

A long-hidden species of *Pimelodella* (Siluriformes: Heptapteridae) from the upper and middle Orinoco, and western Amazon tributaries



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A new species of *Pimelodella* is described from the upper and middle basin of the Orinoco River, upper basin of Negro River, and upper basin of the Apaporis River. The new species is distinguished from its congeners by its unique dark saddle on the predorsal region, and also by its maxillary barbel reaching or slightly exceeding the adipose-fin insertion; anterior margin of pectoral fin-spine with minute straight dentitions covering the middle third of the spine, serrae along its distal third, and posterior margin with 8–10 retrorse dentitions along 40–45% of the middle section of the spine; adipose fin short (23.5–27.2% of SL); caudal fin lobes subequal; 38 total vertebrae; and diffuse dark band along the sub-distal region of the dorsal fin. Polymorphism of fusion pattern of the epiphyseal branches of the supraorbital sensory canals is reported for the new species, and its Negro–Orinoco biogeographic pattern is discussed.

Keywords: Apaporis, Colombia, Morphology, Rhamdiinae, Rio Negro, Taxonomy.

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Una especie nueva del género *Pimelodella* es descrita para la cuenca alta y media del río Orinoco, cuenca alta de río Negro y cuenca alta del río Apaporis. La especie nueva se distingue de sus congéneres por su mancha oscura única en forma de silla de montar en la región predorsal y también por su barbilla maxilar alcanzando o excediendo ligeramente la inserción de la aleta adiposa; margen anterior de la espina pectoral con dentaciones pequeñas rectas cubriendo el tercio medio de la espina, sierras a lo largo de su tercio distal y margen posterior con 8–10 dentaciones retrorsas a lo largo de 40–45% de la sección media de la espina; aleta adiposa corta (23.5–27.2% de LE); lóbulos de la aleta caudal sub-iguales; 38 vértebras totales; y una banda oscura difusa a lo largo de la región sub-distal de la aleta dorsal. Se reporta polimorfismo en el patrón de fusión de las ramas epifisiales de los canales sensoriales supraorbitales en la especie nueva, y se discute su patrón biogeográfico Negro–Orinoco.

Palabras clave: Apaporis, Colombia, Morfología, Rhamdiinae, Río Negro, Taxonomía.

INTRODUCTION

Current knowledge on the internal relationships of Heptapteridae has advanced significantly by recently published molecular phylogenetic studies (Sullivan *et al.*, 2013; Faustino-Fuster *et al.*, 2021; Silva *et al.*, 2021), which support the monophyly of the family and its subdivision into two subfamilies (Rhamdiinae and Heptapterinae). Rhamdiinae is currently the most species-rich subfamily, comprising five genera and 128 valid species (Fricke *et al.*, 2025), with the genera *Pimelodella* Eigenmann & Eigenmann (1888) and *Rhamdia* Bleeker (1858) being the most taxonomically diverse (Angrizani, Malabarba, 2020; Fricke *et al.*, 2025). However, the limited knowledge about the actual taxonomic diversity within these two genera, partly reflects a poor understanding of its internal phylogenetic relationships. One of the most important issues related to Rhamdiinae is the monophyly of *Pimelodella*, where *Brachyrhamdia* Myers (1927) is phylogenetically placed as nested within *Pimelodella* (Bockmann, 1998; Silva *et al.*, 2021), resulting in a paraphyletic *Pimelodella*. *Pimelodella* is still distinguished within Heptapteridae mostly by a combination of plesiomorphic characters, *i.e.*, orbital rim free, cranial fontanels long, supraoccipital process long, usually reaching the anterior nuchal plate (Slobodian *et al.*, 2017; Slobodian, Pastana, 2018). A single putatively apomorphic character has been proposed for its diagnosis, innermost two caudal-fin rays not articulated to the hypural plate (Bockmann, 1998; Slobodian *et al.*, 2017).

Pimelodella comprises 84 valid species (Fricke *et al.*, 2025) and includes small to medium-sized species (< 30 cm SL), distributed in cis- and trans-Andean drainages from southeastern Costa Rica to northern Argentina (Slobodian *et al.*, 2017; Slobodian, Pastana, 2018; Conde-Saldaña *et al.*, 2019; Cortés-Hernández *et al.*, 2020; Slobodian *et al.*, 2021; Cortés-Hernández *et al.*, 2023a; Pierre, Slobodian, 2024). Since the revisionary taxonomic work of Eigenmann (1917), no comprehensive updates have been published, leaving most species within the genus still awaiting proper taxonomic and geographical delimitation (Slobodian *et al.*, 2021).

In Colombia, 22 species of *Pimelodella* have been recorded, with 13 species distributed in the Amazon and Orinoco basins: *P. bockmanni* Slobodian & Pastana, 2018, *P. buckleyi* (Boulenger, 1887), *P. chaparae* Fowler, 1940, *P. conquetaensis* Ahl, 1925, *P. cristata* (Müller & Troschel, 1849), *P. cruxenti* Fernández-Yépez, 1950, *P. figueroai* Dahl, 1961, *P. gracilis* (Valenciennes, 1835), *P. linami* Schultz, 1944, *P. longibarbata* Cortés-Hernández, DoNascimento & Ramírez-Gil, 2020, *P. megalops* Eigenmann, 1912, *P. metae* Eigenmann, 1917, and *P. serrata* Eigenmann, 1917 (DoNascimento *et al.*, 2023). However, new records and descriptions of new species of *Pimelodella* from these basins suggest that the taxonomic diversity of the genus is still underestimated (Cortés-Hernández *et al.*, 2020; 2023a). As part of a taxonomic revision focused on the Orinoco River basin in Colombia, we detected numerous specimens of a very distinctive species with a striking pigmentation pattern, from tributaries of the upper and middle basins of the Orinoco River, and from the Guainía and Pacoa rivers, tributaries of the upper basin of the Negro and Caquetá rivers, respectively. These specimens are therefore described as a new species, based on a comprehensive morphological comparison.

MATERIAL AND METHODS

Morphometric data were taken on the left side of specimens using a digital caliper (0.1 mm) whenever possible, following Slobodian *et al.* (2017) and Slobodian, Pastana (2018). Cleared and stained (c&s) specimens were prepared according to Taylor, Van Dyke (1985), following the modifications proposed by Springer, Johnson (2000). Osteological nomenclature follows Bockmann, Miquelarena (2008). Vertebral counts include five vertebrae of the Weberian complex and the compound caudal centrum ($PU_1 + U_1$) was counted as one element (Lundberg, Baskin, 1969). Nomenclature of pectoral and dorsal-fin spines ornamentation follows Vanscoy *et al.* (2015), and terminology for the distal segments of the pectoral-fin spine follows Kubicek *et al.* (2019).

Morphometric data of *Pimelodella megalops* were obtained from paratypes (USNM 66262) and additional specimens cataloged at USNM from the Cuyuní River, Essequibo River basin in Guyana. Principal component analysis (PCA) of morphometric data was carried out with “stats” package in Rstudio. Missing measures were imputed by chained random forests, whose iterative adjustment of the model offers the option of matching predictive means by species, avoiding imputation with values that are not present in the original data, and increases the variance to a realistic level. These analyses were performed in the “missRanger” package. We transformed the measures expressed as percentage of SL to log values to reduce the lack of homogeneity of variance due to size variation, following Humphries *et al.* (1981) and Bookstein (1992). A linear regression analysis of log-transformed lower caudal-fin lobe length data and an analysis of covariance (ANCOVA) were performed, using SL as a covariate. Osteological data of *Pimelodella buckleyi*, *P. grisea* (Regan, 1903), *P. hasemani* Eigenmann, 1917, *P. howesi* Fowler, 1940, *P. leptosoma* (Fowler, 1914), *P. macturki* Eigenmann, 1912, *P. megalops*, *P. metae*, and *P. notomelas* Eigenmann, 1917 were obtained from x-ray images (xr) of their type-series, available at All Catfish Species Inventory (ACSI) Image Base (Morris *et al.*, 2006), Digital Imaging of the Primary Type Fish Specimens at the Academy of Natural Sciences, Philadelphia (<http://clade.ansp.org/ichthyology/>

FTIP/search.php?mode=search&tbl=Species&contains=&Submit=Search), the Natural History Museum (https://data.nhm.ac.uk/?_ga=2.6151667.1378510653.1590362534-435128425.1589952862), and the Museum of Comparative Zoology, Harvard University, Cambridge websites (<https://mczbase.mcz.harvard.edu/guid/MCZ:Ich:30075>). Institutional abbreviations follow Sabaj (2025). Localities were projected onto cartographic projections of South America, using Quantum Gis v. 3.30.0.

RESULTS

Pimelodella nuchalis, new species

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(Figs. 1–5; Tab. 1)

Pimelodella megalops Mesa-Salazar *et al.*, 2019:30 (taxonomic list, IAvH-P 16640). —Cortés-Hernández *et al.*, 2020:504 (taxonomic treatment). —DoNascimento *et al.*, 2023 (taxonomic list). —Cortés-Hernández, Ramírez-Gil, 2024:94–97 (morphometric analysis).

