

# A Multilocus Molecular Phylogeny for *Chaetostoma* Clade Genera and Species with a Review of *Chaetostoma* (Siluriformes: Loricariidae) from the Central Andes

Nathan K. Lujan<sup>1,2,3</sup>, Vanessa Meza-Vargas<sup>4,5</sup>, Viviana Astudillo-Clavijo<sup>1,2</sup>, Ramiro Barriga-Salazar<sup>6</sup>, and Hernán López-Fernández<sup>1,2</sup>

**The rubbernose-pleco genus *Chaetostoma* comprises 47 currently valid and many undescribed species distributed along Atlantic and Pacific slopes of the Andes Mountains from Panama to southern Peru, the Coastal Mountains of Venezuela, and drainages of the Guiana and Brazilian shields. We present a five-locus molecular phylogeny for 21 described and six undescribed species of *Chaetostoma* spanning the geographic range of the genus. Bayesian and maximum likelihood analyses found *Chaetostoma* to be well supported as monophyletic and sister to a clade of central and northern Andean genera that have also been hypothesized to be closely related based on morphology (i.e., *Andeancistrus*, *Cordylancistrus*, *Dolichancistrus*, *Leptoancistrus*, and *Transancistrus*). Species of *Chaetostoma* were divided into a trichotomy consisting of: a Pacific Coast, Central American, Magdalena Basin, Lake Valencia, and Guiana Shield clade; a western Orinoco, Lake Maracaibo, and Lake Valencia clade; and a widespread upper Amazon/Orinoco clade inclusive of a single species on the Brazilian Shield. We also conducted a systematic review of species from the central Andes of northern Peru and Ecuador. Based on our phylogenetic results and direct examination of historical and recently collected type and non-type material, we describe two new species of *Chaetostoma* (*C. bifurcum*, from the Pacific Coast, and *C. trimaculineum*, from the Atlantic Slope), redescribe four species (*C. breve*, *C. carrioni*, *C. dermorhynchum*, and *C. microps*, all from the Atlantic Slope), transfer four species from *Chaetostoma* to *Ancistrus* and find two species to be junior synonyms.**

**Las carachamas nariz de goma del género *Chaetostoma* comprenden 47 especies válidas y algunas especies no descritas distribuidas a lo largo de las vertientes Atlántico y Pacífico de la Cordillera de los Andes desde Panamá hasta el sur de Perú, las montañas costeras de Venezuela, y cuencas de los escudos de Guayana y Brasil. Presentamos una filogenia molecular de cinco loci para 21 especies descritas y seis no descritas de *Chaetostoma*, que abarcan el área de distribución geográfica del género. Los análisis de probabilidad bayesiana y máxima verosimilitud muestran que *Chaetostoma* está bien soportado como grupo monofilético y grupo hermano del clado de los géneros andinos del centro y norte, que también se ha hipotetizado que están estrechamente relacionados en base a la morfología (p.e., *Andeancistrus*, *Cordylancistrus*, *Dolichancistrus*, *Leptoancistrus* y *Transancistrus*). Las especies de *Chaetostoma* se dividieron en una tricotomía que consiste en: un clado de la costa del Pacífico, Centroamérica, cuenca del Magdalena, Lago de Valencia y del Escudo Guayanés; un clado del oeste del Orinoco, Lago de Maracaibo y Lago de Valencia; y un clado ampliamente distribuido del alto Amazonas/Orinoco incluyendo la única especie en el Escudo Brasileño. Realizamos también una revisión sistemática de las especies de los Andes centrales del norte de Perú y Ecuador. Basados en nuestros resultados filogenéticos y en la examinación directa de colectas históricas y recientes de material tipo y no tipo, se describen dos nuevas especies de *Chaetostoma* (*C. bifurcum*, de la costa Pacífica y *C. trimaculineum*, de la vertiente del Atlántico), se redescriben cuatro especies (*C. breve*, *C. carrioni*, *C. dermorhynchum*, *C. microps*, todas de la vertiente del Atlántico), se transfieren cuatro especies de *Chaetostoma* a *Ancistrus* y se encuentran dos especies que son sinónimo junior.**

**T**HE genus *Chaetostoma* was erected by Tschudi (1846) for the new species *Ch. lobarhynchos* from the Ucayali River drainage in east-central Peru. For nearly a century, *Chaetostoma* was used as a catch-all taxon to which many new species that are now broadly distributed throughout the subfamily Hypostominae were assigned (e.g., *Chaetostomus aspidolepis* Günther, 1867 = *Hypostomus aspidolepis*; *Chaetostomus nigrolineatus* Peters, 1877 = *Panaque nigrolineatus*; *Chaetostomus furcatus* Fowler, 1940 = *Peckoltia furcata*; Lujan et al., 2015a). Taxonomic revisions by Eigenmann and Eigenmann (1889, 1890), Eigenmann (1922), Regan (1904), Isbrücker (1980), and Burgess (1989),

and morphology-based phylogenetic analyses by Armbruster (2004, 2008) restricted the genus to species having the following five internal osteological synapomorphies (from Armbruster, 2004): 1) hyomandibular free from the compound pterotic posterior to the cartilaginous condyle of the hyomandibular (character 34, state 0), 2) posterior region of the hyomandibular not greatly deflected (character 42, state 0), 3) anterior process of the compound pterotic absent or only slightly deflected (character 111, state 0), 4) sphenotic with a thin ventral process less than one fourth as wide as the main body of the sphenotic (character 116, state 0), 5) tip of transverse process of the Weberian complex

<sup>1</sup>Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6; E-mail: (HLF) h.lopez.fernandez@utoronto.ca.

<sup>2</sup>Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks St., Toronto, Ontario, Canada M5S 3B2; E-mail: (VAC) viviana.astudillo@utoronto.ca.

<sup>3</sup>Present address: Center for Systematic Biology and Evolution, Academy of Natural Sciences of Drexel University, 1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103; E-mail: nklujan@gmail.com. Send reprint requests to this address.

<sup>4</sup>Departamento de Vertebrados, Museu Nacional, Quinta da Boa Vista, 20940-040 Rio de Janeiro, RJ, Brazil; E-mail: meza.sv@gmail.com.

<sup>5</sup>Departamento de Ictiología, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Av. Arenales 1256, Lima, Perú.

<sup>6</sup>Instituto de Ciencias Biológicas, Escuela Politécnica Nacional, Quito, Ecuador; E-mail: ramiro.barriga@epn.edu.ec.

Submitted: 14 November 2014. Accepted: 7 May 2015. Associate Editor: R. E. Reis.

© 2015 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CI-14-194 Published online: September 25, 2015

centrum at least partially contacting the compound pterotic (character 135, state 0). Several more recent species descriptions and taxonomic revisions have helped to further clarify boundaries of both the genus, clades within the genus, and species (e.g., Ballen, 2011; Salcedo, 2006a, 2006b, 2013).

In a molecular phylogenetic study examining two mitochondrial (Cyt *b*, 16S) and three nuclear (RAG1, RAG2, MyH6) loci and 12 species of *Chaetostoma* among a wide range of other Hypostominae taxa, Lujan et al. (2015a) found strong support for monophyly of the genus as defined by Armbruster (2004, 2008; i.e., inclusive of the genera *Lipopterichthys* and *Loraxichthys*, which are therefore treated herein as junior synonyms). Both morphological and molecular phylogenetic evidence support a sister relationship between *Chaetostoma* and a clade consisting of five northern Andean genera: *Andeancistrus*, *Cordylancistrus*, *Dolichancistrus*, *Leptoancistrus*, and *Transancistrus*.

Externally, all but one of the 47 currently valid species of *Chaetostoma* can be distinguished from most other loracarids by having at least one vertical column of five plate rows at the thinnest part of the caudal peduncle (vs. three in *Ancistrus*), by having eight or more branched dorsal-fin rays (vs. seven in *Ancistrus*), and by having the anterior and anterolateral snout margins free of plates, with this region instead being covered by a broad band of naked (i.e., unplated) skin lacking tentacles (vs. tentacles present in *Ancistrus*). *Chaetostoma platyrhyncha*, which is unique in the genus for having a plated snout, is the only exception to the last characteristic. Variation in the extent or pattern of snout plating distinguishes *Chaetostoma* from *Transancistrus aequinoctialis*, *T. santarosensis*, *Paulasquama callis*, and *Pseudolithoxus stearleyi*. The naked snout region of *Chaetostoma* generally takes the shape of a broad crescent around the anterior and anterolateral margins of the snout, whereas in *T. aequinoctialis* and *T. santarosensis*, the anteriormost unplated snout region is almost absent (Tan and Armbruster, 2012), and in *Paulasquama* and *Pseudolithoxus stearleyi* the unplated region is limited to medial lobes extending posteriorly from the anterior snout margin to the nares (Lujan and Armbruster, 2011).

In this study, we reexamine and expand upon relationships found by Lujan et al. (2015a) by conducting a molecular phylogenetic analysis inclusive of more species and populations of *Andeancistrus*, *Chaetostoma*, *Cordylancistrus*, *Dolichancistrus*, *Leptoancistrus*, and *Transancistrus*. We also present new morphometric, meristic, geographic range, and live color data for two new and four described species of *Chaetostoma* distributed along the Pacific and Atlantic slopes of the Andes from central Peru to southern Colombia. We redescribe the Atlantic slope species *Ch. breve* Regan, 1904, *Ch. carrioni* (Norman, 1935), *Ch. dermorhynchum* Boulenger, 1887, and *Ch. microps* Günther, 1864, based on combinations of original type specimens and recently collected material from at or near type localities. We describe the new Atlantic Slope species *Ch. trimaculineum* based on material from the Marañon and Santiago river drainages, and describe the new Pacific Slope species *Ch. bifurcum* based on material from the Esmeraldas, Guayas, Santa Rosa, and Tumbes river drainages in Ecuador and Peru. In addition to these phylogenetic and taxonomic results, we provide as comprehensive an overview of the distinguishing morphological characteristics of *Chaetostoma* from throughout the Amazon Basin as is possible given limitations on the availability of specimens of certain rare species. Finally, we

present a summary of all genera and species that we conclude are valid within the *Chaetostoma* Clade (*sensu* Lujan et al., 2015a), including several taxonomic changes based on our direct and photographic examination of type specimens.

## MATERIALS AND METHODS

**Phylogenetic taxon sampling.**—We sampled as broadly as possible throughout *Chaetostoma* Clade genera and species, including all valid genera, approximately half of all valid species (Tables 1, 2), several undescribed species, and representatives from almost the entire geographic range of the clade. Lots that have been examined in our molecular phylogenetic analysis are indicated with an asterisk (\*, text) or bullet (•, Table 1). As with any attempt to comprehensively sample a diverse, widespread, and relatively poorly known group of organisms, there are species and drainages missing from our analysis.

**Tissue and DNA sources.**—Newly generated sequence data (Table 2) were obtained from tissue samples or DNA extracts collected by the authors or provided by the Academy of Natural Sciences of Drexel University in Philadelphia, Pennsylvania (ANSP), the Auburn University Museum in Auburn, Alabama (AUM), the Muséum d'Histoire Naturelle in Geneva, Switzerland (MHNG), the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos in Lima, Peru (MUSM), the Royal Ontario Museum in Toronto, Canada (ROM), and the Smithsonian Tropical Research Institute in Panama (STRI), or obtained through the ornamental fish trade. Voucher specimens (Table 2) were identified either directly by the first author, directly by curators and collection managers at contributing institutions, or by exchange of photographs.

**Molecular markers, DNA extraction, amplification, and sequencing.**—Molecular methods followed those of Lujan et al. (2015a) and will only be briefly reviewed here. We amplified and sequenced an approximately 600 base pair (bp) fragment of the mitochondrial 16S gene, an approximately 1150 bp fragment of the mitochondrial Cyt *b* gene, an approximately 1020 bp fragment of the nuclear gene RAG1, an approximately 950 bp fragment of the nuclear RAG2 gene, and an approximately 660 bp fragment of the nuclear MyH6 gene. Each fragment was amplified using combinations of previously published (Sullivan et al., 2006; Li et al., 2007) and recently developed primers (Lujan et al., 2015a). The total alignment equaled 4293 base pairs.

Whole genomic DNA (gDNA) was extracted from fin or muscle tissues preserved in 95% ethanol following manufacturer's instructions for the DNeasy Blood & Tissue Kit (Qiagen N.V., Venlo, Netherlands). Fragment amplifications were performed following the methods of Lujan et al. (2015a). For all genes, the entire volume of PCR product was run on a 1% agarose gel with 0.01% SYBR Safe DNA gel stain (LTI: Life Technologies Inc., Carlsbad, CA). For all markers, the band corresponding to the target locus was cut from the gel and the target PCR product extracted by centrifuge filtration through the top of a P-200 pipette filter tip in a labeled 1 ml snap-top tube (5 min at 15,000 rpm). Forward and reverse sequencing reactions followed the manufacturer's recommendations for sequencing on an Applied Biosystems 3730 DNA analyzer (LTI).

**Table 1.** Summary of valid genera and species in the *Chaetostoma* Clade (*sensu* Lujan et al., 2015). Species included in our molecular phylogenetic analysis are designated with a bullet (•) after their name. Institutional abbreviations follow Sabaj Pérez (2014). Drainages indicated are those for the principal type locality only, followed by the following larger watershed abbreviations: AD = Amazon Drainage ( $n = 19$ ), CC = Caribbean Coastal ( $n = 6$ ), MD = Magdalena Drainage ( $n = 9$ ), OD = Orinoco Drainage ( $n = 5$ ), PC = Pacific Coastal ( $n = 13$ ). Taxonomic conclusions for *Dolichancistrus* from Ballen and Vari (2012). Abbreviation: syn = syntype.

Species	Author	Year	Holotype	Paratypes	Country	Drainage
<b><i>Andeancistrus</i> Lujan, Meza-Vargas, and Barriga-Salazar, 2015</b>						
<i>A. eschwartzae</i> •	Lujan et al.	2015	MEPN 14780	19	Ecuador	Pastaza (AD)
<i>A. platycephalus</i> •	(Boulenger)	1898	BMNH 1898.11.4.42	2 (syn)	Ecuador	Santiago (AD)
<b><i>Chaetostoma</i> Tschudi, 1846</b>						
<i>Ch. aburrensis</i>	Posada	1909	type unknown	—	Colombia	Cauca (MD)
<i>Ch. anale</i>	(Fowler)	1943	ANSP 70525	—	Colombia	Caqueta (AD)
<i>Ch. anomalum</i> •	Regan	1903	BMNH syntypes	13 (syn)	Venezuela	L. Maracaibo
<i>Ch. bifurcum</i> n. sp. •	Lujan et al., this study	2015	MEPN 14687	136	Ecuador	Guayas (PC)
<i>Ch. branickii</i>	Steindachner	1881	NMW syntypes	5 (syn)	Peru	Marañon (AD)
<i>Ch. breve</i> •	Regan	1904	BMNH, MSNM, MZUT	12 (syn)	Ecuador	Santiago (AD)
<i>Ch. brevilabiatum</i> •	Dahl	1942	ZMUL	—	Colombia	Magdalena (MD)
<i>Ch. carrioni</i> •	(Norman)	1935	BMNH 1933.5.29.1	4	Ecuador	Santiago (AD)
<i>Ch. changae</i> •	Salcedo	2006a	ANSP 179125	16	Peru	Huallaga (AD)
<i>Ch. daidalmatos</i> •	Salcedo	2007	MUSM 25552	7	Peru	Huallaga (AD)
<i>Ch. dermorhynchum</i> •	Boulenger	1887	BMNH 1880.12.8.64–66	3 (syn)	Ecuador	Pastaza (AD)
<i>Ch. dorsale</i> •	Eigenmann	1922	CAS 77093	—	Colombia	Meta (OD)
<i>Ch. dupouii</i>	Fernández-Yépez	1945	AFY	11	Venezuela	Tuy (CC)
<i>Ch. fischeri</i> •	Steindachner	1879	NMW 47170–73	7 (syn)	Panama	Chepo (PC)
<i>Ch. floridablancaensis</i>	Ardila Rodríguez	2013	CAR 633.1	19	Colombia	Lebrija (MD)
<i>Ch. formosae</i> •	Ballen	2011	ICNMHN 17114	many	Colombia	Meta (OD)
<i>Ch. guariense</i> •	Steindachner	1882	NMW 47183–85	7 (syn)	Venezuela	Tuy (CC)
<i>Ch. jegui</i>	Rapp Py-Daniel	1991	INPA 2822	83	Brazil	Uraricoera (AD)
<i>Ch. leucomelas</i>	Eigenmann	1918	CAS 60167	2	Colombia	Patía (PC)
<i>Ch. lepturum</i>	Regan	1912	BMNH 1910.7.11.116–118	3 (syn)	Colombia	San Juan (PC)
<i>Ch. lexa</i> •	Salcedo	2013	ANSP 179128	17	Peru	Huallaga (AD)
<i>Ch. leucomelas</i>	Eigenmann	1917	CAS 60167	2	Colombia	Patía (PC)
<i>Ch. lineopunctatum</i> •	Eigenmann and Allen	1942	CAS 64650	1	Peru	Ucayali (AD)
<i>Ch. lobarhynchos</i> •	Tschudi	1845	NMW 47190	—	Peru	Ucayali (AD)
<i>Ch. machiquense</i>	Fernández-Yépez and Martin S.	1953	MHNS 1558	1	Venezuela	L. Maracaibo
<i>Ch. marginatum</i>	Regan	1904	BMNH 1901.8.3/27–28	3 (syn)	Ecuador	Mira (PC)
<i>Ch. marmorescens</i> •	Eigenmann and Allen	1942	IU 15403	—	Peru	Huallaga (AD)
<i>Ch. microps</i> •	Günther	1864	BMNH 1860.6.16.137–143	7 (syn)	Ecuador	Santiago (AD)
<i>Ch. milesi</i>	Fowler	1941	ANSP 69330	—	Colombia	Magdalena (MD)
<i>Ch. niveum</i>	Fowler	1944	ANSP 71432	—	Colombia	Jurubidá (PC)
<i>Ch. nudirostre</i> •	Lütken	1874	ZMUC P30168	—	Venezuela	L. Valencia (CC)
<i>Ch. palmeri</i>	Regan	1912	BMNH 1910.7.11.120–121	2 (syn)	Colombia	San Juan (PC)
<i>Ch. patiae</i>	Fowler	1945	ANSP 71716	1	Colombia	Patía (PC)
<i>Ch. paucispinis</i>	Regan	1912	BMNH 1910.7.11.119	—	Colombia	San Juan (PC)
<i>Ch. pearsei</i>	Eigenmann	1920	CAS 64655	4	Venezuela	L. Valencia (CC)
<i>Ch. platyrhynchus</i>	(Fowler)	1943	ANSP 70512	3	Colombia	Caquetá (AD)
<i>Ch. sovichthys</i>	Schultz	1944	USNM 121053	171	Venezuela	L. Maracaibo
<i>Ch. stanii</i>	Lütken	1874	ZMUC P30169	—	Venezuela	Yaracuy (CC)
<i>Ch. stroumpoulos</i> •	Salcedo	2006b	MUSM 23491	many	Peru	Huallaga (AD)
<i>Ch. tachiraense</i>	Schultz	1944	USNM 121052	1	Venezuela	L. Maracaibo
<i>Ch. taczanowskii</i>	Steindachner	1883	NMW 47219	1	Peru	L. Maracaibo
<i>Ch. thomsoni</i>	Regan	1904	BMNH 1902.5.15.28–30	3 (syn)	Colombia	Magdalena (MD)
<i>Ch. trimaculineum</i> n. sp. •	Lujan et al., this study	2015	MEPN 14688	6	Ecuador	Santiago (AD)
<i>Ch. vagum</i>	Fowler	1943	ANSP 70521	3	Colombia	Caquetá (AD)
<i>Ch. vasquezzi</i> •	Lasso and Provenzano	1998	MHNS 8791	57	Venezuela	Caura (OD)
<i>Ch. venezuelae</i>	Schultz	1944	NYZS 30064	—	Venezuela	San Juan (CC)
<i>Ch. yurubiense</i>	Ceas and Page	1996	INHS 34942	15	Venezuela	Yaracuy (CC)
<b><i>Cordylancistrus</i> Isbrücker, 1980</b>						
<i>Co. torbesensis</i> •	(Schultz)	1944	USNM 121001	173	Venezuela	Apure (OD)

**Table 1.** Continued.

Species	Author	Year	Holotype	Paratypes	Country	Drainage
<b><i>Dolichancistrus</i> Isbrücker, 1980</b>						
<i>D. atratoensis</i>	(Dahl)	1960	ICNMHN 51	42	Colombia	Atrato
<i>D. carnegiei</i> •	(Eigenmann)	1916	FMNH 58350	11	Colombia	Magdalena (MD)
<i>D. cobrensis</i>	(Schultz)	1944	USNM 121036	160	Venezuela	L. Maracaibo
<i>D. fuesslii</i> •	(Steindachner)	1911	NMW 48026	—	Colombia	Meta (OD)
<b><i>Leptoancistrus</i> Meek and Hildebrand, 1916</b>						
<i>L. canensis</i> •	(Meek and Hildebrand)	1913	FMNH 7581	44	Panama	Tuira (PC)
<i>L. cordobensis</i>	Dahl	1964	type missing	—	Colombia	Magdalena (MD)
<b><i>Transancistrus</i> Lujan, Meza-Vargas, and Barriga-Salazar, 2015</b>						
<i>T. aequinoctialis</i> •	(Pellegrin)	1909	MNH 1904–0017	—	Ecuador	Esmeraldas (PC)
<i>T. santarosensis</i> •	(Tan and Armbruster)	2012	MECN-DP 2061	5	Ecuador	Santa Rosa (PC)
<b><i>incertae sedis</i></b>						
<i>Co. daguae</i>	(Eigenmann)	1912	FMNH 56052	84	Colombia	Magdalena (MD)
<i>Co. perijae</i>	Pérez and Provenzano	1996	MBLUZ 4413	47	Venezuela	L. Maracaibo
<i>D. setosus</i>	(Boulenger)	1887	BMNH 1880.2.26.9–10	2 (syn)	Colombia	Cesar (MD)

**Sequence assembly, alignment, and phylogenetic inference.**

Sequence data were assembled, edited, aligned, and concatenated following the methods of Lujan et al. (2015a). Phylogenetic analysis of the concatenated alignment was conducted using both Bayesian inference (BI) and maximum likelihood (ML) methods with *Vandellia* sp. (Trichomycteridae) designated as the outgroup. A Bayesian Markov chain Monte Carlo search of tree space was conducted using MrBayes (v3.2.2; Ronquist and Huelsenbeck, 2003) on the CIPRES supercomputing cluster (Miller et al., 2010). MrBayes was programmed to run for 40 million generations using eight chains (nchains = 8; with default temperature parameter), sampling every 2666 trees with the first 30% of trees (4500) being discarded as burn-in. The Bayesian search was determined to have reached stationarity when cold chains randomly fluctuated within a stable range of posterior probabilities and when effective sample size for all metrics exceeded 200 as determined by the program Tracer (v1.6; Rambaut et al., 2007). Maximum likelihood analysis was conducted using RAxML (v8.0.0; Stamatakis, 2014) programmed to first conduct a 200 generation search for the best tree and then generate bootstrap support values based on a 2000 generation search of tree space.

**Scope of taxonomic research.**—This study is based largely on fresh material collected by the authors during expeditions to the Atlantic and Pacific slopes of the Andes mountains of Ecuador in 2012 and 2014 and to the Marañon (2006) and Madre de Dios (2010) river drainages of Peru. Our choice of species to formally redescribe is based largely on the material that we had at our disposal as a result of this field work and by our desire to avoid duplicating ongoing work by other researchers.

**Morphometrics and meristics.**—Morphometric and meristic data are presented in tables. Measurement landmarks follow Armbruster (2003); lateral trunk plate row terminology follows Schaefer (1997). Standard length (SL) is expressed in mm and other measurements are expressed as percentages of either standard length or head length. Measurements and counts were taken on the left side of specimens when possible. Institutional abbreviations follow Sabaj Pérez (2014).

**Sexual dimorphism.**—Urogenital pore morphologies differ between male and female *Chaetostoma*, with males having a more elongate and tubular genital pore (Fig. 1; Rapp Py-Daniel, 1991). These primary sexual differences were used to determine sex and to elucidate secondary sexual characteristics.

**Type specimens.**—We directly examined original types of *Chaetostoma alternifasciatum* Fowler, 1945 (ANSP 71711), *Ch. anale* (Fowler, 1941; holotype: ANSP 70525), *Ch. anomalum* Regan, 1903 (holotype: USNM 133135), *Ch. breve* Regan, 1904 (syntypes: BMNH 1898.11.4.33–36), *Ch. carrioni* (Norman, 1935; holotype: BMNH 1933.5.29.1), *Ch. changae* Salcedo, 2006a (holotype: ANSP 179125), *Ch. dermorhynchum* Boulenger, 1887 (syntypes: BMNH 1880.12.8.64–66), *Ch. microps* Günther, 1864 (syntypes: BMNH 1860.6.16.137–143), *Ch. milesi* Fowler, 1941 (holotype: ANSP 69330), *Ch. mollinasum* Pearson, 1937 (syntypes [8]: CAS 64653), *Ch. niveum* Fowler, 1944 (holotype: ANSP 71432), *Ch. patiae* Fowler, 1945 (holotype: ANSP 71716), *Ch. platyrhynchus* (Fowler, 1943; holotype: ANSP 70512), *Ch. sericeum* Cope, 1872 (holotype: ANSP 22005), *Ch. sovichthys* Schultz, 1944 (holotype: USNM 121053), *Ch. tachiraense* Schultz, 1944 (holotype: USNM 121052), and *Ch. vagum* Fowler, 1943 (holotype: ANSP 70521). We also directly examined live or recently collected topotypes (see non-type material listed below) of *Ch. breve* Regan, 1904, *Ch. carrioni* (Norman, 1935), *Ch. dermorhynchum* Boulenger, 1887, *Ch. jegui* Rapp Py-Daniel, 1991 (INPA 33840), and *Ch. microps* Günther, 1864. Original types of *Ch. guairense* Steindachner, 1881, *Ch. lepturum* Regan, 1912, *Ch. leucomelas* Eigenmann, 1918, *Ch. marginatum* Regan, 1904, *Ch. palmeri* Regan, 1912, and *Ch. paucispinis* Regan, 1912 were examined via high resolution digital images hosted by the All Catfish Species Project website.

**L-numbers.**—Several taxa examined in this study are undescribed genera or species that have previously been recognized as distinct by aquarium fish hobbyists and been assigned a standardized alphanumeric code (an L-number; Dignall, 2014) as a way of tracking them pending official description. Given the utility and generally standardized

**Table 2.** Loci sequenced, voucher catalog number, and country and river drainage of origin for the tissue samples analyzed in this study. Non-*Chaetostoma* Clade taxa were included in the analysis only as outgroups and were omitted from Figure 2.

