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Hidden diversity in the Paraná River basin: a new species of *Phenacorhamdia* (Siluriformes: Heptapteridae) from the Bermejo River, Argentina

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Phenacorhamdia comprises 15 species distributed across the major river basins of South America, with *P. tenebrosa* being the only species recorded in Argentina. After the examination of specimens of *Phenacorhamdia* from the upper Bermejo River basin, Paraná River basin, in northwestern Argentina, we conclude that they belong to a new species which is described herein. The new species is distinguished from the remaining members of the genus by a combination of non-unique characters including: maxillary barbel surpassing the distal tip of the adpressed pectoral fin; light-brown background coloration of the body; the conical teeth; 41–42 vertebrae; iii–iv,7–9 anal-fin rays, among other features. The morphological analysis performed shows a clear distinction of the new species from congeners, and the greater genetic distance based on the gen COI between *P. bermejo* with *P. tenebrosa*, provides additional support for the recognition of the new species herein described.

Keywords: Catfish, Genetic divergence, Heptapterinae, Morphological analysis, Species delimitation.

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Phenacorhamdia comprende 15 especies distribuidas en las principales cuencas hidrográficas de América del Sur, siendo *P. tenebrosa* la única especie registrada en Argentina. Tras el examen de ejemplares de *Phenacorhamdia* provenientes de la cuenca alta del río Bermejo, cuenca del río Paraná, en el noroeste de Argentina, concluimos que pertenecen a una nueva especie, la cual se describe en el presente trabajo. La nueva especie se distingue de los demás miembros del género por una combinación de caracteres no exclusivos que incluyen: barbilla maxilar sobrepasando la punta distal de la aleta pectoral adosada; la coloración general del cuerpo de tono marrón claro; la presencia de dientes cónicos; 41–42 vértebras; iii–iv,7–9 radios de la aleta anal, entre otras características. El análisis morfológico realizado muestra una clara distinción de la nueva especie de sus congéneres, y la gran distancia genética entre *P. bermejo* y *P. tenebrosa* basada en el gen COI, proveen soporte adicional para el reconocimiento de la nueva especie aquí descrita

Palabras clave: Análisis morfológico, Bagres, Delimitación de especies, Divergencia genética, Heptapterinae.

INTRODUCTION

Heptapteridae is one of the most species-rich families within Siluriformes and is widely distributed throughout the Neotropical region, from Mexico to southern Argentina (Bockmann, Guazelli, 2003; Bockmann, Slobodian, 2018; Thomas, Sabaj, 2020). According to the last phylogenetic hypothesis (*i.e.*, Faustino-Fuster *et al.*, 2021; Silva *et al.*, 2021; Slobodian, Bockmann, 2025) the family comprises two major clades, the subfamilies Rhamdiinae and Heptapterinae supported, respectively, by five synapomorphies, and 14 discrete and two continuous characters proposed by de Pinna (1993), Lundberg *et al.* (1991), Bockmann (1998), and Bockmann, Miquelarena (2008); see Slobodian, Bockmann (2025) for a complete description of synapomorphies and characters. Heptapterinae includes the tribes Brachyglaniini and Heptapterini, diagnosed by seven and 14 synapomorphies, respectively (Slobodian, Bockmann, 2025). Within Heptapterini, *Phenacorhamdia* Dahl, 1961 was recovered as monophyletic (although the type species, *P. macarenensis*, has never been sampled), and as the sister group of *Magdalenichthys* DoNascimiento, Conde-Saldaña, Albornoz-Garzón, Villa-Navarro in DoNascimiento *et al*. (2025), with *Pariolius* Cope, 1872 as sister to *Phenacorhamdia* and *Magdalenichthys*; those results partially align with the phylogenetic hypothesis proposed by Solabodian, Bockmann (2025), who recovered a clade formed by *Phenacorhamdia* as sister to '*Imparfinis*' *microps* Eigenmann & Fisher, 1916 and an undescribed, *incertae sedis* species, that clade being sister to *Pariolius*.

Phenacorhamdia is a genus composed of small catfishes distinguished from other Heptapteridae by a prognathous mouth, eyes without free orbital margin, the second pore of the supraorbital canal (s2+i2) located far posterior to the anterior nostril, the epioccipital process prominent, and the neural and haemal spines of the posterior vertebrae inclined 30° or less (Britski, 1993; Bockmann, 1998:367). Additionally, members of the genus can be recognized by a combination of non-unique characters that includes a moderate to very elongate body; small eyes, located dorsally; maxillary barbel usually reaching to the last third of the pectoral fin or slightly surpassing its posterior border; the first pectoral-fin ray usually longer than the second one, mostly flexible (except its basal third) and prolonged as a short filament; distal margin of pectoral, dorsal, pelvic, and anal fins convex; pectoral fin usually with 6–9 branched rays; first dorsal-fin ray (spinelet) absent; origin of the pelvic fin at a vertical through the middle of dorsal-fin base or slightly anterior; adipose fin rectangular and moderately long, not confluent with the caudal fin; anal fin short to moderately long, bearing 12–18 rays; caudal fin deeply forked with the ventral lobe slightly to markedly longer than the dorsal lobe, usually with seven branched rays on the dorsal lobe and eight branched rays on the ventral lobe; lateral line continuous to the base of the caudal-fin rays; head and body with uniform brown coloration; anterior and posterior fontanels open; mandibular adductor muscles restricted to the facial region; posterior supraoccipital process short; and usually 7–8 branchiostegal rays (Bockmann, 1998; Bockmann, Slobodian, 2018). *Phenacorhamdia* shares with its closest relatives, *Magdalenichthys* and *Pariolius*, the anal-fin origin usually situated anteriorly to a vertical through the adipose-fin origin (although in *P. macarenensis* they are located on the same vertical); the anteriorly positioned pelvic-fin origin, which commonly is situated anteriorly to a vertical through the dorsal-fin origin; a usually prognathous mouth (isognathous in some species of the clade); and a usually uniformly pigmented body, with no conspicuous dark bars on the dorsum (although lightcolored marks may be present).

Phenacorhamdia currently is composed of 15 valid species, distributed in various watersheds in South America (Castro, Wozniacki, 2022; Silva *et al*., 2022). From the Orinoco River basin, *P. anisura* (Mees, 1987), *P. macarenensis* Dahl, 1961, *P. provenzanoi* DoNascimiento & Milani, 2008 and *P. taphorni* DoNascimiento & Milani, 2008 are recorded. In the Amazon River basin, *P. boliviana* (Pearson, 1924) is found in the Beni River; *P. nigrolineata* Zarske, 1998 occurs in the Branco, Ucayali, Solimões, Purus, Madeira, and Tapajós Rivers; and *P. somnians* (Mees, 1974) in the das Mortes River. In turn, *P. cuspidata* Silva, Castro, Ohara & Oliveira, 2024 is restricted to the upper Tapajós River basin; and *P. suia* Silva, Ochoa & Castro, 2022 to the Xingu River basin. Regarding the river basins in northern South America draining into the Atlantic Ocean, *P. cabocla* Rocha, Ramos & Ramos, 2018 is found in the upper Parnaíba River basin and *P. tenuis* (Mees, 1986) in the Marowijne River basin. Four species are recognized in the Paraná River basin: *P. hoehnei* (Miranda Ribeiro, 1914), in the Taquari River, a tributary of the Paraguay River; *P. roxoi* Silva, 2020, in the upper Paranapanema River basin; *P. unifasciata* Britski, 1993, endemic to the São Bartolomeu River; and *P. tenebrosa* (Schubart, 1964), originally described from the upper Paraná River basin, but also recorded in the lower reaches of the basin in Argentina (Giorgis *et al*., 2012).

