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A new species of *Pimelodella* (Siluriformes: Heptapteridae) from the Paraguai basin, Brazil, with a discussion regarding its distribution

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A new species of *Pimelodella* is described from the rio Paraguai basin in Mato Grosso do Sul and Mato Grosso States, Brazil. The new species distinguishes from all other members of the genus based on a unique combination of characteristics, which include: dorsal profile straight from snout to dorsal-fin, maxillary barbel reaching at least the anal-fin terminus when parallel to main body axis, robust dorsal-fin spine bearing small spinules along three-fourths of its posterior margin, 41–42 total vertebrae (rarely 43 or 44), 13–23 large and retrorse blades at the posterior margin of the pectoral-fin spine, and dorsolateral region of body slightly darkened. This study also discusses the ichthyofaunal similarities between the Paraguai and Amazon basins, shedding light on their biogeographic history. Additionally, the research includes considerations about the sexual dimorphism of *Pimelodella* and provides an identification key for the *Pimelodella* species found in the Paraguai basin.

Keywords: Biogeography, Catfishes, Identification key, Sexual dimorphism, Taxonomy.

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Uma nova espécie de *Pimelodella* é descrita da bacia do rio Paraguai, nos Estados de Mato Grosso do Sul e Mato Grosso, Brasil. A nova espécie se distingue de todas as suas congêneres por apresentar uma combinação exclusiva de características, que incluem: perfil da região anterior do corpo reto do focinho à nadadeira dorsal, barbilhão maxilar alcançando pelo menos o término da nadadeira anal quando paralelo ao eixo principal do corpo, espinho da nadadeira dorsal robusto e apresentando pequenas espínulas nos três-quartos distais da sua margem posterior, 41–42 vértebras totais (raramente 43 ou 44), espinho da nadadeira peitoral apresentando 13–23 lâminas grandes e retrorsas na sua margem posterior, e região dorsolateral do corpo ligeiramente mais escura que o restante. Este estudo também discute as similaridades entre a ictiofauna das bacias do Paraguai e Amazônica, abordando a história biogeográfica entre ambas as regiões. Adicionalmente, considerações acerca do dimorfismo sexual de *Pimelodella* são apresentadas, além de uma chave de identificação para as espécies de *Pimelodella* encontradas na bacia do Paraguai.

Palavras-chave: Bagres, Biogeografia, Chave de identificação, Dimorfismo sexual, Taxonomia.

INTRODUCTION

Pimelodella, as described by Eigenmann and Eigenmann in 1888, stands as the most diverse genus within the Heptapteridae family, currently comprising 83 valid species (Fricke *et al*., 2023). The first comprehensive taxonomic review of this genus was conducted by Eigenmann in 1917. In this review, Eigenmann provided descriptions and geographic distribution information for 34 species and one subspecies of *Pimelodella* known at the time, in addition to a diagnosis for the genus. However, this initial diagnosis had undergone numerous discussions and redefinitions (*e.g*., Mees, 1983; Bockmann, Miquelarena, 2008; Bockmann, Slobodian, 2013; Souza-Shibatta *et al*., 2013; Slobodian *et al*., 2017; Slobodian, Pastana, 2018) primarily due to the discovery of new species. As a result, *Pimelodella* is currently characterized by a distinctive combination of features: body moderately elongated, usually between 12–30 cm of standard length; supraoccipital process long, usually reaching the anterior nuchal plate; anterior and posterior fontanels open, long, separated by the epiphyseal bar; limits of eyes well defined by a free orbital rim, more conspicuous anteriorly and dorsally; pectoral fin with a single, strong and pungent unbranched ray (spine), bearing both anterior and posterior ornamentations, and 7–9 (usually 8) branched rays; branchiostegal rays usually 6; caudal fin deeply forked; median caudal-fin rays not articulated to hypural plate; hypural 5 as a single structure, and not fused to hypural plate; body generally with a dark midlateral stripe, extending from the snout or posterior to the head until the insertion of, or onto, the median caudal-fin rays (Slobodian *et al*., 2017).

The distribution of *Pimelodella* encompasses both cis- and trans- Andean Neotropical drainages from Panamá to Argentina (Bockmann, Guazzelli, 2003; Ferraris, 2007; Fricke *et al*., 2023). These fishes are typically found in the major Neotropical basins, primarily in streams, where they form schools of up to ten individuals, often associated with sandy banks, marginal vegetation, or rock crevices (Bockmann, Guazzelli, 2003; Slobodian *et al*., 2017; Slobodian, Pastana, 2018). Several *Pimelodella* species have been reported to inhabit the Paraguai basin. These include *P. gracilis* (Valenciennes, 1835), *P. griffini* Eigenmann, 1917, *P. laticeps* Eigenmann, 1917, *P. megalura* Miranda Ribeiro, 1918, *P. mucosa* Eigenmann & Ward, 1907 in Eigenmann *et al*. (1907), *P. notomelas* Eigenmann, 1917, and *P. taeniophora* (Regan, 1903) (Britski *et al*., 1999; Koerber *et al*., 2017; Mirande, Koerber, 2020; Slobodian *et al*., 2022). *Pimelodella taenioptera* Miranda Ribeiro, 1914, was also described for the Paraguai basin in Brazil, but indicated as probably a junior synonym of *P. gracilis* in Slobodian (2017). *Pimelodella parva* Günthert, 1942, was described for the Paraguay basin in Paraguay, but is probably a juvenile of *Pimelodus* (Slobodian, 2017). The name *Pimelodus parvus* is previously occupied by *Pimelodus* (*Rhamdia*) *parvus* Boulenger (1898), and the problems related to this species are already being tackled in an ongoing work (M. Rocha and V. Slobodian, work in progress).

The Paraguai basin encompasses drainages in Brazil (in the States of Mato Grosso and Mato Grosso do Sul), Bolivia, Paraguay, and Argentina. This region is susceptible to various anthropic impacts, including hydroelectric and agricultural activities, which induce significant hydrological alterations (Tucci *et al*., 1999; Hamilton, 2002; Ely *et al*., 2020). The Paraguai basin is renowned for its high biological diversity, serving as habitat for approximately three hundred fish species, with about one-third being endemic (Carvalho, Albert, 2011). Some notable examples of these endemic species include *Curimatopsis myersi* Vari, 1982, *Hyphessobrycon rutiliflavidus* Carvalho, Langeani, Miyazawa & Troy, 2008, *Ernstichthys taquari* Dagosta & de Pinna, 2021, and *Paracanthopoma saci* Dagosta & de Pinna, 2021 (Melo *et al*., 2016; Dagosta, de Pinna, 2021; Fricke *et al*., 2023).

During the examination of a *Pimelodella* material from the Paraguai basin in Brazil for an illustrated guide to Pantanal fish species (Gimênes-Junior, Rech, 2022), we encountered specimens that exhibited similarities with *P. serrata* Eigenmann, 1917. As a result, these specimens were identified as belonging to *P. serrata* in the guide (*e.g*., Slobodian *et al*., 2022). *Pimelodella serrata* is a species originally described from San Joaquin, Bolivia, within the upper rio Guaporé basin (Bockmann, Guazzelli, 2003). It has also been observed in various locations within the rio Madeira basin, spanning Bolivia and Brazil (Lauzanne, Loubens, 1985; Chernoff *et al*., 2000; Bockmann, Slobodian, 2013). However, under a more detailed examination, specimens from the Paraguai basin revealed to be distinct from *P. serrata* and other species within the *Pimelodella* genus. In this context, we proceed with a description of this newly discovered *Pimelodella* species, with nine recorded occurrences within the Paraguai basin. Additionally, we provide an identification key for *Pimelodella* species found within the Paraguai basin and discuss the similarities between the ichthyofauna of the Paraguai and Amazon basins.

MATERIAL AND METHODS

Measurements were taken as point-to-point distances using a digital caliper with a precision of 0.01 mm, according to Slobodian *et al.* (2017). All specimens were measured, including the one cleared and stained (c&s) prior to treatment. Measurements of head parts were converted to proportions of head length (HL), except for measurements of barbels, which are shown as proportions of standard length (SL). The HL and measurements of body parts were converted to proportions of SL. Meristics and fin positions followed Bockmann, Castro (2010). Vertebral counts include the Weberian complex elements counted as five, all free vertebrae, and the compound caudal centrum (PU1+U1) counted as one, following Lundberg, Baskin (1969). The number of specimens counted for each meristic characteristic is indicated in parentheses. When a range is presented, the count for the holotype is indicated by an asterisk.

Osteological nomenclature follows Bockmann, Miquelarena (2008); nomenclature for pectoral- and dorsal-fin ornamentations follows Slobodian, Pastana (2018), with modifications of Ballen, de Pinna (2022); nomenclature for lateral-line canals and pores follows Slobodian, Pastana (2018). Osteological data was obtained with X-ray images from the Faxitron LX-60 system, Faxitron DX software, and specimens c&s following the method of Taylor, Van Dyke (1985). Gonadal morphology and development phase identification follow Mazzoni *et al.* (2020).

Illustrations were prepared digitally in Adobe Illustrator CC 2019, with the assistance of photos taken with a Leica M205 stereomicroscope and a Leica DFC295 digital camera. Photos were taken using a Canon EOS 5D Mark II camera and edited in Adobe Photoshop CC 2018. The geographic distribution map was produced using Google Earth Pro v. 7.3 and QGIS v. 3.28.3 softwares, following Calegari *et al.* (2016), with modifications.