Taxa	Tissue #	Topotype	16S	Cyt b	RAG1	RAG2	MyH6	Voucher cat. #	Country	Drainage
Loricariidae										
<i>Chaetostoma</i> Clade										
<i>Andeancistrus eschwartzae</i>	T14249		X	X	X	X	X	AUM 64664	Ecuador	Pastaza R.
<i>Andeancistrus platycephalus</i>	T14019	*	X	X	X	X	X	ROM 93847	Ecuador	Santiago R.
<i>Chaetostoma</i> aff. <i>lineopunctatum</i>	PE08-545		X	X	X	X	X	MHNG 2712.069	Peru	Huallaga R.
<i>Chaetostoma anomalum</i>	T631		X	X		X	X	INHS 55455	Venezuela	L. Maracaibo
<i>Chaetostoma bifurcum</i> n. sp.	T13602	*	X	X	X	X	X	ROM 93687	Ecuador	Esmeraldas R.
<i>Chaetostoma bifurcum</i> n. sp.	T13665		X	X	X	X	X	ROM 93721	Ecuador	Guayas R.
<i>Chaetostoma bifurcum</i> n. sp.	T13896		X	X	X	X	X	ROM 93787	Ecuador	Santa Rosa R.
<i>Chaetostoma breve</i>	PE08-648		X	X	X	X	X	MHNG 2712.074	Peru	Huallaga R.
<i>Chaetostoma breve</i>	P6292	*	X	X	X	X	X	AUM 46515	Peru	Marañon R.
<i>Chaetostoma breve</i>	T14360		X	X	X	X		ROM 93950	Ecuador	Napo R.
<i>Chaetostoma breve</i>	T14224		X	X				ROM 93923	Ecuador	Pastaza R.
<i>Chaetostoma carrioni</i>	T14016	*	X	X	X	X	X	ROM 93845	Ecuador	Santiago R.
<i>Chaetostoma</i> cf. <i>fischeri</i>	T9034		X	X	X	X	X	STRI 11581	Panama	Tuira R.
<i>Chaetostoma</i> cf. <i>loborhynchus</i>	CH204		X	X	X	X	X	MUSM 44889	Peru	Huallaga R.
<i>Chaetostoma changae</i>	PE08-543	*	X	X	X	X	X	MHNG 2712.067	Peru	Huallaga R.
<i>Chaetostoma daidalmatos</i>	PE08-347	*	X	X	X	X	X	MHNG 2712.055	Peru	Huallaga R.
<i>Chaetostoma dermorhynchum</i>	T14258		X	X	X	X	X	ROM 93656	Ecuador	Pastaza R.
<i>Chaetostoma dorsale</i>	T12929		X		X	X	X	ROM 94926	Colombia	Meta R.
<i>Chaetostoma fischeri</i>	T9036	*	X	X	X	X	X	STRI 12274	Panama	Bayano R.
<i>Chaetostoma fischeri</i>	T9026		X	X	X	X	X	STRI 7604	Panama	Chagres R.
<i>Chaetostoma guairense</i>	VZ122	*	X	X	X	X	X	INHS 34786	Venezuela	Limon R.
<i>Chaetostoma lexa</i>	PE08-591	*	X	X	X	X	X	MHNG 2712.071	Peru	Huallaga R.
<i>Chaetostoma lineopunctatum</i>	T10088		X	X	X	X	X	AUM 51166	Peru	Madre de Dios R.
<i>Chaetostoma lineopunctatum</i>	PE08-047	*	X	X	X	X	X	MHNG 2712.041	Peru	Ucayali R.
<i>Chaetostoma marmorescens</i>	CH198		X	X	X	X	X	MUSM unknown	Peru	Huallaga R.
<i>Chaetostoma microps</i>	PE08-190		X	X	X	X	X	MHNG 2712.046	Peru	Huallaga R.
<i>Chaetostoma microps</i>	P6034		X	X		X	X	AUM 45518	Peru	Marañon R.
<i>Chaetostoma microps</i>	T14364		X	X	X	X	X	ROM 93949	Ecuador	Napo R.
<i>Chaetostoma microps</i>	T14125	*	X	X	X	X	X	ROM 93895	Ecuador	Santiago R.
<i>Chaetostoma microps</i>	T14097		X	X	X		X	ROM 93877	Ecuador	Yungantza R.
<i>Chaetostoma</i> n. sp. L402	T621		X	X			X	INHS 56147	Venezuela	Apure R.
<i>Chaetostoma</i> n. sp. L402	T08955		X	X	X		X	AUM 54034	Venezuela	Apure R.
<i>Chaetostoma</i> n. sp. L445	T12930		X	X	X	X	X	ROM 94925	Colombia	Meta R.
<i>Chaetostoma</i> n. sp. Ucayali	PE08-121		X	X	X	X	X	MHNG 2712.042	Peru	Ucayali R.
<i>Chaetostoma</i> n. sp. Xingu	B1487		X	X	X	X	X	ANSP 199686	Brazil	Jaraçu R.
<i>Chaetostoma nudirostre</i>	T2084		X	X			X	ANSP 191471	Venezuela	L. Valencia
<i>Chaetostoma stroumpoulos</i>	PE08-307	*	X	X	X	X	X	MHNG 2712.056	Peru	Huallaga R.
<i>Chaetostoma trimaculineum</i> n. sp.	P6047		X	X	X	X	X	AUM 45524	Peru	Marañon R.
<i>Chaetostoma trimaculineum</i> n. sp.	T14136		X	X	X	X	X	ROM 93894	Ecuador	Santiago R.
<i>Chaetostoma vasquezi</i>	V27		X	X	X	X	X	AUM 36555	Venezuela	Caroni R.

Table 2. Continued.

Taxa	Tissue #	Topotype	16S	Cyt <i>b</i>	RAG1	RAG2	MyH6	Voucher cat. #	Country	Drainage
<i>Chaetostoma vasquezi</i>	T09945	*	X	X	X	X	X	AUM 53812	Venezuela	Caura R.
<i>Cordylancistrus torbesensis</i>	T674	*	X		X	X	X	INHS 55478	Venezuela	Torbes R.
<i>Dolichancistrus carnegiei</i>	6647		X	X	X	X	X	ANSP 189598	Colombia	Magdalena R.
<i>Dolichancistrus fuesslii</i>	T14621	*	X	X	X	X	X	ROM 94484	Colombia	Guaviare R.
<i>Leptoancistrus canensis</i>	T9033	*	X	X	X	X	X	STRI 11580	Panama	Tuira R.
<i>Leptoancistrus cf. canensis</i>	T9031		X	X	X	X	X	STRI AM-55	Panama	Cocle del Norte R.
<i>Leptoancistrus cf. canensis</i>	T9029		X	X	X	X		STRI 11050	Panama	Cocle del Sur R.
<i>Leptoancistrus cf. canensis</i>	T9039		X	X	X	X		STRI 6058	Panama	Indio R.
<i>Transancistrus aequinoctialis</i>	T13525		X	X	X	X	X	ROM 93661	Ecuador	Esmeraldas R.
<i>Transancistrus santarosensis</i>	T13980	*	X	X	X	X	X	ROM 93798	Ecuador	Santa Rosa R.
Ancistrini										
<i>Ancistrus leucostictus</i>	T08143		X	X	X	X		ROM 88561	Guyana	Essequibo R.
<i>Ancistrus ranunculus</i>	B1500	*	X	X	X	X	X	ANSP 199525	Brazil	Xingu R.
<i>Ancistrus clementinae</i>	T13829	*	X	X	X	X	X	ROM 93737	Ecuador	Guayas R.
<i>Lasiancistrus schomburgkii</i>	P6125		X	X	X	X	X	AUM 45548	Peru	Marañon R.
<i>Lasiancistrus tentaculatus</i>	T09686		X	X	X	X	X	AUM 53895	Venezuela	Ventuari R.
<i>Pseudolithoxus kelsorum</i>	T09895	*	X	X	X	X	X	AUM 51644	Venezuela	Orinoco R.
<i>Pseudolithoxus stearleyi</i>	V5533	*	X	X	X	X	X	AUM 43872	Venezuela	Soromoni R.
<i>Corymbophanes kaiei</i>	T12637		X	X	X	X	X	ROM 89856	Guyana	Potaro R.
<i>Hoplancistrus tricornis</i>	T9017		X	X	X	X	X	AUM 39853	Brazil	aquarium trade
<i>Guyanancistrus brevispinis</i>	86.1	*	X	X	X	X	X	MHNG 2725.099	French Guiana	Maroni R.
<i>Dekeyseria scaphirhyncha</i>	T09540		X	X	X	X	X	AUM 54309	Venezuela	Ventuari R.
<i>Neblichthys brevibrachium</i>	T06068	*	X	X	X	X	X	ROM 83692	Guyana	Mazaruni R.
<i>Paulasquama callis</i>	T06189	*	X	X	X	X	X	ROM 83784	Guyana	Mazaruni R.
Peckoltia Clade										
<i>Panaqolus nocturnus</i>	P6126	*	X	X	X	X	X	AUM 45500	Peru	Marañon R.
<i>Peckoltia furcata</i>	P6200		X	X	X	X	X	AUM 45593	Peru	Marañon R.
<i>Hypancistrus debilitera</i>	T09279	*	X	X	X	X	X	AUM 53528	Venezuela	Orinoco R.
<i>Aphanotorulus squalinus</i>	T09528		X	X	X	X	X	AUM 54305	Venezuela	Ventuari R.
Hypostomini										
<i>Cochliodon macushi</i>	T07038	*	X	X	X	X	X	ROM 85939	Guyana	Essequibo R.
<i>Hypostomus niceforoi</i>	T10282		X	X	X	X	X	AUM 51404	Peru	Madre de Dios R.
Hemiancistrus Clade										
<i>'Baryancistrus' beggini</i>	T09392	*	X	X	X	X	X	AUM 54990	Venezuela	Orinoco R.
<i>'Baryancistrus' demantoides</i>	T09361	*	X	X	X	X	X	ROM 93339	Venezuela	Ventuari R.
<i>Hemiancistrus medians</i>	6948	*	X	X	X	X	X	ANSP 187122	Suriname	Maroni R.
<i>Panaque nigrolineatus</i>	T09018	*	X	X	X	X	X	AUM 53764	Venezuela	Apure R.
Acanthicus Clade										
<i>Acanthicus adonis</i>	T9001		X	X	X	X	X	AUM 44605		aquarium trade
Lithoxus Clade										
<i>Exastilithoxus fimbriatus</i>	V049	*	X	X	X	X	X	AUM 36632	Venezuela	Caroni R.
<i>incertae sedis</i>										
<i>Pseudancistrus genisetiger</i>	86.2		X	X	X	X	X	MHNG 2593.061	Brazil	São Francisco R.

Table 2. Continued.

Taxa	Tissue #	Topotype	16S	Cyt b	RAG1	RAG2	MYH6	Voucher cat. #	Country	Drainage
Callichthyidae										
Corydoradinae										
<i>Corydoras aeneus</i>	T12836		X	X	X	X		ROM 90346	Bolivia	Mamoré R.
<i>Corydoras panda</i>	T12932		X	X	X	X		ROM 94924		
<i>Corydoras stenocephalus</i>	T12839		X	X	X	X	X	ROM 90345	Bolivia	Mamoré R.
Callichthyinae										
<i>Callichthys callichthys</i>	T10404		X	X		X		MUSM unknown	Peru	Huallaga R.
Trichomycteridae										
<i>Vandellia</i> sp.	V5509		X		X		X	AUM 43867	Venezuela	Orinoco R.

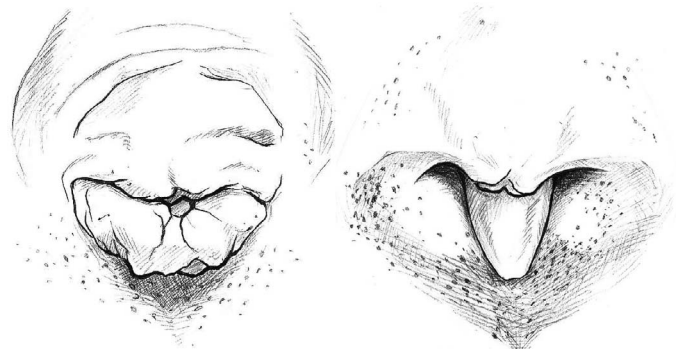


Fig. 1. Illustrations of representative female (left) and male (right) urogenital pores of *Chaetostoma*. Illustrations by VAC.

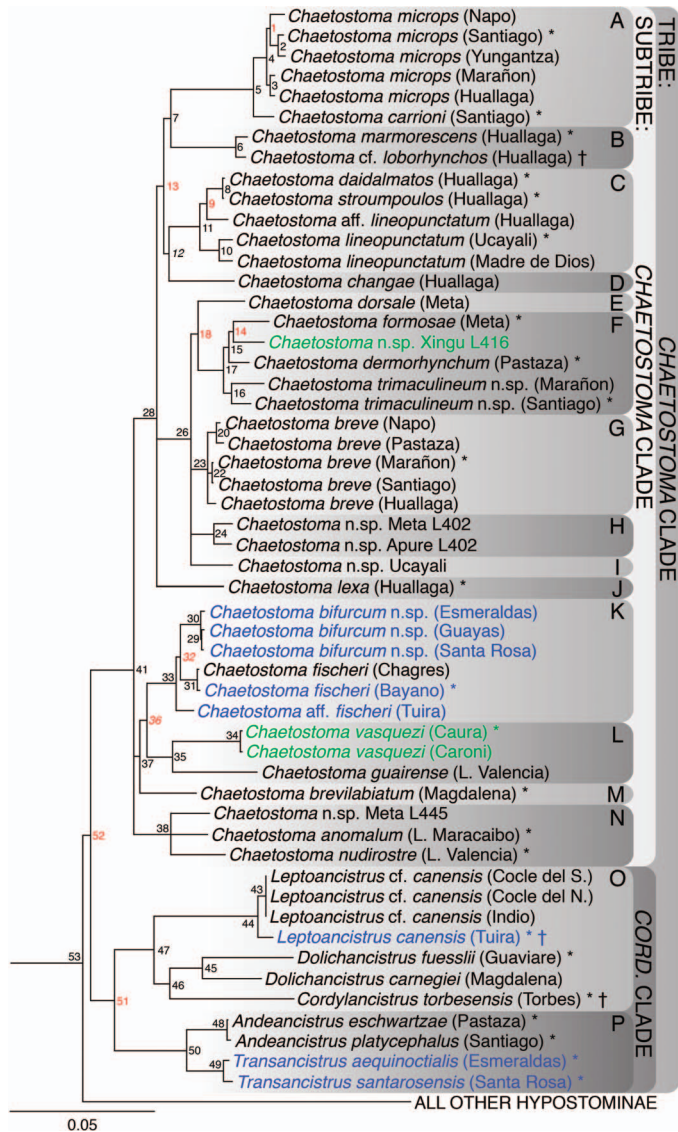
application of these codes, we have adopted them throughout this study.

**Taxonomic diagnoses.**—Due to the broad geographic range and high species richness of *Chaetostoma* and the paucity of institutionally curated specimens from many parts of its range, a comprehensive taxonomic revision of the genus is not currently possible. We therefore restrict our taxonomic diagnoses to valid congeners described from arbitrarily defined geographic regions. For *Ch. bifurcum*, new species, we restrict our diagnosis to the eight *Chaetostoma* currently described from the Pacific Coast of South America. For *Ch. carrioni*, *Ch. breve*, *Ch. dermorhynchum*, *Ch. microps*, and *Ch. trimaculineum*, new species—all species with type localities in Atlantic Slope headwaters of the Amazon Basin within Ecuador—we restrict our diagnoses to all 17 naked-snouted *Chaetostoma* currently recognized as valid from the Amazon Basin. For ease of reference, we present the diagnoses of Amazon Basin species in both a text and tabular format. *Chaetostoma platyrhynchus*, the only Amazon Basin species excluded from our diagnoses, is easily distinguished from all other *Chaetostoma* by having a fully plated snout and will therefore not be considered further herein.

**Color descriptions.**—To the extent possible, we focus on descriptions and images of live specimens—information that has been scarce in the recent literature on this group. As with most fish, coloration of *Chaetostoma* changes dramatically after preservation, including the frequent loss of most or all color and color pattern on the body. Fin color patterns are usually more resistant to the fading effects of long-term preservation. Illustrations and photographs of preserved specimens of most of the species in this paper can be found in the original descriptions and/or online repositories of type images (e.g., the All Catfish Species Inventory Image Base: <http://acsi.acnatsci.org/base/>).

## RESULTS

**Phylogeny.**—With the addition of more species and populations of *Andeancistrus*, *Chaetostoma*, *Cordylancistrus*, *Dolichancistrus*, *Leptoancistrus*, and *Transancistrus* (Fig. 2; vs. Lujan et al., 2015a), statistical support for the sister relationship between *Chaetostoma* and the *Cordylancistrus* Clade (Clade OP) changed little (Table 3, Node 52: BI: 0.70, ML: 53; vs. BI: 0.66, ML: 64), support for monophyly of



**Fig. 2.** Phylogenetic relationships within the *Chaetostoma* Clade (*sensu* Lujan et al., 2015) based on Bayesian analysis of a 4293 base pair alignment consisting of two mitochondrial (16S, Cyt *b*) and three nuclear loci (RAG1, RAG2, MyH6). Taxa from Pacific Coast drainages in blue and Brazilian or Guiana Shield drainages in green. Node numbers correspond to Bayesian posterior probability (BI) and maximum likelihood (ML) support values in Table 3. Numbers in red indicate BI: <90; numbers in italics indicate ML: <50. Samples taken from at or near the type locality for a given species are indicated by asterisks and species that are types for the given genus are indicated

*Chaetostoma* remained strong (Node 41: BI: 1.0, ML: 99; vs. BI: 1.0, ML: 100), and support for monophyly of *Cordylancistrus* Clade genera declined slightly (Node 51; BI: 0.80, ML: 60; vs. BI: 0.87, ML: 72).

Basal relationships within *Chaetostoma* consisted of a trichotomy between the geographically widespread Clade A–J, the northwestern South American Clade N, and the northern South American/Panamanian Clade KLM (Node 41). Clade N also consisted of a strongly monophyletic trichotomy (Node 38: BI: 1.0, ML: 100), in this case between an undescribed species from the upper Meta River drainage in Colombia (*Ch. n. sp.* Meta L445), and respective species from the Lake Maracaibo (*Ch. anomalum*) and Lake Valencia (*Ch. nudirostre*) drainages in western and northern Venezuela. Clade KLM consisted of species distributed from

central Panama (*Ch. fischeri*) in the northwest to the Pacific Coast of southern Ecuador (*Ch. bifurcum*, new species) in the southwest and the Caroni River drainage (*Ch. vasquezzi*) of eastern Venezuela in the east. Within Clade KLM, *Ch. breviliabiatum* (Clade M) from the Magdalena River drainage in Colombia was moderately supported as sister to all other species (Node 37: BI: 0.97, ML: 61). The remaining clades K and L were moderately supported as sister (Node 36: BI: 0.89, ML: 46), with each clade being strongly well supported as monophyletic (Nodes 33 and 35: BI: 1.0, ML: 100).

Clade K was the only *Chaetostoma* clade that contained species from either Central America or the Pacific Coast of South America, and it appears to be entirely restricted to this marginal zone. Within Clade K, the apparently undescribed southeastern Panamanian species *Ch. aff. fischeri* (from the Tuira River) was found to be sister (Node 33) to a weakly supported clade containing species distributed to both the northwest (*Ch. fischeri*) and southwest (*Ch. bifurcum*, new species; Node 32: BI: 0.68, ML: –). Specimens of *Ch. bifurcum*, new species, from across the entire Pacific Coast of Ecuador were strongly monophyletic (Node 30: BI: 1.0, ML: 100) and showed little sequence divergence (i.e., short branch lengths). However, the two more southerly populations from the Guayas and Santa Rosa drainages were more closely related to each other than either were to populations in the Esmeraldas River drainage to the north (Node 29: BI: 0.97, ML: 75).

In contrast to *Chaetostoma* clades K, L, M, and N, Clade A–J comprised species that are broadly distributed across headwaters of the Amazon and Orinoco, from the Meta and Apure river drainages in the north to the Madre de Dios River drainage in the south and the Xingu River in the east. Basal relationships within Clade A–J consisted of a trichotomy (Node 28: BI: 1.0, ML: 100) including *Ch. lexa* (Clade J), a weakly supported Clade A–D (Node 13: BI: 0.56, ML: 57), and a strongly supported Clade E–I (Node 26: BI: 1.0, ML: 99). Of these, Clade J (*Ch. lexa*) was the most geographically restricted, being known only from the upper Huallaga River drainage in central Peru (Salcedo, 2013). Clade A–D comprised species from mostly southwestern headwaters of the Amazon Basin, bounded by the Napo River in the north (*Ch. microps*) to the Madre de Dios River drainage (*Ch. lineopunctatum*)—the southernmost limit to the range of *Chaetostoma*.

Within Clade A–D, Clade A (Node 5: BI: 1.0, ML: 100) comprised the widely distributed and strongly monophyletic species *Ch. microps* (Node 4: BI: 1.0, ML: 89) and its sister species *Ch. carrioni*, which is narrowly endemic to the Santiago River drainage in southeastern Ecuador. Clade A was well supported as sister to Clade B (Node 7: BI: 91, ML: 70), which comprised the Huallaga River sister species *Ch. marmorescens* and *Ch. cf. lobarhynchos* (Node 6: BI: 1.0, ML: 100). The strongly supported Clade C (Node 11: BI: 1.0, ML: 100) comprised species having rows of longitudinal spots along the body, including the Huallaga River sister species *Ch. daidalmatos* and *Ch. stroumpoulos* (Node 8: BI: 1.0, ML: 100), and *Ch. lineopunctatum* from the Ucayali and Madre de Dios rivers (Node 10: BI: 1.0, ML: 100). A possibly new species (*Ch. aff. lineopunctatum*) from the Huallaga River was found to be more closely related to *Ch. daidalmatos* and *Ch. stroumpoulos* than to *Ch. lineopunctatum sensu stricto* (Node 9: BI: 0.81, ML: 94; see *Other undescribed species* below). The Huallaga River species *Ch. changae* (Clade D) was ambiguously supported as sister to Clade C (Node 12: BI: 0.97, ML: 49).



**Table 3.** Support values for each of the nodes in Figure 2, derived from Bayesian inference (BI) and maximum likelihood (ML) optimality criteria. Support values in bold indicate BI: <0.90 or ML: <50.

Node	BI	ML	Clade	Node	BI	ML	Clade	Node	BI	ML	Clade
1	<b>0.84</b>	66	<i>Ch. microps</i> Santiago + Yungantza	19	—	<b>13</b>	<i>Ch. breve</i> Napo + Pastaza	37	0.97	61	<i>Ch. brevilabiatum</i> + (Clades K + L)
2	1.00	100	<i>Ch. microps</i> Marañon + Huallaga	20	1.00	99		38	1.00	100	Clade N
3	0.91	50		21	—	<b>43</b>	<i>Ch. breve</i> Marañon + Santiago	39	—	<b>43</b>	<i>Ch. anomalum</i> + <i>Ch. n. sp.</i> L445
4	1.00	89	<i>Chaetostoma microps</i> <i>Ch. carrioni</i> + <i>Ch. microps</i>	22	1.00	100	<i>Chaetostoma breve</i> <i>Chaetostoma n. sp.</i>	40	—	<b>46</b>	Clade N + Clade A–J
5	1.00	100	<i>Ch. marmorescens</i> + <i>Ch. cf. lobo</i>	23	1.00	100	L402	41	1.00	99	<i>Chaetostoma</i>
6	1.00	100		24	1.00	94		42	—	62	<i>L. cf. canensis</i> Cocle <i>L. cf. canensis</i> (North/Caribbean)
7	0.91	70	Clade A + B <i>Ch. daidalmatos</i> + <i>Ch. stroump</i>	25	—	<b>13</b>		43	1.00	100	
8	1.00	100		26	1.00	99	Clade E–I	44	1.00	100	<i>Leptoancistrus</i>
9	<b>0.81</b>	94	<i>Ch. lineopunctatum</i>	27	—	<b>33</b>	<i>Ch. lexa</i> + Clade A–D widespread	45	1.00	100	<i>Dolichancistrus</i> <i>Co. torbesensis</i> + <i>Dolichancistrus</i>
10	1.00	100	Ucayali + MdD	28	1.00	100	<i>Chaetostoma</i> clade <i>Ch. marginatum</i>	46	0.98	81	
11	1.00	100	Clade C	29	0.97	75	Guay. + Sta. Ros.	47	1.00	100	Clade O ' <i>Co.</i> ' <i>platycephalus</i> + ' <i>Co.</i> ' n. sp.
12	0.97	<b>49</b>	<i>Ch. changae</i> + Clade C	30	1.00	100	<i>Ch. marginatum</i>	48	1.00	100	' <i>Co.</i> ' <i>aequinoctialis</i> + ' <i>Co.</i> ' <i>santoros</i>
13	<b>0.56</b>	57	Clades A, B, C, D <i>Ch. formosae</i> + <i>Ch. n. sp.</i> Xingu	31	1.00	100	Chagres <i>Ch. marginatum</i> + <i>Ch. fischeri</i>	49	1.00	100	all ' <i>Cordylancistrus</i> ' of Ecuador
14	<b>0.79</b>	53		32	<b>0.68</b>	—		50	1.00	100	Subtribe: <i>Cordylancistrus</i>
15	0.99	71	<i>Ch. n. sp.</i> Marañon + Santiago	33	1.00	100	Clade K <i>Ch. vasquezi</i> Caura + Caroni	51	<b>0.80</b>	60	Clade Tribe: <i>Chaetostoma</i>
16	1.00	98		34	1.00	100	<i>Ch. guairense</i> + <i>Ch. vasquezi</i>	52	<b>0.70</b>	53	Clade
17	1.00	96	Clade F	35	1.00	100		53	0.98	50	Hypostominae
18	0.60	—	<i>Ch. dorsale</i> + Clade F	36	0.89	46	Clade K + L				

Clade E–I (Node 26) comprised species distributed across almost the entire Atlantic Slope range of the genus *Chaetostoma*, from the Meta and Apure rivers in the north to the Huallaga River in the south and the Xingu River in the east. Basal relationships within this clade consist of a four-way polytomy between an undescribed species from the Ucayali River drainage (Clade I), an undescribed and strongly monophyletic species from the Meta and Apure river drainages (L402, Clade H, Node 24: BI: 1.0, ML: 94), the geographically widespread and strongly monophyletic species *Ch. breve* (Clade G, Node 23: BI: 1.0, ML: 100), and the weakly supported Clade EF (Node 18: BI: 0.60, ML: –). Clade E comprised only *Ch. dorsale* from the upper Meta River drainage in central Colombia. Clade F was found to be strongly monophyletic (Node 17: BI: 1.0, ML: 96) and contained species from the upper Meta River drainage (*Ch. formosae*), the Pastaza River drainage (*Ch. dermorrhynchum*), an undescribed species (L416) from the Xingu River drainage in Brazil, and a new species from the Marañon and Santiago river drainages of southern Ecuador and northern Peru (described herein as *Ch. trimaculineum*, new species). The first three of these species comprise a previously morphologically defined subclade within

*Chaetostoma* called the *Ch. anale* species group (Ballen, 2011); molecular data supported their monophyly (Node 15: BI: 0.99, ML: 71) and their sister relationship to *Ch. trimaculineum*, new species.

Monophyly of the *Cordylancistrus* Clade (Clade OP) was moderately supported (Node 51: BI: 0.80, ML: 60). This clade comprised the respectively strongly supported clades O and P (Nodes 47 and 50: BI: 1.0, ML: 100). Clade O comprised three genera (*Cordylancistrus*, *Dolichancistrus*, and *Leptoancistrus*) distributed from northwestern Panama to western headwaters of the Orinoco River in central Colombia and western Venezuela. The entirely Panamanian and northwestern Colombian genus *Leptoancistrus* was found to be strongly monophyletic (Node 44: BI: 1.0, ML: 100) and to comprise the type species, *L. canensis* (from the Tuira River drainage in southeastern Panama), plus a likely undescribed species, *L. cf. canensis* (from the Cocle and Indio rivers in northwestern Panama; Node 43: BI: 1.0, ML: 100). *Leptoancistrus* was sister (Node 47) to a strongly supported clade (Node 46: BI: 0.98, ML: 81) comprising two species of *Dolichancistrus* (Node 45: BI: 1.0, ML: 100) and *Cordylancistrus torbesensis* (type species of *Cordylancistrus*). This latter clade spans the Cordillera Central of the northern Andes Mountains, being present in the



**Fig. 3.** *Chaetostoma dermorhynchum* from the Pastaza River drainage, Ecuador: (A) immature male (type locality; ROM 93946, 84.4 mm SL) and (B) adult male (ROM 93656\*, 171.7 cm SL). Scale bars = 1 cm. Photos by NKL.

Magdalena River drainage (*Dolichancistrus carnegiei*) and two left-bank (western) tributaries of the Orinoco River: the upper Apure River drainage in southwestern Venezuela (*Cordylancistrus torbesensis*), and the upper Guaviare River drainage in central Colombia (*D. fuesslii*). Clade P comprised two recently described genera (Lujan et al., 2015b) from opposite sides of the Andes Mountains in Ecuador. The Pacific Coastal genus *Transancistrus* was strongly monophyletic (Node 49: BI: 1.0, ML: 100) and sister (Node 50: BI: 1.0, ML: 100) to the Atlantic Slope genus *Andeancistrus*, which was also strongly monophyletic (Node 48: BI: 1.0, ML: 100).