Pimelodella sp. Acosta-Santos *et al.*, 2019:74 (visual guide). —Villa-Navarro *et al.*, 2022:160 (taxonomic list).

Holotype. CZUT-IC 27776, 67.3 mm SL; Colombia, Guainía, río Arabapo, isla Chamochina, border between Colombia and Venezuela, 03°46'57.11"N 67°37'59.1"W, 24 Aug 2008, C. A. Lasso, M. Sierra, M. Patiño & F. A. Villa-Navarro.

Paratypes. Colombia: CZUT-IC 16674, 2, 45.1–55.6 mm SL, collected with the holotype. CZUT-IC 16675, 30, 34.5–67.3 mm SL (3 c&s, 44.8–56.0 mm SL), collected with the holotype. CIACOL 3238, 3, 49.1–69.1 mm SL, Vaupés, cachivera Morroco, río Pacoa, tributary of río Apaporis, adjacent to community El Morroco, 00°08'37.4"N 70°57'30.8"W, 25 Feb 2018, E. Agudelo-Córdoba & A. Acosta-Santos. CIACOL 3239, 2, 60.4–70.0 mm SL, Vaupés, cachivera Morroco, río Pacoa, tributary of río Apaporis, adjacent to community El Morroco, 00°08'38.9"N 70°57'25.3"W, 26 Feb 2018, E. Agudelo-Córdoba & A. Acosta-Santos. CZUT-IC 16521, 3, 39.7–41.1 mm SL (2 c&s, 40.0–41.0 mm SL), Guainía, río Inírida, upstream of community Remanso, 03°27'39"N 67°58'23.5"W, 18 Feb 2008, C. A. Lasso, M. Sierra, M. Patiño, F. A. Villa-Navarro, A. Ortega-Lara & J. S. Usma-Oviedo. CZUT-IC 24773, 1, 56.1 mm SL, Guainía, vereda San Felipe, río Guainía, indigenous community Frito, 02°15'08.0"N 67°13'32.0"W, 86 m a.s.l., 10 Oct 2021, F. A. Villa-Navarro & A. Méndez-López. CZUT-IC 24774, 2, 53.3–57.9 mm SL, Guainía, vereda San Felipe, río Guainía, dock at community Punta Barbosa, 01°58'37.0"N 67°07'12.0"W, 80 m a.s.l., 14 Oct 2021, F. A. Villa-Navarro & A. Méndez-López. IAvH-P 16640, 8, 42.7–54.3 mm SL (1 c&s, 53.3 mm SL), Vichada, Puerto Carreño, caño Terecay, tributary of río Tomo, 05°34'57.9"N 68°29'55.4"W, 3 Mar 2017, L. M. Mesa-Salazar, C. DoNascimento, C. A. Lasso & Z. Rivas.

Diagnosis. *Pimelodella nuchalis* differs from all congeners by having a dark saddle on the predorsal region (Figs. 1–2, 5) (*vs.* absent). Additionally, *P. nuchalis* is distinguished from most congeners (except *P. bockmanni*, *P. buckleyi*, *P. geryi*, *P. grisea*, *P. hasemani*,

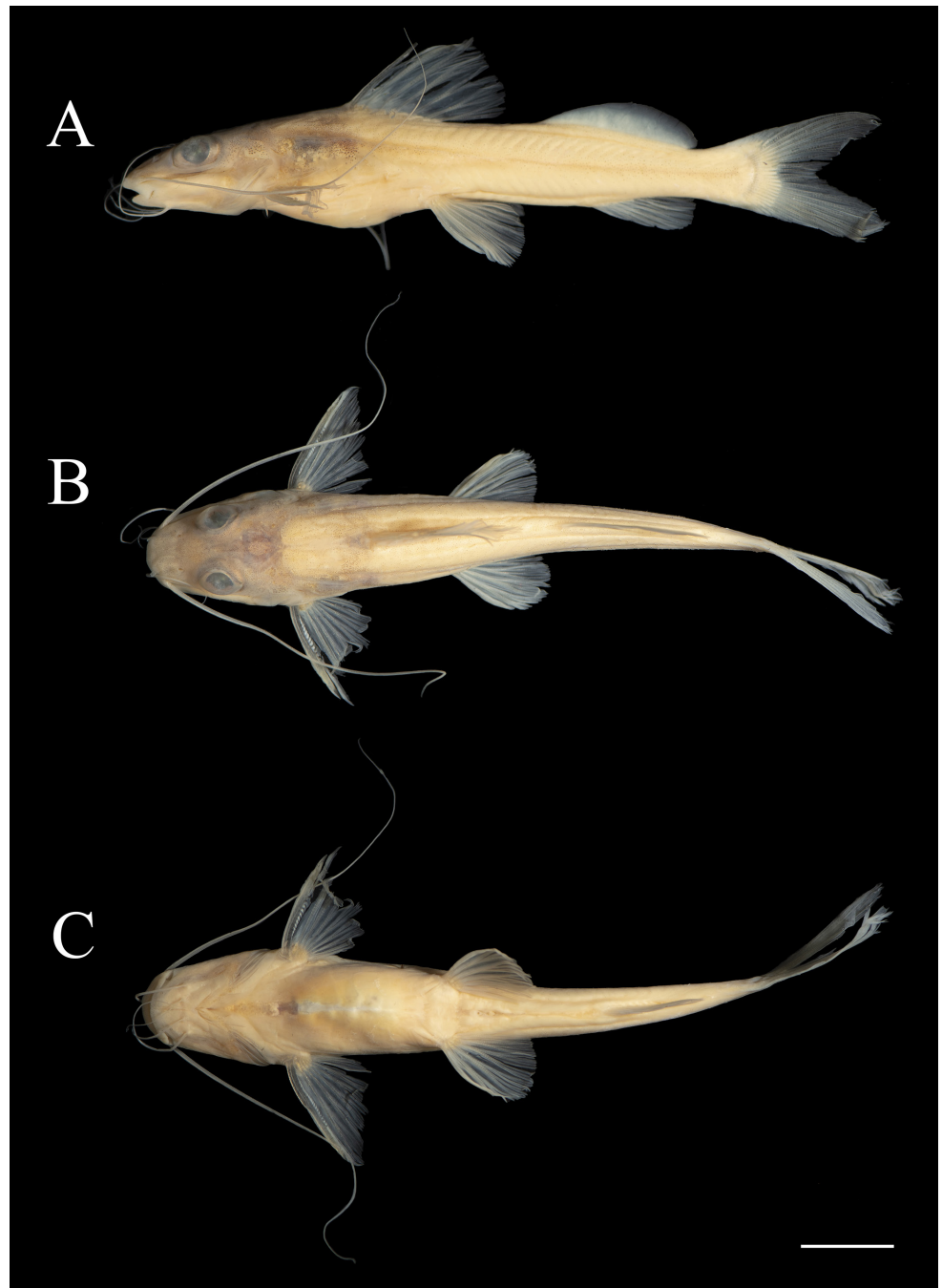


FIGURE 1 | *Pimelodella nuchalis*, holotype, CZUT-IC 27776, 67.3 mm SL. **A.** Left lateral view, **B.** Dorsal view, **C.** Ventral view. Scale bar = 1 cm.

P. howesi, *P. leptosoma*, *P. macturki*, *P. megalops*, *P. metae*, *P. notomelas*, and *P. procera*) by having a dark band on the dorsal fin (*vs.* absent). *Pimelodella nuchalis* differs from *P. bockmanni*, *P. leptosoma*, and *P. metae* by having the supraoccipital process reaching the anterior nuchal plate (*vs.* disconnected, leaving a free space between the supraoccipital process and anterior nuchal plate). *Pimelodella nuchalis* differs from *P. buckleyi*, *P. grisea*, *P. hasemani*, *P. howesi*, *P. macturki*, and *P. megalops* by having fewer total vertebrae