After the examination of specimens from the upper Bermejo River, Paraná River basin, we conclude that they belong to a new species which is described herein, corresponding to the sixteenth species of the genus. In addition, we provide a brief discussion on its phylogenetic relationships within *Phenacorhamdia*, based on the cytochrome oxidase 1 (COI) and cytochrome b (Cytb) genes.

MATERIAL AND METHODS

The specimens were collected by electrofishing and euthanized by immersion in tricaine methanesulfonate (MS222), and fixed following standard methods. In some fresh individuals, a small tissue sample was taken and immediately preserved in absolute ethanol for genetic analysis. The tissue aliquots were deposited in the Ichthyological Tissue Collection of the Fundación Miguel Lillo (CIT-FML). Institution abbreviations follow Sabaj (2025).

Representative individuals were cleared and stained (c&s) following Taylor, Van Dyke (1985). Measurements were taken following DoNascimiento, Milani (2008). Counts include the number of fin rays, branchiostegal rays, ribs, and vertebrae, as well as the number and position of support elements for the dorsal and anal fins, and number of procurrent rays of the caudal fin. Total vertebrae count includes the anterior five, associated with the Weberian complex (Lundberg, McDade, 1986) counted as separate, the free vertebrae, and the compound caudal centrum (PU1+U1) counted as one element (Lundberg, Baskin, 1969). An asterisk indicates counts from the holotype. Morphological data of *Phenacorhamdia* species, including fin rays, vertebral and rib counts and body measurements were obtained from original species descriptions when available, and from DoNascimento, Milani (2008) for *Phenacorhamdia anisura*, and from Azevedo-Santos *et al*. (2025) for *P. tenebrosa.* Additionally, X-ray images were used for assess osteological data of *Phenacorhamdia boliviana* and *P. somnians*, available at the California Academy of Sciences, San Francisco (CAS) Ichthyology Primary Types Imagebase (https://researcharchive.calacademy.org/research/ichthyology/types/Index.asp), and at the Natural History Museum, London (NHMUK) online database (https://data.nhm.ac.uk/dataset/56e711e6-c847-4f99-915a-6894bb5c5dea/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb/record/2536084), respectively.

Morphological analysis. An exploratory PCA was conducted in R Stats package v. 4.4.2 (R Development Core Team, 2024), using the original measurements without transformations or size corrections, excluding standard length from the analyses. The morphological data matrix analyzed comprised eight species, including the new species herein described and *P. boliviana* (3 specimens), *P. cabocla* (5), *P. hoehnei* (4), *P. roxoi* (1), *P. sommians* (2), *P. unifasciata* (7) and *P. tenebrosa* (3), and 24 morphological measurements. Missing data were imputed using the missRanger package v. 2.6.0 (Mayer, 2024). All these analyses were performed in R Studio (R Development Core Team, 2024).

DNA extraction. Total genomic DNA was extracted from ethanol-preserved muscle tissue, using the Qiagen DNeasy kit. PCR amplifications were carried out in 30 μL reactions using 0.2 μL Taq (Genbiotech). Mitochondrial gene Cytochrome oxidase subunit I (COI) was amplified by Polymerase Chain Reaction (PCR) using a cocktail of primers VF2_t1, FishF2_t1, and FishR2_t1, Fr1d_t1 (Ivanova *et al*., 2007); and following conditions implemented by Ward *et al*. (2005). Cytochrome B (Cytb) was amplified using the primers GLUDGL (Palumbi, 1996) and H16460 (Perdices *et al*., 2002), following the PCR protocol proposed by Ríos *et al*. (2017). PCR-amplified products were visualized on 1% agarose gel and cleaned using AccuPrep PCR Purification Kit. Products were sequenced by the Korean company Macrogen (http://www.macrogen.

com) and all samples were sequenced in both directions to check for potential errors. Chromatograms obtained from the automated sequencer were processed and edited using GENEIOUS PRO v. 4.8.5 (www.geneious.com). Genbank accession numbers of the sequences used in the phylogenetic analyses are provided in Tab. **S1**. The sequences generated for the new species herein described have been deposited in GenBank under the accessionnumbers PX978871 (COI) and PX989894 (CYTB).

Phylogenetic analysis. Phylogenetic analyses were performed based on a concatenated dataset including 55 sequences of the cytochrome oxidase subunit 1 gene (COX1) and 22 sequences of the cytochrome b gene (CYTB) to have some estimation of the relationships of the new species within the family. The dataset is composed of 1,494 sites (577 parsimony informative) and 55 terminal specimens obtained from Genbank (Tab. **S1**). Analyses were rooted on *Pimelodus maculatus* Lacepède, 1803. These analyses, however, should be taken as provisional, given that no data from most species of the genus are available and its main aim is to assess the generic assignment of the new species. Analyses were performed both under parsimony in TNT (Goloboff, Morales, 2023) and maximum likelihood in RAxML (Stamatakis *et al*., 2014). Parsimony analyses were done under equal weighting and implied weighting (Goloboff, 1993). We explored a broad range of the concavity constant K, which determines how strong the analysis downweights the characters according to their homoplasy (Goloboff, 1993). Results herein presented and calculations of support correspond to K = 10 that, considering the size of the dataset, produces a mild weight against homoplasy. Searches were done from Wagner trees, whose branches were swapped with complete cycles of TBR (*i.e*., connecting each terminal taxon and internal clade on every position of the tree, using all the possible rootings in the case of prunned branches). After that, trees were refined with sectorial searches and tree fusing (Goloboff, 1999). Clade supports were calculated through symmetric resampling and expressed as values of GC (Goloboff *et al*., 2003).

Maximum likelihood analysis was carried out with defaults parameters of RAxML (Stamatakis, 2014) under the GTR+Gamma model. Analyses started from 10 random plus 10 parsimony trees that were swapped by 1000 bootstrap cycles in which fast SPR rounds were performed (*i.e*., computing the likelihoods according to the branch lengths of the initial tree). As default in RaxML, during the SPR cycles, the distance at which each prunned taxon or clade (its SPR radius) is connected was set to “auto” (Togkousidis *et al*., 2023). Support estimation was done under Bootstrap, using convergence as stopping criterion (Pattengale *et al*., 2010).

RESULTS

Phenacorhamdia bermejo, new species

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(Figs. 1–2; Tab. 1)

FIGURE 1 | Lateral, dorsal, and ventral views of holotype of *Phenacorhamdia bermejo*, CI-FML 8284, 42.6 mm SL.

Holotype. CI-FML 8284, 42.6 mm SL, Argentina, Ledesma department of Jujuy Province, San Francisco River at Yuto, 23°40’02.0”S 64°28’44.6”W, 345 m asl, 10 Oct 2024, G. Aguilera, G. Terán, M. A. Cortés Hernández & A. López-Méndez.