**Biogeography.**—An explicit, quantitative biogeographical analysis of the *Chaetostoma* Clade is beyond the scope of this paper and will be provided elsewhere. However, two broad biogeographical trends can be inferred from the phylogeny (Fig. 2). The first is suggestive of a northwestern South American origin for the clade as a whole, with several depauperate sister lineages that branch from basal nodes being restricted to this region (e.g., clades K, L, M, and O) and more species-rich and broadly distributed clades being generally more deeply nested (e.g., clades A, B, C, D, G, J). The second trend, within the broadly distributed *Chaetostoma* Clade A–J, is suggestive of a secondary point of origin in the Huallaga River drainage of central Peru, with this drainage being represented in six of the ten lettered subclades A–J. Moreover, despite the poor resolution at several points in this clade, it is clear that several depauperate lineages restricted to the Huallaga (e.g., clades B, D, J) are closely related to more geographically widespread clades (e.g., A, C, E, F, G, H).

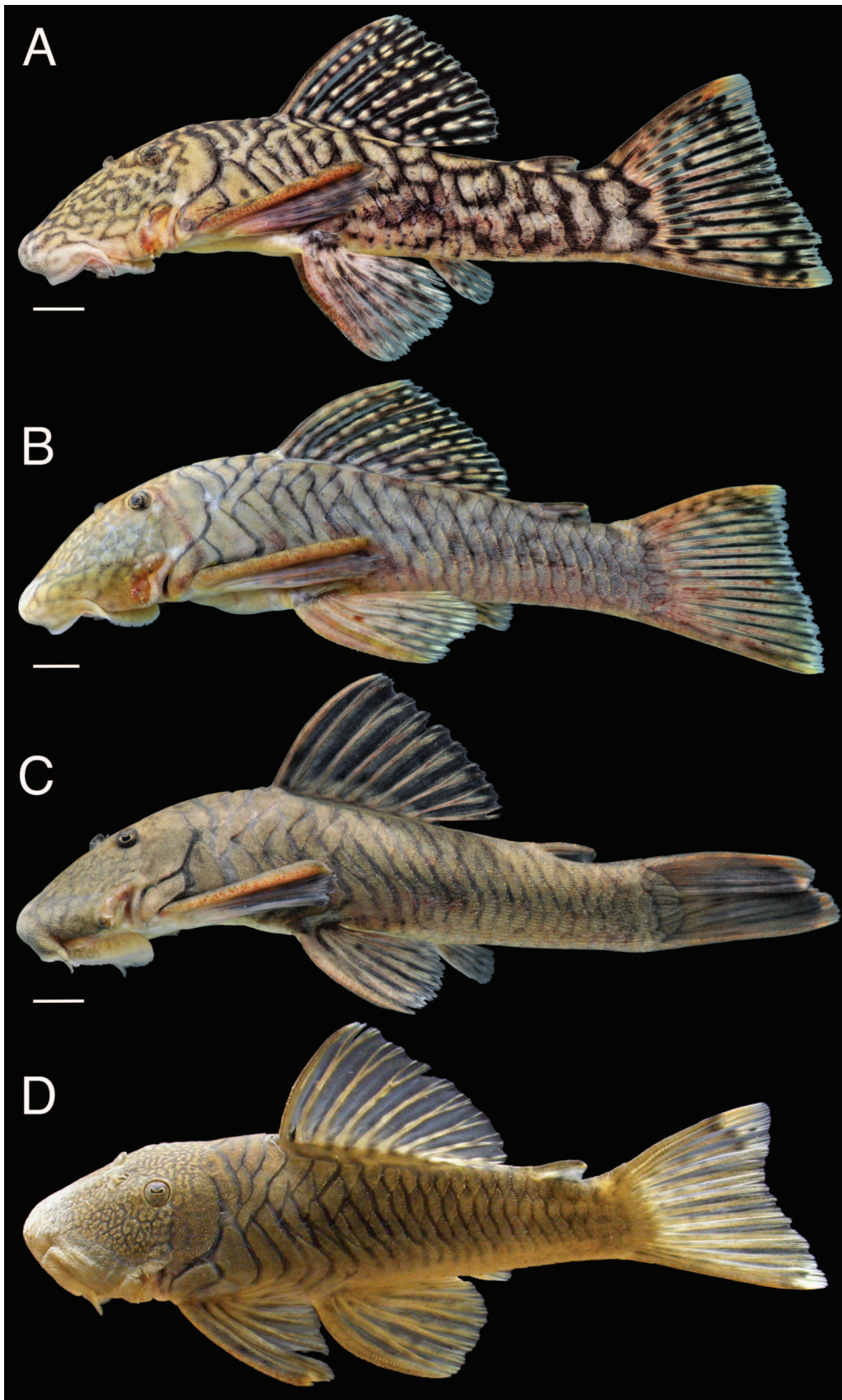
**Sexual dimorphism.**—Unlike many other loricariids (Rapp Py-Daniel and Cox Fernandes, 2005), members of the genus *Chaetostoma* generally do not display extensive hypertrophy or elongation of odontodes when sexually mature. Instead, males of many species develop a more enlarged and fleshy unplated anterior snout region, an elongation of various fin regions, sometimes accompanied by longitudinal dermal folds along the dorsal or lateral ridges of fin rays (e.g., *Ch.*

*dermorhynchum*, Fig. 3, immature male [A] versus mature male [B]). The coloration of some species can also change, with base colors becoming more intensified and pattern contrasts either increasing (e.g., *Ch. breve*, Fig. 4A) or decreasing (e.g., *Ch. dermorhynchum*, Fig. 3B).

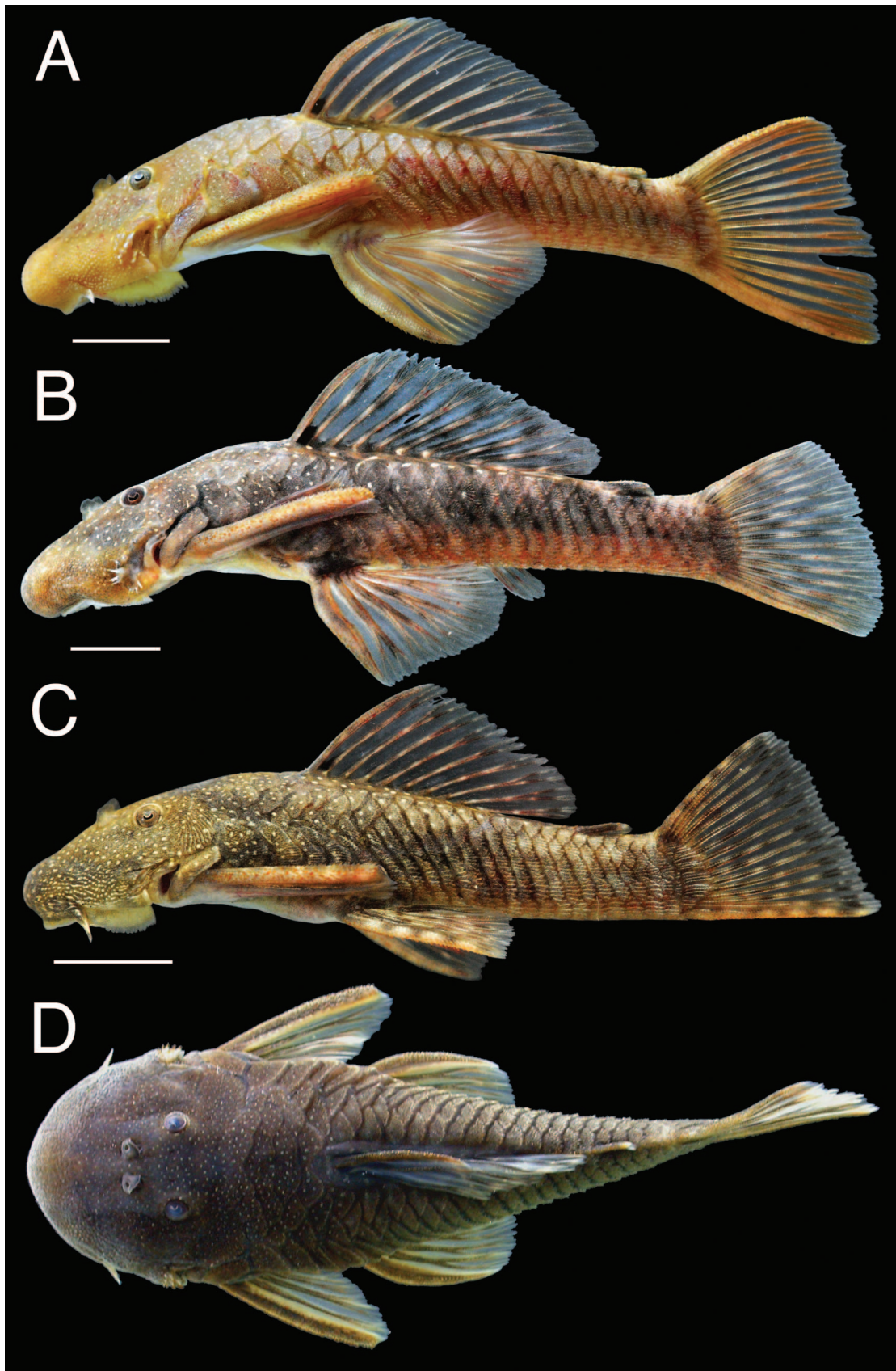
We recognized four distinct types of sexual dimorphism related to fin morphology in *Chaetostoma*, each of which is illustrated either alone or in combination by species described herein: Type 1 fin modifications involve the elongation of proximal, branched pelvic-fin rays so that the proximomedial posterior margin of the pelvic fin is elongated into a lobe (e.g., *Ch. dermorhynchum*, Fig. 3; *Chaetostoma microps*, Fig. 5, male [A and B] vs. female [C and D]). Type 2 modifications involve the development of a dermal fold or flap along the proximal posterodorsal margin of the unbranched pelvic-fin ray, with this fold being deeper than all other skin folds on branched rays (if present) and being adnate to the body at the pelvic-fin insertion (e.g., *Ch. dermorhynchum*, Fig. 3). Type 3 modifications involve the development of low dermal folds along the length of branched fin rays (e.g., *Ch. dermorhynchum*, Fig. 3B). These dermal folds can develop on the dorsal surfaces of pelvic-fin rays and on the lateral or posterior surface of anal-fin rays, but have not been observed on rays of either the pectoral, dorsal, or caudal fin. Type 4 fin modifications involve the elongation of outer, unbranched rays of the pelvic and/or anal fins into short filaments, typically accompanied by the overall enlargement of the anal fin (e.g., *Ch. dermorhynchum*, Fig. 3B).

**Cheek odontode shape and size.**—*Chaetostoma* exhibit a range of taxonomically important cheek odontode morphologies (Ballen, 2011; Salcedo, 2013). To facilitate diagnoses, we categorize this variation into four distinct types (Fig. 6): Type 1 cheek odontodes are thin, short, and straight; Type 2 cheek odontodes are thin, more elongate, and slightly hooked; Type 3 odontodes are relatively short, thick, and strongly hooked; and Type 4 cheek odontodes are more elongate than all others and moderately hooked.

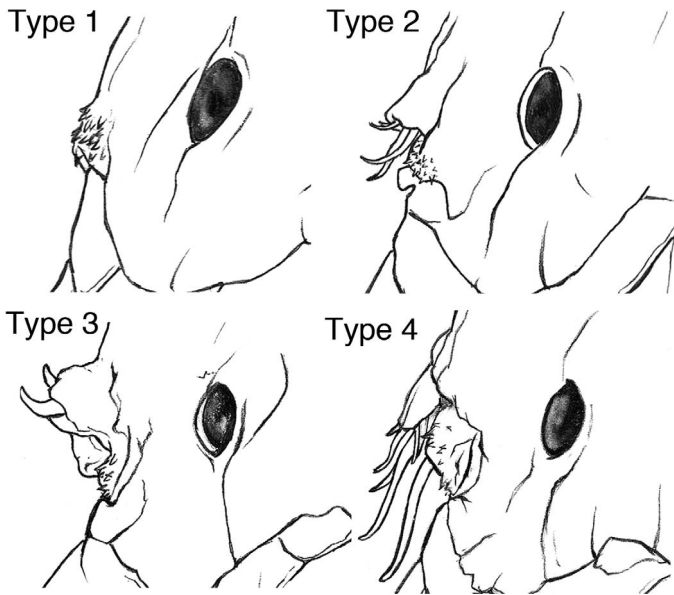
**Taxonomic changes.**—Based on our direct and photographic examination of type material, we transfer the following three species from *Chaetostoma* to the genus *Ancistrus*: *Chaetostoma greeni* Isbrücker et al., 2001 (replacement name for *Chaetostomus maculatus* Regan, 1904) is recognized as *Ancistrus greeni*, new combination; *Chaetostomus marcapatae* Regan, 1904 is recognized as *Ancistrus marcapatae*, new combination; and *Chaetostomus sericeus* Cope, 1872 is recognized as *Ancistrus sericeus*, new combination. The type specimens of each of these species have unplated snout margins, but only three plate rows at the thinnest part of the caudal peduncle and seven branched dorsal-fin rays, confirming their proper placement in the genus *Ancistrus*. *Chaetostomus trinitatis* Günther, 1864, described from the island of Trinidad, is a fourth species that we believe should be transferred to *Ancistrus*, based in part on its original description stating that it only has seven branched dorsal-fin rays. Unfortunately, the whereabouts of the syntypes of *Chaetostomus trinitatis* are unknown. Further justification for this transferral is derived from the absence of any vouchered record of a *Chaetostoma* ever having been collected in Trinidad, and the modern occurrence of only a single species of ancistrine loricariid on this island: a species currently referred to as *Ancistrus maracasae* (Phillip et al., 2013). We



**Fig. 4.** *Chaetostoma breve* from various drainages along the Atlantic Slope of the Andes: the (A, B) Napo (Ecuador: ROM 93950\*, A: 117.4 mm, B: 137.1 mm SL), (C) Santiago (Ecuador: type locality; ROM 93848, 127.2 mm SL), and (D) Marañon (Peru: AUM 46515\*, 91.5 mm SL) river drainages. Scale bars = 1 cm. Photos by NKL.



**Fig. 5.** *Chaetostoma microps* from various Atlantic Slope drainages of the Andes: the (A) Napo (Ecuador, ROM 93948, 72.3 mm SL), (B, C) Santiago (Ecuador, type locality; B: ROM 93902, 74.5 mm SL, C: ROM 93895\*, 56.2 mm SL), and (D) Marañon (Peru, AUM 45525) river drainages. Scale bars = 1 cm. Photos by NKL.



**Fig. 6.** Illustrations of four odontode shape and size types observed across species of *Chaetostoma*. Illustrations by VAC.

therefore recognize *Chaetostomus trinitatis* Günther, 1864 as *Ancistrus trinitatis*, new combination, and agree with Phillip et al. (2013) that this species is likely a synonym of *Ancistrus maracasae* Fowler, 1946.

Within *Chaetostoma*, we consider *Ch. alternifasciatum* Fowler, 1945 to be a junior synonym of *Ch. vagum* Fowler, 1943 based on a lack of characteristics differentiating the type specimens and on their overlapping distribution in the upper Japurá River (Caquetá River drainage), Colombia. We believe that the holotype of *Ch. alternifasciatum* (143.0 mm SL) is an adult, and that of *Ch. vagum* (85.8 mm SL) is a juvenile, of the same species. We also consider *Ch. mollinasum* Pearson, 1937, from the upper Marañón River drainage in Peru, to be a synonym of *Ch. microps* Günther, 1864, from the Santiago River drainage in Ecuador, based on a review of type and non-type specimens spanning the geographic range between both type localities. Specimens of *Ch. microps* spanning this geographic range are not only morphologically similar, but also monophyletic in our molecular phylogenetic analysis (Fig. 2, Node 4: BI: 1.0, ML: 89). A summary of species that we consider valid within the *Chaetostoma* Clade is provided in Table 1.

Finally, given the strong molecular phylogenetic evidence for the nested position of *Lipopterygion carrioni* Norman, 1935 and *Loraxichthys lexa* Salcedo, 2013 within *Chaetostoma*, and the overall morphological similarity of these species to other species of *Chaetostoma*, we transfer these species to genus *Chaetostoma*: *Chaetostoma carrioni*, new combination; and *Chaetostoma lexa*, new combination.

***Chaetostoma branickii* and *Ch. taczanowskii*.**—Specimens correctly identified as either *Chaetostoma branickii* or *Ch. taczanowskii* are rare in collections, and the two species are challenging or impossible to distinguish based only on original descriptions and the limited availability of type or non-type material. Both species share a relatively tall and slender body, Type 1 cheek odontodes, eight branched dorsal-fin rays, absence of a supraoccipital excrescence and absence of any detectable color pattern or sexual dimorphism (Table 4). Both species were described by Steindachner in sequential years (*Ch. branickii*

in 1881 and *Ch. taczanowskii* in 1882) from neighboring drainages (Marañón and Huallaga, respectively). For this study, we had only two lots tentatively identified as *Ch. branickii* (ROM 54720, ROM 54723) and no tissue available for genetic analysis. We therefore had little basis from which to draw conclusions regarding differences between these species and refer to them in diagnoses as the undifferentiated species pair *Ch. branickii/taczanowskii*. The information we have for these species applies, to the best of our knowledge, to both. More specimens, data, and redescrptions of these species are needed in order to clearly diagnose them from each other and other species.

***Chaetostoma lobarhynchos* and *Ch. marmorescens*.**—Differentiating the sister species *Chaetostoma lobarhynchos* from *Ch. marmorescens* can also be a source of confusion. Both share Type 1 cheek odontodes, marbled light and dark green to gray coloration on the body, indistinct banding of the dorsal- and paired-fin rays with all fin membranes being hyaline, absence of a supraoccipital excrescence, and Type 1 and 2 sexual dimorphism of the pelvic fins. Moreover they were described from neighboring drainages (*Ch. lobarhynchos* from the upper Ucayali River, and *Ch. marmorescens* from the upper Huallaga River), but appear to have at least partially overlapping ranges within the Huallaga River drainage. In addition to the meristic differences listed in Table 4 (e.g., non-overlapping ranges of premaxillary and dentary teeth, differing numbers of branched anal- and dorsal-fin rays), we found that *Ch. lobarhynchos* can be distinguished morphometrically from *Ch. marmorescens* by having a smaller orbit diameter ( $3.1 \pm 0.4\%$  SL, vs.  $4.5 \pm 0.4$ ), a greater snout length ( $22.0 \pm 1.0\%$  SL, vs.  $19.4 \pm 1.4$ ), and greater pelvic-dorsal distance ( $22.2 \pm 1.4\%$  SL, vs.  $20.1 \pm 0.7$ ). See also *Other undescribed species* below for a description of interdrainage morphological variation observed in *Ch. lobarhynchos*.

#### ***Chaetostoma bifurcum*, new species**

urn:lsid:zoobank.org:act:9349BF35-726C-43EA-AE4D-C4708BBAAA78

Figure 7; Tables 5, 6

**Holotype.**—MEPN 14687 (ex. ROM 93721\*), 132.4 mm SL, Ecuador, Santo Domingo de las Tsáchilas Province, Guayas River drainage, Otongo River upstream of confluence with Baba River,  $00^{\circ}21'06.90''S$ ,  $79^{\circ}12'52.32''W$ , 24 August 2012, H. López-Fernández, D. Taphorn, N. Lovejoy, R. Barriga, F. Hauser, J. Arbour, D. Brooks.

**Paratypes.**—Ecuador, Pacific Coast, Esmeraldas River drainage, Imbadura Province: ROM 93662, 2, 61.3–139.3 mm SL, confluence of the Chontal and Guallabamba rivers,  $00^{\circ}14'23.13''N$ ,  $78^{\circ}45'52.10''W$ , 20 August 2012, N. Lujan, D. Taphorn, D. Brooks (electrofishing), local fisherman (cast-netting). Pichincha Province: ROM 93668, 3, 58.2–140.1 mm SL, Nanegalito, Pachijal River alongside road,  $00^{\circ}10'08.01''N$ ,  $78^{\circ}56'13.80''W$ , 21 August 2012, N. Lujan, D. Taphorn, H. López-Fernández, J. Arbour, F. Hauser, D. Brooks; ROM 93670, 2, 69.0–81.1 mm SL, Blanco River west of Puerto Quito,  $00^{\circ}07'12.77''N$ ,  $79^{\circ}14'04.46''W$ , 22 August 2012, D. Taphorn, N. Lovejoy, J. Arbour, F. Hauser, E. Wagner Obando Mina; ROM 93687\*, 3, 49.5–103.4 mm SL, Silanchi River downstream of community of Silanchi,  $00^{\circ}09'32.28''N$ ,  $79^{\circ}14'36.42''W$ , 22 August 2012, N. Lujan,

**Table 4A.** Summary of characters variable across Amazon Basin species of *Chaetostoma* (exclusive of *Ch. platyrhynchus*). Data summarized from examination of types, comparative material, Rapp Py-Daniel (1991), and Salcedo (2006a, 2006b, 2013).

	<i>Chaetostoma anale</i> <i>n</i> = 1; Fowler, 1943	<i>Ch. branickii/</i> <i>taczanowskii</i> <i>n</i> = 4	<i>Chaetostoma breve</i> <i>n</i> = 26, Fig. 4	<i>Chaetostoma carrioni</i> <i>n</i> = 6, Fig. 10	<i>Chaetostoma changae</i> <i>n</i> = 27
<b>Head</b>					
depth (% SL)	—	22.6±1.3	26.6±1.2	23.4±1.3	24.8±0.7
spots (color; distinct/indistinct; shape; size; spacing)	black; distinct; 1/2 naris size; 1–2 spot widths apart	absent	absent or (rarely) white; indistinct; irregularly reticulated; naris size or smaller; variable spacing	white; indistinct; irregularly round to vermiculate; < 1/2 size of naris; 2–3 spot widths apart	absent
male snout enlargement	present	none observed	present	present	present
occipital excrescence	present	absent	present	absent	present
<b>Cheek odontodes</b>					
shape/length	Type 2	Type 2	Type 3	Type 1	Type 2
number	5	6–10	3–16	5–13	3,4
<b>Dentition</b>					
premaxillary teeth	60	87–90	123±21	56±6	75±15
dentary teeth	75	115–132	170±33	76±10	105±15
<b>Body</b>					
cleithral width (% SL)	—	31.1±1.7	35.6±2.7	33.7±1.1	32.9±1.8
spots (color; distinct/indistinct; shape; size; spacing)	black; distinct; round; naris sized; 3–5 spot widths apart; forming 4 linear rows	absent	absent	black; indistinct; round; orbit diameter or larger; 1 spot width apart; anteriorly absent, more distinct caudally; irregularly distributed	absent
stripes/bands	absent	absent	stripe along	absent	absent
<b>Fins</b>					
branched dorsal-fin rays	8	8	7,(8),9	7,(8)	8,(9),10
dorsal-fin coloration	uniform	uniform	uniform or (rarely) reticulated with band width similar to naris diameter	variable, indistinct black bands, bands orbit diameter or smaller	uniform distinct white spots on rays, spots half naris diameter
branched anal-fin rays	5	4	3,(4),5	fin absent or (1),2	(4),5
anal-fin odontodes	present	present	present	present if fin present	absent
paired-fin coloration	uniform	uniform	unpatterned or (rarely) reticulated with band width similar to naris diameter	variable, indistinct black spots/ bands, bands orbit diameter or smaller	unpatterned
pelvic-fin dimorphism	Type 1, 2, 3, 4	none observed	Type 1 (weak), 2 (weak)	Type 1, 2, 3	Type 1, 2 (weak), 3 (weak), 4

**Table 4B.** Summary of characters variable across Amazon Basin species of *Chaetostoma* (exclusive of *Ch. platyrhynchus*). Data summarized from examination of types, comparative material, Rapp Py-Daniel (1991), and Salcedo (2006a, 2006b, 2013).