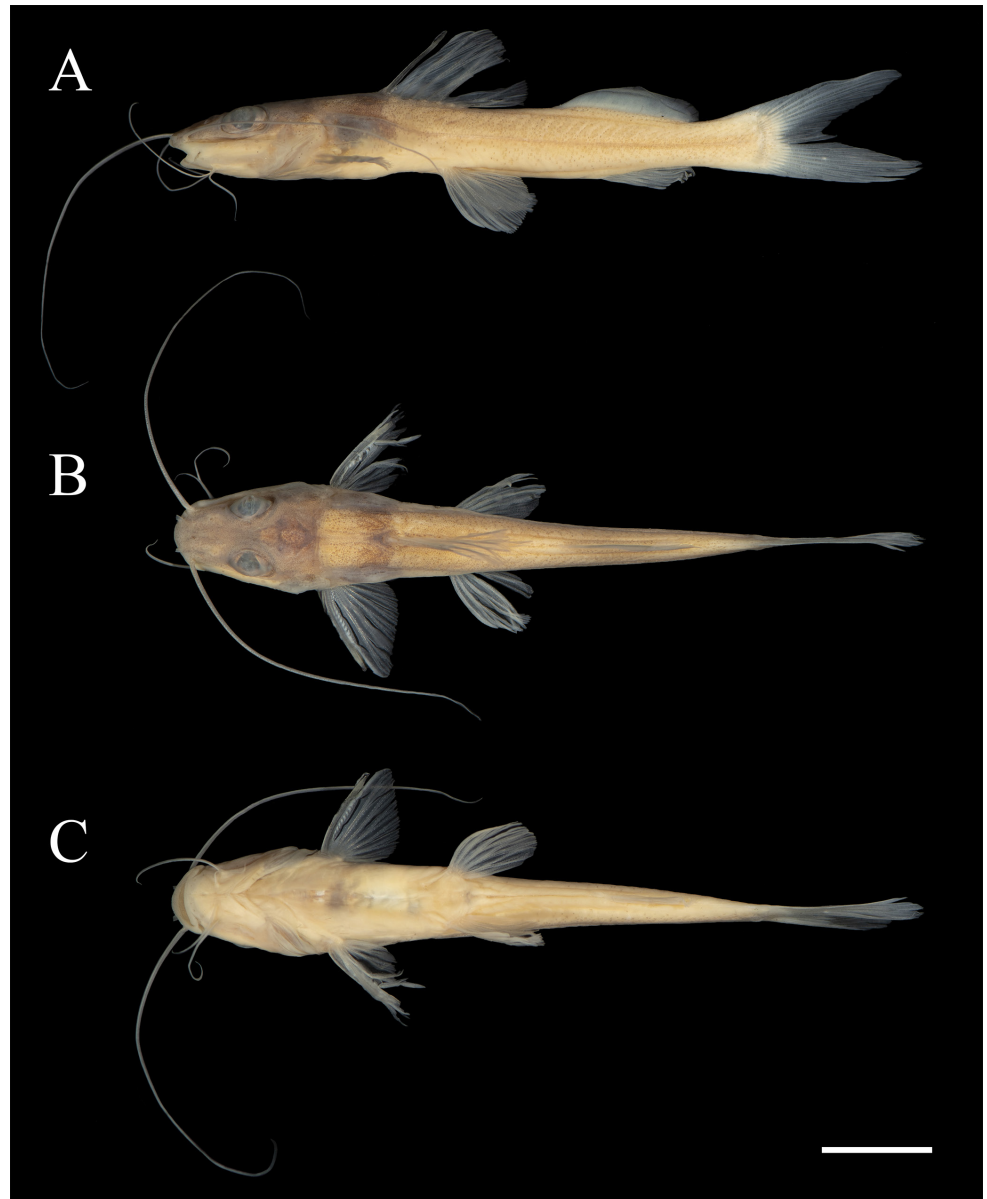


FIGURE 2 | *Pimelodella nuchalis*, paratype, CZUT-IC 16675, 52.3 mm SL. **A.** Left lateral view, **B.** Dorsal view, **C.** Ventral view. Scale bar = 1 cm.

(38 *vs.* 39–40 in *P. grisea*, 39–42 in *P. megalops*, 40–41 in *P. macturki*, 42–43 in *P. hasemani*, 43–44 in *P. buckleyi* and *P. howesi*). *Pimelodella nuchalis* differs from *P. geryi*, *P. notomelas*, and *P. procera* by having a shorter maxillary barbel (not exceeding the anterior fourth of the adipose-fin base *vs.* reaching the caudal-fin base in *P. geryi*; reaching the tip of middle caudal-fin rays or a little shorter in *P. notomelas*; reaching from mid-length of adipose-fin base to its posterior end in *P. procera*); anterior margin of pectoral-fin spine with minute straight dentations covering 60% of basal portion, and serrae restricted to its distal third (Fig. 3) (*vs.* serrae covering two-thirds in *P. geryi* and *P. procera*; basal two thirds smooth in *P. notomelas*); and posterior margin with 8–10 retrorse dentations (Fig. 3) (*vs.* 4–6 dentations in *P. notomelas*). *Pimelodella nuchalis* is

furtherly distinguished from *P. hasemani* by having a shorter maxillary barbel, never exceeding the anterior fourth of the adipose-fin base (*vs.* reaching between middle of adipose fin base to its distal posterior end), epiphyseal branches fused medially or giving origin to two or three unfused pores, aligned anteroposteriorly along sagittal plane (*vs.* unfused paired pores, symmetrically placed to both sides of sagittal plane), anterior margin of pectoral-fin spine with minute straight dentations covering approximately 60% of basal portion (*vs.* covering almost entire margin), and posterior margin with 8–10 retrorse dentations (*vs.* 12–14).

Description. Morphometric data summarized in Tab. 1. Body elongate, compressed towards caudal fin. Greater depth of body at dorsal-fin insertion. Dorsal profile of body convex from snout to base of supraoccipital process, then straight to dorsal-fin insertion, and descending along dorsal-fin base, slightly concave from posterior end of dorsal-fin base to adipose-fin insertion, straight and descending along adipose-fin base, and slightly concave along caudal peduncle. Ventral profile of body straight to slightly convex from jaw tip to pelvic-fin insertion, almost straight between pelvic-fin insertion to anal-fin insertion, straight and ascending along anal-fin base, and slightly concave along caudal peduncle (Figs. 1–2).

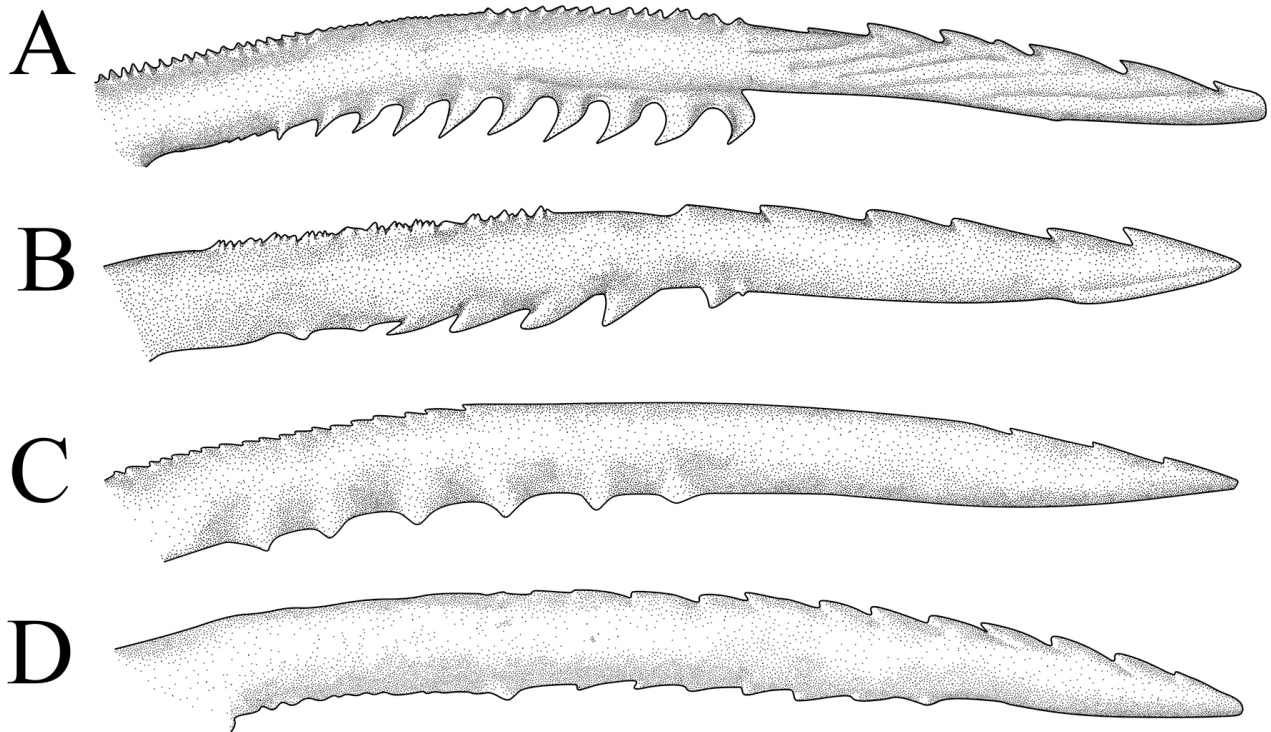


FIGURE 3 | Ventral view of left pectoral-fin spine. **A.** *Pimelodella nuchalis*, paratype, CZUT-IC 16675, 56.0 mm SL; spine length 10.6 mm. **B.** *P. geryi*, holotype, ZMA 102235, 58.0 mm SL; spine length 10.0 mm (modified from Slobodian *et al.*, 2017). **C.** *P. notomelas*, holotype, FMNH 57967, 38.9 mm SL (modified from Eigenmann, 1917). **D.** *P. procera*, paratype, 83.0 mm SL; spine length 14.8 mm.

TABLE 1 | Morphometric data of *Pimelodella nuchalis* and *P. megalops* (2 paratypes and 5 non-types). N = number of specimens; SD = standard deviation.