The delimitation of the Amazonas-Paraguai lowlands follows Dagosta, de Pinna (2019). Amazon bioregion delimitation follows Dagosta, de Pinna (2017), and Paraguai ecoregion delimitation follows Abell *et al.* (2008). Specimens were preserved in 70% ethanol, except for those c&s, which were preserved in glycerol. X-rayed specimens are marked as “xr”.

The specimens of *P. gracilis*, *P. griffini*, *P. howesi* Fowler, 1940, *P. laticeps*, *P. megalura*, *P. mucosa*, *P. notomelas*, *P. serrata*, and *P. taeniophora* included in the examined material were identified according to their original descriptions (*i.e.*, Valenciennes, 1835; Regan, 1903; Eigenmann, Ward, 1907; Eigenmann, 1917; Miranda Ribeiro, 1918; Fowler, 1940), in addition to comments provided by Bockmann, Slobodian (2013) and Slobodian (2017), which are based on osteological characters and external morphology. Information of *P. longibarbata* is based on original description and additional photos requested to the authors. The identification key was produced using our findings and the literature above. Institutional codes follow Sabaj (2023).

RESULTS

Pimelodella guato, new species

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(Figs. 1, 2A, 3A; Tab. 1)

Pimelodella serrata non Eigenmann, 1917. —Slobodian *et al*., 2022:340 (rio Taquari, rio Paraguai basin; geographic distribution).

FIGURE 1 | *Pimelodella guato*, holotype, ZUFMS-PIS 8515, 78.5 mm SL, Brazil, Mato Grosso do Sul, Corumbá municipality, rio Paraguai basin, rio Miranda, sandy beaches at Passo do Lontra region, 19°34’37”S 57°00’42”W. **A.** Dorsal; **B.** Left lateral; and **C.** Ventral views. Scale bar = 1 cm.

Holotype. ZUFMS-PIS 8515, xr, 78.5 mm SL, Brazil, Mato Grosso do Sul, Corumbá municipality, rio Paraguai basin, rio Miranda, sandy beaches at Passo do Lontra region, 19°34'37"S 57°00'42"W, 31 Oct 1991, J. C. Louzan & V. M. F. Jesus.

Paratypes. All from Brazil, rio Paraguai basin. CIUnB 1772, 7, 3 xr, 79.1–99.9 mm SL, 1 c&s, 91.2 mm SL, Mato Grosso do Sul, Corumbá municipality, rio Miranda, sandy beaches at Passo do Lontra region, 19°34'37"S 57°00'42"W, 17 Sep 1993, O. Froehlich. MZUEL 11088, 1, 103.7 mm SL, Mato Grosso do Sul, Corumbá municipality, corixo, fifth bridge after the entrance to Passo do Lontra, Estrada Parque, 19°38'S 57°02'W, 3 Sep 2002, O. A. Shibatta *et al*. MZUEL 16829, 1, 79.6 mm SL, Mato Grosso do Sul, Corumbá municipality, rio Miranda, BEP/UFMS (Base de Estudos do Pantanal), 19°34'36"S 57°1'5"W, 22 Aug 2016, O. A. Shibatta *et al*. NUP 14295, 1, 72.3 mm SL, Mato Grosso, Cáceres municipality, baía de Cáceres, tributary of rio Paraguai, 16°04'02"S 57°41'38"W, 28 Mar 2012, Nupelia. NUP 19919, 3, 64.8–83.2 mm SL, Mato Grosso do Sul, Coxim municipality, rio Coxim, tributary of rio Taquari, 18°33'32"S 54°44'37"W, 8 Oct 2017, Nupelia. ZUFMS-PIS 647, 5, xr, 37.1–94.3 mm SL, Mato Grosso do Sul, Corumbá municipality, rio Miranda, Passo do Lontra, across from the BEP, 19°34'37"S 57°00'42"W, 6 Sep 1990, O. Froehlich. ZUFMS-PIS 676, 15, 62.3–107.4 mm SL, Mato Grosso do Sul, Corumbá municipality, rio Miranda, sandy beaches at Passo do Lontra region, 19°34'37"S 57°00'42"W, 17 Sep 1993, O. Froehlich. ZUFMS-PIS 4843, 2, xr, 64.6–65.4 mm SL, Mato Grosso do Sul, Corumbá municipality, rio Miranda, across from the BEP, 19°34'37"S 57°00'42"W, 5 Sep 2008, O. Froehlich. ZUFMS-PIS 6370, 2, xr, 98.6–127.9 mm SL, Mato Grosso do Sul, Coxim municipality, rio Taquari, 18°31'32"S 54°44'30"W, 16 Dec 2019, H. Gimenes-Jr, M. B. Mendonça, P. Camelier, M. Kaluza, F. Severo-Neto, R. Rech, F. Vasconcelos & R. Mochi. ZUFMS-PIS 8516, 4, xr, 49.7–109.0 mm SL, same data as holotype.

Diagnosis. *Pimelodella guato* differs from all *Pimelodella* species except *P. boliviana*, *P. chaparae*, *P. cristata*, *P. cruxenti*, *P. dorseyi*, *P. geryi*, *P. gracilis*, *P. howesi*, *P. humeralis*, *P. laurenti*, *P. longibarbata*, *P. longipinnis*, *P. martinezi*, *P. megalops*, *P. mucosa*, *P. notomelas*, *P. odynea*, *P. ophthalmica*, *P. parnahybae*, *P. serrata*, *P. steindachneri*, *P. taeniophora*, *P. tapatapae*, *P. wesselii*, and *P. witmeri* by the long maxillary barbel, reaching at least the anal-fin terminus when parallel to main body axis (*vs*. reaching at best posterior limit of anal-fin base). It differs from *P. longipinnis* and *P. tapatapae* by having the supraoccipital process reaching the anterior nuchal plate (*vs.* not reaching, gap between distal terminus of supraoccipital process and anterior nuchal plate *ca*. 20–25% of supraoccipital process length). It differs from *P. boliviana*, *P. cruxenti*, *P. geryi*, *P. laurenti*, *P. martinezi*, *P. megalops*, *P. notomelas*, *P. odynea*, and *P. taeniophora* by having a robust dorsal-fin spine, bearing small, straight spinules along three-fourths of its posterior margin (*vs.* dorsal-fin spine not particularly robust, with posterior margin spinules inconspicuous or absent). It differs from *P. cristata*, *P. dorseyi*, *P. gracilis*, *P. howesi*, *P. humeralis*, *P. ophthalmica*, *P. parnahybae*, *P. steindachneri*, *P. wesselii*, and *P. witmeri* by usually having 41–42 (rarely 43 or 44) total vertebrae (*vs.* always 43–44 in *P. howesi;* 46 or more in the remaining species). It further differs from *P. howesi* by having the dorsolateral region of body slightly darkened (*vs.* not darkened), dorsal fin with light brown stripe near its origin, followed by a hyaline stripe, and distal half dark (*vs.* basal half of dorsal fin hyaline, and distal half dark), and by the dorsal lamina of the

Weberian apparatus reaching the ventral margin of the supraoccipital process only at its first third (*vs.* dorsal lamina reaching the supraoccipital process along all its extension). It differs from *P. mucosa* and *P. longibarbata* by the preoperculomandibular laterosensory canal openings at dentary not particularly large (*vs.* large openings). It differs from *P. chaparae*, *P. longibarbata*, and *P. serrata* by the wide midlateral stripe (*vs.* narrow) and by the dorsal lamina of the Weberian apparatus reaching the ventral margin of the supraoccipital process only at its first third (*vs.* first half in *P. longibarbata*; and almost its entire extension in *P. chaparae* and *P. serrata*) (Figs. 2A, D).

Furthermore, *P. guato* can be diagnosed from all congeners by the following exclusive character combination: dorsal profile straight from snout to dorsal fin; maxillary barbel reaching at least the anal-fin terminus when parallel to main body axis; supraoccipital process reaching anterior nuchal plate; dorsal-fin spine robust, bearing small, straight spinules along three-fourths of its posterior margin; posterior margin of pectoral-fin spine bearing 13–23 large, retrorse blades along basal two-thirds (Fig. 3A); adipose fin 2.5 to 3.0 times in SL; usually 41–42 (rarely 43 or 44) total vertebrae; epiphyseal branch of supraorbital canal on the head (S6) emerging as a single pore; brown midlateral stripe wide, not well delimited, extending from snout to caudal-fin origin.