Paratypes. Argentina. CI-FML 8289, 2 c&s, 41.3–47.7 mm SL, collected with the holotype. CI-FML 7747, 1, 49.2 mm SL, confluence between San Francisco and San Lorenzo rivers, Ledesma department of Jujuy Province, 23°50’27.9”S 64°37’38.1”W, 16 Aug 2019, G. Aguilera, G. Terán & M. Casalinuovo. CI-FML 7790, 1, 45.0 mm SL, San Francisco River under bridge of Route N. 1, Ledesma department of Jujuy Province, 23°42’2.4”S 64°32’08.1”W, 350 m a.s.l., 15 Aug 2019, G. Aguilera, G. Terán & M. Casalinuovo. CI-FML 8285, 9, 1 c&s, 40.5–51.0 mm SL, confluence between San Francisco and San Lorenzo rivers, Ledesma department of Jujuy Province, 23°50’27.9”S 64°37’38.1”W, 365 m a.s.l., 20 Dec 2016, G. Aguilera, G. Terán & D. Delgado. CI-FML 8286, 2, 38.0–38.7 mm SL, confluence between San Francisco and San Lorenzo rivers, Ledesma department of Jujuy Province, 23°50’27.9”S 64°37’38.1”W, 365 m a.s.l., 10 Dec 2019, G. Aguilera, G. Terán & M. Casalinuovo. CI-FML 8287, 1, 51.1 mm SL, Bermejo River, Orán department of Salta Province, 23°11’30.4”S 64°11’02.1”W, 300 m a.s.l., Sep 2016, M. Casalinuovo. CI-FML 8288, 4, 32.4–45.6 mm SL, San Lorenzo River, Ledesma department of Jujuy Province, 23°49'46.4"S 64°39'09.3"W, 370 m a.s.l., Dec 2022, G. Aguilera, G. Terán, A. López-Méndez & H. Bugeau. MACN-Ict 13513, 2, 41.4–43.6 mm SL, confluence between Sauzalito and San Francisco rivers, Ledesma department of Jujuy Province, 23°42'29.7"S 64°31'51.1"W, 350 m a.s.l., 7 Dec 2019, M. Casalinuovo.

Diagnosis. *Phenacorhamdia bermejo* is distinguished from the other congeners, except *P. anisura*, *P. hoehnei*, *P. macarenensis*, *P. nigrolineata*, *P. tenebrosa*, by having fewer number of total vertebrae (41–42 *vs.* 39 in *P. taphorni*, 43 in *P. boliviana*, 43–45 in *P. suia*, 44 in *P. cabocla*, 48–52 in *P. cuspidata*, 47–48 in *P. provenzanoi*, 45–46 in *P. roxoi*, 45 in *P. somnians,* 46 in *P. unifasciata*, and 53–55 in *P. tenuis*). Additionally, it can be distinguished by having a longer maxillary barbel (29.8–38.0% of SL *vs.* 26.2–28.3 in *P. anisura*, 12.5–23.3 in *P. cabocla*, 10.5–18.7 in *P. cuspidata*, 19.3–23.0 in *P. hoehnei*, 21.0–27.8 in *P. provenzanoi*, 15.9–22.1 in *P. roxoi*, 19.6–21.1 in *P. somnians*, 16.5–21.7 in *P. suia,* 22.6–27.4 in *P. tenebrosa* and 14.6–18.8 in *P. unifasciata*); longer outer mentonian barbel (16.1–19.9% of SL *vs.* 6.2–13.4 in *P. cuspidata*, 11.0–15.0 in *P. roxoi*, 11.8–14.2 in *P. suia*, and 9.6–15.1 in *P. unifasciata*); longer inner mentonian barbel (12.8–16.2% of SL *vs.* 5.8–10.4 in *P. cuspidata*, 9.9–12.4 in *P. roxoi*, 8.7–14.7 in *P. suia*, and 6.9–11.2 in *P. unifasciata*); conical teeth in the jaws (*vs.* multicuspidate teeth in *P. cuspidata*, *P. suia*, and *P. taphorni*); 11–12 anal-fin rays (*vs.* 10 in *P. somnians*, 16 in *P. tenuis*, and 16–18 in *P. provenzanoi*); 15 branched caudal-fin rays (*vs.* 14 in *P. unifasciata* and 16–17 in *P. tenuis*); and longer head (20.9–24.5% of SL *vs.* 15.1–19.0 in *P. provenzanoi* and 16.5–20.7 in *P. suia*). *Phenacorhamdia bermejo* is distinguished from *P. anisura*, *P. hoehnei*, *P. nigrolineata*, *P. provenzanoi*, and *P. unifasciata* by having longer upper caudal-fin lobe (24.2–28.6% of SL *vs.* 21.4–23.7 in *P. anisura*, 20.4–24.0 in *P. hoehnei*, 17.6–23.1 in *P. nigrolineata*, and 14.0–18.2 in *P. provenzanoi*, and 15.0–23.4 in *P. unifasciata*). It is distinguished from *P. hoehnei*, *P. macarenensis* and *P. nigrolineata* by having more branched pectoral-fin rays (7–8 *vs.* 5–6 in *P. hoehnei*, 6 in *P. macarenensis* and *P. nigrolineata*). From *P. hoehnei*, *P. taphorni*, and *P. tenebrosa* by having longer lower caudal-fin lobe (29.0–33.8% of SL *vs.* 24.0–28.0 in *P. hoehnei*, 21.5–28.6 in *P. taphorni*, and 21.7–24.2 in *P. tenebrosa*). From *P. nigrolineata* and *P. tenebrosa* by having longer caudal peduncle (20.1–23.4% of SL *vs.* 12.3–18.6% in *P. nigrolineata* and 17.5–17.9% in *P. tenebrosa*). From *P. hoehnei* and *P. nigrolineata* by the mouth gape (30.8–36.6% of HL vs. 14.5–20.1 in *P. hoehnei* and 37.2–53.7 in *P. nigrolineata*). From *P. nigrolineata* and *P. provenzanoi* by the shorter anal-fin base (11.4–14.8% of SL *vs.* 15.1–22.1 in *P. nigrolineata* and 16.2–19.4 in *P. provenzanoi*). From *P. nigrolineata* and *P. roxoi* by having deeper body (11.5–17.0% of SL *vs.* 6.8–10.6 in *P. nigrolineata* and 8.2–10.2 in *P. roxoi*). From *P. anisura* and *P. provenzanoi* by having deeper caudal peduncle (7.0–8.6% of SL *vs.* 5.7–6.9 in *P. anisura* and 4.3–5.1 in *P. provenzanoi*).

