeatus*, USNM 52594. *Neblichthys*: *N. pilosus*, ANSP 157587 (paratypes); *N. roraima*, ANSP 174914 (paratypes). *Panaque*: *P. maccus*, ICNMHN 15728; *P. gibbosus*, ICNMHN 369. *Peckoltia*: *P. bachi*, ICNMHN 13952; *P. brevis*, ICNMHN 7952; *P. vittata*, ICNMHN 7954, 12792. *Pseudacanthicus*: *P. leopardus*, AUM 35550, USNM 197105; *P. spinosus*, USNM 52594. *Pseudancistrus*: *P. sidereus*, ANSP 185297. *Pseudolithoxus*: *P. dumus*, ANSP 185255. *Spectracanthicus*: *S. punctatissimus*, MNHN 1999-0021.