	<i>Chaetostoma daidalmatos</i> <i>n</i> = 3; Salcedo, 2006b	<i>Chaetostoma dermorhynchum</i> <i>n</i> = 11, Fig. 3	<i>Chaetostoma jeguí</i> Rapp Py-Daniel, 1991	<i>Chaetostoma lexa</i> <i>n</i> = 2; Salcedo, 2013	<i>Chaetostoma lineopunctatum</i> <i>n</i> = 10, Fig. 11	<i>Chaetostoma laborhynchus</i> <i>n</i> = 8
<b>Head</b>						
depth (% SL)	22.3±0.9	22.5±0.6	14.9±0.9*	16.2±0.7*	25.4±1.0	23.8±1.0
spots (color; distinct/indistinct; shape; size; spacing)	black; distinct; round to oblong; half size of naris; densely spaced <1 spot width apart	black; distinct; round; size of naris; evenly distributed 1 spot width apart	uniform	absent	absent (Urubamba and Madre de Dios) or black; distinct; round to vermiculate; <1/2 naris size; evenly spaced 1 spot width apart	light green to gray; indistinct; round to oblong; <1/2 naris diameter; <1 spot width apart
male snout enlargement	absent	present	none observed	present	weak	present (strong)
occipital excrescence	present	present	present	absent	present	absent
<b>Cheek odontodes</b>						
shape/length number	Type 2 5–8	Type 2 2–5	Type 3 2–5	Type 4 9–14	Type 2 3,4	Type 1/2 6–17
<b>Dentition</b>						
premaxillary teeth	60±11	105±14	46–102	31–41	105±10	87±8
dentary teeth	97±21	131±14	62–121	41–50	159±18	138±6
<b>Body</b>						
cleithral width (% SL)	29.7±2.5	31.4±0.8	—	34.4±1.0	33.3±0.8	35.8±0.9
spots (color; distinct/indistinct; shape; size; spacing)	black; round or irregularly oblong; distinct; orbit size or smaller; evenly spaced 1 spot width apart; loosely arranged in 5–6 rows	white to gray; indistinct; round; diameter of orbit; arranged in 4–5 rows from pelvic to caudal fin; more distinct posteriorly	absent	absent	black; round to vermiculate; distinct; 1/2 size of naris; 2–4 spot widths apart; 5–7 irregular rows or series of oblique columns	absent; indistinctly blotched or marbled; pattern widths > orbit diameter
stripes/bands	absent	absent	absent	midlateral stripe (indistinct), width of orbit	absent	absent, see spots above
<b>Fins</b>						
branched dorsal-fin rays	8	8	9,10	(9),10	(8), 9	8
dorsal-fin coloration	black spots; round; diameter of naris; <1 spot width apart; centered on rays; 6–8 per ray	white spots; up to 10; <1/2 diameter of naris; on rays or membranes; more distinct in juveniles	absent	3–5 black bands across all rays; band as wide as orbit diameter; spaced 1 band width apart; membranes hyaline	two series of black spots <1/2 diameter of naris on most or all interradiial membranes, single series on most rays	4–6 irregular bands across all rays; band width similar to naris diameter; membranes hyaline

**Table 4B.** Continued.

	<i>Chaetostoma daidalmatos</i> <i>n</i> = 3; Salcedo, 2006b	<i>Chaetostoma dermorhynchum</i> <i>n</i> = 11, Fig. 3	<i>Chaetostoma jegui</i> Rapp Py-Daniel, 1991	<i>Chaetostoma lexa</i> <i>n</i> = 2; Salcedo, 2013	<i>Chaetostoma lineopunctatum</i> <i>n</i> = 10, Fig. 11	<i>Chaetostoma loborhynchos</i> <i>n</i> = 8
branched anal-fin rays	(4),5	4	2,3,4	fin absent or 1,(2),3	3,(4),5	3,(4)
anal-fin odontodes	present	present	present	absent	present	present
paired-fin coloration	black spots; round or merging into bands; diameter or width of naris	uniformly gray	uniform	uniform or rays indistinctly banded, membranes hyaline	indistinct black spots or lines bordered by hyaline along interradial membranes	approximately 5 indistinct bands across all rays; membranes hyaline
pelvic-fin dimorphism	none observed	Type 1, 2, 3, 4	Type 2, 4	Type 1 (crenulate), 2, 3	Type 1, 2	Type 1, 2

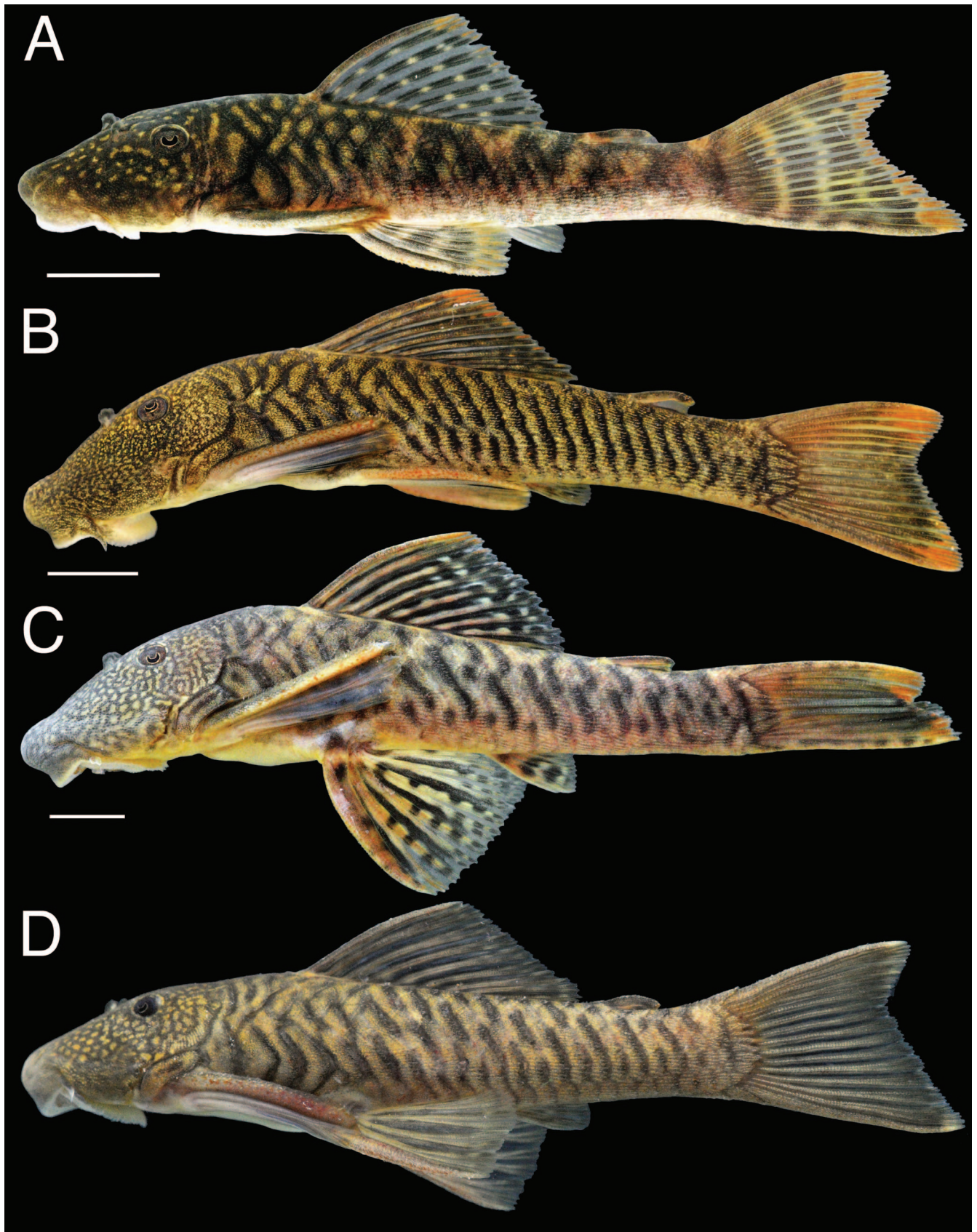
**Table 4C.** Summary of characters variable across Amazon Basin species of *Chaetostoma* (exclusive of *Ch. platyrhynchus*). Data summarized from examination of types, comparative material, Rapp Py-Daniel (1991), and Salcedo (2006a, 2006b, 2013).

	<i>Chaetostoma marmoreoscens</i> <i>n</i> = 10	<i>Chaetostoma microps</i> <i>n</i> = 23, Figs. 5, 12	<i>Chaetostoma stroumpoulos</i> <i>n</i> = 31; Salcedo, 2006b	<i>Chaetostoma trimaculineum</i> , new species <i>n</i> = 5, Figs. 13, 14	<i>Chaetostoma vagum</i> <i>n</i> = 9
<b>Head</b>					
depth (% SL)	23.6±1.5	24.8±1.4	23.7±1.0	23.3±0.2	23.5±0.6
spots (color; distinct/indistinct; shape; size; spacing)	none observed	white, blue, or yellow; distinct; round or vermiculate; <1/2 size of naris; 3 or more spot widths apart	absent or black; indistinct; round to oblong; 1/3 or 1/4 size of naris; densely spaced <1 spot width apart	black; distinct; round; 1/2 naris size; 1–3 spot widths apart	black; distinct; round; 1/2 naris size; 1 spot width apart
male snout enlargement	present (weak)	present	weak	absent	present
occipital excrecence	absent	absent	present	present	present
<b>Cheek odontodes</b>					
shape/length	Type 1/2	Type 1	Type 2	Type 2/3	Type 2
number	3–16	5–20	3–6	4,5	2–6
<b>Dentition</b>					
premaxillary teeth	63±15	49±18	86±21	100±31	82±14
dentary teeth	95±15	80±23	135±27	138±44	102±13
<b>Body</b>					
cleithral width (% SL)	36.4±2.4	34.6±2.0	32.0±2.2	31.7±1.2	32.5±2.3



Table 4C. Continued.

	<i>Chaetostoma marmorescens</i> <i>n</i> = 10	<i>Chaetostoma microps</i> <i>n</i> = 23, Figs. 5, 12	<i>Chaetostoma stroumpoulos</i> <i>n</i> = 31; Salcedo, 2006b	<i>Chaetostoma trimaculineum</i> , new species <i>n</i> = 5, Figs. 13, 14	<i>Chaetostoma vagum</i> <i>n</i> = 9
spots (color; distinct/indistinct; shape; size; spacing)	absent; indistinctly blotched or marbled; pattern widths > orbit diameter	white, blue, or yellow; distinct; round or vermiculate; <1/2 size of naris; 3 or more spot widths apart; anterodorsally clustered	black; indistinct; round or irregularly oblong; 1/2 orbit size or less; evenly spaced 1 spot width apart; loosely arranged in rows (sometimes absent)	black; distinct; round; naris size; 1–2 spot widths apart; 3–4 linear rows on median, mid-dorsal, and dorsal plate series	black; distinct; round; 1/2 naris size; irregular, 1–4 spot widths apart
stripes/bands	absent, see spots above	faint midlateral stripe	absent	absent	absent
<b>Fins</b>					
branched dorsal-fin rays	8,(9),10	8,(9),10	8	8	8
dorsal-fin coloration	3–4 irregular bands across all rays; band width similar to orbit diameter; membranes hyaline	unpatterned or indistinctly patterned rays; hyaline membranes	uniform and hyaline or black spots; round; diameter of naris; 1 spot width apart; centered on rays; 6–7 per ray	rays uniform, membranes hyaline or with few black spots	uniform
branched anal-fin rays	2,(3),4	2,(3)	3,4,(5)	4	3,4,(5)
anal-fin odontodes	absent	present	present	present	present
paired-fin coloration	uniform pectoral fins; 3–4 indistinct and irregular bands on pelvic fins	uniform or (rarely) irregularly banded, bands indistinct and broadly reticulate	uniform and hyaline or black spots; round; diameter of naris; 1–2 spot widths apart; centered on rays	uniformly gray to light brown	uniform
pelvic-fin dimorphism	Type 1, 2	Type 1, 2, 3	Type 2, 4	none observed	none observed



**Fig. 7.** *Chaetostoma bifurcum*, new species, from three drainages along the Pacific Coast of Ecuador: (A) Esmeraldas (ROM 93662, 59.7 mm SL), (B, C) Guayas (B: ROM 93721\*, 83.7 mm SL; and C: ROM 93729, 91.9 mm SL), and (D) Santa Rosa (ROM 93787\*, 96.3 mm SL) river drainages. Scale bars = 1 cm. Photos by NKL.

**Table 5.** Selected morphometric characters and tooth counts for *Chaetostoma bifurcum*, new species, *Chaetostoma breve* Regan, 1904 (syntype: BMNH 1898.11.4.33–36), and *Chaetostoma carrioni* (Norman, 1935; holotype: BMNH 1933.5.29.1). Interlandmarks (ILM) are the two points between which measurements were taken (from Armbruster, 2003). Morphometric characters other than standard length presented as percents of either standard length or head length. Abbreviations: Min = minimum value, Max = maximum value, *n* = number of specimens examined, StDev = standard deviation.

ILM	Measurement	<i>Chaetostoma bifurcum</i> , new species						<i>Chaetostoma breve</i> Regan, 1904						<i>Chaetostoma carrioni</i> (Norman, 1935)					
		Holotype	<i>n</i>	Mean	StDev	Min	Max	Syntype	<i>n</i>	Mean	StDev	Min	Max	Holotype	<i>n</i>	Mean	StDev	Min	Max
1–20	Standard length (mm)	132.4	12			71.5	132.4	126.2	26			56.1	134.8	55.9	7			46.9	60.2
<b>Percents of standard length</b>																			
1–10	Predorsal length	41.6	12	41.7	2.2	39.3	47.9	42.8	26	44.0	1.3	41.7	47.2	42.8	7	44.8	2.0	42.7	47.9
1–7	Head length	31.8	12	31.7	1.9	29.6	36.4	31.6	26	34.8	1.3	31.6	36.7	32.4	7	31.7	1.1	30.3	33.7
7–10	Head-dorsal length	10.1	12	10.5	1.3	9.5	14.2	12.7	26	10.0	0.9	8.3	12.7	9.7	7	14.0	2.1	9.7	15.7
8–9	Cleithral width	31.9	12	31.6	2.0	29.1	36.9	34.0	26	35.6	2.7	30.7	40.0	34.8	7	33.7	1.1	32.1	35.1
1–12	Head-pectoral length	27.3	12	26.8	1.3	25.2	30.1	28.1	26	29.3	1.1	27.3	31.9	30.3	7	29.8	1.3	27.4	31.3
12–13	Thorax length	19.4	12	21.3	1.5	19.0	24.2	20.7	26	22.0	1.8	19.3	25.8	26.7	7	24.0	2.0	20.8	26.7
12–29	Pectoral-spine length	28.5	12	28.6	1.0	27.2	30.3	29.1	26	29.0	2.0	24.7	32.9	27.4	7	26.6	1.2	24.3	27.8
13–14	Abdominal length	23.3	12	23.9	0.8	22.8	25.5	23.7	26	24.4	1.5	20.6	28.2		6	25.4	1.7	23.5	27.9
13–30	Pelvic-spine length	24.2	12	24.8	1.6	21.3	26.5	25.6	26	25.1	3.8	8.8	28.5	29.6	7	23.9	2.9	21.0	29.6
14–15	Postanal length	35.8	12	35.0	1.6	30.7	37.3	35.0	26	33.5	2.5	26.4	36.3		6	28.4	1.5	26.8	31.2
14–31	Anal-fin spine length	11.8	12	11.2	1.4	9.0	13.7	9.8	26	10.1	1.4	8.0	13.5		6	4.1	1.4	2.3	6.5
7–12	Head depth	22.2	12	22.9	1.6	21.0	26.8	24.3	26	26.6	1.2	24.3	28.9	21.3	7	23.4	1.3	21.3	25.3
10–12	Dorsal-pectoral depth	26.9	12	27.3	0.9	25.9	28.8	29.0	26	30.9	1.5	28.6	34.3	25.7	7	29.5	2.3	25.7	32.2
10–11	Dorsal spine length	26.1	12	27.2	2.1	24.0	30.0	29.1	26	26.9	1.9	24.2	31.0	26.6	7	22.5	2.3	18.8	26.6
10–13	Dorsal-pelvic depth	22.2	12	21.0	1.0	19.5	22.6	24.6	26	24.9	1.9	21.6	30.5	19.7	7	21.0	1.9	19.2	24.7
10–16	Dorsal-fin base length	25.8	12	25.2	1.0	22.9	26.6	26.7	26	27.3	1.6	24.2	31.8	24.0	7	26.7	1.6	24.0	28.4
16–17	Dorsal-adipose depth	16.7	12	17.1	1.7	14.4	20.9	16.3	26	15.3	1.3	13.0	18.9		3	14.8	0.8	13.9	15.6
17–18	Adipose-spine length	7.9	12	8.9	0.9	7.6	10.2	7.2	26	9.7	1.1	7.2	12.0		3	6.9	1.1	6.2	8.1
17–19	Adipose-upper caudal length	17.9	12	17.7	1.0	15.9	19.2	18.1	26	15.8	1.5	12.7	18.5		3	14.5	2.5	11.8	16.9
15–19	Caudal peduncle depth	14.6	12	13.3	0.6	12.5	14.6	16.9	26	15.4	0.8	13.5	16.9	11.5	7	12.0	0.7	11.3	13.3
15–17	Adipose-lower caudal depth	22.8	12	23.1	1.0	22.0	25.5	26.3	26	24.7	1.0	23.1	26.6		3	22.7	2.2	21.1	25.2
14–17	Adipose-anal depth	22.1	12	20.8	1.3	18.1	22.3	22.7	26	22.4	1.0	19.9	23.8		3	19.1	3.6	15.8	22.9
14–16	Dorsal-anal depth	15.5	12	15.5	0.4	14.7	16.1	20.2	26	18.3	0.9	16.1	20.2		6	14.8	0.5	14.4	15.8
13–16	Pelvic-dorsal depth	26.9	12	26.5	1.3	23.5	28.2	28.2	26	29.0	1.5	25.8	31.3	20.8	7	27.9	3.3	20.8	30.3
<b>Percents of head length</b>																			
5–7	Head-eye length	28.5	12	30.5	2.2	27.1	34.8	9.7	26	11.1	4.0	8.9	28.5	32.7	7	33.3	3.4	26.5	36.9
4–5	Orbit diameter	13.3	12	14.3	1.1	11.8	16.3	4.1	26	5.1	1.7	3.8	13.1	10.8	7	14.2	1.6	10.8	15.5
1–4	Snout length	67.3	12	64.3	2.5	61.5	68.2	20.8	26	25.1	8.9	20.4	68.4	66.6	7	65.5	2.4	61.8	69.5
2–3	Internares width	12.4	12	10.9	1.0	9.8	13.2	3.8	26	3.7	1.5	2.2	10.4	8.8	7	13.7	2.3	8.8	16.2
5–6	Interorbital width	29.3	12	30.8	1.7	28.0	34.3	10.0	26	11.7	3.9	9.9	30.5	32.8	7	44.0	5.3	32.8	48.7
1–24	Mouth length	61.3	12	54.9	3.8	49.2	61.3	62.3	26	60.8	2.6	55.7	67.3	20.8	7	20.2	0.5	19.5	20.9
21–22	Mouth width	77.7	12	74.6	4.2	68.8	83.9	78.0	26	83.1	5.0	74.4	90.4	25.5	7	25.3	1.2	23.1	26.7
22–23	Barbel length	8.4	12	8.2	2.8	3.5	14.1	8.1	26	9.0	1.4	5.4	12.0	4.3	7	3.0	0.8	1.9	4.3
25–26	Dentary tooth cup length	30.5	12	29.6	1.8	26.6	32.5	33.7	26	34.3	2.3	29.1	38.6	10.3	7	10.2	0.9	8.8	11.4
27–28	Premax. tooth cup length	26.3	12	25.4	1.4	22.4	27.0	28.4	26	29.4	1.8	26.3	32.3	9.0	7	8.7	0.7	7.3	9.5
<b>Tooth counts</b>																			
	Left premaxillary teeth	132	12	107	21	67	137	86	26	123	21	86	166		6	56	6	45	59
	Left dentary teeth	185	12	151	34	52	185	92	26	170	33	92	223		6	76	10	63	84

**Table 6.** Selected meristic characters for *Chaetostoma bifurcum*, new species, *Chaetostoma breve* Regan, 1904 (syntype: BMNH 1898.11.4.33–36), and *Chaetostoma carrioni* (Norman, 1935; holotype: BMNH 1933.5.29.1). Abbreviations: Min = minimum value, Max = maximum value, *n* = number of specimens examined.

	<i>Chaetostoma bifurcum</i> , new species					<i>Chaetostoma breve</i> Regan, 1904					<i>Chaetostoma carrioni</i> (Norman, 1935)				
	Holotype	<i>n</i>	Mode	Min	Max	Syntype	<i>n</i>	Mode	Min	Max	Holotype	<i>n</i>	Mode	Min	Max
Median plates	24	12	24	22	24	23	26	23	23	24	24	7	23	22	24
Supramedian plates	25	12	24	23	25	23	26	24	22	24	23	7	22	22	23
Inframedian plates	25	12	24	23	25	24	26	24	23	24	23	7	22	22	23
Caudal peduncle plate rows	5	12	5	5	5	5	26	5	5	5	5	7	5	5	5
Dorsal-fin branched rays	8	12	8	8	8	8	26	8	7	9	7	7	8	7	8
Pectoral-fin branched rays	6	12	6	6	6	6	26	6	6	7	6	7	6	6	6
Pelvic-fin branched rays	5	12	5	5	5	5	26	5	5	5	5	7	5	5	5
Anal-fin branched rays	4	12	4	4	5	4	26	4	3	5	0	7	0	0	2
Caudal-fin branched rays	14	12	14	14	14	14	26	14	14	14	12	7	12	12	12
Dorsal procurent caudal-fin rays	5	12	5	3	5	5	26	5	2	6	6	7	4	3	6
Ventral procurent caudal-fin rays	4	12	3	2	4	2	26	3	1	5	4	7	2	1	4
Preadipose plates	1	12	1	1	1	1	26	1	1	2	0	7	1	0	1
Dorsal–adipose plates	6	12	6	4	6	4	26	5	3	6	0	7	5	0	5
Infraorbital plates	5	12	5	5	6	6	26	6	5	6	5	7	5	5	5

D. Taphorn, H. López-Fernández, J. Arbour, F. Hauser, E. Wagner Obando Mina. Esmeraldas Province: ROM 93712, 1, 82.4 mm SL, Otongo River at bridge crossing, 00°22'59.76"N, 79°12'26.20"W, 24 August 2012, N. Lujan, D. Taphorn, V. Meza, H. López-Fernández, F. Hauser, D. Brooks. Guayas River drainage, Los Ríos Province: ANSP 182817, 10, 60.7–104.4 mm SL, same data as holotype; AUM 64433, 10, 65.4–97.1 mm SL, same data as holotype; FMNH 80708, 1, 91.6 mm SL, Palenque River at Centro Científico Río Palenque, 1975, G. S. Glodek; FMNH 93101, 68, 83.8–137.2 mm SL, Palenque River at Centro Científico Río Palenque, 7 November 1978, G.S. Glodek, D. Taphorn, J. Gourley, J. Carter; ROM 93729, 9, 43.2–114.1 mm SL, Umbe River at bridge crossing in Las Palmitas, 01°12'42.56"S, 79°18'40.25"W, 25 August 2012, local children from community of Las Palmitas; ROM 93739, 2, 58.6–58.8 mm SL, Clara River at La Clara around bridge and downstream, 01°40'28.68"S, 79°23'13.22"W, 26 August 2012, local children from community of La Clara. Santo Domingo de las Tsáchilas Province: ROM 93704, 2, 29.9–38.0 mm SL, Chihuilpe River at bridge crossing and downstream, 00°19'20.92"S, 79°12'59.11"W, 23 August 2012, N. Lujan, N. Lovejoy, V. Meza, J. Arbour, F. Hauser; ROM 93721\*, 4, 58.2–74.7 mm SL, Ecuador, same data as holotype. Santa Rosa River drainage, El Oro Province: ROM 93787\*, 10, 61.3–99.0 mm SL, Santa Rosa River at La Avanzada bathing area, 03°33'31.18"S, 79°56'49.19"W, 29 August 2012, N. Lujan, D. Taphorn, V. Meza, R. Barriga, H. López-Fernández, F. Hauser, J. Arbour; ROM 93842, 9, 68.3–99.5 mm SL, Santa Rosa River downstream of town of Avanzada, 9 km S of town of Santa Rosa, 03°31'49.80"S, 79°57'35.40"W, 30 August 2012, D. Taphorn, N. Lovejoy, J. Arbour, V. Meza.

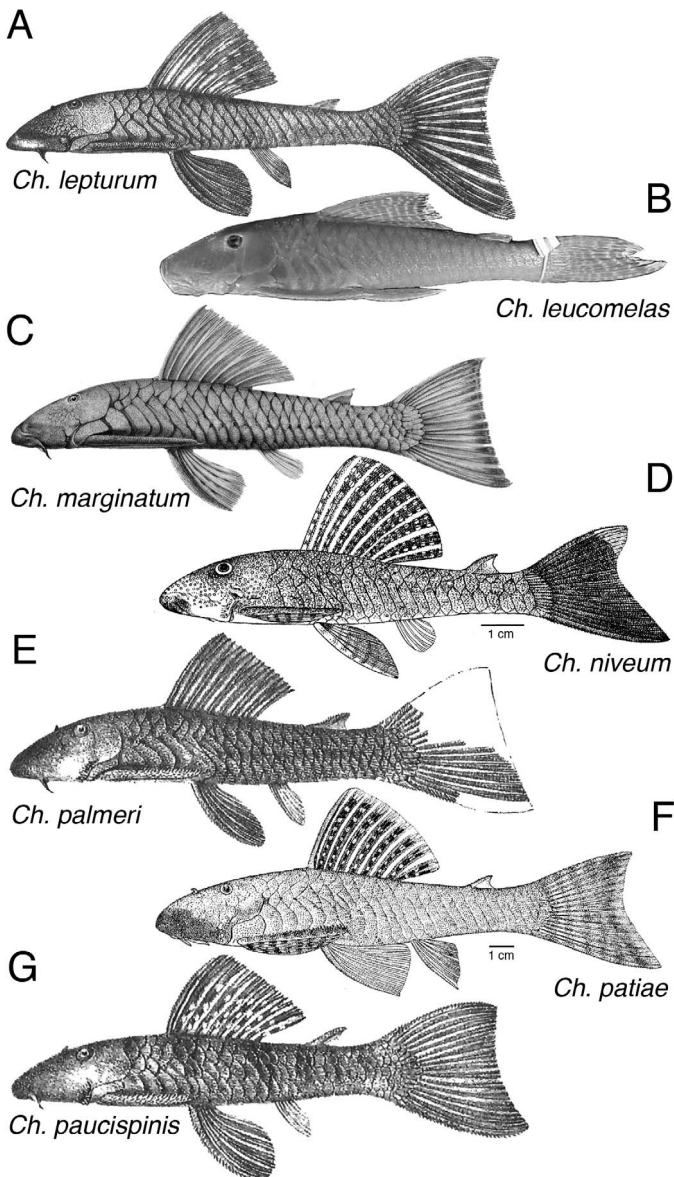
**Non-type material.**—Peru, Tumbes Region: AUM 21561, 3, Puyango River 5 km W of Puyango, 19 km NW of Alamor, approx. 03°54'S, 80°07'W; MHNG 2359.009, 2, Tumbes River at Rica Playa; MUSM 5830, Tumbes River, Quebrada

Don Pablo; ROM 66743, 1, 119 mm SL, Tumbes River at Rica Playa, Carillos, approx. 03°48'S, 80°31'W; ROM 66746, 3, 43–105 mm SL, Quebrada Honda, Ucumares, approx. 03°52'S, 80°30'W.

**Diagnosis.**—*Chaetostoma bifurcum* can be diagnosed from all other *Chaetostoma* along the Pacific Coast of South America except *Ch. palmeri* and *Ch. paucispinis* by having only one or two evertible cheek odontodes (vs. three to six); from *Ch. niveum*, *Ch. palmeri*, *Ch. patiae*, and *Ch. paucispinis* by having most frequently four branched anal-fin rays (vs. five); from *Ch. palmeri* and *Ch. paucispinis* by living adults having body with black, indistinct, vertically elongate, irregularly broken or complete bars ½ to ⅔ width of orbit (vs. body uniform or with transverse cross-bars wider than two times orbit centered on dorsal midline, Fig. 8); and from *Ch. paucispinis* by having eight branched dorsal-fin rays (vs. nine).

**Description.**—Morphometrics in Table 5 and meristics in Table 6. Largest specimen 140.1 mm SL. Body depth increasing from tip of snout to greatest body depth at predorsal plates, decreasing to posterior margin of adipose fin with slight increase at base of caudal fin. Dorsal profile slightly convex between snout and predorsal plates then straight and descending to base of dorsal fin. Ventral profile flat from snout to base of caudal fin. Ossified dermal plates with small odontodes covering head and body flanks. Plates missing from broad crescent around snout margin and abdomen. Cheek plates having zero, one, or two slightly enlarged, distally hooked (Type 3, Fig. 6) odontodes; odontodes typically obscured by thick fleshy lobe. Orbit positioned dorsolaterally on head with opening sloped ventrolaterally at approximately 45° from sagittal plane in anterior view. Snout broadly triangular in dorsal view.

Oral disk occupying majority of ventral surface of head anterior of cleithrum. Teeth minute, bicuspid, with cusps bent 90° toward mouth opening. Single digitate papilla



**Fig. 8.** Original illustrations (A, C–G) and photograph (B) of the types of seven species of *Chaetostoma* from the Pacific Coast of South America. Illustrations (A, G, E) from Regan (1912), (C) from Regan (1904), (D) from Fowler (1944), and (F) from Fowler (1945). Photograph (B; CAS 60167) courtesy of the California Academy of Sciences.

extending ventrally from dorsal part of premaxillary symphysis; single thick cluster of low papillae at middle of interior surface of each mandible. Maxillary barbel short, unattached along most of length; ventral surface of labial disk with low hemispherical papillae decreasing in size distally.

Dorsal-fin spinelet small and round; posteriormost dorsal-fin ray free from body; reaching to within one plate width from adipose-fin spine when adpressed. Pectoral fin reaching just beyond pelvic-fin base when adpressed, spine having modestly enlarged odontodes along posterodorsal and distal surfaces. Pelvic-fin spine reaching middle of anal-fin base when adpressed. Second unbranched anal-fin ray longest; anal fin spanning total of six plate widths when adpressed. Adipose-fin spine straight, adnate to caudal peduncle via fleshy membrane. Caudal-fin margin obliquely emarginate with ventral lobe slightly longer than dorsal lobe.

Body broadest at cleithrum; posterior margin of exposed posterior process of cleithrum rounded. First two to three midventral plates gently bent forming rounded lateral ridge between verticals through pectoral- and dorsal-fin origins.

**Coloration in life.**—Highly variable (Fig. 7). Base color of head black to dark gray with white to cream colored, indistinct, irregularly round to oblong spots; head spots size of naris or smaller and spaced from less than one to three spot widths apart. Body base color white to cream with black, indistinct, vertically elongate, irregularly broken or complete bars, bar width of orbit or smaller, spaced one spot or bar width apart. Dorsal fin irregularly colored, sometimes uniformly light brown to gray, sometimes with three to four white to cream colored spots less than half naris diameter along branched rays. Paired fins irregularly colored, sometimes uniformly light brown to gray, sometimes with three to four alternating light and dark colored bands width of orbit or smaller, bands sometimes irregularly broken into spots. Caudal uniformly light brown to gray or with bands wider than orbit diameter. Tips of caudal and/or dorsal fin often colored red to orange.