The new species is also distinguished from *P. boliviana* by the insertion of dorsal-fin pterygiophore behind vertebra 11 (*vs.* 14); from *P. cabocla* by having fewer upper caudal-fin lobe branched rays (7, one with 6, *vs.* 8–9), and longer snout length (36.0–45.7% of HL *vs.* 30.0–35.9); from *P. suia* by the shorter distance between dorsal fin to adipose fin (17.9–21.4% of SL *vs.* 25.5–34.9); from *P. macarenensis* by having more branched anal-fin rays (7–9 *vs.* 6); from *P. tenebrosa* by the insertion of dorsal-fin first basal radial between neural spine of 11th–12th vertebrae (*vs.* 9th–10th), and last basal radial between neural spine of 16th–17th vertebrae (*vs.*13th–14th or 14th–15th). *Phenacorhamdia bermejo* is additionally distinguished from *P. provenzanoi* and *P. tenuis* by the greater number of gill rakers on first branchial arch (7 *vs.* 4–5 in *P. provenzanoi* and 2 in *P. tenuis*). It is also distinguished from the remaining species of the genus, except *P. macarenensis*, *P. nigrolineata*, *P. provenzanoi*, *P. roxoi*, *P. taphorni*, *P. tenuis* and *P. unifasciata*, by the maxillary barbel surpassing the distal tip of the adpressed pectoral fin and reaching up to the dorsal-fin base in some specimens (*vs.* reaching up to the distal tip of the adpressed pectoral fin in *P. anisura*, *P. boliviana* and *P. tenebrosa*; to the pectoral-fin base in *P. cabocla*, *P. hoehnei*, and *P. suia*; to the end of the opercle in *P. somnians*; and not reaching to pectoral-fin origin in *P. cuspidate*, Fig. **S2**).

Description. Morphometric data are summarized in Tab. 1. Body elongated, elliptical in cross section through dorsal-fin origin. Greater body depth at dorsal-fin origin; body becoming compressed towards caudal peduncle. Dorsal profile of body, from snout tip to dorsal-fin origin, convex (except for concave area between anterior margin of posterior nostril to posterior margin of eye). Straight or slightly convex from end of dorsal fin to adipose-fin origin, straight and descending along adipose-fin base, and straight from that point to caudal-fin origin. Ventral profile of body, from snout tip to pelvic-fin origin, convex; thence almost straight to anal-fin end; and concave or almost straight from that point to caudal-fin origin.

Head depressed, deepest and widest at occipital region. Snout short, anterior margin rounded in dorsal view. Mouth terminal or slightly prognathous; lower jaw slightly longer than upper jaw. Premaxillary and dentary teeth conical, arranged in rectangular patch with four to eight irregular rows. Anterior nares tubular, smaller than posterior nares, situated closer to snout tip than to posterior nares. Posterior nares ovoid, closer to eye than to anterior nares, with fleshy anterior flap covering nostril when retracted. Eyes small, dorsally positioned and covered with skin, located closer to snout tip than to posterior opercular margin. Maxillary barbel long, surpassing distal tip of pectoral fin when adpressed, reaching pelvic-fin origin or dorsal-fin origin in some specimens. Mental barbels (inner and outer) aligned in straight line; outer barbel longer, reaching pectoral-fin origin; inner barbel extending just anterior to vertical through opercular margin. Branchiostegal membranes free, anteriorly united to isthmus, bearing seven rays (3 c&s). Gill rakers seven, along anterior margin of first ceratobranchial.

Dorsal fin with i,6(21)* rays; its origin anterior to midbody. First basal radial between neural spines of vertebrae 11–12; last between vertebrae 16–17(3 c&s). Long supraneural, anterior to first dorsal-fin pterygiophore, spanning two vertebrae in length. Adipose fin moderate in length (16.7–20.3% of SL), not confluent with caudal fin and far from reaching first caudal-fin ray. Pectoral fin with i,7(18)* or i,8(3) rays; unbranched ray prolonged into short filament, extending beyond distal fin margin. Pelvic fin with i,5 rays and rounded margin; insertion anterior to or at vertical through dorsal-fin origin. Anal fin with iii(8) or iv(12)* unbranched rays and 7(1), 8(17)* or 9(2) branched rays, in combinations: iv,7(1), iii,8(8), iv,8(9)*, iv,9(2). Origin posterior to midbody; first basal radial between hemal spine of vertebrae 22–23, and last distal radial between vertebrae 28–29.

Caudal fin deeply forked, with i,7+8,i (20)* principal rays (one specimen with i,6 rays on dorsal lobe). Lobes elongate and pointed; ventral lobe longer (29.0–33.8% SL) than dorsal (24.2–28.6% SL). Procurrent rays 9–10 in dorsal lobe, and 8–9 on ventral lobe. Caudal skeleton of ventral lobe with hypurals 1+2 fused into single plate; parahypural

TABLE 1 | Morphometric measurement of *Phenacorhamdia bermejo*. N = 21 specimens; SD = Standard deviation.

	Holotype	Range	Mean	SD
Standard length (mm)	42.6	32.4–52.3	–	–
Percents of standard length				
Body depth	13.8	11.5–17.0	13.6	1.4
Cleithral width	14.4	13.0–16.7	14.9	0.9
Predorsal length	41.6	37.9–42.0	40.4	1.2
Dorsal-fin base	10.8	9.5–12.6	11.1	0.7
Dorsal fin to adipose fin	20.3	17.9–21.4	19.5	0.9
Preadipose length	72.4	67.3–72.4	70.1	1.3
Adipose-fin length	18.1	16.7–20.3	18.5	1.1
Prepelvic length	39.7	38.0–43.9	40.4	1.2
Preanal length	66.4	63.6–69.6	65.8	1.4
Anal-fin base	12.5	11.4–14.8	12.8	0.9
Caudal-peduncle length	21.8	20.1–23.4	21.5	1.0
Caudal-peduncle depth	7.0	7.0–8.6	7.6	0.4
Upper caudal lobe length	26.2	24.2–28.6	26.5	1.3
Lower caudal lobe length	29.7	29.0–33.8	31.3	1.5
Head length	22.5	20.9–24.5	22.5	1.0
Maxillary-barbel length	35.0	29.8–38.0	34.2	2.4
Outer mental-barbel length	18.2	16.1–19.9	18.0	1.0
Inner mental-barbel length	14.9	12.8–16.2	14.5	1.2
Percents of head length				
Head width	58.9	56.4–76.5	66.0	4.7
Head depth	44.8	42.9–55.9	49.4	4.0
Mouth gape	30.8	30.8–36.6	33.5	1.7
Snout length	40.3	36.0–45.7	39.5	2.3
Fleshy interorbital	28.2	22.2–29.2	25.6	2.1
Eye diameter	8.6	8.6–11.3	9.8	0.8

closely adjacent but separated from it. Dorsal lobe with hypural 3+4 fused into single plate; hypural 5 ossified and free; uroneural ossified, fused to complex centrum (preural centrum 1+ural centrum 1). Precaudal vertebrae 15(2) and 16(1), caudal vertebrae 25(1), 26(1), 27(1), 41(2) or 42(1) total vertebrae. First hemal spine on 16th (2) or 17th (1) vertebra. Bifid hemal spine on vertebra 24th (3) to 29th (2) or 30th (1). Pleural ribs 8(1) or 9(2).

Supraorbital sensory canal with 4 pores: s1, opening medially adjacent to anterior nares, s2 fused to infraorbital pore i2 (s2+i2) and opening approximately half length between anterior and posterior nares, s3 on internal posterior margin of posterior nare, s4 and s5 absent, supraorbital canals connected medially by epiphysial membranous canal, above anterior fontanel, without superficial pore (s6), and s8 at the posterior surface of frontal. Infraorbital canal with six pores: i1, located at vertical through posterior margin of anterior nares, near the groove of maxillary barbel, i2 fused to s2, i3 located half distance between anterior and posterior nares, into maxillary groove, i4 located just anterior to vertical through anterior eye margin, i5 behind eye in lateral margin of maxillary groove, and i6 placed behind eye. Preoperculomandibular canal with 11 pores, pm 1 displaced just from midventral line at dentary, pm2 and pm3 on posterior margin of ventral lip, pm4 anterior to outer mentonian barbel insertion, pm5 at outer mentonian barbel level, pm6 at vertical through anterior margin of posterior nares, pm7 at vertical through half distance between posterior nares and anterior eye margin, pm8 at vertical through eye, pm9 and pm10 separated by a short stretch from principal preoperculomandibular canal, and pm11 in preopercle at eye level.