	<i>Pimelodella nuchalis</i>					<i>Pimelodella megalops</i>	
	Holotype	Mean	N	Range	SD	Paratypes	Non-types
						Range	Range
Standard length	67.3	52.1	17	39.7–67.3	-	55.7–67.2	52.8–70.3
Body depth	16.6	15.3	17	13.6–17.3	1.1	13.6–14.1	10.1–14.9
Body width	17.3	16.8	17	15.8–17.5	0.5	15.0–15.0	14.7–15.4
Maxillary-barbel length	65.3	63.7	16	56.5–71.4	4.0	79.6–88.7	81.2–94.4
Outer-mental barbel length	26.3	25.2	17	19.1–27.9	2.3	35.4–38.3	27.8–45.1
Inner-mental barbel length	13.4	12.8	17	11.1–16.5	1.4	17.3–18.4	17.3–21.1
Predorsal length	36.2	35.4	17	32.7–36.6	1.0	32.6–33.8	21.8–33.4
Dorsal-fin base	15.4	15.3	17	14.4–16.2	0.5	13.6–13.8	13.1–15.1
Dorsal-fin spine length	16	16.8	15	14.4–21.0	1.9	14.5–15.1	13.5–15.7
Dorsal-fin length (first branched ray)	20.9	20.1	16	18.3–21.9	1.2	25.9–26.6	13.6–26.9
Dorsal fin to adipose fin	14.9	14.5	17	13.1–16.5	1	12.2–13.4	9.1–13.3
Preadipose length	66	64.3	17	61.8–66.3	1.3	57.4–58.7	54.9–59.2
Adipose-fin base	24.5	24.8	17	23.5–27.2	1.1	29.4–31.5	29.7–32.6
Adipose-fin depth	4.8	4.6	17	3.9–5.2	0.4	3.8–4.6	3.2–4.9
Caudal-peduncle length	18	18.1	17	16.4–19.4	0.8	21.1–22.3	19.8–22.2
Caudal-peduncle depth	6.4	6.8	17	6.2–7.7	0.4	7.2–7.3	6.9–7.8
Upper caudal-fin lobe length	26.5	27	16	25.1–29.7	1.2	24.1–24.1	26.1–32.7
Lower caudal-fin lobe length	25.9	28.1	16	25.3–31.5	1.8	33.9–33.9	28.1–36.0
Preanal length	74.3	73.4	17	71.5–74.5	0.8	64.5–64.8	65.8–67.5
Anal-fin length	8.7	9.2	17	8.2–11.1	0.7	22.6–23.3	22.3–23.7
Prepelvic length	48.5	46.7	17	44.9–48.5	1	43.0–44.3	44.1–46.3
Pelvic-fin length	16	16.6	17	14.6–19.0	1.1	16.2–17.1	15.7–17.7
Prepectoral length	23.5	24.2	17	22.7–26.0	1	21.1–21.4	20.6–23.4
Pectoral-fin spine length	17.4	17.5	17	15.1–20.2	1.6	18.9–19.7	16.4–18.3
Snout to anus distance	53.5	52.1	16	49.5–54.7	1.3	49.4–50.6	49.8–51.0
Anus to anal-fin origin	20	20	16	18.6–22.1	1.1	16.0–16.5	16.1–17.9
Head length	26.1	26.2	17	24.2–27.5	1	22.2–22.8	21.2–22.3
Head width	62.1	59.0	17	54.8–65.9	3.2	52.6–57.5	64.2–69.0
Head depth	49.7	47.7	17	41.7–54.5	3.2	51.9–55.8	57.8–63.1
Snout length	37	34.9	17	31.7–37.2	1.4	38.3–38.4	36.4–38.7
Orbital diameter	28.7	30.6	17	26.0–36.3	3.3	38.5–41.1	33.0–35.9
Mouth width	36.8	35.3	17	32.4–38.2	1.4	27.5–28.5	26.6–31.1
Postorbital distance	35.3	34.3	17	30.4–37.7	2.1	28.3–30.5	28.8–33.5
Interorbital width	11.1	10.8	17	8.5–13.7	1.4	13.2–19.2	13.8–17.6
Internostril distance	16.7	18.2	17	15.8–21.8	1.6	16.3–17.4	14.7–18.0
Anterior nostril width	19.4	16.9	17	14.8–19.4	1.2	12.7–14.1	11.7–13.7
Posterior nostril width	18.1	17	17	14.9–19.0	1.2	17.0–17.6	14.7–18.2

Head conical. Mouth subterminal, upper jaw more pronounced than lower jaw. Premaxilla with 4–5 rows and dentary with four rows of villiform teeth. Anterior naris tubular. Posterior naris ovoid, closer (half of internarial distance) to anterior ocular margin than to anterior naris, bordered by a fleshy margin leaving a narrow notch on posterior margin. Nares disposed in rectangular arrangement. Barbels thin and slightly depressed. Maxillary barbel reaching or slightly exceeding insertion of adipose fin, but never exceeding anterior fourth of adipose-fin base. Outer mental barbel reaching vertical through spinelet base. Inner mental barbel reaching half of length of pectoral-fin spine when adpressed. Eye large and rounded, occupying most of dorsolateral surface of head. Orbital rim well defined. Supraoccipital process subrectangular in shape and long, reaching anterior nuchal plate. Branchiostegal membranes almost entirely free, united to isthmus only at medial apex and not joined to each other anteriorly. Branchiostegal rays six (6). Gill rakers on first gill arch 12–16; 9–12 associated to ceratobranchial, one to cartilage between ceratobranchial and epibranchial, and 2–3 to epibranchial (6).

Dorsal fin with spinelet, spine, and six branched rays; originating at vertical through posterior end of pseudotympanum. Distal margin of fin slightly convex. Spinelet large with wide base and rounded distal tip. Spine straight, slender, pungent, shorter than first branched ray (14.4–21.0% of SL). Anterior margin of spine with feeble, almost imperceptible serrae along distal third, remaining two thirds completely smooth, posterior margin entirely smooth. Anteriormost pterygiophore inserted above complex vertebra; posteriormost pterygiophore anterior to neural spine of vertebrae 10(2) or 11(4).

Pectoral fin with spine and seven (4), eight (12) or nine* (3) branched rays (c&s specimen of 41.0 mm SL with six branched rays on right side). Distal margin of fin slightly convex. Spine almost straight, entirely ossified, and pungent. Anterior margin of spine with minute straight dentations covering approximately 60% of basal portion, and serrae extending along its distal third. Posterior margin with 8–10 retrorse dentations covering 40–45% of margin, with proximal-most dentation closer to base of spine than distal-most dentation to distal tip of spine (Fig. 3A).

Pelvic fin with one unbranched and five branched rays, originating at vertical through last dorsal-fin ray. First ray distinctly shorter than second and third rays (first and second branched rays, respectively). Distal margin of fin convex. Tip of fin not reaching adipose-fin insertion.

Anal fin with two (2) or three (4) procurrent, two (2) or three (4) unbranched, and six (1), seven (4) or eight (1) branched rays. Base of anteriormost two or three rays embedded in thick skin. Distal margin of fin convex. Insertion of fin approximately at level of first third of adipose-fin base. Terminus of adpressed fin slightly surpassing adpressed terminus of adipose fin. Anteriormost pterygiophore inserted posterior to hemal spine of vertebrae 22(1) or 23(5); posteriormost pterygiophore inserted anterior to hemal spine of vertebrae 27(2) or 28(4).

Adipose fin short (23.5–27.2% of SL), with rounded margin and deepest point approximately at its mid-length. Distance from dorsal fin to adipose fin (13.6–16.5% of SL) equal than length of dorsal-fin base (14.4–16.2% of SL). Insertion of fin posterior to mid-length of trunk, approximately at vertical through vertebral centrum 20(1), 21(4) or 22(1). Terminus of fin at vertical through vertebral centrum 32(1) or 33(5).

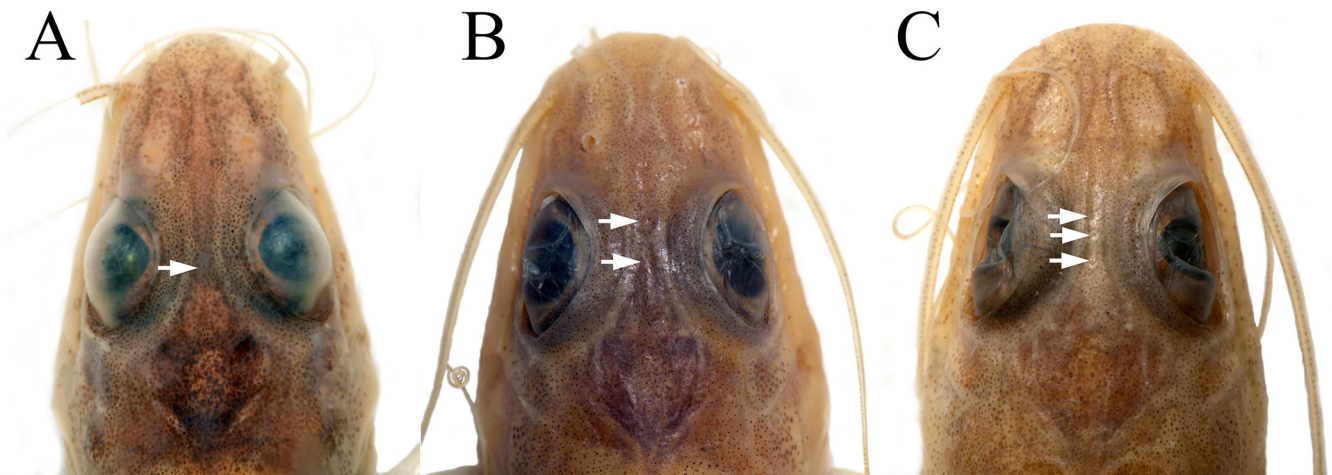


FIGURE 4 | Dorsal view of head of *Pimelodella nuchalis*. **A.** Fused epiphyseal branches (CZUT-IC 16675, 55.4 mm SL). **B.** Unfused epiphyseal branches with two sensory pores s6 (CZUT-IC 27776, holotype, 673 mm SL). **C.** Unfused epiphyseal branches with three sensory pores s6 (CZUT-IC 16674, 55.6 mm SL).