**Coloration in preservative.**—Uniformly dark gray to black.

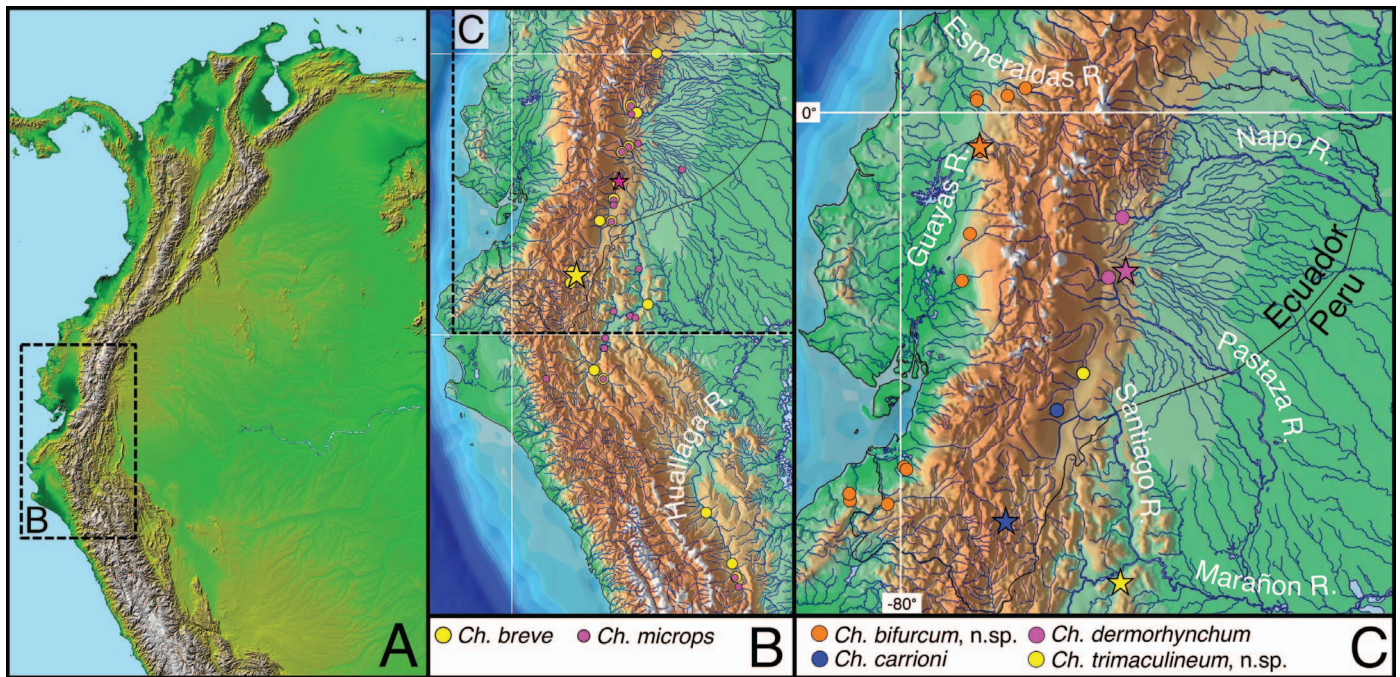
**Sexual dimorphism.**—None observed.

**Distribution.**—Known from piedmont elevations (approximately 100 to 650 masl) of Pacific Coast drainages of western Ecuador and northwestern Peru (Fig. 9C), including (from north to south) the Esmeraldas, Guayas, Santa Rosa, and Tumbes river drainages.

**Etymology.**—The species epithet *bifurcum* is a Latin adjective meaning “two-pronged,” which is in reference to the two evertible cheek odontodes characteristic of this species.

**Remarks.**—*Chaetostoma bifurcum* displays relatively little genetic divergence in the loci sequenced for this study from the Esmeraldas River drainage in the north to the Santa Rosa River drainage in the south (see branch lengths, Fig. 2). However, molecular data do suggest that Guayas and Santa Rosa river drainage populations are more closely related to each other (Fig. 2, Node 29: BI: 0.97, ML: 75) than either are to the Esmeraldas River population (Node 30: BI: 1.0, ML: 100).

Molecular phylogenetic evidence (Fig. 2) and morphological similarities (i.e., only one to three evertible cheek odontodes, reddish tinged fin tips, absence of sexual dimorphism) place *Ch. bifurcum* with *Ch. palmeri* and *Ch. paucispinis* as part of the *Ch. fischeri* group, which appears to be limited to Panama and the Pacific Coast of South America in Colombia, Ecuador, and Peru. Throughout its range, *Ch. bifurcum* appears to be the only species of *Chaetostoma* present, although at higher elevations it is often sympatric with *Transancistrus* (i.e., *T. aequinoctialis* in the north and *T. santarosensis* in the south) which may be confused with *Chaetostoma* due to their both having a partially naked snout, eight branched dorsal-fin rays, and five rows of caudal-peduncle plates. However, *Transancistrus* can be easily distinguished from *Ch. bifurcum* by having a more narrowly restricted unplated snout region and by having a much higher number of evertible cheek odontodes (16–31, mode 19; Tan and Armbruster, 2012; Lujan et al., 2015b).



**Fig. 9.** (A) Map of northwestern South America and southern Central America, and (B, C) enlargements of Ecuador and northern Peru showing the distributions of specimens of (B) *Chaetostoma breve* and *Ch. microps*, and (C) *Ch. bifurcum*, new species, *Ch. carrioni*, *Ch. dermorhynchum*, and *Ch. trimaculineum*, new species, that were examined in this study. Star = type locality.

### *Chaetostoma breve* Regan, 1904

Figure 4; Tables 4, 5, 6

**Syntypes.**—All specimens eastern Ecuador, Santiago River drainage: BMNH 1898.11.4.33–36, 4, Zamora River; MSNM 40 [ex MSNM 5592], 1, Zamora River; MZUT 1488, 2, Bomboiza River; MZUT 1489, 13, Zamora River [15 total specimens at MZUT but evidently only 1 designated as syntype; see Tortonese (1940), type catalog].

**Non-type material.**—Ecuador, Napo River drainage, Napo Province: ROM 93950\*, 6, 68.2–135.3 mm SL, Tena River at bridge crossing 9.3 km NW of Tena, 00°55'27.62"S, 77°52'34.10"W; ROM 93951, 2, 67.7–72.9 mm SL, Napo River near Tena, 01°02'38.08"S, 77°47'34.68"W. Pastaza River drainage, Morona-Santiago Province: ROM 93923\*, 1, 61.5 mm SL, Lumbaima River at bathing area 27 km S of Puyo, 01°42'37.66"S, 78°00'03.53"W; ROM 93930, 3, 81.4–94.6 mm SL, Amundalo River 10.3 km WSW of Palora, 01°44'54.90"S, 78°02'39.78"W. Pastaza Province: ROM 93939, 6, 78.8–139.7 mm SL, Puyo River upstream of confluence with Pastaza River, 20.4 km SSE of Puyo, 01°39'09.59"S, 77°55'29.26"W. Santiago River drainage, Morona-Santiago Province: ROM 93879, 2, 93.4–117.4 mm SL, Yungantza River downstream of bridge S of the town of Limón, 02°58'16.26"S, 78°26'29.88"W; ROM 93888, 1, 72.5 mm SL, Yunquiantza River at bridge crossing on road between Santiago and Mendez, just upstream of confluence with Santiago River, 02°58'56.16"S, 78°13'36.12"W; ROM 93893, 2, 98.9–100.4 mm SL, confluence of the Changachangasa and Tutanangosa rivers and upstream in both, 02°35'51.18"S, 78°11'10.38"W; ROM 93921, 2, 123.6–127.5 mm SL, Upano River, 02°18'05.76"S, 78°06'47.04"W. Zamora-Chinchipec Province: ROM 93848, 3, 124.2–134.2 mm SL, Bomboscara River 2.42 km SE of Zamora, downstream of

Podocarpus National Park, 04°05'08.08"S, 78°57'26.98"W; ROM 93856, 1, 88.3 mm SL, Piunza River at bridge in community of Piunza, 03°52'28.12"S, 78°52'41.78"W; ROM 93861, 8, 80.1–122.6 mm SL, Yacuambi River at community of Piunza, upstream of mouth of Piunza R., 03°52'44.48"S, 78°53'06.40"W; ROM 93863, 23, 86.7–107.6 mm SL, confluence of the Jambue and Zamora rivers, 03°57'37.30"S, 78°50'49.18"W. Peru, Marañon River drainage, Amazonas Region: AUM 45583, 1, Marañon River at pongo above Borja, 35.5 km NE of Santa Maria de Nieva, 04°27'30.64"S, 77°34'53.52"W; AUM 45597, 25, same data as AUM 45583; AUM 45634, 17, Marañon River at Pongo de Renema, 05°38'16.66"S, 78°31'53.72"W; AUM 45641, 2, Río Utcubamba, 23 km SE of Bagua Chica, 05°46'32.34"S, 78°22'28.74"W; AUM 46515\*, 41, same data as AUM 45641. Huallaga River drainage, San Martín Region, Tocache Province: MHNG 2712.074\*, 2, Tocache River at Uchiza (RFC 23), 08°10'07.50"S, 76°32'32.50"W. Huánuco Region, Leoncio Prado Province: MHNG 2712.047, 2, Huallaga River between Tingo Maria and Aucayacu (RFC 07), 09°04'42"S, 76°04'44"W; MHNG 2712.081, 10, Huallaga River at Tingo Maria (RFC 25), 09°18'53.8"S, 76°00'34.2"W; MHNG 2712.048, 1, same data as MHNG 2712.047; MHNG 2712.078, 1, same data as MHNG 2712.081; MUSM 16471, Tingo Maria, Huallaga River, 09°18"S, 76°00"W; MUSM 35826, Tingo Maria, Huallaga River; MUSM 35828, Huallaga River between Tingo Maria and Aucayacu; MUSM 41082, Huánuco District, Huallaga River, 09°40'33.00"S, 75°51'01.07"W.

**Diagnosis.**—*Chaetostoma breve* can be diagnosed from all other Amazon Basin *Chaetostoma* except *Ch. jegui* and *Ch. trimaculineum*, new species, by having Type 3 cheek odontodes (vs. Types 1, 2, or 4); from all other Amazon Basin species except *Ch. dermorhynchum*, *Ch. lineopunctatum*, *Ch. stroumpoulos*, and *Ch. trimaculineum*, new species, by

having more teeth per premaxillary ramus (an average of  $123 \pm 21$ , vs. typically fewer than 102); from all other Amazon Basin species except *Ch. dermorhynchum*, *Ch. lineopunctatum*, *Ch. lobarhynchos*, *Ch. stroumpoulos*, and *Ch. trimaculineum*, new species, by having more teeth per mandible (an average of  $170 \pm 33$ , vs. typically fewer than 137); from all other Amazon Basin species except *Ch. branickii/taczanowskii*, *Ch. changae*, *Ch. jegui*, *Ch. lexa*, *Ch. lobarhynchos*, and *Ch. marmorescens* by lacking round spots on the body (vs. black or white spots present on body); from all other Amazon Basin species except *Ch. anale*, *Ch. branickii/taczanowskii*, *Ch. jegui*, *Ch. microps*, *Ch. stroumpoulos*, and *Ch. vagum* by lacking distinct spots or bands on the dorsal fin (vs. dorsal-fin spots or bands present); from all other Amazon Basin species except *Ch. branickii/taczanowskii*, *Ch. daidalmatos*, *Ch. lineopunctatum*, *Ch. lobarhynchos*, *Ch. marmorescens*, *Ch. trimaculineum*, new species, and *Ch. vagum* by lacking Types 3 and 4 sexual dimorphism of the pelvic and anal fins (vs. Type 3 and/or 4 sexual dimorphism present); from *Ch. daidalmatos*, *Ch. dermorhynchum*, *Ch. lexa*, *Ch. stroumpoulos*, *Ch. trimaculineum*, new species, and *Ch. vagum* by having greater head depth ( $26.6 \pm 1.2\%$  SL, vs.  $\leq 24.7$ ); from *Ch. anale*, *Ch. daidalmatos*, *Ch. dermorhynchum*, *Ch. microps*, *Ch. trimaculineum*, new species, and *Ch. vagum* by lacking round spots or having indistinct and irregularly reticulate white spots on the head (vs. distinct black spots or distinctly round to vermiculate white, yellow, or blue spots smaller than naris on head); from *Ch. branickii/taczanowskii*, *Ch. carrioni*, *Ch. lexa*, *Ch. lobarhynchos*, *Ch. marmorescens*, and *Ch. microps* by having a supraoccipital excrescence (vs. excrescence absent); from *Ch. daidalmatos*, and *Ch. dermorhynchum* by having a wider cleithral width ( $35.6 \pm 2.7\%$  SL, vs.  $< 32.9$ ); from *Ch. carrioni* and *Ch. lexa* by having an anal fin with most frequently four branched rays (sometimes three or five, vs. anal fin missing or if present with most frequently one or two rays, rarely three).

**Description.**—Morphometrics in Table 5 and meristics in Table 6. Largest specimen 139.7 mm SL. Body depth increasing from tip of snout to greatest body depth at predorsal plates or dorsal-fin origin, decreasing to posterior margin of adipose fin then increasing slightly to base of caudal fin. Dorsal profile convex between snout and dorsal-fin origin then straight and descending to base of dorsal fin. Ventral profile flat from snout to base of caudal fin. Ossified dermal plates with small odontodes cover head and body flanks. Plates missing from broad crescent around snout margin and abdomen. Cheek plates having three to 16 slightly enlarged, distally hooked odontodes (Type 3, Fig. 6). Orbit positioned dorsolaterally on head with opening sloped ventrolaterally at approximately  $45^\circ$  from sagittal plane in anterior view. Snout broadly rounded in dorsal view.

Oral disk occupying majority of ventral surface of head anterior of cleithrum. Teeth minute, bicuspid, with cusps bent  $90^\circ$  toward mouth opening. Single digitate papilla extending ventrally from dorsal part of premaxillary symphysis; clusters of low papillae at middle of interior surface of each premaxilla and mandible, mandibular clusters larger. Maxillary barbel short, adnate along most or all of length; ventral surface of labial disk with low hemispherical papillae decreasing in size distally.

Dorsal-fin spinelet small and triangular, sometimes covered with flesh; posteriormost dorsal-fin ray free from body; reaching to within one plate width from adipose-fin spine

when adpressed. Pectoral fin reaching just beyond pelvic-fin base when adpressed, spine having modestly enlarged odontodes along posterodorsal and distal surfaces. Pelvic-fin spine not reaching anal fin or reaching middle of anal-fin base when adpressed. Second unbranched anal-fin ray longest; anal fin spanning total of four to four and a half plate widths when adpressed. Adipose-fin spine straight, adnate to caudal peduncle via fleshy membrane. Caudal-fin margin vertically or slightly obliquely emarginate with ventral lobe coequal or slightly longer than dorsal lobe.

Body broadest at cleithrum; posterior margin of exposed posterior process of cleithrum rounded or pointed. First one to two midventral plates gently bent, forming rounded lateral ridge between verticals through pectoral- and dorsal-fin origins.

**Coloration in life.**—Highly variable (Fig. 4). Base color of head dark brown to black with light gray to cream colored, generally indistinct (excepting mature males, e.g., Fig. 4A), irregularly round to reticulated spots; spots half size of naris to half orbit diameter. Body sometimes uniformly light brown to gray, sometimes with darker gray to black, generally indistinct (excepting mature males, e.g., Fig. 4A), irregular reticulations with patterns being width of orbit or smaller. Dorsal fin irregularly colored, sometimes uniformly light brown to gray, sometimes with irregular spotting aligned with rays. Paired fins uniformly light brown to gray or with irregular, indistinct bands or reticulations. Caudal fin uniformly light brown to gray. Tips of caudal fin sometimes colored white. Indistinct black spot sometimes present along anterior base of dorsal fin, between second unbranched and first branched ray.

**Coloration in preservative.**—Body uniformly dark gray to light brown. Fins sometimes showing faint pattern of spots aligned with rays.

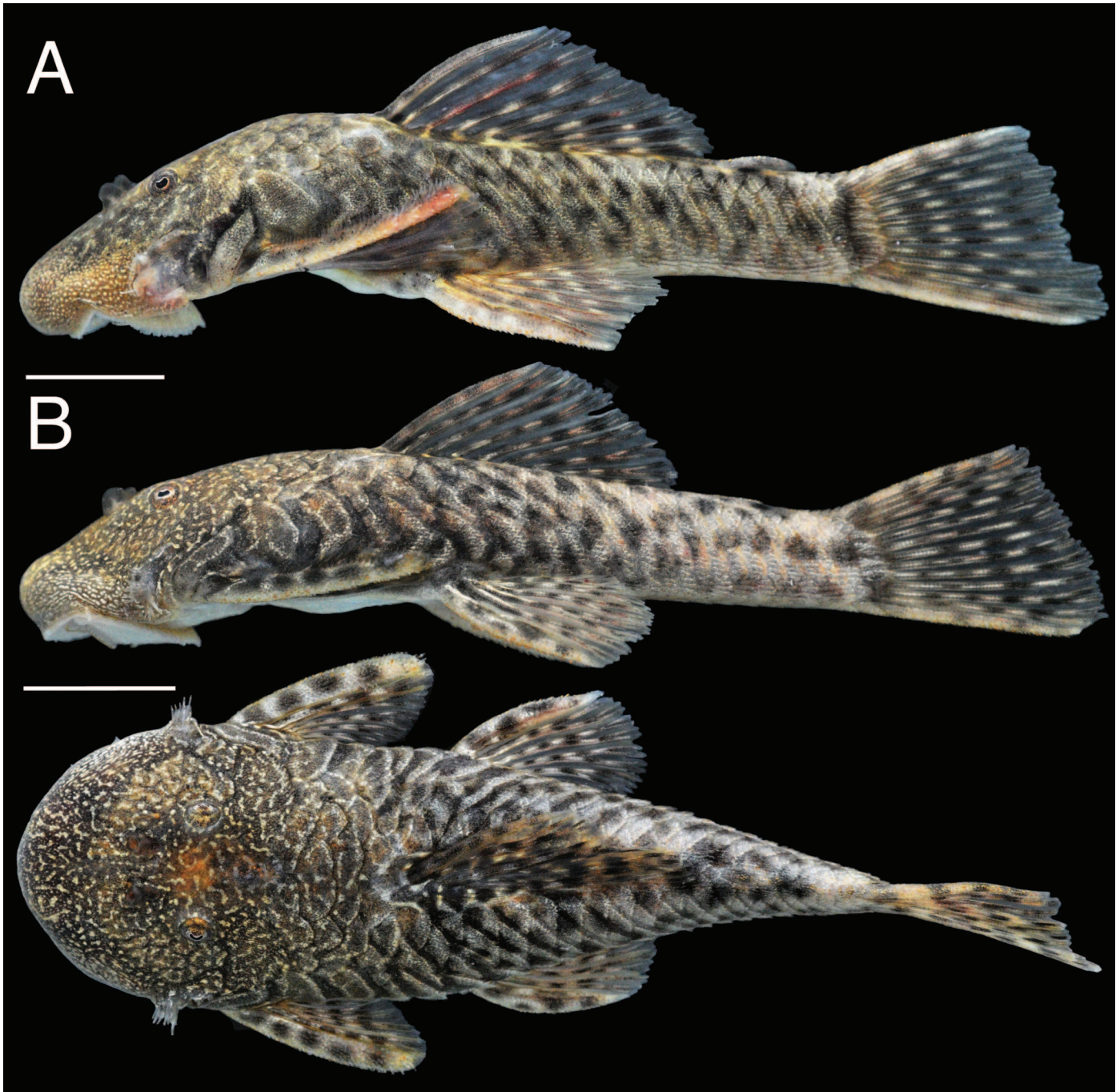
**Sexual dimorphism.**—Mature males with slightly elongated proximal, branched pelvic-fin rays so that proximomedial posterior pelvic-fin margin is slightly elongated into a modest lobe (Type 1 dimorphism), posterodorsal margin of pelvic-fin spine with modest dermal fold (Type 2 dimorphism). Mature males may also display some enlargement of the unplated, fleshy snout region and more intense color pattern contrasts (e.g., Fig. 4A).

**Distribution.**—*Chaetostoma breve* is widespread across headwaters of the western Amazon Basin in Ecuador and Peru, from at least the Aguarico River in the north to the Huallaga River in the south (Fig. 9B). It appears to be restricted to piedmont habitats and elevations (approximately 250 to 1100 masl). *Chaetostoma breve* is not currently known from the Ucayali River drainage, and it seems unlikely, given the considerable sampling that has occurred in this drainage, that *Ch. breve* exists there but remains undetected. It seems more likely that the Huallaga River drainage forms the southernmost extent of its range. Drainages to the immediate north of the Aguarico River are poorly sampled, but it seems plausible that the range of *Ch. breve* extends further northward, possibly even into Colombia.

#### ***Chaetostoma carrioni* (Norman, 1935)**

Figure 10; Tables 4, 5, 6

*Lipopterichthys carrioni* Norman, 1935.



**Fig. 10.** Topotypes of *Chaetostoma carrioni* from the Zamora River (Ecuador, Santiago River drainage, Atlantic Slope, ROM 93845\*): (A) 60.2 mm and (B) 56.3 mm SL. Scale bars = 1 cm. Photos by NKL.

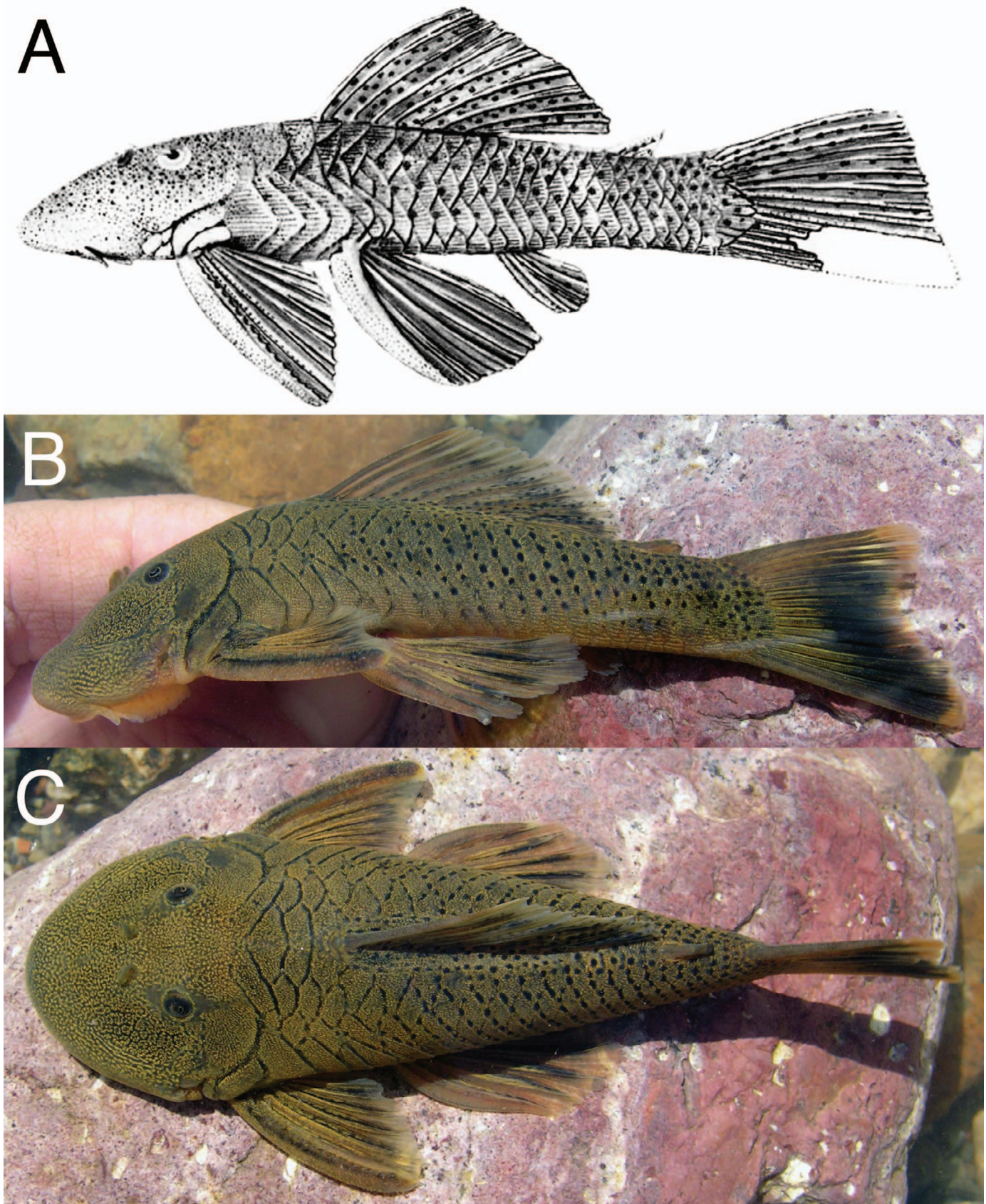
**Holotype.**—BMNH 1933.5.29.1, 78 mm SL, Río Zamora near Loja, upper Amazon River basin, eastern Ecuador.

**Paratypes.**—BMNH 1933.5.29.2–5, 4, same data as holotype.

**Non-type material.**—Ecuador, Santiago River drainage: AUM 4233, 1, Loja Province, tributary to San Lucas River at “El Puente” 33 km N of Loja; ROM 93845\*, 6, 48.0–61.1 mm SL, Zamora-Chinchipec Province, Bomboscara River 2.42 km SE of Zamora, downstream of Podocarpus National Park, 04°05′10.08″S, 78°57′19.50″W; ROM 93877\*, 2, 54.4–72.7 mm SL, Morona-Santiago Province, Yungantza River downstream of bridge S of the town of Limón, 02°58′16.26″S, 78°26′29.88″W.

**Diagnosis.**—*Chaetostoma carrioni* can be diagnosed from all other Amazon Basin *Chaetostoma* by having only 12 branched caudal-fin rays (vs. 14); from all other Amazon Basin species except *Ch. lexa* by lacking an anal fin or (if present) having most frequently one or two branched anal-fin rays (vs. anal fin present, with most frequently three or more branched rays) and by having the adipose fin often absent or rudimentary; from all other Amazon Basin species except *Ch. lobarhynchos*, *Ch. marmorescens*, and *Ch. microps* by having Type 1 cheek odontodes (vs. Types 2–4); from all other Amazon Basin species except *Ch. branickii/taczanowskii*, *Ch. breve*, Urubamba and Madre de Dios populations of *Ch. lineopunctatum* (Fig. 11), and *Ch. microps* by having white, indistinct, irregularly round to vermiculate spots less





**Fig. 11.** Original illustration (A, from Eigenmann and Allen, 1942) and photos (B, C) of *Chaetostoma lineopunctatum*. Photographed specimen from the Ucayali River drainage (Rio Coribeni, ANSP 180442, 80.5 mm SL). Photos by M. H. Sabaj Pérez.

than half naris size spaced two to three spot widths apart on head (vs. head without spots or with black spots); from all other Amazon Basin species except *Ch. breve*, *Ch. carrioni*, *Ch. lexa*, *Ch. lobarhynchus*, *Ch. marmorescens*, and *Ch. microps* by having 11–13 evertible cheek odontodes (vs. typically less than 11 or more than 13); from all other Amazon Basin species except *Ch. branickii/taczanowskii*, *Ch. lexa*, *Ch. lobarhynchus*, *Ch. marmorescens*, and *Ch. microps* by lacking a supraoccipital excrescence (vs. excrescence present); from all other Amazon Basin species except *Ch. changae*, *Ch. jegui*, *Ch. lexa*, *Ch. marmorescens*, and *Ch. microps* by having most frequently nine branched dorsal-fin rays (vs. eight); from all other Amazon Basin species except *Ch. anale*, *Ch. changae*, *Ch. dermorhynchum*, *Ch. lexa*, and *Ch. microps* by exhibiting Type 3 sexual dimorphism of the pelvic fins (vs. lacking Type 3 sexual dimorphism); from all other Amazon Basin species except *Ch. anale*, *Ch. daidalmatos*, *Ch. jegui*, *Ch. marmorescens*, and *Ch. microps* by having an average of  $76 \pm 10$  teeth per mandible (vs. typically less than 66 or greater than 86 teeth); from *Ch. changae*, *Ch. daidalmatos*, *Ch. dermorhynchum*, *Ch. lineopunctatum*, *Ch. stroumpoulos*, *Ch. trimaculineum*, new species, and *Ch. vagum* by having a wider average cleithral width ( $36.3 \pm 1.1\%$  SL, vs.  $<35.2$ ); from *Ch. breve*, *Ch. dermorhynchum*, *Ch. lexa*, *Ch. lineopunctatum*, *Ch. lobarhynchus*, *Ch. trimaculineum*, new species, and *Ch. vagum* by having an average of  $56 \pm 6$  teeth per premaxillary ramus (vs. less than 50 or more than 62 teeth); from *Ch. breve*, *Ch. changae*, *Ch. dermorhynchum*, *Ch. lexa*, *Ch. lobarhynchus*, *Ch. marmorescens*, and *Ch. microps* by having indistinct black spots larger than orbit diameter on body (vs. spots absent or white and naris size or smaller); from *Ch. anale*, *Ch. changae*, *Ch. dermorhynchum*, *Ch. jegui*, and *Ch. stroumpoulos* by lacking Type 4 sexual dimorphism of the paired or anal fin (vs. having Type 4 sexual dimorphism); and from *Ch. breve* by having a lesser head depth ( $24.4 \pm 1.6\%$  SL, vs.  $26.6 \pm 1.2$ ).