Coloration in alcohol. Coloration after fixation: body background light beige dorsally and laterally, almost white ventrally. The pectoral, pelvic, anal, and dorsal fins remain hyaline, while the pigmentation pattern in the adipose and caudal fins persists, although it becomes less pronounced. In fixed specimens, the small indentation of the lateral line system appears as a thin, grayish line.

Coloration in life. Coloration in live specimens (Fig. 2): the overall pigmentation consists of uniform, minute mottling, producing a homogeneous reddish-brown hue across the body. The head is slightly darker than the rest of the body, while pigmentation on the caudal peduncle is concentrated midlaterally, gradually fading towards the dorsal and ventral regions. The pectoral, pelvic, and anal fins are hyaline, with the dorsal fin similarly transparent but displaying chromatophores concentrated along the rays, which becoming less conspicuous towards the distal tips. The adipose fin exhibits chromatophores concentrated at the base, extending to about middle depth of the fin, with a gradual fading towards the distal margin. The caudal fin shows denser pigmentation near the base, which progressively fades towards the distal margin. Head, in ventral view, with chromatophores restricted to the preoperculomandibular laterosensory canal. Clear absence of pigmentation from the origin of the pectoral fin to the anal-fin origin, giving it a silvery appearance.

FIGURE 2 | Live specimen of *Phenacorhamdia bermejo*, CI-FML 8289, 47.7 mm SL, in dorsal, lateral, and ventral views. Photo by Alejandro López-Méndez.

Geographical distribution. *Phenacorhamdia bermejo* inhabits the upper Bermejo River basin, where it was found at four localities, three on the San Francisco River basin in Jujuy Province and one at the Bermejo River in Salta (Fig. 3).

Conservation status. *Phenacorhamdia bermejo* is exposed to some environmental pressures within its range, including agricultural runoff, deforestation, and industrial pollution affecting freshwater ecosystems. However, no major threats have been identified that would currently place the species at risk across its distribution. The species occur in relatively well-preserved habitats and does not meet the criteria for any threat category. Following the IUCN Red List categories and criteria (IUCN, 2024), *P. bermejo* is best assessed as Least Concern (LC).

Etymology. The specific epithet "bermejo" is a Spanish word meaning reddish in English and refers to both the coloration of live specimens which present a reddish-brown hue across the body, and to the name of the river basin where the specimens of *Phenacorhamdia bermejo* were collected. A noun in apposition.

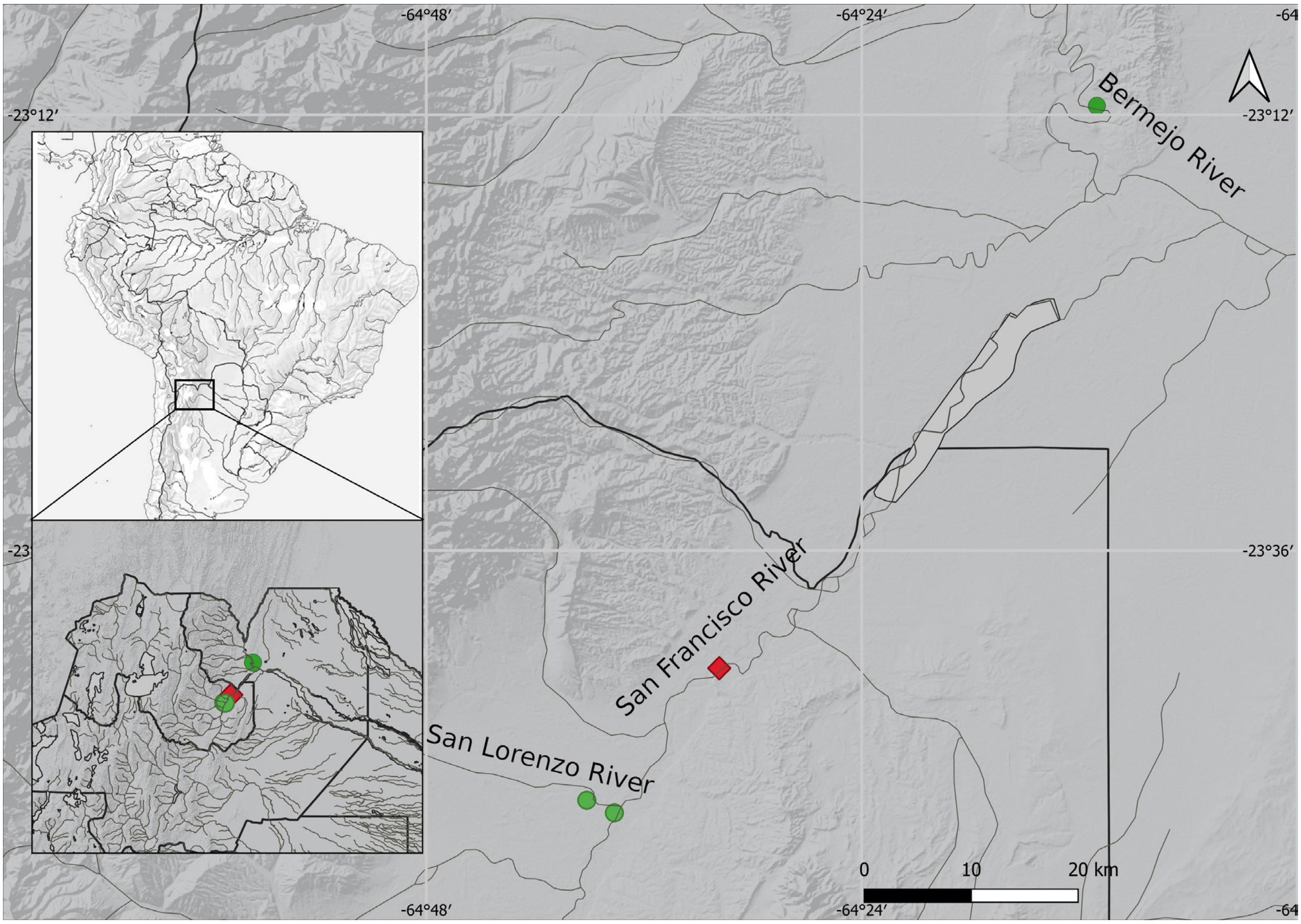

FIGURE 3 | Distributional map of *Phenacorhamdia bermejo*. Red diamond indicates the type locality, and green dots indicate additional localities.