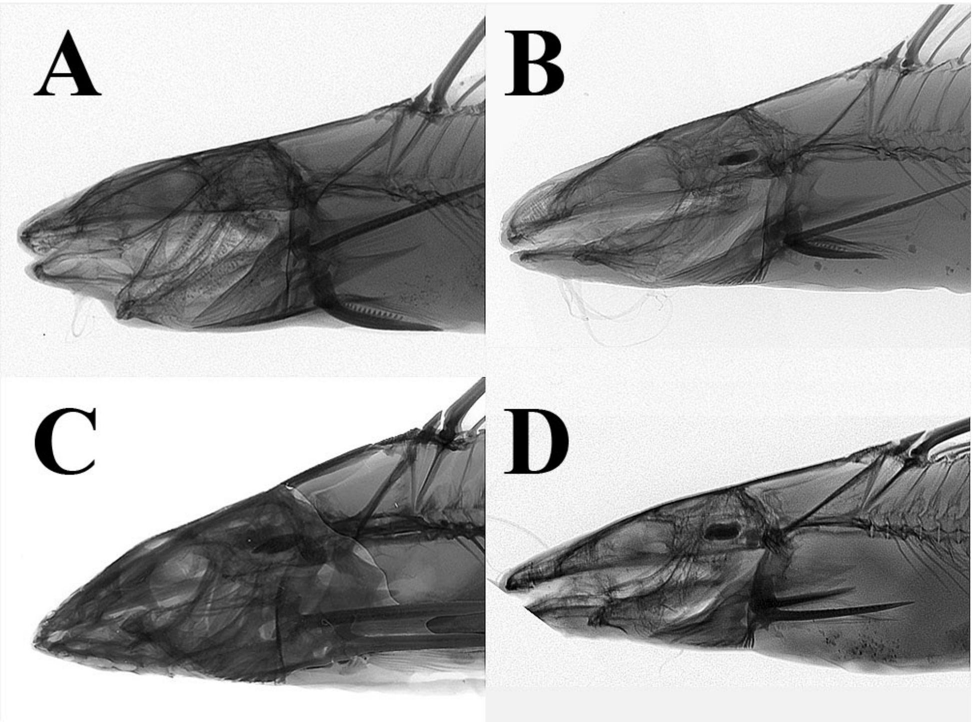

FIGURE 2 | Left lateral view of radiographs of *Pimelodella* species, illustrating the dorsal lamina of Weberian complex vertebrae of **A.** *Pimelodella guato*, paratype, ZUFMS-PIS 647, 90.1 mm SL; **B.** *P. taeniophora*, ZUFMS-PIS 6320, 68.9 mm SL; **C.** *P. mucosa*, holotype, CAS 63720, 97.4 mm SL; and **D.** *P. serrata*, LIRP 10022, 83.6 mm SL.

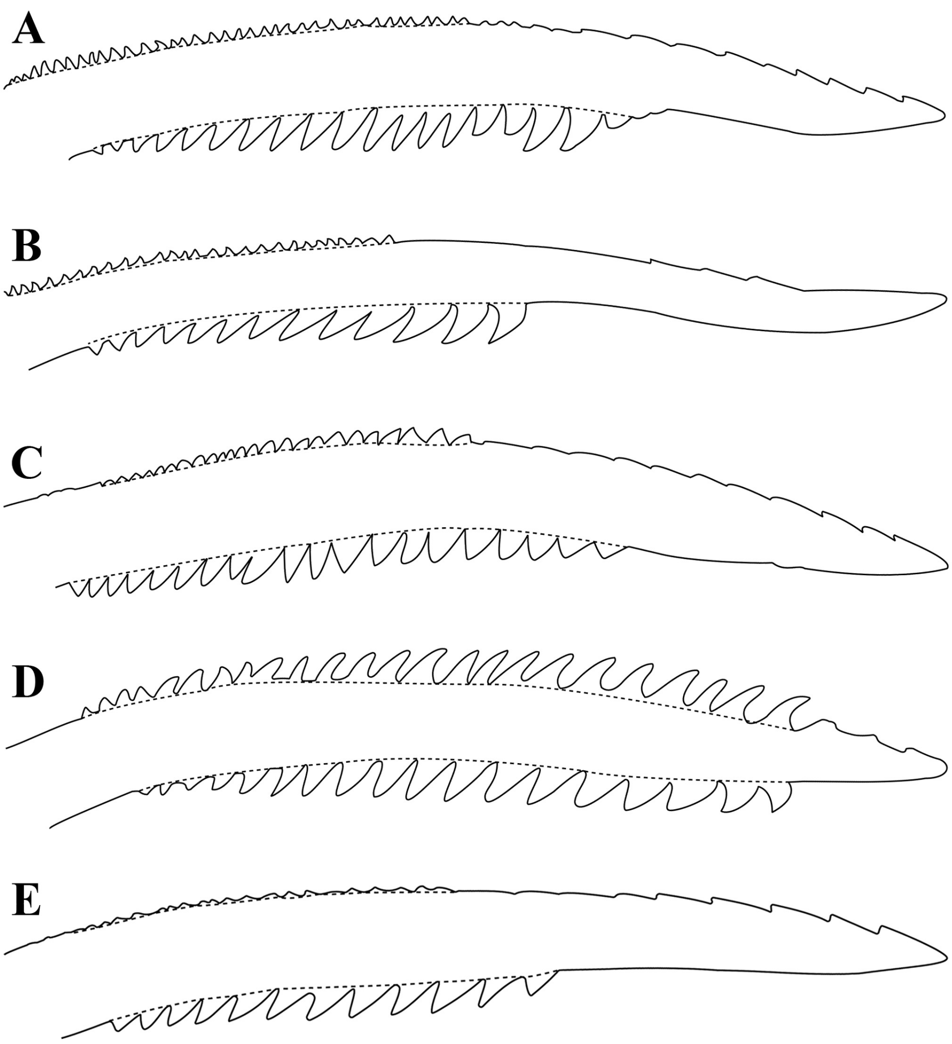

FIGURE 3 | Pectoral-fin spine of **A.** *Pimelodella guato*, paratype, CIUnB 1772, 91.2 mm SL, length of spine 16.7 mm; **B.** *P. taeniophora*, ZUFMS-PIS 6320, 68.9 mm SL, length of spine 11.4 mm; **C.** *P. mucosa*, holotype, CAS 63720, 97.4 mm SL, length of spine 22.8 mm; **D.** *P. serrata*, holotype, FMNH 57979, 55.7 mm SL, length of spine 18.3 mm; and **E.** *P. howesi*, holotype, ANSP 69036, 79.3 mm SL, length of spine 17.8 mm.

Description. Morphometric data are summarized in Tab. 1. Body moderately depressed, depth at dorsal-fin origin 5.0 to 6.5 times in SL; and moderately compressed; body width at dorsal-fin origin 7.0 to 9.0 times in SL (Fig. 1). Greatest body depth at dorsal-fin origin. Dorsal profile straight from snout to dorsal-fin origin, concave from dorsal fin to adipose fin, slightly convex along adipose fin, and concave along caudal peduncle. Ventral profile of body slightly convex from snout to branchiostegal membrane, convex between pectoral and pelvic fins, slightly convex from pelvic fin to anal-fin origin, and concave from this point along the caudal peduncle.

Pseudotympanum externally visible, large, oval, dorsal to posterior process of cleithrum and reaching vertical line of sixth (16) vertebrae. Posterior process of cleithrum triangular, long, its dorsal border slightly concave. Anus and urogenital papilla adjacent. Urogenital papilla tubular, triangular, short. Anus between verticals through half and last third of adpressed pelvic fin; urogenital papilla between verticals through second third and terminus of adpressed pelvic fin. Some specimens might present enlarged urogenital papillae (see Discussion).

TABLE 1 | Morphometric data for the holotype and 42 paratypes of *Pimelodella guato*. N = number of specimens; SD = Standard deviation.

	Holotype	Range	N	Mean	SD
Total length (mm)	97.1	47.5–161.2	42	99.9	
Standard length (mm)	78.5	37.1–127.9	43	82.5	
Percents of standard length					
Body depth (dorsal)	17.6	15.0–20.8	43	17.9	1.3
Body width (dorsal)	12.0	11.1–14.1	43	12.9	0.8
Cleithral width	16.0	15.2–18.2	43	16.7	0.6
Head length	29.2	27.2–31.3	43	29.0	1.0
Maxillary-barbel length (left side)	87.1	81.0–113.6	42	94.6	7.4
Outer mental-barbel length (left side)	36.7	28.7–49.7	43	37.3	3.9
Inner mental-barbel length (left side)	21.2	16.8–32.3	43	22.0	3.0
Predorsal length	32.3	28.5–34.1	43	32.3	1.2
Distance between snout tip and terminus of dorsal-fin base	45.4	42.3–48.9	43	46.2	1.2
Distance between snout tip and dorsal-fin distal end	62.1	54.4–75.2	38	58.3	3.4
Dorsal fin to adipose fin	5.0	3.8–22.2	43	7.3	2.9
Dorsal-fin base	15.2	12.7–18.3	43	14.9	1.0
Length of first dorsal-fin ray (unbranched)	30.5	20.1–42.5	29	24.8	4.3
Length of rigid part of first dorsal-fin ray	20.4	14.3–20.7	38	18.5	1.4
Length of second dorsal-fin ray (first branched)	24.0	18.6–24.0	42	21.3	1.2
Length of third dorsal-fin ray (second branched)	19.3	16.4–23.3	42	19.4	1.6
Prepectoral length	23.2	20.0–27.5	43	24.0	2.0
Distance between snout tip and terminus of pectoral-fin base	24.7	22.5–29.0	43	25.9	1.7
Distance between snout tip and pectoral-fin distal end	43.0	38.8–46.0	42	42.4	1.7
Length of first left pectoral-fin ray (unbranched)	21.2	17.3–21.2	39	19.4	1.1
Length of rigid part of first left pectoral-fin ray	18.7	15.5–18.8	43	17.4	0.9
Length of second left pectoral-fin ray (first branched)	19.2	14.7–19.9	42	17.6	1.2
Length of third left pectoral-fin ray (second branched)	17.9	12.4–17.9	41	15.4	1.2
Prepelvic length	42.1	42.1–49.2	43	45.5	1.5
Distance between snout tip and terminus of pelvic-fin base	43.6	43.6–50.8	43	47.1	1.4
Distance between snout tip and pelvic-fin distal end	61.3	58.6–65.5	43	61.4	1.7
Distance between pelvic fins	3.7	2.7–6.4	43	4.3	0.8
Length of first left pelvic-fin ray (unbranched)	18.1	11.5–18.1	43	14.8	1.4
Length of second left pelvic-fin ray (first branched)	18.2	14.3–18.2	43	16.1	1.0