**Description.**—Morphometrics in Table 5 and meristics in Table 6. Largest specimen 78.0 mm SL. Body depth increasing from tip of snout to greatest body depth at predorsal plates, decreasing to posterior margin of adipose fin then remaining straight to base of caudal fin. Dorsal profile convex between snout and dorsal-fin origin then straight and descending to base of dorsal fin. Ventral profile flat from snout to base of caudal fin. Ossified dermal plates with small odontodes cover head and body flanks. Plates missing from broad crescent around snout margin and abdomen. Cheek plates having five to 13 slightly enlarged, straight odontodes (Type 1, Fig. 6). Orbit positioned dorso-laterally on head with opening sloped ventrolaterally at approximately  $45^\circ$  from sagittal plane in anterior view. Snout broadly rounded or triangular in dorsal view.

Oral disk occupying majority of ventral surface of head anterior of cleithrum. Teeth minute, bicuspid, with cusps bent  $90^\circ$  toward mouth opening. Digitate papilla generally absent from mouth, very small if present. Maxillary barbel short, adnate along most or all of length; ventral surface of labial disk with low hemispherical papillae decreasing in size distally.

Dorsal-fin spinelet obscured by flesh; posteriormost dorsal-fin ray free from body; reaching to adipose-fin spine when adpressed if adipose fin present. Adipose fin sometimes missing, with spine flush with dorsal ridge of caudal peduncle; if present spine straight, adnate to caudal

peduncle via fleshy membrane. Pectoral fin reaching to posterior pelvic-fin base when adpressed, spine having modestly enlarged odontodes along posterodorsal and distal surfaces. Pelvic-fin spine not reaching anal fin or just reaching anal-fin base when adpressed, if anal fin present. Anal fin typically reduced, sometimes missing; if present, spanning total of one to two plate widths when adpressed. Caudal-fin margin obliquely straight or slightly rounded with ventral spine slightly longer than dorsal spine.

Body broadest at cleithrum; posterior margin of exposed posterior process of cleithrum rounded or straight. First three to four midventral plates gently bent forming rounded lateral ridge between verticals through pectoral and pelvic-fin origins.

**Coloration in life.**—Base color of head dark gray with white, indistinct, irregularly round to vermiculate spots; spots less than half size of naris and spaced two to three spot widths apart. Body base color light gray with black, indistinct, round spots; spots orbit diameter or larger and spaced one spot width apart; spots absent or faded anteriorly and increasingly distinct posteriorly; irregularly distributed. Dorsal-, paired-, and caudal-fin coloration variable, often with indistinct black bands width of orbit or smaller. Distinct black spot present along anterior base of dorsal fin, between second unbranched and first branched ray.

**Coloration in preservative.**—Uniformly dark gray with some banding apparent in fins.

**Sexual dimorphism.**—Mature males with elongated proximal, branched pelvic-fin rays so that proximomedial posterior pelvic-fin margin is elongated into a lobe (Type 1 dimorphism); posterodorsal margin of pelvic-fin spine with modest dermal fold (Type 2 dimorphism); low fin folds also along dorsal surface of branched pelvic-fin rays (Type 3 dimorphism). Mature males also often display some enlargement of the unplated, fleshy snout region.

**Distribution.**—*Chaetostoma carrioni* is known only from headwaters of the Santiago River drainage in southeastern Ecuador (Fig. 9C), although additional records in the Marañon River drainage of northern Peru would not be surprising.

**Remarks.**—*Chaetostoma carrioni* was originally assigned to the then new genus *Lipopterichthys* by Norman (1935) based on the absence of adipose and anal fins from the type series. These and other morphological characters were assessed in a phylogenetic analysis by Salcedo (2013), which found support for continued recognition of *Lipopterichthys* as a valid genus. However, recently collected topotypes (ROM 93845\*) revealed continuous gradation in the development of the adipose and anal fins. Comparison of live specimens also showed striking similarities between *Ch. carrioni* (Fig. 10) and *Ch. microps* (Fig. 5), which is consistent with the sister relationship found for these species in our molecular phylogenetic analysis.

#### ***Chaetostoma dermorhynchum* Boulenger, 1887**

Figure 3; Tables 4, 7, 8

**Syntypes.**—BMNH 1880.12.8.64–66, 3, Bobonaza River at Canelos, eastern Ecuador.

**Table 7.** Selected morphometric characters and tooth counts for *Chaetostoma dermorhynchum* Boulenger, 1887 (syntype: BMNH 1880.12.8.64–66), *Chaetostoma microps* Günther, 1864 (syntypes: BMNH 1860.6.16.137–143), and *Chaetostoma trimaculineum*, new species. Interlandmarks (ILM) are the two points between which measurements were taken (from Armbruster, 2003). Morphometric characters other than standard length presented as percents of either standard length or head length. Abbreviations: Min = minimum value, Max = maximum value,  $n$  = number of specimens examined, StDev = standard deviation.

ILM	Measurement	<i>Chaetostoma dermorhynchum</i> Boulenger, 1887						<i>Chaetostoma microps</i> Günther, 1864						<i>Chaetostoma trimaculineum</i> , new species						
		Syntype	$n$	Mean	StDev	Min	Max	Syntype	Syntype	$n$	Mean	StDev	Min	Max	Holotype	$n$	Mean	StDev	Min	Max
1–20	Standard length (mm)	107.3	11			68.4	107.3	43.7	62.3	26			28.8	78.2	128.1	4			68.4	128.1
	<b>Percents of standard length</b>																			
1–10	Predorsal length	41.3	11	41.6	0.6	40.7	42.3	44.8	43.7	26	43.7	2.0	40.9	49.4	41.9	4	40.8	1.4	38.8	41.9
1–7	Head length	31.2	11	32.1	0.6	31.2	33.1	34.3	31.8	26	32.3	2.6	24.7	37.1	31.4	4	30.6	1.4	28.5	31.5
7–10	Head-dorsal length	10.4	11	10.0	0.4	9.3	10.7	12.2	11.7	26	12.3	1.3	9.4	15.4	11.2	4	10.7	0.4	10.4	11.2
8–9	Cleithral width	32.4	11	31.4	0.8	30.2	32.8	38.5	35.2	26	34.6	2.0	31.5	38.5	33.4	4	31.7	1.2	30.6	33.4
1–12	Head-pectoral length	26.8	11	26.0	0.8	24.4	27.0	29.7	28.0	26	28.7	1.6	25.7	32.3	26.7	4	28.0	1.2	26.7	29.0
12–13	Thorax length	21.3	11	21.6	1.4	19.8	23.7	25.4	23.3	26	24.2	1.5	21.8	27.5	21.7	4	21.9	0.7	21.1	22.6
12–29	Pectoral-spine length	31.6	11	28.2	1.5	25.5	31.6	28.8	29.1	26	29.6	1.9	26.8	34.4	30.6	4	28.9	1.3	27.6	30.6
13–14	Abdominal length	24.0	11	24.3	0.6	23.5	25.3	27.7	28.8	26	26.4	1.7	23.6	29.8	25.4	4	25.1	0.5	24.3	25.4
13–30	Pelvic-spine length	28.2	11	26.7	1.4	24.5	29.0	27.7	24.7	26	26.0	2.7	22.2	31.8	24.8	4	25.6	1.2	24.4	26.8
14–15	Postanal length	35.9	11	35.6	1.1	33.9	37.5	31.1	27.1	26	31.9	1.8	27.1	35.5	32.7	4	32.6	0.3	32.3	33.0
14–31	Anal-fin spine length	10.9	11	11.4	0.9	10.4	13.1	10.0	7.2	26	7.8	1.4	4.7	10.5	11.7	4	11.2	0.6	10.5	11.7
7–12	Head depth	21.7	11	22.5	0.6	21.7	23.6	25.3	22.5	26	24.8	1.4	22.5	29.0	23.1	4	23.3	0.2	23.1	23.7
10–12	Dorsal-pectoral depth	25.7	11	27.2	0.7	25.7	28.5	29.7	26.5	26	30.1	1.6	26.5	33.2	28.6	4	28.6	0.5	27.9	29.2
10–11	Dorsal spine length	34.3	11	31.4	1.3	29.6	34.3	26.6	25.9	26	24.3	2.4	19.5	28.1	29.9	4	21.1	14.1	0.0	29.9
10–13	Dorsal-pelvic depth	21.6	11	22.0	0.7	20.8	23.2	18.9	18.5	26	20.3	1.6	17.2	24.3	24.3	4	23.5	1.5	21.5	24.9
10–16	Dorsal-fin base length	27.1	11	26.4	0.8	24.7	27.4	28.6	31.8	26	29.8	2.3	24.9	35.2	26.0	3	25.7	0.3	25.2	26.0
16–17	Dorsal-adipose depth	16.9	11	16.8	0.5	16.1	17.7	11.9	13.5	26	14.1	2.2	11.1	18.4	19.3	4	16.7	1.7	15.5	19.3
17–18	Adipose-spine length	10.4	11	9.6	0.6	8.6	10.6	5.1	5.6	26	8.2	2.9	5.1	15.9	7.2	4	9.0	1.4	7.2	10.6
17–19	Adipose-upper caudal length	16.6	11	17.5	0.5	16.6	18.4	14.7	13.6	26	15.2	2.3	12.0	21.0	15.3	4	14.3	1.8	12.3	16.3
15–19	Caudal peduncle depth	14.3	11	14.2	0.4	13.7	15.1	12.5	12.2	26	13.0	0.7	11.9	14.6	14.1	4	15.2	0.8	14.1	16.1
15–17	Adipose-lower caudal depth	24.6	11	24.5	0.6	23.9	25.8	21.7	19.2	26	21.4	1.5	19.2	25.4	22.5	4	24.0	1.3	22.5	25.6
14–17	Adipose-anal depth	22.4	11	21.4	1.8	16.3	22.6	20.3	16.1	26	19.2	1.5	16.1	23.3	23.3	4	22.0	1.4	20.7	23.3
14–16	Dorsal-anal depth	16.6	11	16.6	0.5	16.0	17.6	17.2	13.3	26	14.1	1.2	11.0	17.2	17.4	4	17.6	0.4	17.2	18.2
13–16	Pelvic-dorsal depth	25.4	11	27.9	1.4	25.4	30.2	30.7	26.8	26	29.1	2.1	24.7	33.5	29.0	4	29.7	1.5	28.5	31.8
	<b>Percents of head length</b>																			
5–7	Head-eye length	27.3	11	28.4	1.1	26.0	29.8	33.2	33.6	26	32.1	2.5	28.3	41.5	29.6	4	30.9	1.4	29.6	32.8
4–5	Orbit diameter	19.8	11	17.6	1.2	16.1	19.8	18.0	14.1	26	15.9	1.6	11.2	20.1	14.4	4	16.0	1.5	14.4	17.8
1–4	Snout length	68.5	11	64.2	2.7	59.8	68.5	63.5	64.0	26	63.9	4.5	55.9	81.3	65.7	4	64.6	1.3	62.7	65.7
2–3	Internares width	12.0	11	10.7	0.7	9.3	12.0	10.5	9.7	26	10.3	1.7	7.7	16.3	11.9	4	15.3	3.1	11.9	18.0
5–6	Interorbital width	29.5	11	28.8	1.2	27.5	30.9	32.1	31.2	26	32.4	2.8	27.5	42.2	31.5	4	47.9	11.0	31.5	54.3
1–24	Mouth length	49.9	11	52.3	2.5	47.5	56.5	62.7	65.2	26	61.0	6.2	44.7	69.9	56.2	4	58.6	1.8	56.2	60.3
21–22	Mouth width	78.6	11	76.5	2.9	70.5	79.5	83.3	83.5	26	87.3	8.3	74.2	113.5	89.5	4	82.5	5.3	77.3	89.5
22–23	Barbel length	13.5	11	9.6	2.0	7.3	13.5	12.9	8.5	26	11.1	4.3	4.0	24.1	6.3	4	10.1	2.6	6.3	12.0
25–26	Dentary tooth cup length	36.6	11	33.2	2.3	30.9	36.9	36.5	28.6	26	32.1	3.2	25.2	39.2	37.2	4	35.5	1.7	33.8	37.2
27–28	Premax. tooth cup length	31.0	11	28.2	2.0	26.3	31.5	29.5	26.3	26	27.6	2.0	23.5	31.7	31.7	4	30.9	0.9	29.8	31.7
	<b>Tooth counts</b>																			
	Left premaxillary teeth	95	11	105	14	86	126	20	35	26	49	18	20	90	147	4	100	31	83	147
	Left dentary teeth	108	11	131	14	108	160	37		26	80	23	37	133	201	4	138	44	105	201

**Table 8.** Selected meristic characters for *Chaetostoma dermorhynchum* Boulenger, 1887 (syntype: BMNH 1880.12.8.64–66), *Chaetostoma microps* Günther, 1864 (syntypes: BMNH 1860.6.16.137–143), and *Chaetostoma trimaculineum*, new species. Abbreviations: Min = minimum value, Max = maximum value, *n* = number of specimens examined.

	<i>Chaetostoma dermorhynchum</i> Boulenger, 1887					<i>Chaetostoma microps</i> Günther, 1864					<i>Chaetostoma trimaculineum</i> , new species					
	Syntype	<i>n</i>	Mode	Min	Max	Syntype	Syntype	<i>n</i>	Mode	Min	Max	Holotype	<i>n</i>	Mode	Min	Max
Median plates	22	11	23	22	24	22	24	26	23	20	24	24	4	24	24	24
Supramedian plates	24	11	24	24	24	23	23	26	22	21	23	24	4	24	24	24
Inframedian plates	25	11	24	23	25	25	23	26	22	21	25	24	4	24	24	24
Caudal peduncle plate rows	5	11	5	5	5	5	5	26	5	4	6	5	4	5	5	5
Dorsal-fin branched rays	8	11	8	8	8	9	9	26	9	8	10	8	4	8	8	8
Pectoral-fin branched rays	6	11	6	6	6	6	6	26	6	6	6	6	4	6	6	6
Pelvic-fin branched rays	5	11	5	5	5	5	5	26	5	5	5	5	4	5	5	5
Anal-fin branched rays	4	11	4	4	4	3	2	26	3	2	3	4	4	4	4	4
Caudal-fin branched rays	14	11	14	14	14	14	14	26	14	8	14	14	4	14	14	14
Dorsal procurvent caudal-fin rays	4	11	5	4	5	4	3	26	5	3	6	5	4	4	4	5
Ventral procurvent caudal-fin rays	4	11	3	2	5	3	3	26	2	1	3	2	4	2	2	2
Preadipose plates	1	11	1	1	1	2	1	26	1	1	2	1	4	1	1	1
Dorsal–adipose plates	6	11	6	5	6	4	5	26	4	4	6	6	4	5	5	6
Infraorbital plates	5	11	5	5	6	5	5	26	5	4	6	5	4	5	5	5
Cheek odontodes	4	11	3	2	5	20	16	26	9	5	20	5	4	4	4	5

**Non-type material.**—Ecuador, Pastaza River drainage, Pastaza Province: ROM 93946, 17, 69.1–95.2 mm SL, Bobonaza River 1.5 km W of Canelos downstream of bridge, 01°35'26.28"S, 77°45'38.40"W; ROM 93656\*, 22, 80.6–182.1 mm SL, Puyo River upstream of confluence with Pastaza River, 20.4 km SSE of Puyo, 01°39'10.02"S, 77°55'28.02"W. Napo River drainage, Napo Province: ROM 93952, 4, 78.8–100.1 mm SL, Napo River near Tena, 01°02'38.08"S, 77°47'34.68"W.

**Diagnosis.**—*Chaetostoma dermorhynchum* can be diagnosed from all other Amazon Basin *Chaetostoma* by having four to five rows of white to gray indistinct round spots the diameter of the orbit or larger on the body (vs. spots absent, black, or diameter of naris or smaller); from all other Amazon Basin species except *Ch. changae* by having up to ten distinct or indistinct white spots less than half naris diameter on each branched dorsal-fin ray or interradial membrane (vs. dorsal-fin spots absent, black, or much fewer in series); from all other Amazon Basin species except *Ch. anale*, *Ch. changae*, *Ch. jegui*, and *Ch. stroumpoulos* by exhibiting Type 4 sexual dimorphism of the pelvic and anal fins (vs. lacking Type 4 sexual dimorphism); from all other Amazon Basin species except *Ch. anale*, *Ch. daidalmatos*, lower Ucayali populations of *Ch. lineopunctatum*, *Ch. stroumpoulos*, *Ch. trimaculineum*, new species, and *Ch. vagum* by having distinct, black, round, naris-sized spots evenly distributed one spot width apart on the head (vs. spots absent or white); from *Ch. anale*, *Ch. carrioni*, *Ch. changae*, *Ch. daidalmatos*, *Ch. lexa*, *Ch. marmorescens*, and *Ch. microps* by having more teeth per premaxillary ramus (an average of  $105 \pm 14$ , vs.  $< 91$ ); from *Ch. breve*, *Ch. carrioni*, *Ch. lexa*, *Ch. lineopunctatum*, *Ch. lobo-rhynchos*, *Ch. marmorescens*, and *Ch. microps* by having lesser cleithral width ( $31.4 \pm 0.8\%$  SL, vs.  $> 32.3$ ); from *Ch. anale*, *Ch. carrioni*, *Ch. daidalmatos*, *Ch. lexa*, *Ch. marmorescens*, *Ch.*

*microps*, and *Ch. vagum* by having more teeth per mandible (an average of  $131 \pm 14$ , vs.  $< 117$ ); from *Ch. branickii/taczanowskii*, *Ch. carrioni*, *Ch. lexa*, *Ch. microps*, *Ch. lobo-rhynchos*, and *Ch. marmorescens* by having a supraoccipital excrescence (vs. excrescence absent); from *Ch. breve*, *Ch. carrioni*, *Ch. jegui*, *Ch. lexa*, and *Ch. microps* by having Type 2 cheek odontodes (vs. Types 1, 3, or 4); from *Ch. changae*, *Ch. jegui*, *Ch. lexa*, *Ch. marmorescens*, and *Ch. microps* by having eight branched dorsal-fin rays (vs. most frequently nine or more); from *Ch. carrioni*, *Ch. lexa*, *Ch. microps*, and *Ch. marmorescens* by having four branched anal-fin rays (vs. anal fin absent or having most frequently three or fewer branched rays); from *Ch. changae*, *Ch. lineopunctatum*, and *Ch. microps* by having lesser head depth ( $22.5 \pm 0.6\%$  SL, vs.  $> 23.1$ ); and from *Ch. branickii/taczanowskii* and *Ch. lexa* by having four or five evertible cheek odontodes (vs. six or more).

**Description.**—Morphometrics in Table 7 and meristics in Table 8. Largest specimen 182.1 mm SL. Body depth increasing from tip of snout to greatest body depth at predorsal plates or dorsal-fin origin, decreasing to posterior margin of adipose fin then increasing slightly to base of caudal fin. Dorsal profile convex between snout and dorsal-fin origin then straight and descending to base of dorsal fin. Ventral profile flat from snout to base of caudal fin. Ossified dermal plates with small odontodes cover head and body flanks. Plates missing from broad crescent around snout margin and abdomen. Cheek plates having two to five slightly enlarged, gently curved odontodes (Type 2, Fig. 6). Cheek odontodes typically obscured by thick fleshy lobe. Orbit positioned dorsolaterally on head with opening sloped ventrolaterally at approximately 45° from sagittal plane in anterior view. Snout broadly rounded in dorsal view.

Oral disk occupying majority of ventral surface of head anterior of cleithrum. Teeth minute, bicuspid, with cusps bent 90° toward mouth opening. Single digitate papilla extending ventrally from dorsal part of premaxillary symphysis; clusters of low papillae at middle of interior surface of each premaxilla and mandible, mandibular clusters larger. Maxillary barbel short, adnate or free along most of length; ventral surface of labial disk with low hemispherical papillae decreasing in size distally.

Dorsal-fin spinelet small and round, sometimes covered with flesh; posteriormost dorsal-fin ray free from body; reaching to within one plate width from adipose-fin spine when adpressed. Pectoral fin reaching to or beyond pelvic-fin base when adpressed, spine having modestly enlarged odontodes along posterodorsal and distal surfaces. Pelvic-fin spine reaching middle of anal-fin base when not sexually mature, well beyond anal-fin base when sexually mature. Second unbranched anal-fin ray longest; anal fin spanning four and a half plate widths when not sexually mature, almost to caudal fin when sexually mature. Adipose-fin spine straight, adnate to caudal peduncle via fleshy membrane. Caudal-fin margin obliquely straight or slightly emarginate with ventral lobe slightly longer than dorsal lobe.

Body broadest at cleithrum; posterior margin of exposed posterior process of cleithrum rounded or pointed. First one to three midventral plates gently bent forming rounded lateral ridge between verticals through pectoral- and dorsal-fin origins.

**Coloration in life.**—Base color of head light to dark gray with black, distinct, round spots; spots size of naris, evenly distributed one spot width apart. Body base color darker gray than head with white to light gray indistinct round spots; spots diameter of orbit and arranged in four to five horizontal rows from pelvic to caudal fin; spots more distinct caudally, fading to absent anteriorly. Dorsal fin with up to 10 distinct or indistinct white spots aligned with rays but present on rays and/or membranes; spots less than half diameter of naris; spots more distinct in juveniles. Paired fins uniformly gray.

**Coloration in preservative.**—Preserved individuals distinguished by retention of black spots on head and light gray spots on dorsal fin; body and paired fins uniformly dark gray to black.

**Sexual dimorphism.**—Mature males with elongated proximal, branched pelvic-fin rays so that proximomedial posterior pelvic-fin margin is elongated into a lobe (Type 1 dimorphism); posterodorsal margin of pelvic-fin spine with dermal fold (Type 2 dimorphism); low fin folds also along dorsal surface of branched pelvic-fin rays (Type 3 dimorphism); and unbranched pelvic- and anal-fin rays elongated as short filaments (Type 4 dimorphism). Mature males also display enlargement of the unplated, fleshy snout region and an overall decrease in color pattern contrast (Fig. 3B).

**Distribution.**—*Chaetostoma dermorhynchum* is known only from the Pastaza and Napo river drainages in Ecuador (Fig. 9C), although it likely also occurs in lower reaches of both rivers in Peru.

**Remarks.**—*Chaetostoma dermorhynchum* is a member of the *Ch. anale* species group (i.e., *Ch. anale*, *Ch. formosae*, *Ch.*

*jegui*; Fig. 2, Clade F), defined by Ballen (2011) as having the second unbranched anal-fin ray in mature males enlarged and bearing two posterior fleshy ridges. The type specimens represent immature individuals. Intriguingly, all 17 specimens (ROM 93946) collected from the type locality in the upper Bobonaza River (a tributary of the Pastaza River) during this study were also at an immature developmental stage similar to the types (Fig. 3A). In contrast, all 22 specimens (ROM 93656\*) collected from a nearby main channel of the Pastaza River exhibited extreme sexual dimorphisms of the snout and pelvic fins (Fig. 3B), even at body sizes similar to individuals at the headwater site (although individuals at the main channel site were on average larger than individuals at the headwater site).

Despite the morphological distinctiveness of individuals from the main channel site, mitochondrial and nuclear genes sequenced from individuals at both localities were invariant, confirming their conspecificity. The concentration of immature individuals in a headwater habitat and adults in a main channel habitat suggests that either A) there is some degree of migratory behavior in this species, a behavior otherwise unknown in the Loricariidae outside of the Rineleptinae, B) that sexual dimorphism in this species is seasonal and that the headwater population was out of sync with the main channel population, or C) that the headwater population is in some way pedomorphic and does not develop sexual dimorphisms present in adults of the main channel population.

#### ***Chaetostoma microps* Günther, 1864**

Figures 5, 12; Tables 4, 7, 8

*Chaetostoma mollinasum* Pearson, 1937.

**Syntypes.**—BMNH 1860.6.16.137-143, 7, Andes of western Ecuador.

**Non-type material.**—Ecuador, Napo River drainage, Orellana Province: ROM 93948, 19, 43.8–73.8 mm SL, Talag River ~200 m upstream of confluence with Napo River, 10.8 km SSW of Tena, 01°04'08.76"S, 77°51'42.36"W; ROM 93949\*, 60, 35.5–72.1 mm SL, Tena River at bridge crossing 9.3 km NW of Tena, 00°55'30.54"S, 77°52'33.00"W. Pastaza River drainage, Morona-Santiago Province: ROM 93928, 12, 35.0–57.5 mm SL, Amundalo River 10.3 km WSW of Palora, 01°44'54.90"S, 78°02'39.78"W. Pastaza Province: ROM 93938, 8, 44.9–60.5 mm SL, Puyo River upstream of confluence with Pastaza River, 20.4 km SSE of Puyo, 01°39'10.02"S, 77°55'28.02"W; ROM 93947, 3, 50.5–52.2 mm SL, Bobonaza River 1.5 km W of Canelos downstream of bridge, 01°35'26.28"S, 77°45'38.40"W; USNM 163925, 1, 64.4 mm SL, Bobonaza River at Pacayacu, 02°03'S, 76°59'W. Santiago River drainage, Morona-Santiago Province: ROM 93884, 1, 64.3 mm SL, Yungantza River at bridge crossing on road between Santiago and Mendez, just upstream of confluence with Santiago River, 02°58'56.16"S, 78°13'36.12"W; ROM 93895\*, 2, 35.6–56.5 mm SL, confluence of the Changachangasa and Tutanangosa rivers and upstream in both, 02°35'51.18"S, 78°11'10.38"W; ROM 93902, 15, 41.5–76.7 mm SL, Yumbiza River at bridge crossing 42.4 km S of Macas on Shuar reservation, 02°41'33.48"S, 78°11'07.20"W; ROM 93905, 3, 49.4–60.0 mm SL, Domono River at dirt road fork 15 km N of Macas, 02°10'56.82"S, 78°05'41.34"W; ROM 93913, 12,

37.4–73.3 mm SL, Copueno River at major bridge crossing 1.6 km S of Macas, 02°18'05.76"S, 78°06'46.04"W. Peru, Marañon River drainage, Amazonas Region: AUM 45518\*, 40, 61.8–78.2 mm SL, Almendro River 50.1 km NNE of Bagua Grande, 121 km NNW of Chachapoyas, 10.1 km S of Chiriaco, 05°14'40.60"S, 78°21'40.00"W; AUM 45525, 100, Quebrada Siasme at Nuevo Siasme, 04°41'21.77"S, 77°48'34.74"W; AUM 45530, 6, Cenepa River at Tsantsa gravel bar, 58 km N of Imacita, 04°33'37.76"S, 78°11'07.08"W; AUM 45534, 5, 43.6–55.1 mm SL, Quebrada Shaapan at Tutino, 57 km N of Imacita, 04°34'37.06"S, 78°11'27.64"W; AUM 45566, 3, Nieva River 7.4 km SSW of Juan Velasco (Sta Maria de Nieva), 04°39'38.45"S, 77°53'02.00"W; AUM 45622, 9, Marañon River at Imacita, 05°03'28.98"S, 78°20'06.43"W; AUM 46516, 1, Utcubamba River 23 km SE of Bagua Chica, 05°46'32.34"S, 78°22'28.74"W; MUSM 19111, Santiago River drainage, CCNN Soledad, Quebrada Soledad, 03°30'47.42"S, 77°46'06.17"W. Cajamarca Region: AUM 45514, 7, 28.8–38.5 mm SL, Huancabamba River 47 km ENE of Olmos, 98.2 km W of Bagua, 05°46'33.49"S, 79°22'35.77"W. Huallaga River drainage, Huánuco Region, Leoncio Prado Province, José Crespo y Castillo District: MHNG 2712.054, 4, Aucayacu River (RFC 10), 08°55'18.30"S, 76°06'35.30"W; MHNG 2712.058, 7, Aucayacu River (RFC 10), 08°55'18.30"S, 76°06'35.30"W; MUSM 35709, Aucayacu River, 08°55'43.87"S, 76°06'11.78"W; MUSM 40999, Quebrada Santa Clara, 09°38'25.86"S, 75°50'40.84"W. San Martín Region: MUSM 35460, 3, 45.9–51.7 mm SL, Uchiza River; MUSM 35463, 4, 51.8–69.7 mm SL, Pacota River; MUSM 35464, 1, 33.5 mm SL, Cashiyacu River at Santa Ana; MUSM 35465, 1, 32.8 mm SL, Quebrada Shapaja. Huánuco Region: MUSM 35466, 1, 56.1 mm SL, Aucayacu River; MUSM 44228, 2, 56.0 and 56.6 mm SL, Derrepente River, 09°29'13.53"S, 75°57'34.35"W; MUSM 44313, Quebrada Oro, 09°20'07.99"S, 76°02'42.35"W; MUSM 44314, same data as MUSM 44313. Tocache Province, Nuevo Progreso District: MHNG 2712.062, 1, Pacota River, tributary of Uchiza River (RFC 14), 08°23'56.30"S, 76°18'30.20"W; MHNG 2712.065, 1, Rio Huantanamo, affluent du Rio Huainabe (RFC 15), 08°21'57.20"S, 76°15'47.60"W. Uchiza District: MHNG 2712.070, 3, Santa Rosa de Cachiyacu River (RFC 20), 08°14'16.50"S, 76°24'16.50"W; MHNG 2712.072, 7, Shapaja River (RFC 22), 08°17'41.10"S, 76°21'49.90"W; MHNG 2712.076, 14, Tocache River (RFC 23), 08°10'07.5"S, 76°32'32.5"W; MUSM 35825, Tocache River; MUSM 35906, Mantencion River. Tingo Maria District: MHNG 2712.046\*, 2, Monzon River at confluence with Quebrada Bella, downstream of Tingo Maria (RFC 06), 09°19'22.90"S, 76°01'50.90"W.