Morphological analysis. The PCA revealed clear morphological differentiation among the examined species of *Phenacorhamdia*. The first two principal components accounted for 86.3% of the total variation (PC1: 72.5%; PC2: 13.8%). Along PC1, *P. bermejo* was distinctly separated from all other species, indicating that morphological proportions such as preadipose length, preanal length, prepelvic length, caudal fin lower lobe length, predorsal length and maxillary barbel length allow clear distinction from other congeners (Fig. 4). In contrast, *P. cabocla*, *P. somnians*, *P. hoehnei*, and *P. tenebrosa* partially overlapped, reflecting shared morphometric characteristics while still maintaining species-level distinctions. Overall, the PCA supports the morphological distinctiveness of the new species, *P. bermejo*, within the genus.

A

Component	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Standard deviation	9.9295	4.3051	2.6427	1.8641	1.4218	1.1628	0.9600	0.7572	0.6503	0.5685
Proportion of variance	0.7336	0.1379	0.0520	0.0259	0.0150	0.0101	0.0069	0.0043	0.0032	0.0024
Cumulative proportion	0.7336	0.8716	0.9235	0.9494	0.9644	0.9745	0.9813	0.9856	0.9887	0.9911

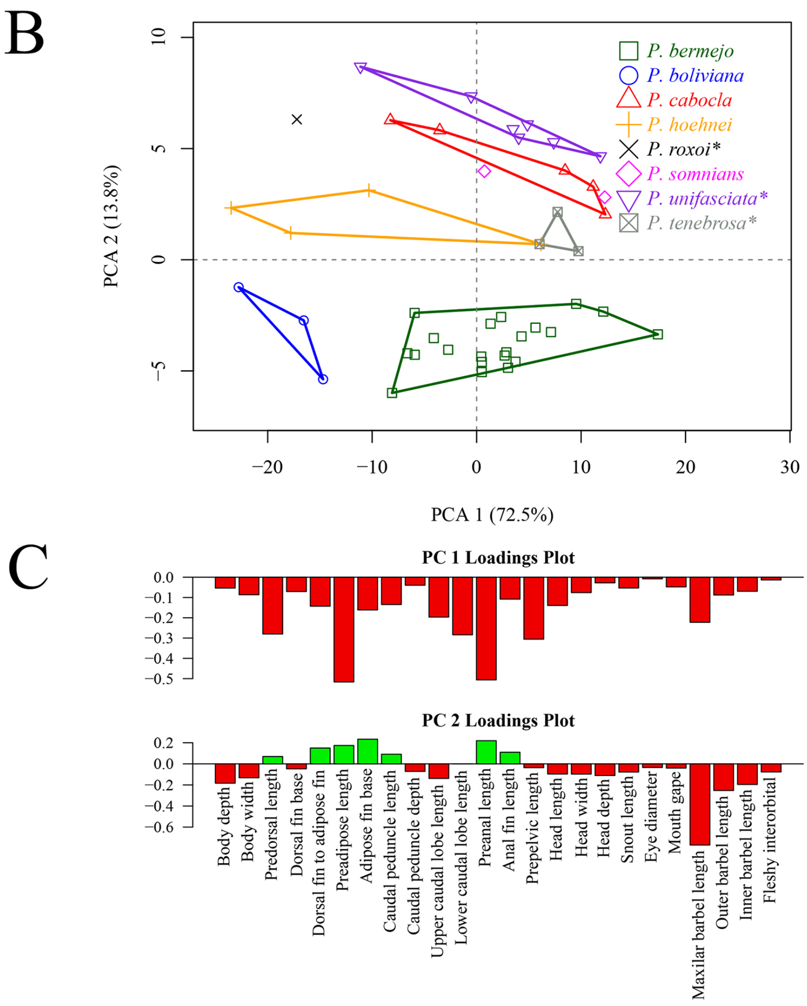

FIGURE 4 | Results of the principal component analysis. **A.** Importance of each component; **B.** Biplot of first two principal components, with the proportion of explained variance shown in parenthesis; **C.** Loading of each variable on the principal components.

Phylogenetic analysis. Both Parsimony and Maximum Likelihood analyses recovered the new species nested with other species of *Phenacorhamdia*, which formed a well-supported monophyletic group (ML: Freq = 93%; P: GC = 90), supporting the inclusion of the new species in this genus (Fig. 5). In both analyses, *Phenacorhamdia* was recovered as the sister group to the recently described genus *Magdalenichthys*. Together, these genera form a clade sister to *Mastiglanis*, and this larger clade is, in turn, sister to *Pariolius*. Within *Phenacorhamdia* two clades were recovered, one with *P. boliviana* and *P. somnians*, and the other one including *P. bermejo* as sister to the clade including *P. unifasciata*, *P. roxoi* and *P. tenebrosa*. The mean genetic distances based on the COI marker indicated a divergence of 8.8% between *P. bermejo* and *P. tenebrosa*, both occurring in the Paraná River basin (Tab. 2). Moreover, *P. bermejo* exhibited genetic divergences exceeding 6% from *P. unifasciata* and 13% from *P. boliviana*, reinforcing the genetic distinctiveness of the new species.