Caudal fin deeply forked with lobes subequal, and margin of tips rounded. Lower lobe with 17–21 procurrent rays, one unbranched, and eight branched principal rays. Upper lobe with 19–21 procurrent rays, one unbranched, and seven branched principal rays. Ventral caudal-fin plate with eight rays articulated (two to parhypural and six to hypurals 1+2) and dorsal caudal-fin plate with seven rays articulated (five rays to hypurals 3+4 and two rays to hypural 5). Upper innermost ray not articulated to caudal skeleton. Parhypural not fused to hypural 1. Hypurals 1 and 2 completely fused. Hypurals 3 and 4 completely fused. Hypural 5 free. Total vertebrae 38(6). Ribs 7(4) or 8(2).

Lateral line canal complete, extending to basal portion of interradiial membrane of middle caudal-fin rays. Head laterosensory canals with non-dendritic branches, ending in single pores. Supraorbital pore s1 medially adjacent to anterior naris, s2 + i2 between anterior and posterior nares, slightly closer to anterior naris. Sensory pore s3 just posterior to rim of posterior naris and s4 (one specimen of 56 mm SL with two pores on left side) located anteromedial to anterior ocular margin. Branches of sensory pores s6 fused to each other medially (13) or failing to fuse in most specimens (26), giving origin to two or three pores, aligned anteroposteriorly along sagittal plane (Fig. 4). Postorbital sensory pore (s7) located anterior to the posterior orbital edge. Parietal sensory pore (s8) posterior to eye and aligned with its dorsal margin. Infraorbital canal with six sensory pores: i1, s2+i2, i3, i4, i5, and i6. Preoperculomandibular canal with 11 sensory pores with relative positions similar to those described for other congeneric species. Postotic canal with three sensory pores, po1 + pm11, po2 slightly posterior to dorsal corner of gill opening, emerging from a posteroventrally directed branch (pterotic branch), and po3 between first two lateral line sensory pores (slightly closer to vertical through second sensory pore), emerging dorsal to lateral line canal.

Coloration in alcohol. Background coloration of body yellow. Sides of body with uniformly spaced chromatophores. Ventral region of head and body pale, with few sparse chromatophores around chin region. Dorsal surface of head with dense

concentration of dark brown chromatophores, framing a pair of slightly lighter elliptical areas corresponding to nasal capsules. Occipital surface around fontanel darker, forming a conspicuously v-shaped spot, continuous posteriorly with dark area on pseudotympanum, connected to its counterpart through a transverse predorsal band, forming a conspicuous dark saddle on predorsal region. Dorsal surface of maxillary barbel darkly pigmented. Mental barbels pale. Subdistal region of dorsal fin with black melanophores on interradiat membrane, forming a conspicuous band between spine and third ray (inconspicuous in specimens less than 40 mm SL). Pectoral, pelvic, adipose, anal, and caudal fins hyaline with few sparse chromatophores along fin rays, but not forming any evident macroscopic dark pattern (Figs. 1–2, 5).

Etymology. From the Latin *nuchalis* (neck), alluding to the dark saddle on the predorsal region (Fig. 5).



FIGURE 5 | Lateral and dorsal views of *Pimelodella nuchalis*. **A.** CZUT-IC 16675, 60.5 mm SL, **B.** CZUT-IC 24773, 56.2 mm SL, **C.** CZUT-IC 24774, 53.4 mm SL, **D.** CZUT-IC 16675, 46.4 mm SL, **E.** CZUT-IC 16675, 43.7 mm SL. Scale bars = 1 cm.

Geographical distribution. *Pimelodella nuchalis* is known from the Atabapo and Inírida rivers of the upper basin of the Orinoco River, and the Tomo River, a direct tributary of the middle basin of the Orinoco River. Additionally, the new species occurs in the Amazon River basin, in the Guainía River, tributary of the upper basin of the Negro River, and in the Pacoa stream, a tributary of the Apaporis River from the Caquetá River drainage (Fig. 6).

Ecological notes. The diet of *Pimelodella* species consists mainly of crustaceans and aquatic insects (e.g., copepods, ostracods, and chironomid and ephemeropteran larvae) (Mazzoni, Costa, 2007; Mazzoni *et al.*, 2010; García *et al.*, 2017). However, the digestive tract of a c&s specimen of *P. nuchalis* (46.7 mm SL) contained an Acestrorhamphidae tetra of approximately 18.1 mm SL (Fig. 7), probably a specimen of *Thayeria* Eigenmann, 1908; *Hemigrammus analis* Durbin, 1909; or *H. hyanuary* Durbin, 1918 (J. M. Miranda and F. C. T. Lima, 2024, pers. comm.). The size ratio between the *P. nuchalis* specimen and its fish prey highlights the great capacity to ingest large food items, which is especially true when considering the actual volume capacity of the abdominal cavity.

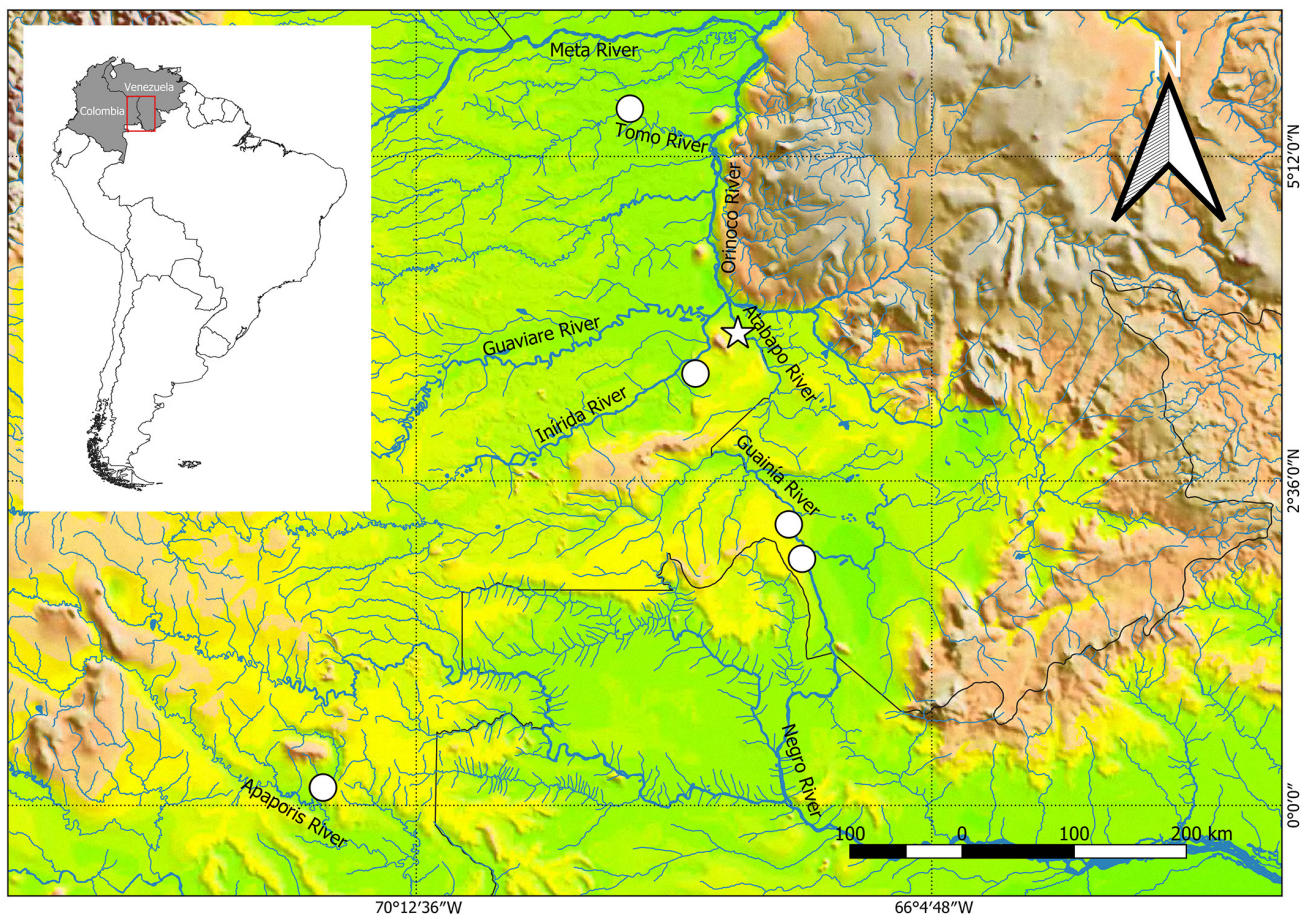


FIGURE 6 | Geographic distribution of *Pimelodella nuchalis*. Type-locality: white star.