**Diagnosis.**—*Chaetostoma microps* can be diagnosed from all other Amazon Basin *Chaetostoma* by having distinct round or vermiculate white, yellow, or blue spots less than half diameter of naris three or more spot widths apart, clustered anterodorsally on the body (vs. spots absent, black, or orbit size or larger); from all other Amazon Basin species except *Ch. carrioni* by having distinct round or vermiculate spots less than half diameter of naris spaced three or more spot widths apart on head (vs. spots on head absent, black, or less than one spot width apart); from all other Amazon Basin species except *Ch. carrioni*, *Ch. lobarhynchos*, and *Ch. marmorescens* by having Type 1 cheek odontodes (vs. Types 2–4); from all other Amazon Basin species except

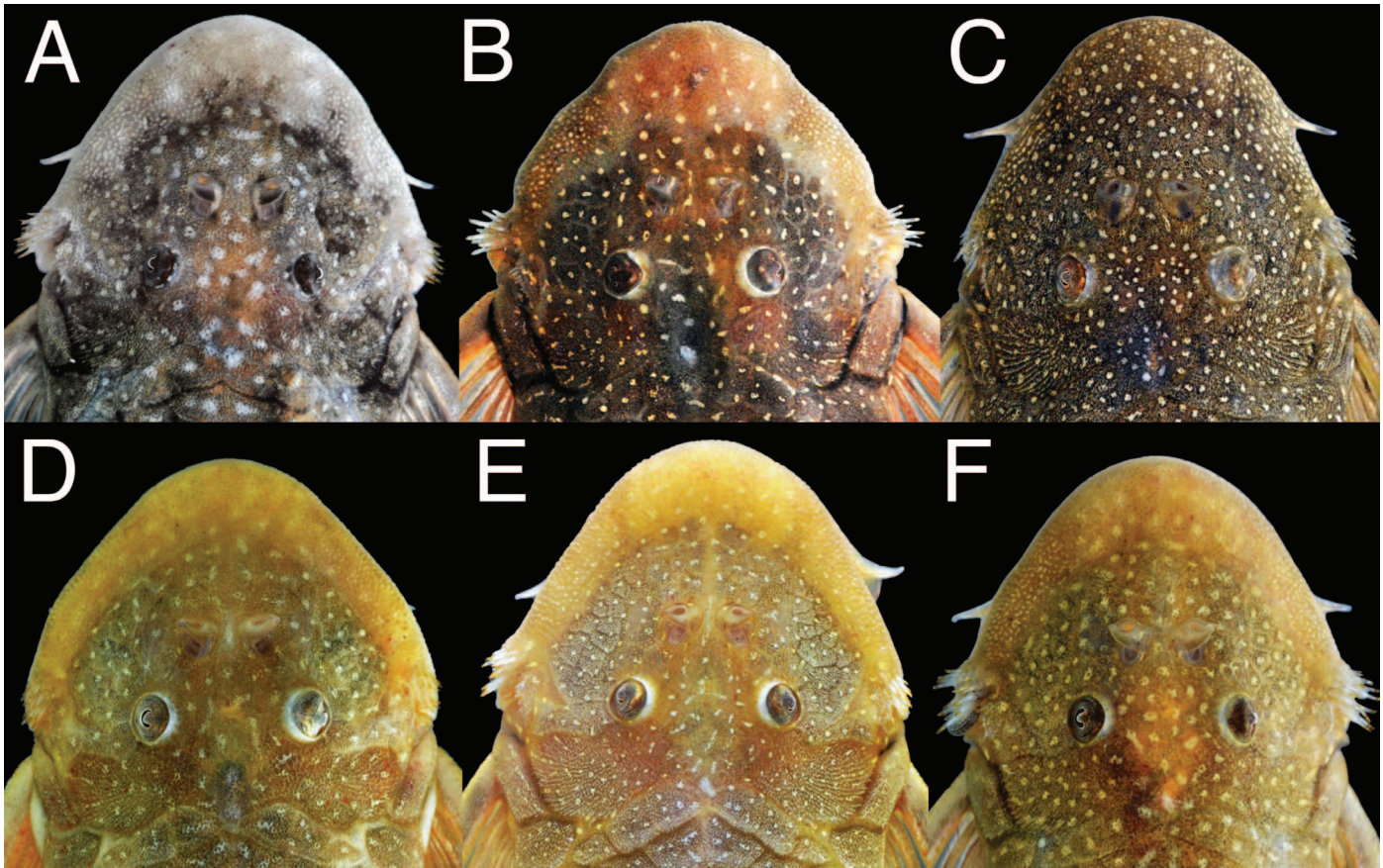
*Ch. carrioni*, *Ch. jegui*, *Ch. lexa*, and *Ch. marmorescens* by having fewer anal-fin rays (most frequently three, sometimes two, vs. most frequently four or five); from all other Amazon Basin species except *Ch. changae*, *Ch. jegui*, *Ch. lexa*, and *Ch. marmorescens* by having more branched dorsal-fin rays (most frequently nine, sometimes 10, vs. most frequently eight); from all other Amazon Basin species except *Ch. branickii/taczanowskii*, *Ch. carrioni*, *Ch. lexa*, *Ch. lobarhynchos*, and *Ch. marmorescens* by lacking a supraoccipital excrescence (vs. excrescence present); from all other Amazon Basin species except *Ch. branickii/taczanowskii*, *Ch. breve*, *Ch. carrioni*, *Ch. lobarhynchos*, *Ch. marmorescens*, and *Ch. microps* by having more evertible cheek odontodes (nine to 15, vs. eight or less); from *Ch. breve*, *Ch. dermorhynchum*, *Ch. lineopunctatum*, *Ch. lobarhynchos*, *Ch. trimaculineum*, new species, and *Ch. vagum* by having fewer teeth per premaxillary ramus ( $49 \pm 17$ , vs.  $>66$ ) and per mandible ( $78 \pm 23$ , vs.  $>101$ ); from *Ch. branickii/taczanowskii*, *Ch. daidalmatos*, *Ch. jegui*, *Ch. stroumpoulos*, *Ch. trimaculineum*, new species, and *Ch. vagum* by exhibiting Type 1 sexual dimorphism (vs. Type 1 dimorphism absent); from *Ch. daidalmatos*, *Ch. dermorhynchum*, and *Ch. trimaculineum*, new species, by having greater head depth ( $25.0 \pm 1.5\%$  SL, vs.  $<23.5$ ); and from *Ch. daidalmatos* and *Ch. dermorhynchum* by having greater cleithral width ( $34.5 \pm 2.1$ , vs.  $<32.4$ ).

**Description.**—Morphometrics in Table 7 and meristics in Table 8. Largest specimen 78.2 mm SL. Body depth increasing from tip of snout to greatest body depth at predorsal plates, decreasing to posterior margin of adipose fin then increasing slightly to base of caudal fin. Dorsal profile convex between snout and dorsal-fin origin then straight and descending to base of dorsal fin. Ventral profile flat from snout to base of caudal fin. Ossified dermal plates with small odontodes cover head and body flanks. Plates missing from broad crescent around snout margin and abdomen. Cheek plates having five to 20 slightly enlarged, straight odontodes (Type 1, Fig. 6). Orbit positioned dorsolaterally on head with opening sloped ventrolaterally at approximately 45° from sagittal plane in anterior view. Snout broadly and roundly triangular in dorsal view.

Oral disk occupying majority of ventral surface of head anterior of cleithrum. Teeth minute, bicuspid, with cusps bent 90° toward mouth opening. Digitate papilla generally absent from mouth, very small if present. Maxillary barbel short, adnate along most of length; ventral surface of labial disk with low hemispherical papillae decreasing in size distally.

Dorsal-fin spinelet typically covered by skin; posterior-most dorsal-fin ray free from body; reaching to within one plate width from adipose-fin spine when adpressed. Pectoral fin reaching to or beyond pelvic-fin base when adpressed, spine having modestly enlarged odontodes along posterodorsal and distal surfaces. Pelvic-fin spine reaching origin of anal fin when adpressed. Second unbranched anal-fin ray longest; anal fin spanning total of two to three and a half plate widths when adpressed. Adipose-fin spine straight, adnate to caudal peduncle via fleshy membrane. Caudal-fin margin obliquely straight with ventral spine slightly longer than dorsal.

Body broadest at cleithrum; posterior margin of exposed posterior process of cleithrum rounded. First two to three midventral plates gently bent forming rounded lateral ridge between verticals through pectoral- and dorsal-fin origins.



**Fig. 12.** *Chaetostoma microps* head shape and color variation found in populations from the: Napo (A, D, E, F), and Santiago (B, C; type locality) river drainages of Ecuador (A, F: ROM 93949\*; B: ROM 93902, C: ROM 93895\*, D: ROM 93948, E: ROM 93948). Photos by NKL.

**Coloration in life.**—Base color of head light to dark gray, brown, or golden yellow (Fig. 12) with white, light blue, or yellow distinct, round to vermiculate spots; spots less than half diameter of naris, spaced three or more spot widths apart. Body base color light to dark gray, brown, or golden yellow (Fig. 5) with white, light blue, or yellow distinct, round to vermiculate spots; spots less than half diameter of naris, spaced three or more spot widths apart; spots restricted to anterodorsal region in front of and below dorsal fin and above inframedian plate series, remainder of body uniform. Dorsal and paired fins uniform or irregularly and indistinctly banded. Distinct black spot approximately diameter of naris present along anterior base of dorsal fin, between second unbranched and first branched ray.

**Coloration in preservative.**—Head and body uniformly light to dark gray or with faint spotting on head and anterior body, indistinct banding on fins usually apparent.

**Sexual dimorphism.**—Mature males with elongated proximal, branched pelvic-fin rays so that proximomedial posterior pelvic-fin margin is elongated into a lobe (Type 1 dimorphism); posterodorsal margin of pelvic-fin spine with modest dermal fold (Type 2 dimorphism); low fin folds also along dorsal surface of branched pelvic-fin rays (Type 3 dimorphism). Mature males also often display some enlargement of the unplated, fleshy snout region. Within some populations, the base color of a few males may also shift to a golden yellow (Fig. 5A, Fig. 12D–F).

**Distribution.**—*Chaetostoma microps* is widespread across headwaters of the Amazon River basin in Ecuador and Peru, from the Napo and Pastaza river drainages in the north to the Huallaga River drainage in the south (Fig. 9B). *Chaetostoma microps* is not currently known from the Ucayali River drainage in the south or from north of the Napo River drainage. It seems unlikely, given the amount of sampling that has occurred in the Ucayali, that *Ch. microps* exists there but remains undetected, and more likely that the Huallaga River drainage forms the southernmost extent of its range. Recent sampling by the first author in the Aguarico River drainage (a northern tributary of the Napo River in northern Ecuador) yielded no specimens of *Ch. microps*, but rather a species of *Chaetostoma* that has a fully plated snout (allied with *Ch. platyrhyncha*) but otherwise very similar morphology, coloration, and size to *Ch. microps*. This suggests that the Napo River proper is the northernmost limit to the range of this species.

***Chaetostoma trimaculineum*, new species**

urn:lsid:zoobank.org:act:4FDC535F-4E71-4A6A-9F31-5428BBECE361

Figures 13, 14; Tables 4, 7, 8

**Holotype.**—MEPN 14688 (ex. ROM 93894\*), 127.1 mm SL, Ecuador, Santiago River drainage, Morona-Santiago Province, confluence of the Changachangasa and Tutanangosa rivers and upstream in both, 02°35'51.18"S, 78°11'10.38"W, 6 September 2012, N. Lujan, D. Taphorn, V. Meza, A. Jackson, V. Roman (seine crew), two local fishermen (castnet).



**Fig. 13.** Lateral views of *Chaetostoma trimaculineum*, new species. (A) Holotype from the Santiago River drainage (ROM 93894\*, 127.1 mm SL) and (B) paratype from the Marañón River drainage (AUM 45524\*, 77.2 mm SL). Scale bar = 1 cm. Photos by NKL.

**Paratypes.**—Ecuador, Santiago River drainage, Zamora-Chinchipe Province: MEPN 11662, 1, Quebrada Nayumbe, tributary of Nangaritza River, 04°11'20"S, 78°36'26"W, 24 January 2013, R. Barriga; MEPN 11663, 1, 45 mm SL, Nangaritza River, 04°17'04"S, 78°36'44"W, 13 January 2013, R. Barriga. Peru, Marañón River drainage, Amazonas Region, Condorcanqui Province, Nieva District: AUM 45524\*, 2, 68.4 and 75.6 mm SL, Quebrada Siasme at Nuevo Siasme, tributary of Nieva River, 04°41'21.77"S, 77°48'34.74"W, 30 July 2006, N. Lujan, D. Werneke, D. Taphorn, A. Flecker, K. Capps, D. German, B. Rengifo, D. Osorio; MUSM 49738, 2, 58.7 and 81.2 mm SL, same data as AUM 45524.

**Non-type material.**—Peru, Marañón River drainage, Amazonas Region: ROM 54722, 93, 33–67 mm SL, tributary of Marañón River at Tsutsunha near Tutumberos, downstream from Aramango at Aguaruno village, 05°02'57.35"S, 78°15'12.97"W, 2 July 1986, B. Reyes, H. Bazan, E. Holm, S. Norriega; ROM 54724, 10, 32–47 mm SL, tributary of Marañón River approximately 14 km W of Bagua, 05°40'59.80"S, 78°38'59.84"W, 30 June 1986, E. Holm, A. Miranda, B. Reyes, H. Bazan.

**Diagnosis.**—*Chaetostoma trimaculineum* can be diagnosed from all other Amazon Basin *Chaetostoma* except *Ch. anale* by having three to four linear rows of distinct, round, naris-sized black spots on the median, mid-dorsal, and

dorsal plate series of the trunk (vs. black spots absent, larger than orbit, or also present on mid-ventral plate series); from all other Amazon Basin species except *Ch. anale*, *Ch. daidalmatos*, *Ch. dermorhynchum*, middle Ucayali populations of *Ch. lineopunctatum* (including type locality), *Ch. stroumpoulos*, and *Ch. vagum* by having distinct round black spots half naris diameter spaced less than one spot width apart on head (vs. spots absent on head or white); from *Ch. anale*, *Ch. carrioni*, *Ch. lexa*, *Ch. marmorescens*, *Ch. stroumpoulos*, and *Ch. vagum* by having an anal fin with four branched rays (vs. anal fin absent or with most frequently three or less or five branched rays); from *Ch. branickii/taczanowskii*, *Ch. carrioni*, *Ch. lexa*, *Ch. lobarhynchos*, *Ch. marmorescens*, and *Ch. microps* by having a supraoccipital excrescence (vs. excrescence absent); from *Ch. changae*, *Ch. jegui*, *Ch. lexa*, *Ch. marmorescens*, and *Ch. microps* by having fewer branched dorsal-fin rays (eight, vs. most frequently nine or sometimes ten); from *Ch. anale*, *Ch. carrioni*, *Ch. daidalmatos*, *Ch. lexa*, and *Ch. microps* by having more teeth per premaxillary ramus (an average of  $112 \pm 32$ , vs. typically  $< 80$ ); from *Ch. anale*, *Ch. carrioni*, *Ch. lexa*, *Ch. marmorescens*, and *Ch. microps* by having more teeth per mandible (an average of  $156 \pm 45$ , vs. typically  $< 111$ ); from *Ch. breve*, *Ch. lineopunctatum*, and *Ch. microps* by having lesser head depth ( $23.0 \pm 0.3\%$  SL, vs.  $> 23.3$ ); from *Ch. lobarhynchos* and *Ch. marmorescens* by having lesser cleithral width ( $32.7 \pm 0.8\%$  SL, vs.  $> 33.5$ ); and from



*Ch. branickii/taczanowskii* and *Ch. lexa* by having four or five evertible cheek odontodes (vs. six or more).

*Chaetostoma trimaculineum* is most similar to *Ch. anale*, from which it can be diagnosed by tooth and anal-fin branched ray counts (see above and Table 7), by the absence of spots from most or all of the compound pterotic (Fig. 13; vs. spots covering the pterotic), by having generally straighter rows of spots along the body, and by lacking spots from the mid-ventral plate series (Fig. 13; vs. spots often present on at least some mid-ventral plates).

**Description.**—Morphometrics in Table 7 and meristics in Table 8. Largest specimen 160.0 mm SL. Body depth increasing from tip of snout to greatest body depth at dorsal-fin origin, decreasing to posterior margin of adipose fin then straight or increasing slightly to base of caudal fin. Dorsal profile convex between snout and dorsal-fin origin then straight and descending to base of dorsal fin. Ventral profile flat from snout to base of caudal fin. Ossified dermal plates with small odontodes cover head and body flanks. Plates missing from broad crescent around snout margin and abdomen. Cheek plates having four or five slightly enlarged, distally hooked odontodes (Type 3, Fig. 6). Orbit positioned dorsolaterally on head with opening sloped ventrolaterally at approximately 45° from sagittal plane in anterior view. Snout broadly rounded in dorsal view.

Oral disk occupying majority of ventral surface of head anterior of cleithrum. Teeth minute, bicuspid, with cusps bent 90° toward mouth opening. Single digitate papilla extending ventrally from dorsal part of premaxillary symphysis; clusters of low papillae at middle of interior surface of each mandible. Maxillary barbel short, adnate along most or all of length; ventral surface of labial disk with low hemispherical papillae decreasing in size distally.

Dorsal-fin spinelet small and round, sometimes covered by skin; posteriormost dorsal-fin ray free from body; reaching to within one plate width from adipose-fin spine when adpressed. Pectoral fin reaching just beyond pelvic-fin base when adpressed, spine having modestly enlarged odontodes along posterodorsal and distal surfaces. Pelvic-fin spine reaching anal-fin origin when adpressed. Second unbranched anal-fin ray longest; anal fin spanning total of four and a half plate widths when adpressed. Adipose-fin spine straight, adnate to caudal peduncle via fleshy membrane. Caudal-fin margin obliquely straight or slightly emarginate with ventral lobe slightly longer than dorsal.

Body broadest at cleithrum; posterior margin of exposed posterior process of cleithrum squared or rounded. First one to two midventral plates gently bent forming rounded lateral ridge between verticals through pectoral- and dorsal-fin origins.

**Coloration in life.**—Head base color light gray with distinct round black spots approximately half the diameter of the naris; spots spaced one to three spot widths apart, spots largely absent from the compound pterotic (Fig. 14). Body base color light gray with distinct round black spots approximately the diameter of the naris; spots spaced one to two spot widths apart and arranged in three to four horizontal rows on median, mid-dorsal and dorsal plate series (absent from mid-ventral and ventral plate series; Fig. 13). Dorsal fin uniformly gray or with few black spots extending up from base; spots aligned with rays and limited

to proximal portion of fin. Paired fins uniformly gray to light brown. Caudal fin often with white tips.

**Coloration in preservative.**—As with live color but faded.

**Sexual dimorphism.**—None observed, see *Remarks* below.

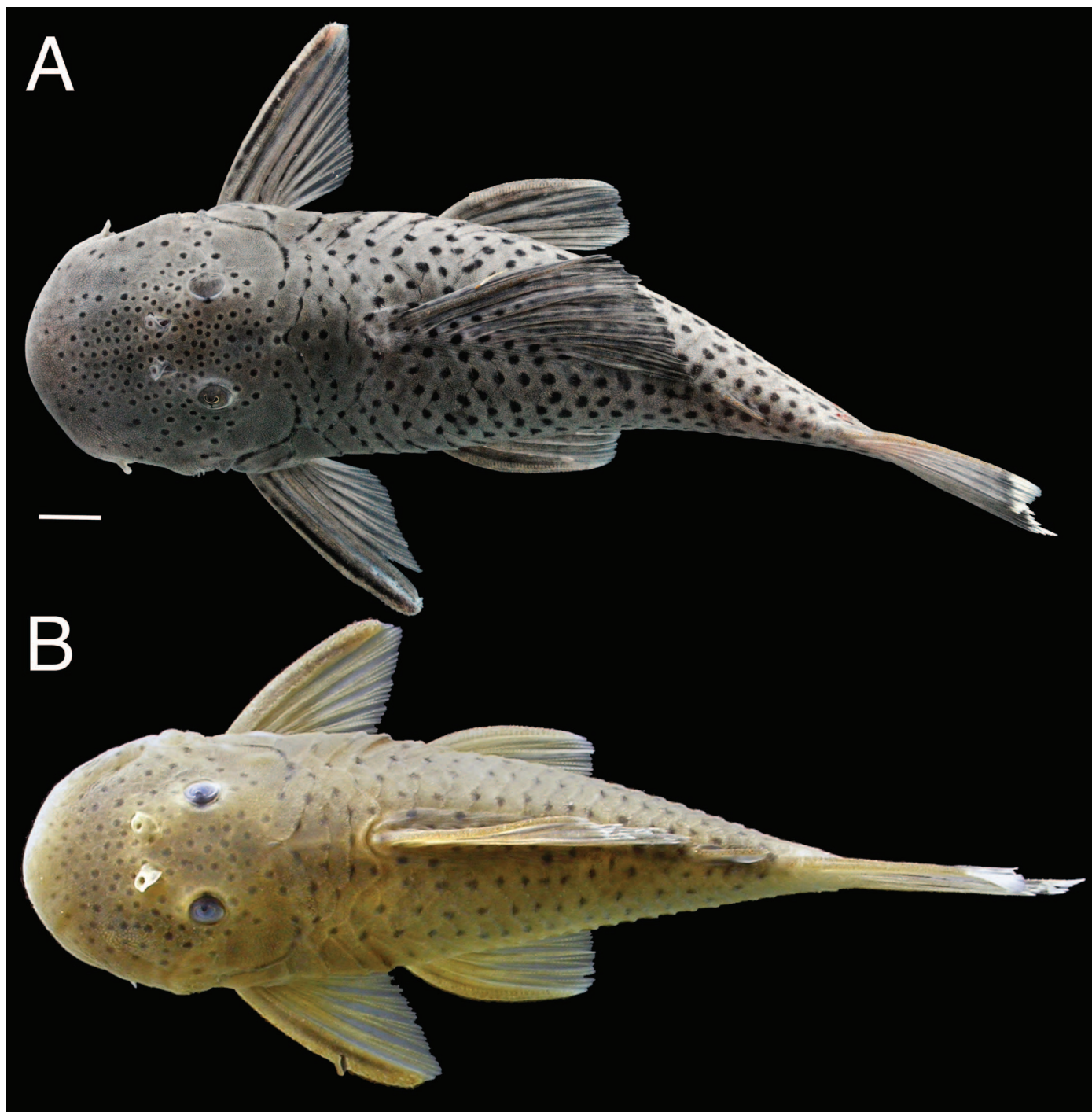
**Distribution.**—*Chaetostoma trimaculineum* is only known from the upper Santiago and middle Marañon river drainages in eastern Ecuador and northern Peru (Fig. 9C). The presence of a very similar but diagnosable species in the Aguarico River drainage in northern Ecuador (see *Remarks* below) suggests that the range of *Ch. trimaculineum* extends no further north than at most the Napo River proper.

**Etymology.**—The species epithet *trimaculineum* is derived from the Latin prefix *tri* = “three,” and nouns *macula* = “spot,” and *linea* = “line;” in reference to the three distinctive rows of spots along the flanks of this species.

**Remarks.**—Despite the lack of sexual dimorphism from all 15 examined specimens, molecular evidence places *Chaetostoma trimaculineum* as sister to the *Ch. anale* species group, defined by Ballen (2011) as consisting of species having the second unbranched anal-fin ray in mature males enlarged and bearing two posterior fleshy ridges (i.e., *Ch. anale*, *Ch. dermorhynchum*, *Ch. formosae*, and *Ch. jegui*; Fig. 2, Clade F). Although *Ch. anale* itself was not included in our phylogenetic analysis, the coloration of the head, body, and fins of *Ch. trimaculineum* is very similar to that of *Ch. anale*, further supporting close relationship. A potential explanation for the apparent absence of sexual dimorphism in *Ch. trimaculineum* is that the type series consists mostly of immature individuals. Alternatively, there may be intraspecific, population-level variation in the extent of sexual dimorphism as was suggested by our observations of *Ch. dermorhynchum*. Regardless, it seems likely that individuals of *Ch. trimaculineum* that exhibit sexual dimorphisms of the anal and pelvic fins may yet be collected. Despite this possibility, *Ch. trimaculineum* should still be morphologically diagnosable from *Ch. anale* based on several additional characteristics listed above (see *Diagnosis*).

While reviewing material for this study and conducting fieldwork in northern Ecuador following completion of this study, we observed many specimens of *Chaetostoma* from the Aguarico River drainage that are very similar to *Ch. trimaculineum*, but differ in having a broader distribution of spots on the head (including the compound pterotic) and body (including some mid-ventral plates) and by exhibiting Types 1–4 sexual dimorphism (for cataloged specimens, see *Material Examined* below, *Ch. cf. trimaculineum*). The more extensive spotting pattern of specimens from the Aguarico makes them more similar in appearance to original illustrations of *Ch. anale*, which was described from the Caqueta River drainage—the next major river drainage north of the Aguarico River. It is therefore conceivable that specimens from the Aguarico River are conspecific with *Ch. anale*. However, without access to fresh material of *Ch. anale* from anywhere in the Caqueta River, we are unable to further clarify the identity of Aguarico individuals.