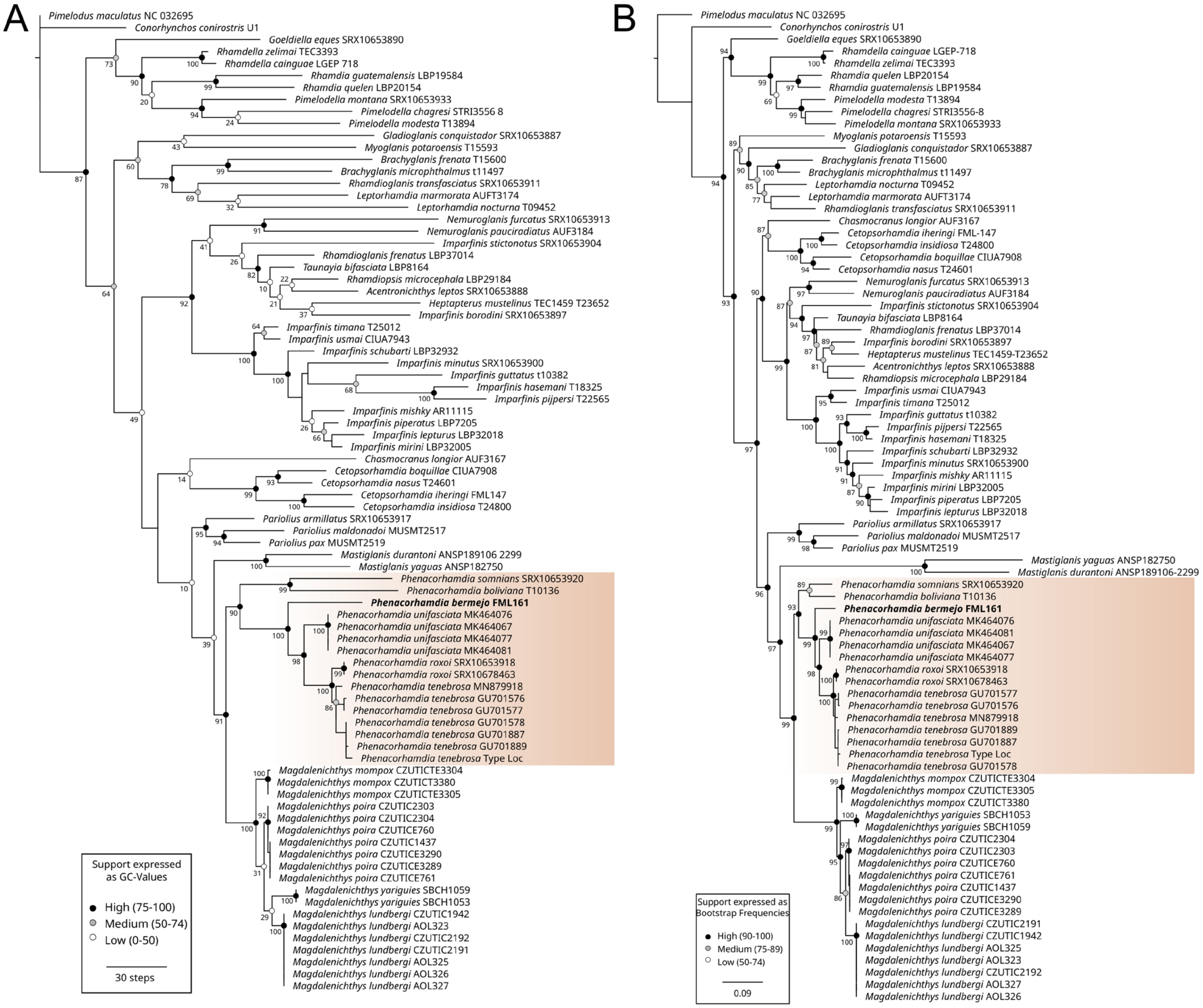

FIGURE 5 | Phylogenetic analyses performed under parsimony (**A**) and maximum likelihood (**B**).

TABLE 2 | Genetic distances interspecific and intraspecific of *Phenacorhamdia* under K2 substitution model. Values are represented as percentages.

	1	2	3	4	Intraspecific distance
1. *Phenacorhamdia bermejo*					-
2. *Phenacorhamdia unifasciata*	6.2				0
3. *Phenacorhamdia tenebrosa*	8.8	6.5			1.4
4. *Phenacorhamdia boliviana*	13.5	14.2	14.9		-

DISCUSSION

Silva *et al*. (2021), Faustino-Fuster *et al*. (2021), Slobodian, Bockmann (2025), and DoNascimiento *et al.* (2025) corroborated the monophyly of Heptapteridae, and recovered two major clades within it, the subfamilies Rhamdiinae and Heptapterinae, as in the present analyses. The Rhamdiinae includes *Brachyrhamdia* Myers, 1927, *Goeldiella* Eigenmann & Norris, 1900, *Pimelodella* Eigenmann & Eigenmann, 1888, *Rhamdella* Eigenmann & Eigenmann, 1888 and *Rhamdia* Bleeker, 1858, and a non-circumscribed genus that includes the species of the group *P. leptosoma* sensu Slobodian, Pastana (2018) (see Slobodian, Bockmann, 2025). For its part, Heptapterinae is divided in two tribes (Brachyglaniini and Heptapterini), the latter composed of *Acentronichthys* Eigenmann & Eigenmann, 1916, *Cetopsorhamdia* Eigenmann & Fisher, 1916, *Chasmocranus* Eigenmann, 1912, *Heptapterus* Bleeker, 1858, *Horiomyzon* Miranda Ribeiro, 1918, *Imparfinis* Eigenmann & Norris, 1900, *Magdalenichthys*, *Mastiglanis* Bockmann, 1994, *Nannoglanis* Boulenger, 1887, *Nemuroglanis* Eigenmann & Eigenmann, 1889, *Pariolius* Cope, 1872, *Phenacorhamdia* Dahl, 1961, *Rhamdioglanis* Ihering, 1907, *Rhamdiopsis* Haseman, 1911, *Taunayia* Miranda Ribeiro, 1918, and a few clades treated as undescribed genera (see Bockmann, Slobodian 2018; Slobodian, Bockmann, 2025).

The phylogenetic hypothesis proposed in this study does not seek to evaluate the position of *Phenacorhamdia* within Heptapterinae, as it is based on two mitochondrial genes (COI and CytB), it should be regarded as exploratory and of limited robustness and explanatory power. Nevertheless, the topologies under Parsimony and ML analyses confirm the close relationships obtained by DoNascimiento *et al*. (2025) between the new genus they described *Magdalenichthys* and *Phenacorhamdia*. DoNascimiento *et al*. (2025) recovered *Pariolius* in a close relation to that clade, and *Mastiglanis* as sister to the remaining species within the tribe Hetapterini, unlike the present analyses in which *Pariolius* and *Mastiglanis* are successive sister taxa to the clade including *Phenacorhamdia* and *Magdalenichthys*. For their part, Slobodian, Bockmann (2025) recovered *Pariolius* as closely related to a clade comprising *Phenacorhamdia* as the sister group to '*Imparfinis*' *microps* plus a new undescribed genus. Although the tree topologies obtained in the present analyses differs from those recovered in previous studies, *Pariolius* is consistently recovered in closely relationship to *Phenacorhamdia* in all cases. Resolution of phylogenetic relationships within Heptapterinae remains limited, which is likely attributable, at least in part, to incomplete taxon sampling in molecular analyses (*e.g*., *Horiomyzon retropinnatus* Stewart, 1986, *Nannoglanis fasciatus* Boulenger, 1887, *Rhamdiopsis moreirai* Haseman, 1911, '*Imparfinis*' *microps*, etc.).

Generic allocation. *Phenacorhamdia* is one of the best-known genera of Heptapteridae, whose phylogenetic relationships for its recognition as a monophyletic group have been addressed through morphological and molecular data (Bockmann, 1998; Silva *et al.*, 2021; Slobodian, Bockmann, 2025), although none of these studies has included the type species of the genus *P. macarenensis*. Bockmann (1998:367) proposed six synapomorphies to define the genus: (a) posterior process of epioccipital very prominent, (b) prognathous mouth, (c) neural and haemal spines of posterior vertebrae inclined 30 degrees or less relative to the longitudinal axis of the body, (d) first ray of pectoral-fin slightly longer than the second ray, (e) eight branched rays on the lower lobe of the caudal-fin, (f) second pore of the supraorbital canal (s2+i2) located farthest from the anterior nostril. All the above-mentioned character-states were verified in *P. bermejo* (Figs. 1, 6) justifying its inclusion in the genus from its morphology and corroborating our phylogenetic results. Thus, with the addition of *P. bermejo*, the genus is currently composed of 16 species widely distributed in the main basins of South America.

The new taxon is the fifth species of the genus described from the Paraná River basin, in addition to *P. hoehnei*, *P. roxoi*, *P. tenebrosa*, and *P. unifasciata*. *Phenacorhamdia bermejo* can be readily distinguished from these species by its yellowish body background and the absence of a dark brown lateral stripe. Additional characters also reinforce the differences among *P. bermejo* and the remaining members of the genus from the Paraná River basin, such as the number of vertebrae and the length of the maxillary barbels.