➡

TABLE 1 | (Continued)

	Holotype	Range	N	Mean	SD
Length of third left pelvic-fin ray (second branched)	17.4	14.0–17.9	42	15.8	1.0
Anal-fin base	10.3	8.6–12.9	43	10.5	0.9
Preanal length	65.7	65.1–71.4	43	67.8	1.4
Distance between snout tip and terminus of anal-fin base	76.7	74.8–82.5	43	77.4	1.5
Distance between snout tip and anal-fin distal end	84.3	82.0–90.3	42	85.2	1.7
Adipose-fin length	39.1	32.5–39.4	43	36.4	1.5
Preadipose length	51.6	51.1–56.4	43	53.2	1.2
Distance between snout tip and adipose-fin base end	86.9	86.3–91.1	43	88.2	1.0
Adipose-fin depth	4.4	3.6–5.2	42	4.4	0.4
Caudal-peduncle length posterior to adipose-fin	10.9	8.1–12.9	43	10.5	0.9
Caudal-peduncle depth at adipose-fin terminus	8.2	6.5–9.2	43	8.0	0.5
Snout-anus distance	48.6	48.2–54.4	42	51.0	1.3
Snout-urogenital papilla distance	55.4	53.2–60.0	40	56.3	1.5
Anus-urogenital papilla distance	6.8	3.9–9.4	40	5.4	1.3
Dorsal lobe of caudal fin length	23.6	21.2–29.2	39	25.8	2.2
Ventral lobe of caudal fin length	26.7	20.8–29.8	42	25.1	1.9
Percents of head length					
Head depth	48.4	42.3–63.5	43	51.4	4.0
Head width	48.9	46.1–57.7	43	51.8	3.1
Eye diameter (left)	19.3	17.6–25.3	43	20.3	1.6
Fleshy interorbital	28.2	22.1–28.4	43	24.9	1.7
Bony interorbital	18.0	12.0–20.5	43	17.2	1.5
Mouth gape	32.0	27.3–37.2	42	32.2	2.4
Snout length (left)	35.8	31.2–38.2	43	35.0	1.5
Distance between snout tip and posterior nare (left side)	18.6	15.6–21.5	43	18.5	1.3
Anterior internarial width	12.1	9.1–15.3	43	12.0	1.1
Posterior internarial width	12.1	11.3–15.5	43	13.7	1.0
Intranarial length (left side)	11.9	10.9–15.4	43	12.8	0.9

Head moderately depressed, depth at supraoccipital-process base 1.5 to 2.5 times in HL. Mouth sub-terminal. Eyes elliptical, 4.0 to more than 5.5 times in HL. Bony interorbital distance roughly equal to eye diameter. Barbels thin, slightly depressed, elliptical in cross-section. Maxillary barbel reaching at least the anal-fin terminus when parallel to main body axis. Outer mental barbel, when parallel to main body axis, reaching between second third of adpressed pectoral fin and first third of adpressed pelvic fin. Inner mental barbel, when parallel to main body axis, reaching between pectoral-fin origin and second third of adpressed pectoral-fin. Supraoccipital process subrectangular to triangular, wide. Dorsal lamina of Weberian complex vertebrae moderately deep, usually reaching the ventral margin of the supraoccipital process along its first third (Fig. 2A). Branchiostegal 6(17).

Dorsal fin triangular, distal margin convex, moderate in length (second branched dorsal-fin ray almost 4.5 to 6.0 times in SL), depressed tip reaching between vertical line through half and terminus of adpressed pelvic fin. Dorsal fin with II,6(24), being the anteriormost the spinelet. Distance between terminus of dorsal-fin base and adipose-fin origin at least a third shorter than dorsal-fin base. Anteriormost dorsal-fin pterygiophore posterior to neural spine of vertebra 4(17); posteriormost dorsal-fin pterygiophore anterior to neural (or pseudoneural) spine of vertebra 10*(7)–12(2). Second unbranched dorsal-fin ray mostly ossified as a spine, long (spine three-fourths of first dorsal-fin ray total length). Dorsal-fin spine robust, bearing small, straight spinules along distal three-fourths of its posterior margin. Second unbranched dorsal-fin ray may present a non-spinuous filamentous portion (see Discussion).

Pectoral-fin rays I,7(4)–I,9(5) (holotype I,8), pectoral-fin triangular with convex or slightly straight distal margin. First pectoral-fin ray curved, with proximal part rigid, forming a spine, and short distal tip, flexible and distinctly segmented. Pectoral-fin spine long, 5.5 to 6.5 times in SL. Anterior margin of pectoral-fin spine with small, straight spinules along its basal two-thirds and flat spinules along its distal third (Fig. 3A). Posterior margin of pectoral-fin spine bearing 13–23 (holotype 17) retrorse blades along basal two-thirds (Fig. 3A). Blades larger and more inclined, hook-like, near distal tip, meanwhile smaller, less inclined, near pectoral-fin base.

Pelvic-fin rays i,5(23), pelvic fin triangular with convex distal margin when expanded. Pelvic-fin origin at vertical through penultimate branched dorsal-fin ray. Tip of adpressed pelvic fin between verticals through second eighth and second fifth of adipose fin. First unbranched ray distinctly shorter than subequal branched second and third rays; remaining rays progressively shorter.

Anal-fin rays iv,7(6); v,7*(4); iv,8(3); or v,8(2); distal border of expanded anal fin convex. One or two anteriormost anal-fin rays vestigial, unsegmented, embedded in thick skin fold. Anal-fin origin between verticals through second third and half adipose-fin base; adpressed anal-fin terminus between verticals through last eighth and terminus of adipose fin. Anteriormost anal-fin pterygiophore posterior to hemal spine of vertebrae 20(1), 21*(5), 22(7) or 23(4); posteriormost anal-fin pterygiophore anterior to hemal spine of vertebrae 27(2), 28*(9), 29(5) or 30(1).

Adipose fin 2.5 to 3.0 times in SL, forming ascending elevated curve in lateral profile, with deepest point approximately midlength. Adipose fin emerging gradually, its posterior limit as a rounded, free lobe. Adipose-fin origin usually at vertical through vertebral centra 16*(6)–18(4), rarely 15(1) or 19(1); adipose-fin terminus usually at vertical through vertebral centra 35(2)–37(7) (holotype 36), rarely 34(1) or 38(1).

Caudal fin deeply forked, lobes subequal, or ventral lobe slightly longer than dorsal. Caudal peduncle length posterior to adipose fin roughly equal to or slightly larger than its depth. Dorsal lobe with 7(18) branched, 1(18) unbranched principal, and 13(2)–23(1) (holotype 17) procurrent fin-rays. Ventral lobe with 7(2)–8*(14) branched, 1(18) unbranched principal, and 14(2)–22(1) (16*) procurrent fin-rays. Hypural 5 completely free, not fused to hypural 3+4. Median caudal-fin rays not articulated directly to caudal plate. Seven* (13) or 8(3) rays articulated to dorsal caudal-fin plate (5 or 6 on hypurals 3+4, and 2 on hypural 5) and 7*(14) or 8(2) rays articulated to ventral caudal-fin plate (5 or 6 on hypurals 1+2, and 2 on parahypural). Total vertebrae usually 41(7)–42*(7), rarely 43(2) or 44(2). Ribs 7*(6)–9(1).

Epiphyseal branch of supraorbital canal on the head (S6) with contralateral canals connecting at midline, proceeding posteriorly as a single canal and opening in a single pore (diaulic S6+S6 pore).

Coloration in alcohol. Background body coloration pale yellow, dorsal and lateral regions of body with sparsely distributed dark brown chromatophores, more concentrated dorsal to midlateral stripe. Ventral region of body and head lacking pigmentation. Brown midlateral stripe wide, faint, not well-delimited, extending from snout to eye and posterior to eye onto the caudal-fin origin. Dorsal region of body with slightly more concentrated brown chromatophores from dorsal-fin origin to half adipose-fin base, fading posteriorly. Pseudotympanum area darker than surrounding areas. Dorsal region of head with scattered dark brown chromatophores. Cephalic brown pigment at posterior fontanel region. Paired dorsal dark-brown stripes, weakly delimited, extending along supraoccipital process. Maxillary barbel dorsal surface brown; mental barbels weakly pigmented along their dorsal surfaces. Dorsal fin with scattered brown chromatophores, more heavily pigmented at the dorsal-fin spine. Dorsal fin with light brown stripe near its base, followed by a hyaline stripe, and distal half darkened. Pectoral-fin spine and branched rays with scattered chromatophores along their extension. Pelvic, anal and caudal fins almost hyaline, with sparse brown chromatophores along rays. Adipose fin hyaline.