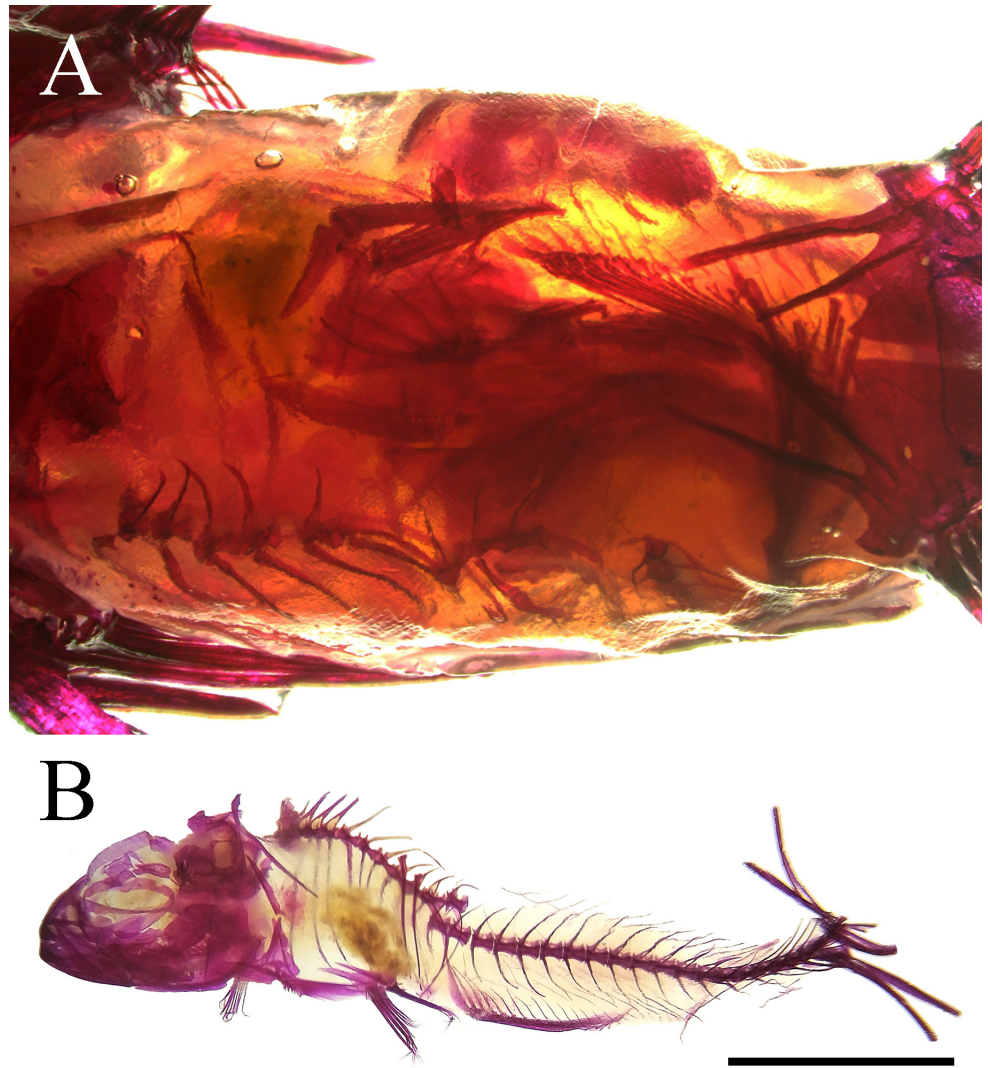


FIGURE 7 | Gut content of *Pimelodella nuchalis*. **A.** Ventral view of abdomen of c&s specimen (CZUT-IC 16675, 46.7 mm SL). **B.** Lateral view of the remains of the ingested acestrorhamphid tetra. Scale bar = 5 mm.

Morphometric analysis. We found a clear morphometric differentiation between *Pimelodella megalops* and *P. nuchalis* along PC 1 that accounts for 74.1% of total variability of our data (Fig. 8). The variables with highest values on the positive axis of PC 1 were anterior nostril width, mouth width, postorbital distance, internostril distance, and dorsal fin to adipose fin; and for the negative axis were anal-fin length, maxillary-barbel length, outer mental-barbel length, inner mental-barbel length, adipose-fin length, lower caudal-fin lobe length and interorbital width (Tab. S1). Simple linear regressions of lower caudal-fin lobe length for these species show that *P. megalops* has a significantly longer lobe than *P. nuchalis* through its growth (ANCOVA $F = 26.85$, $p = 5.31e-05$) (Fig. 9).

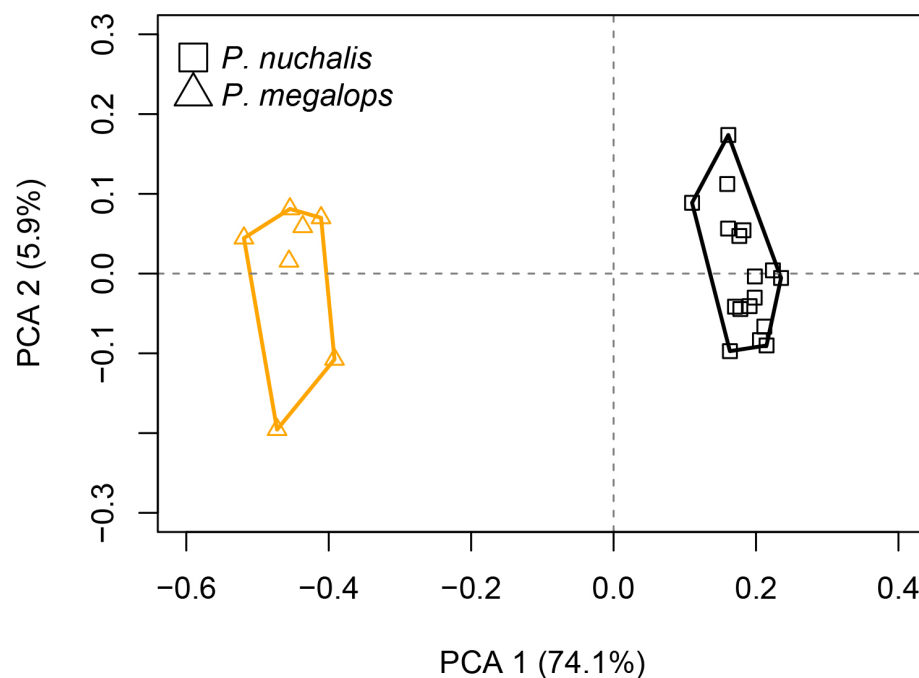


FIGURE 8 | Scatter plot of principal component analysis (PCA 1 and PCA 2) of *Pimelodella nuchalis* and *P. megalops*.

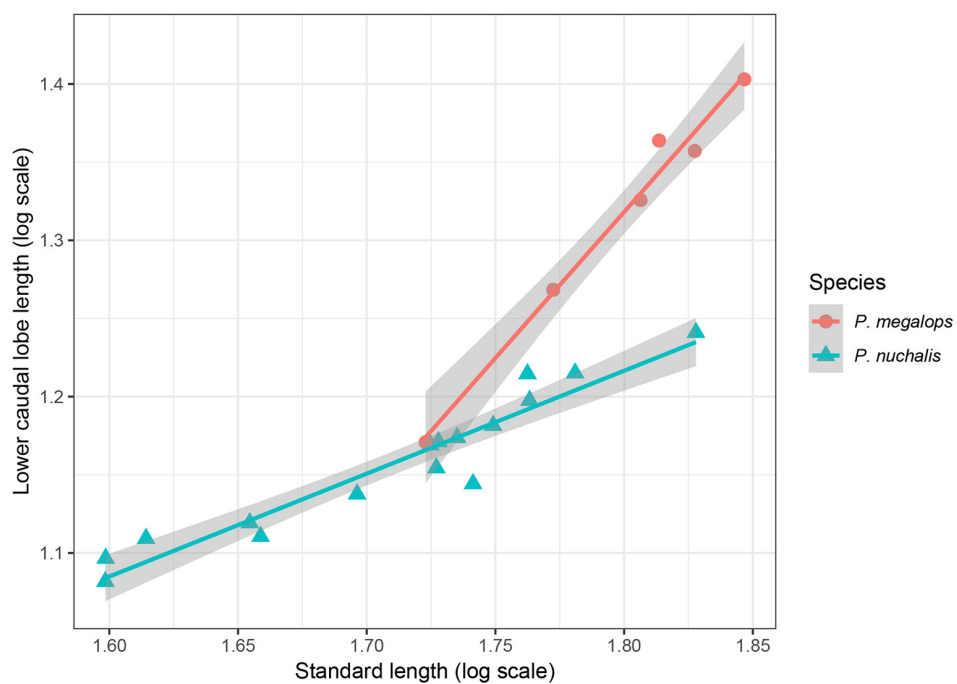


FIGURE 9 | Bivariate plot of linear regression analysis, with 95% confidence interval calculated for *Pimelodella nuchalis* and *P. megalops*.