**Other undescribed species.**—In addition to *Chaetostoma bifurcum* and *Chaetostoma trimaculineum*, our phylogeny



**Fig. 14.** Dorsal views of *Chaetostoma trimaculineum*, new species. (A) Holotype from the Santiago River drainage (ROM 93894\*, 127.1 mm SL) and (B) paratype from the Marañon River drainage (AUM 45524\*, 77.2 mm SL). Scale bar = 1 cm. Photos by NKL.

included six other species of *Chaetostoma* that appear to be undescribed based on combinations of morphology and phylogenetic placement: *Ch.* aff. *lineopunctatum* from the Huallaga River drainage (Clade C), *Ch.* n. sp. Xingu L416 from the Xingu River drainage (Clade F), *Ch.* n. sp. L402 from the Meta and Apure river drainages (Clade H), *Ch.* n. sp. from the Ucayali River drainage (Clade I), *Ch.* aff. *fischeri* from the Tuirá River drainage (Clade K), and *Ch.* n. sp. L445 from the Meta River drainage (Clade N).

For various reasons, including the geographic focus of this manuscript and the ongoing efforts of other researchers, we do not describe any of these species here. Given its direct

relevance to species discussed herein, though, we note that *Ch.* aff. *lineopunctatum* from the Huallaga River drainage is not only phylogenetically distinct from *Ch. lineopunctatum sensu stricto* (i.e., Ucayali and Madre de Dios river drainages), but also morphologically distinct, in that the undescribed species has only a single series of black spots on interradial dorsal-fin membranes versus twin series in the holotype of *Ch. lineopunctatum* and conspecifics thereof. We also observed that there is variation within *Ch. lineopunctatum sensu stricto* in the presence of black spots on the head. Distinct black spots approximately one half naris size and evenly spaced less than one spot width apart are present on

the head of the holotype and conspecifics in the middle Ucayali (i.e., Pachitea, Aguaytia, Pisqui), but are missing from populations in the lower Ucayali, Madre de Dios, and Urubamba drainages.

Notable interdrainage morphological variation was also observed in *Ch. lobarhynchos*, with individuals from the Huallaga River drainage having far more cheek odontodes (14–17) than individuals in the Ucayali River (6–9) drainage, where the holotype was collected.

## DISCUSSION

*Chaetostoma* comprises an important component of the ichthyofauna of the Andean piedmont north of Bolivia, and contains species that are most diverse and abundant in many streams and rivers that are currently imperiled by hydroelectric development throughout the Andes (Finer and Jenkins, 2012). Many specimens examined in this study were collected for the purpose of assessing the environmental impacts of proposed hydroelectric dams, and the likelihood of many more such projects in the near future adds urgency to our efforts to fully document the species-level diversity, diagnostic characteristics, and geographic distributions of this group.

With 47 valid species, *Chaetostoma* is the third most species rich genus of Loricariidae (after *Hypostomus*, ca. 120 spp., and *Ancistrus*, ca. 60 spp.). None of these diverse and geographically widespread groups have undergone recent comprehensive taxonomic revision or phylogenetic analysis throughout their range, making them important foci of current and future ichthyological research. To resolve our currently highly fragmentary understanding of the systematics of *Chaetostoma*, our ultimate goal should be to clearly diagnose each species from all others regardless of geographic range. However, this will require more specimens, genetic data from more species, and more live coloration and morphometric data than are currently available. For the moment, incremental and regionally delimited studies such as this, including the re-descriptions of species described over a century ago, constitute valuable and necessary steps toward a broader synthesis.

In our phylogenetic analysis, we examined 19 valid and six undescribed species of *Chaetostoma*, and in our taxonomic analysis 26 species: eight species from the Pacific Coast of South America and 18 species from the Amazon Basin. The remaining 20 valid species of *Chaetostoma* that we did not examine have ranges limited to Central America, coastal drainages of northwestern South America, or the Magdalena, Maracaibo, or Orinoco drainage basins. Our phylogenetic analysis of species distributed across all these basins indicates that no single region contains a monophyletic radiation. Rather, most drainages—particularly in the Amazon Basin—have phylogenetically diverse assemblages that will ultimately require broad geographic comparison to achieve a more comprehensive systematic understanding of the genus.

Despite the limited scope of this study, the combination of a molecular phylogenetic analysis with a survey of interspecific morphological variation allows for the elucidation of specific traits that define select clades within *Chaetostoma*. To this end, we have attempted to subdivide continuous variation in select characters into natural groupings or types that often corresponded with select clades. Strong secondary sexual dimorphisms of the snout and pelvic and/or anal fins, for example, were divided into discrete categories only observed in subclades within Clade

A–J, differentiating this clade from Clades KLM and N. Clade F, which contains the *Chaetostoma anale* group *sensu* Ballen (2011), displays some of the most pronounced development of the sexual dimorphisms described herein, including one of only two instances of unbranched pelvic- and anal-fin rays being elongated as filaments (Type 4 dimorphism)—the other example being the relatively distantly related *Chaetostoma changae* (Clade D). Likewise, the shape and size of evertible cheek odontodes appeared to be informative of phylogenetic relationships, with straight odontodes (Type 1) being restricted to Clades AB and N, long hooked odontodes (Type 4) being restricted to *Ch. lexa* (Clade J), and all other species having Type 2 or 3 odontodes.

Color, particularly live color, may be one of the richest sources of traits that are variable among species of *Chaetostoma* and potentially informative of clade identity. As a step toward a comprehensive analysis of color patterns of *Chaetostoma*, we have implemented systematic and concise color descriptions: We focus on spot presence, spot color, spot distinctiveness, spot shape, spot size, spot spacing and spot arrangement, and separately describe each of these characteristics for the head, body, dorsal, and paired fins. Species of *Chaetostoma* are frequently spotted and subtle variation in spot pattern is an important means of distinguishing many species (e.g., *Ch. lineopunctatum* vs. *Ch. trimaculineum*). Unfortunately, live color data are currently unavailable for many species described long ago, whose coloration has been mostly or completely lost from long-preserved type specimens. For these species, the only solution is to collect fresh specimens and live color photographs from at or near type localities—a major goal that this study accomplished in Ecuador and northern Peru.

## MATERIAL EXAMINED

*Chaetostoma cf. branickii*: Peru, Huallaga River drainage, Amazonas Region: ROM 54720, 5, 55–137 mm SL, Huallabamba River, Station 22, 4 km SE of Mendoza, approx. 06°21'S, 77°21'W; ROM 54723, 2, 59–81 mm SL, Huallabamba River 4 km SE of Mendoza.

*Chaetostoma changae*: Peru, Huallaga River drainage, Huánuco Region, Leoncio Prado Province: MHNG 2712.044, 2, Monzon River at the confluence of Quebrada Bella near Tingo Maria (RFC 06), 09°19'22.90"S, 76°01'50.90"W; MHNG 2712.059, 3, Aucayacu River near José Crespo y Castillo-Aucayacu (RFC 10), 08°55'18.3"S, 76°06'35.3"W; MHNG 2712.077, 2, Huallaga River at Tingo Maria (RFC 25), 09°18'53.8"S, 76°00'34.2"W. San Martín Region, Tocache Province, Nuevo Progreso District: MHNG 2712.063, 8, Uchiza River drainage, Pacota River (RFC 14), 08°23'56.3"S, 76°18'30.2"W; MHNG 2712.064, 1, Huainabe River drainage, Huantanamo River (RFC 15), 08°21'57.20"S, 76°15'47.60"W. Uchiza District: MHNG 2712.066, 2, Huainabe River at confluence with Huantanamo River (RFC 16), 08°21'30"S, 76°20'11.4"W; MHNG 2712.067\*, 1, Huallaga River at confluence with Cachiyacu River (RFC 18), 08°18'49.90"S, 76°22'40.70"W.

*Chaetostoma daidalmatos*: Peru, Huallaga River drainage, Huánuco Region, Leoncio Prado Province, Tingo Maria district: MHNG 2712.045, 3, Monzon River at the mouth of Quebrada Bella, tributary of Huallaga River near Tingo Maria (RFC 06), 09°19'22.90"S, 76°01'50.90"W; MHNG

2712.051, 1, Huallaga River between Tingo Maria and Aucayacu (RFC 07), 09°04'42"S, 76°04'44"W; MHNG 2712.079, 1, Huallaga River (RFC 25), 09°18'53.8"S, 76°00'34.2"W; MHNG 2712.083, 3, Huallaga River upstream of Tingo Maria on the road to Huánuco (RFC 26), 09°26'03.8"S, 75°58'08.3"W. José Crespo y Castillo District: MHNG 2712.052, 1, Aspuzana River, tributary of Huallaga River near Maronilla (RFC 08), 08°39'46.90"S, 76°08'03.70"W; MHNG 2712.053, 1, Aspuzana River drainage, Pucayacu River (RFC 09), 08°43'44.8"S, 76°06'54.4"W; MHNG 2712.055\*, 3, Aucayacu River, tributary of Huallaga River (RFC 10), 08°55'18.30"S, 76°06'35.30"W; MUSM 35830, Aucayacu River, 08°55'43.87"S, 76°06'11.78"W; MUSM 35913, Huallaga River. San Martín Region, Tocache Province, Uchiza District: MHNG 2712.073, 11, Tocache River, tributary of Huallaga River (RFC 23), 08°10'07.50"S, 76°32'32.50"W.

*Chaetostoma jegui*: Brazil, Branco River drainage, Roraima State: INPA 33840, 4, Uraricoera River at Maracá Island.

*Chaetostoma lexa*: Peru, Huallaga River drainage, San Martín Region, Tocache Province, Uchiza District: MHNG 2712.071\*, 2, Mantencio River (RFC 21), 08°13'41.30"S, 76°26'09.60"W. Huánuco Region, Leoncio Prado Province: MUSM 44322, Quebrada Tambillo Grande, 18L 396392 m E 895988 m S [southing coordinate missing a digit].

*Chaetostoma lineopunctatum*: Peru, Ucayali River drainage, Loreto Region, Ucayali Province: MHNG 2613.04, 3, tributary of the upper Pisqui River, 07°36'22.5"S, 75°56'28"W; MHNG 2613.041, 3, tributary of the upper Pisqui River, 07°36'22.5"S, 75°56'28"W; MHNG 2613.042, 3, tributary of the upper Pisqui River, 07°36'22.5"S, 75°56'28"W; MHNG 2613.043, 3, tributary of the upper Pisqui river, 07°36'22.5"S, 75°56'28"W; MUSM 17945, Cordillera Azul, Alto Pisqui. Ucayali Region, Padre Abad Province: MHNG 2395.05, 3, Huacamayo River near Aguaytia, at km 155 on the road to Huánuco; MHNG 2712.041\*, 3, Huacamayo River near Aguaytia, at km 155 on the Pucallpa-Aguaytia road, tributary of the Aguaytia River (RFC 01), 09°00'14.10"S, 75°29'00.00"W; MHNG 2712.043, 2, Santa Anita River, right bank tributary of Aguaytia River downstream of Aguaytia (RFC 04), 09°04'50"S, 75°31'26"W. San Martín Region: MHNG 2359.003, 10, Huacamayo River at km 155 on the Pucallpa-Huánuco road. Urubamba Province: MUSM 43104, Quebrada Sabeti, 12°04'04.45"S, 72°54'58.67"W. Madre de Dios River drainage, Cusco Region: AUM 51166\*, 3, Araza River, right bank just above the bridge past Quincemil, 13°15'48.17"S, 70°46'48.25"W; AUM 51175, 19, Huacymbre River, upstream of Limonchayo bridge, 9 km N of Quincemil, 13°11'08.63"S, 70°37'35.90"W; AUM 51186, 8, Nusiniscato River, downstream of confluence with the Huactumbrei River, 9.1 km N of Quincemil, 13°11'08.56"S, 70°37'07.39"W; AUM 51201, 8, Araza River between Quincemil and Limonchayoc, 10.9 km WNW of Quincemil, 13°13'05.45"S, 70°43'16.25"W; AUM 51213, 14, Araza River downstream of the mouth of the Nusiniscato River, 11.6 km ENE of Quincemil; AUM 57518, 3, unnamed stream under Interoceanic Hwy bridge, approx. 1 hour E of Quincemil, 13°11'29.22"S, 70°33'15.62"W; AUM 51331, 1, Araza River at its mouth, 27.7 km from Quincemil; MUSM 26421, Inambari Province, Quincemil District, Quebrada Yanamayo, 13°13'28.23"S, 70°44'32.66"W. Madre de Dios Region: AUM 51341, 35, Loromayo River at Interoceanic Hwy bridge

crossing, 29.7 km ENE of Quincemil, 13°10'25.07"S, 70°22'58.58"W; AUM 57495, 2, Inambari River downstream of Puerto Carlos, 12°53'25.33"S, 70°20'22.27"W; AUM 57511, 1, Inambari River, 12°47'06.50"S, 70°00'35.78"W; MHNG 2650.044, 4, Manu, Diamante, upper Madre de Dios River, approx. 12°13'S, 71°44'W. Pachitea River drainage, Huánuco Region, Pachitea Province: ROM 55766, 4, 26.2–41.5 mm SL, Huambo River upstream of confluence with Pachitea River, approx. 09°39'S, 74°56'W; ROM 55768, 2, 27.7–43.3 mm SL, Llullapichis River upstream of confluence with Pachitea River, approx. 09°37'S, 74°57'W; ROM 55772, 1, 55.3 mm SL, Llullapichis River 300 m E of Panguana Camp, approx. 09°37'S, 74°57'W; ROM 55773, 11, 45.1–73.6 mm SL, Llullapichis River 300 m E of Panguana Camp, pool near H88-10, approx. 09°37'S, 74°57'W; ROM 55774, 46, 21.1–76.6 mm SL, Llullapichis River 1.5 km W of Panguana Station, approx. 09°37'S, 74°57'W; ROM 55775, 1, 52.4 mm SL, Llullapichis River at Panguana, approx. 09°37'S, 74°57'W.

*Chaetostoma aff. lineopunctatum*: Peru, Huallaga River drainage, Huánuco Region: MHNG 2712.057, 1, Leoncio Prado Province, José Crespo y Castillo District, Aucayacu River, tributary of Huallaga River (RFC 10), 08°55'18.30"S, 76°06'36.30"W; MUSM 35467, Aucayacu River; MUSM 44253, Huallaga River. San Martín Region: MHNG 2359.004, 1, San Martín Province, Cumbaza River, 06°28'22"S, 76°22'57"W; MHNG 2712.069\*, 21, Tocache Province, Uchiza District, Huallaga River at confluence with Cachiyacu River (RFC 18), 08°18'49.90"S, 76°22'40.70"W. Ucayali Region, Padre Abad Province: MHNG 2712.042\*, 2, Aguaytia River at confluence with Boca Yurac River (RFC 02), 09°05'41.50"S, 75°30'31.30"W.

*Chaetostoma lobarhynchos*: Peru, Ucayali River drainage, Pasco Region: MUSM 20289, Paucartambo River, 10°44'33.50"S, 75°32'09.20"W; MUSM 20307, Paucartambo River, 10°44'34.70"S, 75°31'56.00"W. Junín Region: MUSM 20291, Tulumayo River, 7 August 2003.

*Chaetostoma cf. lobarhynchos*: Peru, Huallaga River drainage, Huánuco Region: MUSM 41039, Tambo River, 09°41'05.42"S, 75°47'18.58"W; MUSM 44901, Quebrada Acomayo, 09°48'58.17"S, 76°03'37.47"W.

*Chaetostoma marmorescens*: Peru: Huallaga River drainage, Huánuco Region, Pachitea Province, Panao District: MUSM 44898, 3, 81.5–141.8 mm SL, Huallaga River.

*Chaetostoma stroumpoulos*: Peru, Huallaga River drainage, Huánuco Region, Leoncio Prado Province, José Crespo y Castillo District: MHNG 2712.056\*, 12, Aucayacu River (RFC 10), 08°55'18.30"S, 76°06'35.30"W; MHNG 2712.06, 3, Aucayacu River (RFC 10), 08°55'18.30"S, 76°06'35.30"W; MHNG 2712.049, 1, Huallaga River between Tingo Maria and Aucayacu (RFC 07), 09°04'42.00"S, 76°04'44.00"W; MHNG 2712.05, 1, Huallaga River between Tingo Maria and Aucayacu (RFC 07), 09°04'42.00"S, 76°04'44.00"W. Tingo Maria District: MHNG 2712.08, 4, Huallaga River (RFC 25), 09°18'53.8"S, 76°00'34.2"W; MHNG 2712.082, 5, Huallaga River upstream of Tingo Maria, south of the Huánuco Rd. (RFC 26), 09°26'03.80"S, 75°58'08.30"W; MUSM 35710, Huallaga River; MUSM 35827, Huallaga River between Tingo Maria and Aucayacu; MUSM 35915, Huallaga River. San Martín Region, Tocache Province, Nuevo Progreso District: MHNG 2712.061, 3, Pacota River, tributary of

Uchiza River (RFC 14), 08°23'56.3"S, 76°18'30.2"W. Uchiza District: MHNG 2712.068, 1, Huallaga River at confluence with Cachiyacu River (RFC 18), 08°18'49.90"S, 76°22'40.70"W; MHNG 2712.075, 2, Tocache River (RFC 23), 08°10'07.5"S, 76°32'32.5"W; MUSM 35823, Pacota River, tributary of Uchiza River; MUSM 35832, Tocache River.

*Chaetostoma* cf. *trimaculineum*: Ecuador, Napo River drainage, Sucumbíos Province: MEPN 1301, 3, 118 mm SL, Aguarico River near Lumbacui, 00°03'05"S, 77°20'05"W; MEPN 11712, 5, 145–160 mm SL, unnamed stream crossing road from Quito to Lago Agrio, sector 51, 00°00'29"N, 77°30'39"W; MEPN 11916, Aguarico River at confluence with the Puchuchoa River, 00°05'06"N, 77°16'03"W.

#### ACKNOWLEDGMENTS

We gratefully acknowledge our principal foreign collaborators O. Castillo (MCNG, Venezuela), O. Leon Mata (MCNG, Venezuela), M. Hidalgo and H. Ortega (MUSM, Peru), and L. Rapp Py-Daniel (INPA, Brazil) for ensuring the legal collection and export of specimens; the collection managers and museum workers M. Burrige (ROM), R. Covain (MHNG), S. Fisch-Muller (MHNG), E. Holm (ROM), J. Maclaine (BMNH), R. Reina (STRI), M. Sabaj Pérez (ANSP), D. Werneke (AUM), D. Wylie (INHS), and M. Zur (ROM), and aquarium fish importer O. Lucanus for generously sharing information, processing specimen loans, and gifting tissues and gDNA extracts; and the expedition participants J. Arbour (U of Toronto), J. Birindelli (MZUSP), D. Brooks, K. Capps (CU), A. Flecker (CU), D. German (UF), F. Hauser (U of Toronto), A. Jackson (TAMU), N. Lovejoy (U of Toronto), O. Leon Mata (MCNG), M. Hidalgo and M. Rengifo (MUSM), K. Roach (TAMU), V. Roman (UCE), M. Sabaj Pérez (ANSP), D. Taphorn (ROM), and D. Werneke (AUM) for helping to collect specimens and tissues. Funding for this research came from NSF DEB-0315963 (Planetary Biodiversity Inventory: All Catfish Species), NSF OISE-1064578 (International Research Fellowship) to NKL, National Geographic Committee for Research and Exploration grant #8721-09 to NKL and #8465-08 to HLF, the Coypu Foundation, the Aquatic Critter Inc., and the estate of George and Carolyn Kelso via the International Sportfish Fund. Additional funding for fieldwork and research came from NSF grant DEB 0516831 to K. O. Winemiller, R. L. Honeycutt, and HLF, a Conservation Research grant from the Life in Crisis: Schad Gallery of Biodiversity, Museum Volunteers research grants (2009, 2010) from the Royal Ontario Museum to HLF, Discovery Grants from the Natural Sciences and Engineering Research Council of Canada to HLF, and grants to D. German and A. Flecker. Salary support for NKL and comparative material from the Rio Xingu provided by NSF DEB-1257813 (the iXingu Project).

#### LITERATURE CITED

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

**Armbruster, J. W.** 2004. Phylogenetic relationships of the suckermouth armoured catfishes (Loricariidae) with emphasis on the Hypostominae and the Ancistrinae. *Zoological Journal of the Linnean Society* 141:1–80.

**Armbruster, J. W.** 2008. The genus *Peckoltia* with the description of two new species and a reanalysis of the phylogeny of the genera of the Hypostominae (Siluriformes: Loricariidae). *Zootaxa* 1822:1–76.

**Ballen, G. A.** 2011. A new species of *Chaetostoma* Tschudi (Siluriformes: Loricariidae) from Colombia with a definition of the *C. anale* species group. *Papeis Avulsos de Zoologia* 51:383–398.

**Ballen, G. A., and R. P. Vari.** 2012. Review of the Andean armored catfishes of the genus *Dolichancistrus* Isbrücker (Siluriformes: Loricariidae). *Neotropical Ichthyology* 10:499–518.

**Boulenger, G. A.** 1887. An account of the fishes collected by Mr. C. Buckley in eastern Ecuador. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London* 1887:274–283.

**Burgess, W. E.** 1989. *An Atlas of Freshwater and Marine Catfishes. A preliminary survey of the Siluriformes.* T.F.H. Publications, Neptune City, New Jersey.

**Cope, E. D.** 1872. On the fishes of the Ambyiacu River. *Proceedings of the Academy of Natural Sciences of Philadelphia* 23:250–294, pls. 253–216.

**Dignall, J.** 2014. List of original I-numbers. [http://www.planetcatfish.com/shanesworld/shanesworld.php?article\\_id=514](http://www.planetcatfish.com/shanesworld/shanesworld.php?article_id=514). First published online: 16 May 2014.

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

**Eigenmann, C. H., and W. R. Allen.** 1942. The Fishes of western South America, Part I. The intercordilleran and Amazonian lowlands of Peru. II. The high pampas of Peru, Bolivia, and northern Chile. With revision of the Peruvian Gymnotidae, and of the genus *Orestias*. University of Kentucky.

**Eigenmann, C. H., and R. S. Eigenmann.** 1889. Preliminary notes on South American Nematognathi. II. *Proceedings of the California Academy of Sciences (Series 2)* 2:28–56.

**Eigenmann, C. H., and R. S. Eigenmann.** 1890. A revision of the South American Nematognathi or cat-fishes. *Occasional Papers California Academy of Sciences* 1:1–508.

**Finer, M., and C. N. Jenkins.** 2012. Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. *PLOS ONE* 7:1–9.

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

**Fowler, H. W.** 1945. Colombian zoological survey. Part I. The fresh-water fishes obtained in 1945. *Proceedings of the Academy of Natural Sciences of Philadelphia* 97:93–135.

**Günther, A.** 1864. Catalogue of the fishes in the British Museum. Catalogue of the Physostomi, containing the families Siluridae, Characinidae, Haplochitonidae, Sternopychidae, Scopelidae, Stomiatidae in the collection of the British Museum 5:i–xxii + 200–271.

**Isbrücker, I. J. H.** 1980. Classification and catalogue of the mailed Loricariidae (Pisces, Siluriformes). *Verslagem en Technische Gegevens* 22:1–181.

**Li, C., G. Ortí, G. Zhang, and G. Lu.** 2007. A practical approach to phylogenomics: the phylogeny of ray-finned fish (Actinopterygii) as a case study. *BMC Evolutionary Biology* 7:44.

- Lujan, N. K., and J. W. Armbruster. 2011. Two new genera and species of Ancistrini (Siluriformes: Loricariidae) from the western Guiana Shield. *Copeia* 2011:216–225.
- Lujan, N. K., J. W. Armbruster, N. R. Lovejoy, and H. López-Fernández. 2015a. Multilocus molecular phylogeny of the suckermouth armored catfishes (Siluriformes: Loricariidae) with a focus on subfamily Hypostominae. *Molecular Phylogenetics and Evolution* 82:269–288.
- Lujan, N. K., V. Meza-Vargas, and R. Barriga-Salazar. 2015b. Two new *Chaetostoma* group (Loricariidae: Hypostominae) sister genera from opposite sides of the Andes Mountains in Ecuador, with the description of one new species. *Copeia* 103:651–663.
- Miller, M. A., W. Pfeiffer, and T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees, p. 1–8. *In*: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 November 2010, New Orleans, Louisiana.
- Norman, J. R. 1935. Description of a new loricariid catfish from Ecuador. *Annals and Magazine of Natural History, Series 10* 15:627–629.
- Pearson, N. E. 1937. The fishes of the Atlantic and Pacific slopes near Cajamarca, Peru. *Proceedings of the California Academy of Sciences* 23:87–98.
- Phillip, D. A. T., D. C. Taphorn, E. Holm, J. F. Gilliam, B. A. Lamphere, and H. López-Fernández. 2013. Annotated list and key to the stream fishes of Trinidad & Tobago. *Zootaxa* 3711:1–64.
- Rambaut, A., A. J. Drummond, and M. Suchard. 2007. Tracer v1.6. Available from <http://tree.bio.ed.ac.uk/software/tracer/>
- Rapp Py-Daniel, L. H. 1991. *Chaetostoma jegui*, a new mailed catfish from the rio Uraricoera, Brazil (Osteichthys: Loricariidae). *Ichthyological Exploration of Freshwaters* 2:239–246.
- Rapp Py-Daniel, L. H., and C. Cox Fernandes. 2005. Dimorfismo sexual em Siluriformes e Gymnotiformes (Ostariophysi) da Amazônia. *Acta Amazonica* 35:91–110.
- Regan, C. T. 1904. A monograph of the fishes of the family Loricariidae. *Transactions of the Zoological Society of London* 17:191–350.
- Regan, C. T. 1912. Descriptions of new fishes of the family Loricariidae in the British Museum Collection. *Proceedings of the Zoological Society of London* 1912 (part 3): 666–670.
- Ronquist, F., and J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
- Sabaj Pérez, M. H. (Ed.). 2014. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 5.0 (22 September 2014). Electronically accessible at <http://www.asih.org/>, American Society of Ichthyologists and Herpetologists, Washington, D.C.
- Salcedo, N. J. 2006a. New species of *Chaetostoma* (Siluriformes: Loricariidae) from central Peru. *Copeia* 2006:60–67.
- Salcedo, N. J. 2006b. Two new species of *Chaetostoma* (Siluriformes: Loricariidae) from the Huallaga River in central Peru. *Ichthyological Exploration of Freshwaters* 17:207–220.
- Salcedo, N. J. 2013. Description of *Loraxichthys lexa*, new genus and species (Siluriformes: Loricariidae) from the Río Huallaga Basin, central Peru, with notes on the morphology of the enigmatic *Lipopterichthys carrioni* Norman, 1935. *Zootaxa* 3640:557–571.
- Schaefer, S. A. 1997. The neotropical cascudinhos: systematics and biogeography of the *Otocinclus* catfishes (Siluriformes: Loricariidae). *Proceedings of the Academy of Natural Sciences of Philadelphia* 148:1–120.
- Stamatakis, A. 2014. RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313.
- Steindachner, F. 1881. Beiträge zur Kenntniss der Flussfische Südamerika's. II. Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften in Wien 43:103–146.
- Steindachner, F. 1882. Beiträge zur Kenntniss der Flussfische Südamerika's (IV). *Anzeiger der Kaiserlichen Akademie der Wissenschaften (Wien)* 19:175–180.
- Sullivan, J. P., J. G. Lundberg, and M. Hardman. 2006. A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using rag1 and rag2 nuclear gene sequences. *Molecular Phylogenetics and Evolution* 41:636–662.
- Tan, M., and J. W. Armbruster. 2012. *Cordylancistrus santarosensis* (Siluriformes: Loricariidae), a new species with unique snout deplation from the Río Santa Rosa, Ecuador. *Zootaxa* 3243:52–58.
- Tortonese, E. 1940. Elenco dei tipi esistenti nella collezione ittologica del R. Museo di Torino. *Bollettino dei Musei di Zoologia ed Anatomia Comparata della R. Università di Torino (Ser. 3)* 48:133–144.
- Tschudi, J. J. von. 1846. *Ichthyologie*, p. ii–xxx + 1–35, pls. 31–36. *Untersuchungen über die Fauna Peruana*. Scheitlin and Zollikofer, St. Gallen, Switzerland.