Geographical distribution. *Pimelodella guato* is known from the rio Paraguai basin, which includes all rivers where the new species was sampled, *i.e.* the rio Miranda, rio Coxim, rio Taquari, and rio Paraguai itself (Fig. 4). The rio Miranda drains from Mato Grosso do Sul State, ultimately joining the rio Paraguai on its left bank within the municipality of Corumbá. Moreover, the rio Miranda basin interconnects with the northwest region of the rio Taquari basin (Mendes *et al*., 2004). The rio Taquari originates in the highlands of Mato Grosso State and courses into Mato Grosso do Sul, in Brazil (Galdino *et al*., 2003). In the latter State, the rio Taquari flows east-to-west, with the rio Coxim serving as its primary tributary before its confluence with rio Paraguai on its left bank (Galdino *et al*., 2003).

Ecological notes. Within the rio Taquari, *Pimelodella guato* was sampled at the Palmeiras waterfall, in an area characterized by shallow waters, moderate water flow, and a sandy substrate (Slobodian *et al*., 2022). This species exhibits abundance during the rainy season and is notably easy to capture, particularly during the nighttime (Slobodian *et al*., 2022).

Etymology. The species name *guato* is in honor of the indigenous Guató people, who are affectionately known as “people of the Pantanal waters” due to their primary mode of transportation, canoes. Historically, the Guató people inhabited an extensive area along the rio Paraguai (Schmidt, 1942). However, in the 1940s, they began to lose their territory due to cattle ranching, and many relocated to cities such as Cáceres and Corumbá. This dispersal led to a reduction in the Guató population, and since then, they have been fighting for recognition of their ethnicity and the demarcation of their lands (Costa, 2015). The choice of *guato* is a homage to the resilience and cultural

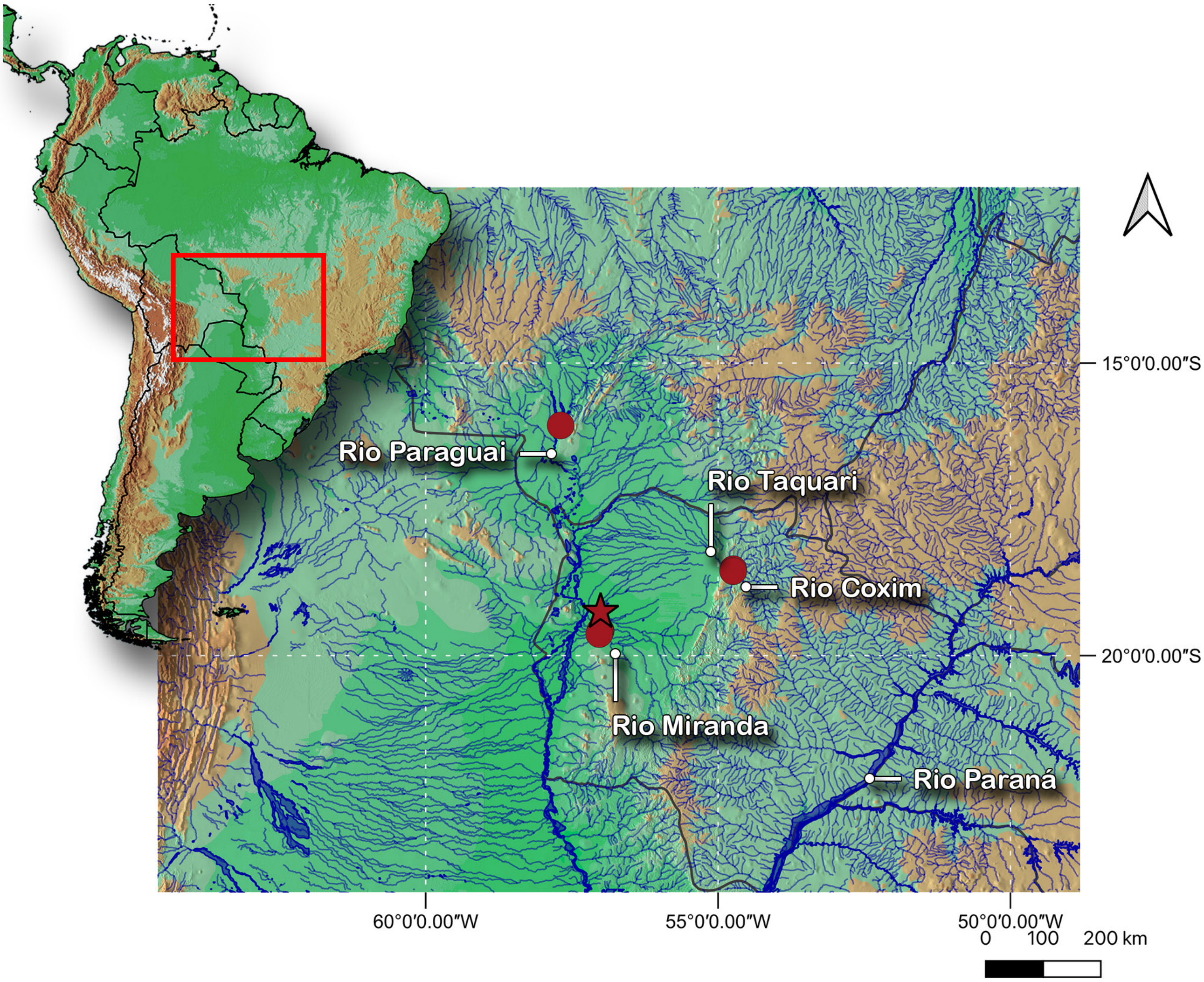

FIGURE 4 | Geographic distribution of *Pimelodella guato* in the rio Paraguai basin (red star, type-locality; red dots, paratype localities). The symbols might represent more than one voucher specimen each.

significance of these people who inhabit the same region where the new species is found. It also recognizes the ongoing struggles with land delimitation that indigenous communities continue to face, particularly in Brazil. A noun in apposition.

Conservation status. *Pimelodella guato* has predominantly been documented within the rio Miranda in the rio Paraguai basin. Despite several anthropic activities in this region, such as ecotourism and land use, which adversely affect water quality, comprehensive conservation plans and projects are notably lacking (Boin *et al*., 2019; Leite *et al*., 2022). Moreover, both the rio Taquari and rio Coxim confront significant challenges related to erosion and river siltation (Galdino *et al*., 2003, 2006; Rabelo, Souza, 2021), also correlated to road paving in the Coxim municipality region (H. Gimênes-Júnior, 2023, pers. comm.). While geological factors in the region render it more susceptible to these issues, deforestation and livestock activities exacerbate erosion and siltation to alarming levels (Galdino *et al*., 2003, 2006; Rabelo, Souza, 2021). Biological and ecological information on *P. guato* remains unavailable, posing a challenge to accurately categorizing its conservation status. Nevertheless, despite the restrictive known distribution of the species, we suggest that *P. guato* be classified as Least Concern (LC), according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2022).

Key to the species of *Pimelodella* from the Paraguai basin

1a. Total vertebrae 46 (rarely 45); anal-fin adpressed terminus always anterior to adipose-fin terminus, reaching at least the vertical through three-fourths of adipose fin; adipose fin very long, slightly more than 2.0 to 2.5 times in SL .... *P. gracilis*

1b. Total vertebrae 39–44; anal-fin adpressed terminus between verticals through adipose-fin terminus and slightly posterior to adipose-fin terminus; adipose fin 2.5 or more times in SL 2

2a. Openings of preoperculomandibular laterosensory canal at dentary large and conspicuous; posterior margin of pectoral-fin spine bearing 14–20 small, retrorse blades along basal two-thirds (Fig. 3C); head roof heavily ornamented .... *P. mucosa*

2b. Openings of preoperculomandibular laterosensory canal at dentary not large or particularly conspicuous; posterior margin of pectoral-fin spine not as above; head roof ornamentation inconspicuous 3

3a. Supraoccipital process not reaching the anterior prenuchal plate; dorsal-fin spine small, approximately half or slightly more of second dorsal-fin ray total length; dorsal lobe of caudal fin notably longer than ventral caudal-lobe; hypural 5 variably fused to hypural 3+4 .... *P. megalura*

3b. Supraoccipital process reaching the anterior prenuchal plate; dorsal-fin spine at least a third of second dorsal-fin total ray length (excepting the filamentuous portion, if present); caudal-fin lobes subequal or ventral lobe slightly longer than dorsal; hypural 5 completely free 4

4a. Maxillary barbels always surpassing caudal-fin origin; posterior margin of pectoral-fin spine bearing 4–6 notably triangular, short and straight blades along basal two-thirds; dorsal fin distal third notably dark brown to black .... *P. notomelas*

4b. Maxillary barbels reaching between pelvic-fin origin and may extend beyond caudal-fin origin; posterior margin of the pectoral-fin spine not as above; dorsal fin not presenting a notably dark brown to black coloration 5

5a. Dorsal profile straight from snout to dorsal fin; dorsal-fin spine robust, large, bearing small, straight spinules along three-fourths of its distal posterior margin; posterior margin of pectoral-fin spine bearing 13–23 retrorse blades along basal two-thirds (Fig. 3A) .... *P. guato*