DISCUSSION

Pimelodella nuchalis is herein unambiguously assigned to *Pimelodella* by having the single exclusive autapomorphy proposed by Bockmann (1998) to distinguish this genus among heptapterids, *i.e.*, middle caudal-fin rays not articulated to hypural plates, along with the combination of morphological characters listed by Slobodian *et al.* (2017) and Slobodian, Pastana (2018): body moderately elongated (39.7–67.3 mm SL); supraoccipital process long, reaching the anterior nuchal plate; anterior and posterior fontanels long and separated by the epiphyseal bar; orbital rim free; pectoral fin with spine, ornamented with anterior and posterior dentations (Fig. 3), and 7–9 branched rays; six branchiostegal rays; caudal fin deeply forked; and hypural 5 free (Figs. 10A–C).

The presence of a dark saddle on the predorsal region in *Pimelodella nuchalis* represents the main diagnostic feature that distinguishes the new species from its congeners. Although the predorsal saddle in *P. nuchalis* seems to be exclusive within *Pimelodella*, some species of Rhamdiinae exhibit a similar condition, as is the case of *Goeldiella eques* (Müller & Troschel, 1849) which shows a conspicuous dark, wide band, extending obliquely from the nuchal plate, along the opercular membrane, and *Brachyrhamdia heteropleura* (Eigenmann, 1912) which presents a dense concentration of chromatophores, extending from the postorbital margin to the insertion of the dorsal fin, and reaching ventrally the pseudotympanum.

Pimelodella nuchalis shows polymorphism in the fusion pattern of the epiphyseal branches of the supraorbital sensory canals. Most specimens (26 out of 39) have separate branches, giving rise to two (23) or up to three sensory pores (3), although showing an asymmetrical disposition pattern, where one pore is placed in advance of the other pore, and both pores are longitudinally aligned along the sagittal plane (Fig. 4). Unfused asymmetrical branches of sensory pores s6 were documented for *P. longibarbata* (Cortés-Hernández *et al.*, 2020), but the longitudinally aligned pattern of *P. nuchalis* has not been documented in any other heptapterid (*e.g.*, Lundberg *et al.*, 1991; Bockmann, 1994; Arratia, Gayet, 1995; Arratia, Huaquin, 1995; Bockmann, Ferraris, 2005; Bockmann, Miquelarena, 2008; Slobodian, Bockmann, 2013;

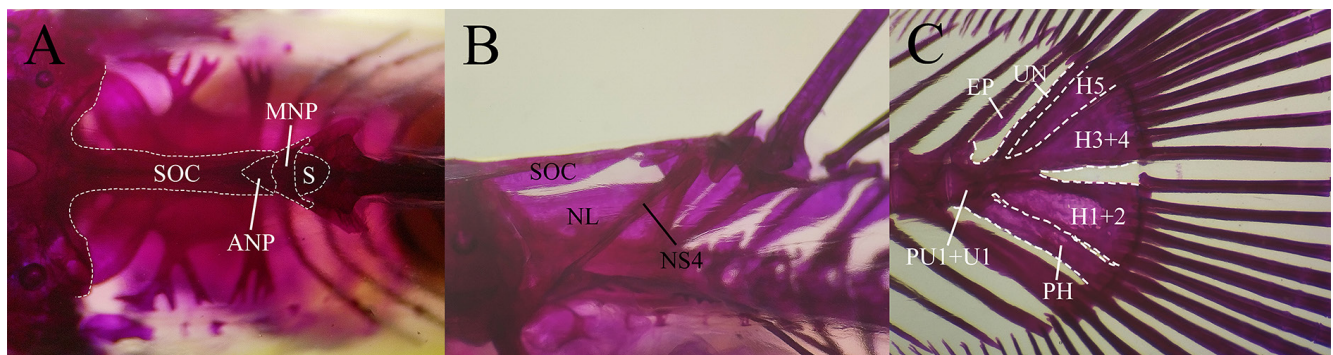


FIGURE 10 | **A.** Dorsal view of skeletal elements associated with articulation of cranium and nuchal plates of *Pimelodella nuchalis*, paratype, CZUT-IC 16675, 46.7 mm SL. **B.** Lateral view of Weberian apparatus. **C.** Lateral view of caudal-fin skeleton. Abbreviations: ANP, anterior nuchal plate; EP, epural; H, hypural; MNP, middle nuchal plate; NL, neural lamina; NS4, neural spine 4; PH, parhypural; PU1+U1, complex caudal centrum (preural centrum 1 and ural centrum 1); S, 1st dorsal-fin spine; SOC, supraoccipital; UN, uroneural.

Slobodian, Pastana, 2018; Bockmann, Reis, 2021; Cortés-Hernández *et al.*, 2023b). The fusion pattern of the epiphyseal branches has been used as a diagnostic character within *Pimelodella* (Slobodian, Pastana, 2018; Pierre, Slobodian, 2024), although it will be important to take into account potential intraspecific variation as we reported here.

Pimelodella nuchalis was originally misidentified in Colombia as *P. megalops*, probably due to their close external resemblance. Both species share small body size (up to 67.3 mm SL in *P. nuchalis* and 75.0 mm SL in *P. megalops*), large eyes (26.0–36.3% of HL in *P. nuchalis* and 33.0–41.1% in *P. megalops*), and posterior margin of the pectoral-fin spine with well-developed retrorse dentitions. *Pimelodella megalops* was formerly listed in Eigenmann (1910) but it was formally described in Eigenmann (1912), based on 60 specimens (56–100 mm TL), coming from the Tumatumari Cataract, in the lower Potaro River, Essequibo River basin of Guyana. Eigenmann (1912:168) distinguished *P. megalops* from the other two recorded species from Guyana (*P. cristata* and *P. macturki*) by its relative length of the maxillary barbel (reaching end of adipose fin or caudal fin), diameter of eye (2.5 in HL, longer than snout), interorbital distance (5.5 in the head), relative length of pectoral-fin spine (little shorter than head), adipose-fin length (3.33 or more in SL), and caudal-fin lobes long and slender, with lower lobe 2.75–3.0 times in the length (Fig. 11). Mees (1986) while comparing specimens of what he identified as *P. megalops* from French Guiana with paratypes of that species, found some subtle differences in eye size, adipose-fin length, and relative length of the lower lobe of the caudal fin, indicating that the eye was smaller than that reported by Eigenmann (1912) (2.7–3.1 times in HL *vs.* 2.5). The length of the adipose fin of *P. megalops* from French Guiana also showed a wider range of variation (3.1–3.55 times in SL *vs.* 3.33),



FIGURE 11 | Left lateral view. **A.** *Pimelodella megalops*, holotype, FMNH 53231, 73.8 mm SL. Photographed by Mike W. Littmann, FMNH Division of Fishes. **B.** *P. nuchalis*, holotype, CZUT-IC 27776, 67.3 mm SL. Scale bars = 1 cm.

and the shape of the caudal fin exhibited some variation, with the lower lobe being slightly longer than the upper lobe (Mees, 1986). Nevertheless, we find that *P. nuchalis* is distinguished from *P. megalops* by having a longer preadipose distance (61.8–66.3% of SL in *P. nuchalis* vs. 54.9–59.2% in *P. megalops*), shorter adipose–fin base (23.5–27.2% of SL vs. 29.4–32.6%), longer preanal distance (71.5–74.5% of SL vs. 64.5–67.5%), shorter anal–fin base (8.2–11.1% of SL vs. 22.3–23.7%), longer head (24.2–27.5% of SL vs. 21.2–22.8%), shorter maxillary barbel (not exceeding anterior fourth of adipose–fin base vs. reaching between posterior end of adipose fin and base of caudal fin), shorter outer mental barbel (reaching mid-length of pectoral–fin spine when adpressed vs. reaching or almost reaching insertion of pelvic fin) and fewer total vertebrae (38 vs. 39–42). Regarding the caudal fin, lobes of *P. nuchalis* are subequal (vs. lower lobe distinctively longer than upper lobe in *P. megalops*). Although variation ranges of lower lobe length overlap (25.3–31.5% of SL in *P. nuchalis* vs. 28.1–36.0% in *P. megalops*), linear regressions show significant differences, expressed both in magnitude and slope for these species (Fig. 9).