5b. Dorsal profile convex from snout to dorsal fin; dorsal-fin spine not particularly robust, nor bearing spinules at its posterior margin; posterior margin of pectoral-fin spine bearing 9–13 retrorse blades along basal two-thirds 6

6a. Maxillary barbels reaching at least anal-fin terminus when parallel to main body axis; adipose fin 2.5 to almost 3.0 times in SL .... *P. taeniophora*

6b. Maxillary barbels reaching between pelvic-fin origin and anal-fin terminus; adipose fin short, more than 3.5 times in SL.. 7

7a. Epiphyseal branch of supraorbital canal on the head (S6) with contralateral canals connecting at midline, proceeding posteriorly as a single canal and opening in a single pore (S6+S6 diaulic pore); total vertebrae 41–42; dorsal region of body usually presenting a well-delimited darker stripe from supraoccipital process to first third of adipose-fin base ....*P. griffini*

7b. Epiphyseal branch of supraorbital canal on the head (S6) emerging as two separated pores; total vertebrae 39–40; dorsal region of head and body slightly darkened, with a dark brown mark extending just between dorsal and adipose fins...*P. laticeps*

DISCUSSION

The genus *Pimelodella* presents several unsettled taxonomic problems despite being an important component of Neotropical ichthyofauna found in all major cis- and trans-Andean basins. Most of them are due to the highly conservative morphology of its species, allied with their putatively broad distributions (Slobodian *et al*., 2017). Many species of *Pimelodella* lack rigorous published taxonomic study, contributing to a high number of specimens undetermined at the species level or wrongly identified in scientific collections (Slobodian *et al*., 2017; pers. obs.). Nevertheless, recent studies are contributing to the taxonomy of *Pimelodella* species (*e.g*., Souza-Shibatta *et al*., 2013; Slobodian *et al*., 2017, 2021; Slobodian, Pastana, 2018; Conde-Saldaña *et al*., 2019; Cortés-Hernández *et al*., 2020, 2023), and a complete revision is underway (V. Slobodian and M. de Pinna, work in progress).

Despite the morphological similarities found among *Pimelodella* species in general, *P. guato* is relatively easy to identify (especially among those species that occur in the rio Paraguai basin) due to its diagnostic features, such as the presence of large blades at the posterior margin of the pectoral-fin spine. Within the *Pimelodella* species of the upper Paraguai basin, only *Pimelodella mucosa* and *P. taeniophora* have pectoral-fin spines that might present large blades at their posterior margin (Figs. 3B, C). In *P. taeniophora*, the pectoral-fin spine is narrower, and smaller specimens (less than 45 mm SL) also have smaller spinules besides proportionally longer adipose fins and maxillary barbels. On the other hand, *P. mucosa* can be promptly distinguished from *P. guato* by its enlarged preopercular and mandibular cephalic lateral-line canals. Such conspicuous cephalic lateral-line canals are also found in *P. longibarbata* from the western rio Orinoco basin.

Pimelodella guato superficially resembles *P. chaparae* Fowler, 1940*, P. howesi*, and *P. serrata*, three species distributed in the Amazon basin. *Pimelodella chaparae* and *P. howesi* were described from Boca Chapare, Bolivia, upper rio Madeira basin (Fowler, 1940), and *P. chaparae* was recently indicated as a senior synonym of *P. pallida* Dahl, 1961, from Río Guayabero, Colombia (Cortés-Hernández *et al*., 2020). *Pimelodella serrata* was described from San Joaquin, Bolivia, probably from upper Guaporé basin (Bockmann, Guazzelli, 2003), and previously reported for the rio Madeira basin, in Bolivia and Brazil (Lauzanne, Loubens, 1985; Chernoff *et al*., 2000; Bockmann, Slobodian, 2013), and from streams draining into the Amazon River channel in Colombia (Cortés-Hernandez *et al*., 2023).

Despite the absence of published phylogenetic relationships among *Pimelodella* species, *P. guato*, *P. chaparae*, *P. howesi*, and *P. serrata* share several morphological characteristics that promptly distinguish them from all other *Pimelodella* species. These characteristics are restricted to a few *Pimelodella* species. They can be interpreted as putatively apomorphic, indicating a possible close phylogenetic relationship between the three species, *e.g.*, head lateral profile straight and robust dorsal-fin spine with large posterior blades (Eigenmann, 1917; Bockmann, Slobodian, 2013; Slobodian, 2017). The long barbels, usually surpassing the caudal-fin insertion, are shared between *P. guato*, *P. howesi*, and *P. serrata,* but could not be ascertained in *P. chaparae* type material due to their damaged condition. In addition, the vertebral count of *P. chaparae* (41 in the holotype), *P. howesi* (44 in the holotype), and *P. serrata* (43 in the holotype) fall into the interval of P. *guato* (41–44). Among these four species, *P. guato* is particularly similar to *P. howesi* since both species exhibit a pectoral-fin spine with a moderately wide shaft and small flat spinules at its anterior margin (Figs. 3A, E); meanwhile, *P. chaparae* and *P. serrata* share an extensive pectoral-fin spine, with conspicuous, antrorse flat spinules at its anterior margin (Fig. 3D). Nevertheless, *P. guato* can be promptly distinguished from *P. howesi*, among other features (see Diagnosis), by having the dorsolateral region of body slightly darkened (*vs.* not darkened), dorsal fin with light brown stripe near its origin, followed by a hyaline stripe (*vs.* basal half of dorsal fin hyaline), and by the dorsal lamina of the Weberian apparatus reaching the ventral margin of the supraoccipital process only at its first third (*vs.* dorsal lamina reaching the supraoccipital process along all its extension).

The taxonomic similarities between the ichthyofauna of the Amazon and Paraguai basins have been discussed for decades (*e.g.*, Eigenmann, Eigenmann, 1891; Jordan, 1896; Eigenmann *et al*., 1907; Pearson, 1937; Hubert, Renno, 2006; Carvalho, Albert, 2011; Ribeiro *et al*., 2013; Ota *et al*., 2014; Dagosta, de Pinna, 2017, 2018, 2019, 2021). Several events might have allowed the sharing of fish fauna between the southern tributary headwaters of the Amazon basins and the Paraguai basin, such as upper Paraguai captures of proto-Amazonas-Orinoco headwaters, the Amazon capture of upper Paraguai headwaters, or other events related to megafans and river captures, involving especially the upper Mamoré and upper Guaporé tributaries along with upper Paraguai tributaries (Pearson, 1937; Lundberg *et al*., 1998; Wilkinson *et al*., 2006, 2010; Carvalho, Albert, 2011; Ota *et al*., 2014; Dagosta, de Pinna, 2019). Therefore, the presence of shared or closely related species on both sides of the Amazon-Paraguai is attributed to the diffusion of species arising from one side to the other by headwater capture events (Carvalho, Albert, 2011), or species being present in a paleo area encompassing both basins before the occurrence of a vicariant event that originated present-day hydrographic configuration (Ribeiro *et al*., 2013). Among the Amazonian headwaters that integrate this route (*i.e*., Mamoré-Guaporé, Tocantins, Xingu, and Tapajós basins), the Mamoré-Guaporé presents the largest divide extension with the Paraguai basin and largest number of shared species (Carvalho, Albert, 2011; Dagosta, de Pinna, 2019).

The Mamoré and Guaporé rivers are tributaries of the upper rio Madeira basin, one of the major Amazonian drainages. The Mamoré sub basin presents headwaters in the Andes region, in Bolivia, and connects with the Paraguai basin, mainly in the Bolivian Chaco, but also in the Bolivian Sub-Andean region (Pearson, 1937; Carvalho, Albert, 2011). The Guaporé sub basin, on the other hand, originates in Brazil, with headwaters in the Chapada dos Parecis (Pearson, 1937), and its connections with the Paraguai basin probably occur in the rio Jauru (Paraguai basin) and its affluents (Reclus, 1895; Pearson, 1937; Carvalho, Albert, 2011). The Aguapeí and Alegre rivers (from Paraguai and Guaporé basins, respectively), for instance, are eventually separated by a narrow isthmus (Reclus, 1895; Carvalho, Albert, 2011), and species migration or shared supra specific taxa between these rivers has already been suggested (Schaefer, 1990). Thus, Carvalho, Albert (2011) indicates that lowland areas separating the headwaters of Paraguai and Mamoré-Guaporé basins allow the diffusion of the ichthyofauna between them.

Ribeiro *et al.* (2013), on the other hand, suggest that the shared ichthyofauna between the Paraguai and Amazon basins could also be possible due to a major central-Brazilian Amazonian paleoplateau rearrangement caused by a subsidence in the upper Paraguai basin. In this way, the lowland areas in the Amazon-Paraguai divide would be more ephemeral than highland areas due to tectonic movements, resulting in lowland fish species more broadly distributed in both basins, in a time when the divide did not exist (Lima, Ribeiro, 2011; Ribeiro *et al.*, 2013). Meanwhile, upland species would have been shared between the basins due to headwaters captures and only present nowadays in the headwaters since such species would not be adapted to the ecological conditions of lowland regions (Lima, Ribeiro, 2011; Ribeiro *et al.*, 2013).

Thus, there are several indications in the literature that the shared taxa between Madeira (especially Guaporé and Mamoré sub basins) and Paraguai basins might be due to several biogeographic events that emerged on different ages, since congruent distributions are partly temporally decoupled, being pseudocongruences (Dagosta, de Pinna, 2019). In that sense, discussions on the common biogeographic history between both regions should highlight which of such events better explain the taxa distribution, depending on them being lowland or highland taxa.

Given the putatively apomorphic characteristics shared between *P. guato* (from the Paraguai basin) and *P. chaparae*, *P. howesi*, and *P. serrata* (from rio Madeira drainage), the occurrence of *P. guato* in the Paraguai basin may be related to the geological and hydrological features of the Amazon-Paraguai divide, that might have allowed the cladogenesis of this group of *Pimelodella*. Since *P. guato* was collected in lowland areas, in sites up to 200 m asl, we infer it is a lowland species, with two main biogeographical events that might explain its distribution: (1) the river avulsion in megafans that lead to taxa shared between upper Mamoré and tributaries to upper Paraguay in Bolivia (following Wilkinson *et al.*, 2006, 2010); and (2) river captures from upper Paraguai tributaries to upper Guaporé, at mid-elevations (following Carvalho, Albert, 2011; Ota *et al.*, 2014). The first mentioned event dates from the Late Miocene (late Tertiary) or later, and this divide is occupied by the modern rio Parapetí megafan nowadays, which leads water into both basins today, despite being well above 200 m a.s.l. (Wilkinson *et al.*, 2006, 2010). The second event is also considerably recent, dating from the late Tertiary or Quaternary (Ota *et al.*, 2014). However, in the absence of a published *Pimelodella* phylogeny, we can scarcely discuss the biogeographic events that led to the presence of *P. guato* in the Paraguai basin.

Anyway, much remains to be understood about the shared ichthyofauna between the Amazon and Paraguai basins. Among the species of *Pimelodella* that are found in the Paraguai basin, *P. gracilis* was described from rio Paraná in Argentina and is known to occur in the Paraguai, upper and lower Paraná basins, in Argentina, Brazil and Paraguay (Bockmann, Guazzelli, 2003; Carvalho, Albert, 2011; Slobodian, 2017, unpublished data), but a few specimens were also reported for the rio Madeira basin (*e.g.*, Pearson, 1924; Bockmann, Slobodian, 2013 [their *Pimelodella* sp. n.]; Slobodian, 2017, unpublished data). Although *P. guato* shares resemblances with *P. gracilis* in certain aspects, such as the length of the maxillary barbel and the morphology of the pectoral-fin spine, there are several characteristics that distinguish both species. *Pimelodella guato* presents 41–42 (rarely 43 or 44) total vertebrae; anal-fin adpressed terminus aligned with the verticals through adipose-fin terminus; and adipose fin 2.5 to 3.0 times in SL. In contrast, *P. gracilis* contains 46 total vertebrae; anal-fin adpressed terminus consistently anterior to the adipose-fin terminus, reaching the vertical through three-fourths of the adipose fin; adipose fin longer, slightly more than 2.0 to 2.5 times in SL; the presence of darker midlateral and dorsolateral stripes; and a notably more elongated body shape. *Pimelodella gracilis* is known to occur syntopically with *P. guato* in the Paraguai basin (pers. obs., ZUFMS-PIS 6678, ZUFMS-PIS 838), being another indication for closely related taxa shared between both Amazon and Paraguai basins.

Lastly, another noteworthy aspect is the reaffirmation of the presence of filaments on the non-spinous portion of the second (unbranched) and the first (unbranched) rays in the dorsal and pectoral fins, respectively, of *P. guato* as a sexually dimorphic trait (Fig. 5A). While this characteristic has been used as a diagnostic feature in the description of several species in the past, such as *Pimelodella boschmai* van der Stigchel, 1964, *P. insignis* (Schubart, 1964), *P. figueroai* Dahl, 1961, *P. griffini*, *P. linami* Schultz, 1944, *P. megalura,* and *P. taenioptera*, the hypothesis of this filament as a secondary sexual character was first introduced by Dahl (1961). Dahl conducted dissections on immature, mature male, and mature female *P. linami* specimens to verify their sex and developmental stage, and the filamentous prolongations were exclusively found in adult males (Dahl, 1961:498). Subsequently, Souza-Shibatta *et al.* (2013) reached the same conclusion based on examinations of *P. griffini* and *P. taenioptera* specimens.

In the specimens we examined for this work, the presence of filamentous prolongation was observed in individuals also displaying an enlarged urogenital papilla (2.4 times the average size of the papilla found in other specimens) (Fig. 5B), which also appears to be a secondary sexual characteristic. An enlarged urogenital papilla and filamentous prolongation were exclusively found in specimens measuring over 73.7 mm SL, suggesting a potential correlation with the size of sexual maturity in males. This finding aligns with observations in other species, such as *P. avanhandavae* Eigenmann, 1917, and *P. meeki* Eigenmann, 1910, whose males reach sexual maturity at sizes of 74 mm SL and 54 mm SL, respectively (Orsi, 2017). Conversely, in *P. lateristriga* (Lichtenstein, 1823) and *P. pappenheimi* Ahl, 1925, no discernible difference was observed in size between males and females at first maturity. Both sexes in these species attain maturity at 44.5 mm SL in *P. lateristriga* (Moraes *et al*., 2013) and 63 mm SL in *P. pappenheimi* (Amaral *et al*., 1998).

In this work, five specimens were dissected to ascertain the correlation between the presence of filamentous prolongation and enlarged urogenital papilla and the sex. Two dissected specimens without the filamentous prolongation were confirmed as females, probably at the spawning-capable phase (CIUnB 1772, 79.1 and 91.0 mm SL). Three dissected specimens were confirmed as males, two of these presenting both a filamentous prolongation (of at least a fourth of the total length of the ray) and an enlarged papilla (CIUnB 1772, 86.0 and 93.8 mm SL), and one presenting only a small filamentous

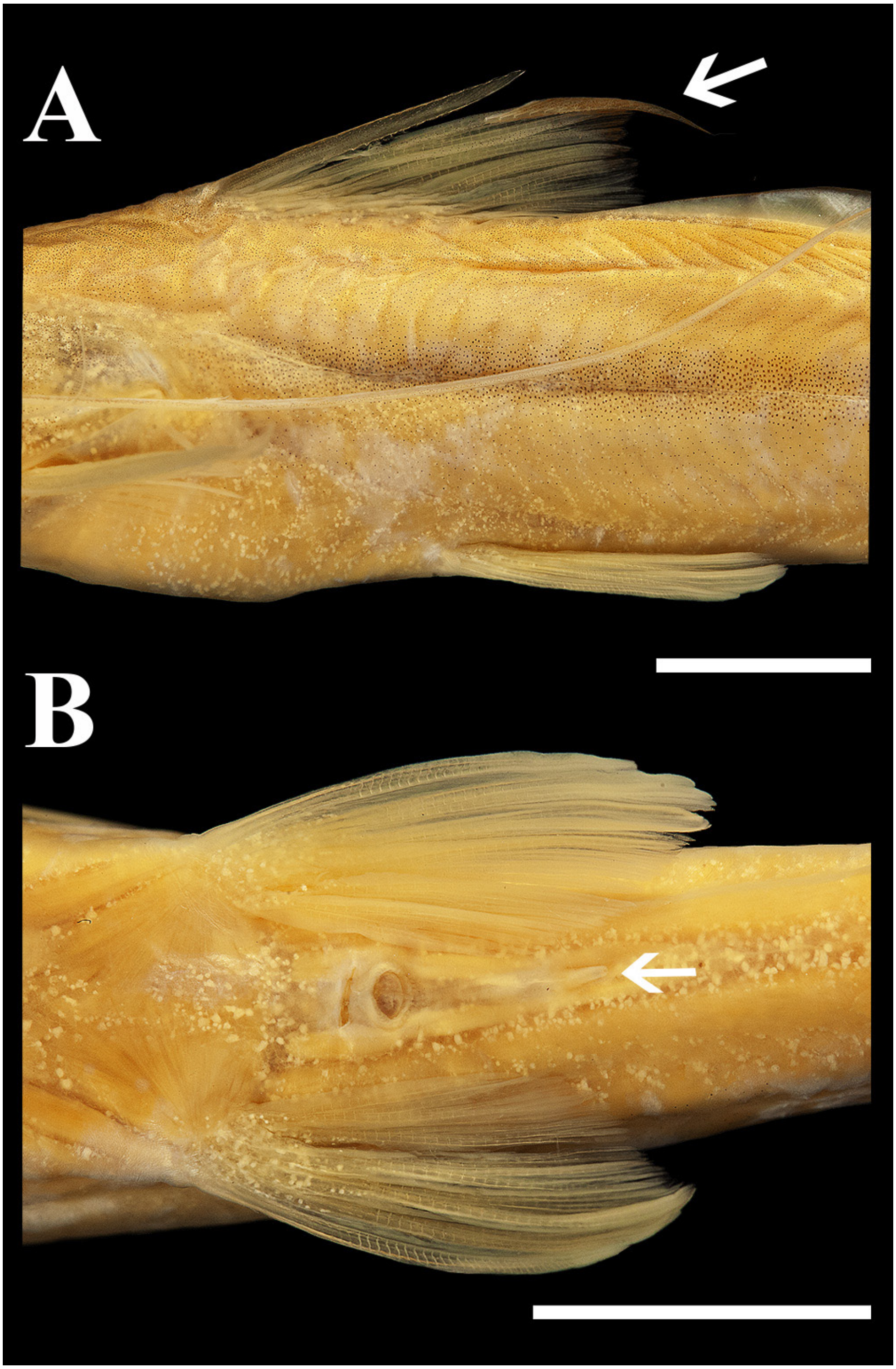

FIGURE 5 | Sexually dimorphic traits in an adult male specimen of *Pimelodella guato* (paratype, CIUnB 1772, 93.8 mm SL). **A.** Filament on the non-spinous portion of dorsal-fin second (unbranched) ray, indicated by a white arrow; and **B.** Enlarged urogenital papilla, indicated by a white arrow. Scale bars = 1 cm.

prolongation (of one sixth of the total length of the ray) and not the enlarged papilla (CIUnB 1772, 89.4 mm SL). However, the testis gross morphology of the three specimens was not different. Therefore, we conclude the presence of the filamentous prolongation is a good indicator for sex determination for males. However, histological studies are needed to ascertain the gonadal development phase of filamentous males. Nevertheless, we highlight the importance of conducting further studies on the biology and systematics of *P. guato* and other species of *Pimelodella* that comprise the Paraguayan basin ichthyofauna, as they are key taxa in advancing our understanding of South American biogeography.