Pimelodella megalops is restricted to the middle basin of the Essequibo River (Mees, 1983; Hardman *et al.*, 2002), while *P. nuchalis* occurs in rivers of the western reaches of the Guiana Shield, in the upper and middle basin of the Orinoco River, and upper basin of Negro and Apaporis rivers. This biogeographic pattern of *P. nuchalis* (Negro and Orinoco: Dagosta, de Pinna, 2019) has been recorded for multiple species across several independent lineages: Acestrorhamphidae: *Hemigrammus barrigona* Eigenmann & Henn, 1914, *H. bellottii* (Steindachner, 1882), *H. vorderwinkleri* Géry, 1963, *Jupiaba anteroides* (Géry, 1965), *Megalomphodus epicharis* (Weitzman & Palmer, 1997), *Petitella bleheri* (Géry & Mahnert, 1986); Acestrorhynchidae: *Heterocharax leptogrammus* Toledo-Piza, 2000; Anostomidae: *Leporinus enyae* Burns, Chatfield, Birindelli & Sidlauskas, 2017, *Pseudanos varii* Birindelli, Lima & Britski, 2012; Characidae: *Odontostilbe pulchra* (Gill, 1858), *Phenacogaster prolata* Lucena & Malabarba, 2010, *Serrabrycon magoi* Vari, 1986; Cichlidae: *Cichla temensis* Humboldt, 1821, *Geophagus abalios* López-Fernández & Taphorn, 2004, *G. dicrozoster* López-Fernández & Taphorn, 2004, *Heros severus* Heckel, 1840, *Hoplarchus psittacus* (Heckel, 1840), *Laetacara fulvipinnis* Staack & Schindler, 2007, *Lugubria lenticulata* (Heckel, 1840), *Mesonauta insignis* (Heckel, 1840), *Pterophyllum altum* Pellegrin, 1903, *Satanoperca daemon* (Heckel, 1840); Crenuchidae: *Microcharacidium gnomus* Backup, 1993, *Poecilocharax weitzmani* Géry, 1965; Ctenoluciidae: *Boulengerella lateristriga* (Boulenger, 1895); Curimatidae: *Curimatopsis macrolepis* (Steindachner, 1876), Hypopomidae: *Racenisia fimbriipinna* Mago-Leccia, 1994; Lebiasinidae: *Copella nattereri* (Steindachner, 1876); Loricariidae: *Acestridium dichromum* Retzer, Nico & Provenzano, 1999 and *A. martini* Retzer, Nico & Provenzano, 1999, *Colossimystax pectegenitor* (Lujan, Armbruster & Sabaj Pérez, 2007), *Hemiancistrus subviridis* Werneke, Sabaj Pérez, Lujan & Armbruster, 2005, *Hypostomus sculpodon* Armbruster, 2003, *Neblinichthys pilosus* Ferraris, Isbrücker & Nijssen, 1986, *Pseudolithoxus nicoi* (Armbruster & Provenzano, 2000), *Stellantia siderea* (Armbruster, 2004); Serrasalminidae: *Tometes makue* Jégu, Santos & Belmont-Jégu, 2002; Stevardiidae: *Creagrutus phasma* Myers, 1927, *C. runa* Vari & Harold, 2001, *C. vexillapinnus* Vari & Harold, 2001, *C. zephyrus* Vari & Harold 2001, *Ptychocharax rhyacophila* Weitzman, Fink, Machado-Allison & Royero, 1994, *Rhinobrycon negrensis* Myers, 1944 (Dagosta, de Pinna, 2019; Bogotá-Gregory *et al.*, 2022). The upper Negro and the upper Orinoco

basins have been proposed as an area with high endemism for Neotropical freshwater fishes (Hubert, Renno, 2006). Part of this fish fauna may have derived from the proto-Orinoco–Amazon landscape, which predates its hydrological separation. However, the diversification of these lineages has been influenced more recently by faunal exchanges facilitated by the Pleistocene/Holocene formation of the Casiquiare Canal, acting as a modern dispersal corridor between these adjacent basins (Willis *et al.*, 2010; Lujan, Armbruster, 2011; Dagosta, de Pinna, 2019).

Comparative material examined. Additional material is listed in Cortés-Hernández *et al.* (2020, 2023a). *Pimelodella buckleyi*. Ecuador: Canelos: BMNH 1880.12.8.98–99, 2 syntypes (xr), 94.0–104.0 mm SL. *Pimelodella figueroai*. Colombia: Meta: La Macarena: ICN-MNH 2900, 12 paratypes, 44.3–107.8 mm SL, Lozada Creek, ca. 17 km above its junction with the Guayabero River. IAvH-P 19354, 3, 75.1–89.8 mm SL, Guayabero River, 02°17'33.1"N 73°52'45.4"W. IAvH-P 19416, 2, 67.7–79.6 mm SL, Guayabero River, 02°17'35.6"N 73°52'32.9"W. IAvH-P 19440, 1, 70.3 mm SL; Guayabero River, 02°17'35.6"N 73°52'32.9"W. IAvH-P 19708, 1, 80.1 mm SL, Guayabero River, 02°32'59.9"N 73°56'27.5"W. IAvH-P 19709, 2, 39.3–50.4 mm SL, 1 c&s, 45.3 mm SL, Duda River, in front of mouth of San José Creek, 02°32'59.9"N 73°56'27.5"W. IAvH-P 22613, 5, 42.4–58.0 mm SL, 1 c&s, 42.8 mm SL, Yarumales Creek, near its confluence with the Guayabero River, 02°23'30.9"N 73°35'24.6"W. *Pimelodella grisea*. Ecuador: BMNH 1902.5.27.36, syntype (xr), 118.5 mm SL, Durango River. BMNH 1902.7.29.47, syntype (xr), 116.3 mm SL, Vaquería River. BMNH 1902.7.29.58, syntype, 98.8 mm SL, Sapayo River. Colombia: Nariño: CZUT-IC 17825, 3, 100.3–121.5 mm SL, Tumaco, Candelillas, Mira River, 01°28'22"N 78°41'14"W. *Pimelodella hasemani*. Brazil: Porto Velho: FMNH 57980, holotype (xr), 61.4 mm SL, San Antonio de Rio Madeira. MCZ 7502, 2 paratypes (xr), 35.6–40.2 mm SL, Óbidos, Amazon River. MCZ 7572, 1 paratype (xr), 50.9 mm SL, Jutai River (tributary of Solimões River). MCZ 7577, 49 paratypes (xr), 35.1–50.1 mm SL, Içá River, Putumayo River (tributary of Solimões River), near the Brazilian–Colombian border. MCZ 7579, 2 paratypes (xr), 50.1–55.5 mm SL, Óbidos, Amazon River. MCZ 7580, 9 paratypes (xr), 37.0–54.2 mm SL, Óbidos, Amazon River. MCZ 7581, 1 paratype, 39.1 mm, Obidos, Amazon River. *Pimelodella howesi*. Bolivia: ANSP 69036, holotype (xr), 80.0 mm SL, Boca Chapare, Chimore River. *Pimelodella leptosoma*. Guyana: ANSP 39340, holotype (xr), 60.0 mm SL, Rupununi River. ANSP 39341, 1 paratype (xr), 60.3 mm SL, Rupununi River. *Pimelodella macturki*. Guyana: FMNH 53234, holotype (xr), 52.2 mm SL, creek in Mora Passage. MCZ 30073, 1 paratype (xr), 48.1 mm SL, creek in Mora Passage. *Pimelodella megalops*. Guyana: FMNH 53231, holotype (xr), 73.8 mm SL, Lower Potaro River at Tumatumari. FMNH 53233, paratype (xr), 44.0 mm SL, Crab Falls. MCZ 30075, paratype (xr), 61.2 mm SL, Lower Potaro River at Tumatumari. USNM 66262, 2 paratypes, 55.7–67.2 mm SL, collected with holotype. USNM 402705, 5, 52.8–70.3 mm SL, Cuyuní River, about 15 km upstream from Waikuni Mountains, in vicinity of mouth of Toropaur River, 06°41'31"N 59°34'38"W. *Pimelodella notomelas*. Brazil: Mato Grosso: FMNH 57967, holotype, 39.3 mm SL, Cáceres.

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acsi.acnatsci.org/base/index.html). Karen L. Álvarez-Álvarez for illustration of the pectoral-fin spines. Juan M. Mirande and Flavio C. T. Lima for providing taxonomic identification of the specimen of *Acestrorhamphidae*, obtained from the digestive tract of c&s paratype of *Pimelodella nuchalis*. MACH thanks the Fondo para la Investigación Científica y Tecnológica (FONCyT) for funding the project “Sistemática de *Pimelodella* (Siluriformes: Heptapteridae), con revisión de las especies argentinas y contexto filogenético en la familia Heptapteridae” (PICT 2020 N° SERIEA-02141), under direction of Juan M. Mirande. CCCS was funded by the Sara E. and Bruce B. Collette Postdoctoral Fellowship in Systematic Ichthyology (NMNH).

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The authors confirm that the data supporting the findings of this study are available within the article.

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The authors declare no competing interests.

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