Comparative material examined. Besides the material indicated in Slobodian *et al.* (2017), the following comparative materials were examined: *Pimelodella gracilis*: **Argentina:** MZUSP 337, 2, 100.4–113.3 mm SL. **Brazil:** CPUFMT 679, 3, 106.8–133.5 mm SL; CPUFMT 850, 4, 100.2–135.2 mm SL; CPUFMT 1546, 1, 162.6 mm SL; CPUFMT 2306, 3, 107.0–107.3 mm SL; LIRP 9531, 1, 88.4 mm SL; MCP 26120, 2, 96.9–97.6 mm SL; MZUEL 6457, 1, 90.0 mm SL; MZUEL 11185, 5, 136.5–185.8 mm SL; MZUEL 11190, 6, 72.3–119.7 mm SL; MZUEL 14001, 6, 56.9–93.7 mm SL; MZUSP 23195, 1, 189.3 mm SL; MZUSP 24856, 1, 107.8 mm SL; MZUSP 27728, 2, 137.4–205.8 mm SL; MZUSP 38033, 3, 65.0–71.6 mm SL; MZUSP 82381, 1, 114.7 mm SL; MZUSP 87788, 1, 147.1 mm SL; NUP 2231, 4, 94.4–158.5 mm SL; NUP 3408, 10, 98.1–118.4 mm SL; NUP 3473, 15, 87.8–103.1 mm SL; NUP 3505, 9, 90.3–114.0 mm SL; NUP 14300, 10, 56.7–71.7 mm SL; ZUFMS-PIS 620, 1, 144.1 mm SL; ZUFMS-PIS 838, 2, 101.8–127.5 mm SL; ZUFMS-PIS 6488, 12, 49.4–166.4 mm SL; ZUFMS-PIS 6678, 4, 135.2–156.6 mm SL. *Pimelodella griffini*: **Brazil:** CPUFMT 5352, 6, 46.4–58.9 mm SL; LIRP 11407, 2, 44.7–51.6 mm SL; MCP 36117, 10, 46.9–56.6 mm SL; MCP 36127, 15, 39.2–53.7 mm SL; MZUEL 3830, 9, 43.2–56.3 mm SL; MZUEL 6460, 2, 71.4–74.6 mm SL; MZUEL 7748, 3, 40.4–56.1 mm SL; MZUEL 9034, 2, 47.6–60.7 mm SL; MZUEL 9035, 3, 51.1–63.6 mm SL; MZUSP 44487, 10, 41.7–54.2 mm SL; MZUSP 90671, 10, 40.1–50.1 mm SL; MZUSP 100564, 2, 67.7–81.1 mm SL; NUP 11627, 10, 52.4–62.9 mm SL; NUP 21728, 3, 47.9–51.7 mm SL; ZUFMS-PIS 876, 20, 45.9–60.0 mm SL; ZUFMS-PIS 1417, 4, 37.3–53.8 mm SL; ZUFMS-PIS 1428, 6, 46.8–67.8 mm SL; ZUFMS-PIS 1433, 1, 55.3 mm SL; ZUFMS-PIS 1465, 10, 43.9–70.6 mm SL; ZUFMS-PIS 1607, 20, 55.4–86.1 mm SL; ; ZUFMS-PIS 3696, 1, 94.8 mm SL; ZUFMS-PIS 3900, 2, 69.0–73.3 mm SL. *Pimelodella longibarbata*: **Colombia:** IAvH 17879, paratype, 1, c&s, 48.8 mm SL (photo). *Pimelodella megalura*: **Brazil:** MCP 15620, 6, 45.1–72.6 mm SL; MCP 15708, 1, 74.3 mm SL; MZUEL 3829, 2, 69.9–79 mm SL; NUP 14702, 15, 42.6–63.9 mm SL; ZUFMS-PIS 1417, 14, 52.9–81.9 mm SL; ZUFMS-PIS 1428, 3, 58.6–67.8 mm SL; ZUFMS-PIS 1477, 1, 66.6 mm SL; ZUFMS-PIS 3900, 3, 71.5–79.7 mm SL; ZUFMS-PIS 4703, 1, 80.8 mm SL. *Pimelodella mucosa*: **Brazil:** CPUFMT 3081, 1, 66.7 mm SL; CPUFMT 3569,1, 70.3 mm SL; CPUFMT 3714, 2, 87.6–97.1 mm SL; CPUFMT 3870, 1, 92.8 mm SL; LIRP 9528, 7, 46.3–66.8 mm SL; MZUEL 11088, 1, 77.5 mm SL; MZUEL 13217, 3, 55.1–78.0 mm SL; MZUEL 14055, 2, 45.5–57.2 mm SL; MZUSP 25091, 1, 86.1 mm SL; NUP 1067, 12, 58.8–101.7 mm SL; NUP 13590, 3, 50.3–59.7 mm SL; NUP 14201, 10, 56.5–82.4 mm SL; NUP 14355, 15, 66.5–91.9 mm SL; ZUFMS-PIS 1613, 1, 44.8 mm SL; ZUFMS-PIS 3256, 2, 75.3–75.4 mm SL; ZUFMS-PIS 3269, 1, 56.5 mm SL; ZUFMS-PIS 3478, 1, 31.0 mm SL; ZUFMS-PIS 4194, 1, 81.6 mm SL. *Pimelodella notomelas*: **Brazil:** MZUEL 7743, 3, 43.9–52.6 mm SL; MZUEL 9032, 1, 39.7 mm SL; MZUEL 9694, 1, 33.0 mm SL. Brazil: ZUFMS-PIS 5438, 2, 34.3–34.4 mm SL. *Pimelodella serrata*: **Brazil:** LIRP 10022, 4, 71.3–83.6 mm SL; LIRP 10029, 12, 66.7–83.9 mm SL. *Pimelodella taeniophora*: **Brazil:** CPUFMT 870, 3, 36.8–68.3 mm SL; CPUFMT 4003, 8, 60.4–75.7 mm SL; LIRP 9528, 2, 47.9–61.2 mm SL; LIRP 9533, 2, 51.3–55.8 mm SL; LIRP 9534, 7, 53.2–71.4 mm SL; LIRP 9535, 6, 50.4–63.3 mm SL; LIRP 10024, 4, 45.1–52.1 mm SL; MCP 10924, 2, 91.2–91.6 mm SL; MCP 15708, 4, 64.8–86.1 mm SL; MCP 15775, 30, 50.1–79.9 mm SL; MCP 36138, 9, 33.7–54.1 mm SL; MZUSP 44289, 1, 61.1 mm SL;

NUP 3390, 16, 56.6–107.0 mm SL; NUP 11390, 5, 70.0–80.0 mm SL; NUP 12222, 2, 38.5–50.2 mm SL; NUP 14189, 15, 55.1–66.9 mm SL; NUP 21860, 2, 79.5–83.5 mm SL; ZUFMS-PIS 648, 1, 51.6 mm SL; ZUFMS-PIS 5549, 3, 45.6–50.0 mm SL; ZUFMS-PIS 6320, 9, 66.8–82.3 mm SL; ZUFMS-PIS 6327, 1, 51.0 mm SL; ZUFMS-PIS 6442, 1, 69.8 mm SL; ZUFMS-PIS 6488, 6, 16.1–64.7 mm SL. *Pimelodella yaharo* (only photos): **Colombia:** CZUT-IC 10922, holotype, 74.7 mm SL; CZUT-IC 10942, paratype, 1, 69.9 mm SL; CZUT-IC 12602, paratypes, 2, 72.4–82.0 mm SL; CZUT-IC 15262, paratypes, 2, 1 c&s, 66.9–76.9 mm SL; IAvH-P 22004, paratypes, 2, 1 c&s, 68.7–72.7 mm SL.

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AUTHORS' CONTRIBUTION

Veida Pierre: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Visualization, Writing-original draft, Writing-review and editing.

Veronica Slobodian: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing-original draft, Writing-review and editing.

ETHICAL STATEMENT

Since we only utilized specimens from scientific collections, no collection permits were required.

COMPETING INTERESTS

The author declares no competing interests.

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