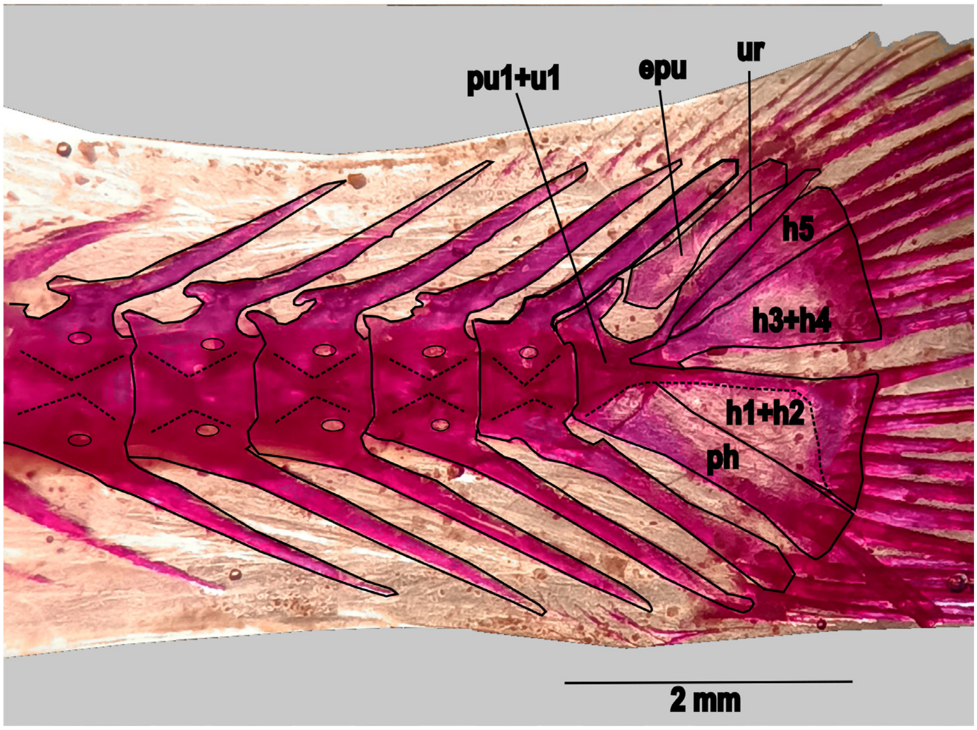

FIGURE 6 | Caudal vertebrae of *Phenacorhamdia bermejo*, CI-FML 8289. Abbreviations: epu, epural; hu1+hu2, ventral hypural plate formed by the fused hypurals 1 and 2; hu3+hu4, dorsal hypural plate formed by the fused hypurals 3 and 4; hu5, dorsal hypural plate 5; ph, parhypural; pu1+u1, complex centrum composed of preural centrum 1 and ural centrum 1; ur, uroneural.

Despite these differences, *P. bermejo* resembles *P. tenebrosa* in external morphology and meristics, highlighting the conservative morphology of these species. Nevertheless, the PCA encompassing all species from the Paraná River basin revealed distinct groupings, thereby indicating a clear morphological differentiation between *P. bermejo* and the remaining species (see Fig. 4). Additionally, the phylogenetic analyses herein performed, under both Parsimony and Maximum Likelihood, recover *Phenacorhamdia* as monophyletic, with *P. bermejo* as the sister group of a clade composed of *P. tenebrosa* and *P. unifasciata*, with *P. boliviana* as the sister group of this clade of three species. In both analyses, *P. bermejo* was recovered as an independent taxon, also showing a high genetic divergence from *P. tenebrosa* (over 8%), which is, by certain morphological similarity, the main species with which the new taxon could be confused.

Giorgis *et al*. (2012) recorded *P. tenebrosa* in Argentina for the first time from the analysis of specimens collected at Yacyretá dam near to Ituzaingó city in Corrientes and the Pre-Delta National Park in Entre Ríos. In that contribution, they mentioned that the maxillary barbel surpasses the distal border of the pectoral fin, and the body presents a reddish-brown coloration in life (see fig. 1 in Giorgis *et al*., 2012), conditions that agree with those exhibited by *P. bermejo*. Although we could not analyze the material from the Paraná River basin, considering the above-mentioned characters, the presence of *P. tenebrosa* in Argentina is dubious and requires further investigation.

Bockmann (1998) recovered two monophyletic clades in *Phenacorhamdia*, one composed of species with short snout and long, slender bodies; and the other, of species with long snout and relatively short bodies. The short snout group, which includes species with snout lengths between 31.5–34.3% HL (Castro, Wosiacki, 2023) is supported by the angle of the neural and haemal spines of caudal vertebrae smaller than 20° (*vs*. between 20° and 30°) as their single known synapomorphy. The long snout group includes *P. anisura*, *P. hoehnei*, *P. macarenensis*, *P. provenzanoi*, *P. roxoi*, *P. somnians*, *P. taphorni*, *P. tenebrosa*, and *P. unifasciata*, which possess snout lengths between 34.3–40.0% HL (Castro, Wosiacki, 2023), and is supported by nine synapomorphies. *Phenacorhamdia bermejo* has a long snout (36.0–45.7% HL), and a relatively short, slender body, and presents the nine synapomorphies supporting the clade according to Bockmann (1998), including a long extension on the postero-lateral angle of premaxilla (ch. 15:2), the lateral margin of the posterior portion of lateral ethmoid sharp and posteriorly directed (ch. 26:2), presence of a foramen on the posterior portion of the lateral ethmoid (ch. 27:1), a vertical fenestra in the anterior portion of the pterosphenoid (ch. 52:1), optic foramen very reduced (ch. 53:2), anterior portion of the corono-meckelian bone tapered (ch. 61:1), the ascending portion of the Meckel cartilage discontinuous (ch. 64:1), and the ventral margin of the metapterygoid without bony contact to the antero-dorsal process of the quadrate (ch. 74:1), which justify its inclusion in the "long-snouted" group and corroborates the phylogenetic results obtained herein.

Material comparative examined. Bolivia. *Phenacorhamdia boliviana*. MZUSP 27813, 5, 44.6–65.6 mm SL, Villa Tunari, Chapare, 17°00'34.0"S 65°18'29.4"W. **Brazil.** *Phenacorhamdia cabocla*. MZUSP 87325, 2, 38.3–39.5 mm SL, Riberão São Raimundo, Tocantins River basin, Estreito, Maranhão, 06°44'22"S 47°07'26"W. MZUSP 84082, 3, 41.0–55.0 mm SL, Formosa do Rio Preto, Brejão, rio Sapão, tributary of rio Preto, São Francisco River basin, Bahia, 10°55'39"S 45°41'54"W. *Phenacorhamdia hoehnei*. MZUSP 103778, 8, 22.8–63.5 mm SL, córrego Cabeceira Comprida, Fazenda Campina Grande, dirt road between Coxim and

Pedro Gomes, upper Taquari basin, Coxim, Mato Grosso do Sul, 18°14'35"S, 54°33'34"W. MZUSP 90022, 1, Tangará da Serra, rio do Sapo, tributary of rio Sepotuba, bellow the waterfall, Mato Grosso, 14°37'04"S 57°44'44"W. MZUSP 59354, 4, 32.6–60.1 mm SL, rio Salobra, about 18 km between Bonito to Bodoquena, Bodoquena, Mato Grosso do Sul. *Phenacorhamdia roxoi*. MZUSP 125819, holotype, 63.4 mm SL, rio Pardo, rio Paranapanema, Botucatu, São Paulo, 22.941178°S 48.584397°W. In addition, material listed in Azevedo-Santos *et al*. (2020), Ferrazi *et al*. (2024), Tinti *et al*. (2024). *Phenacorhamdia somnians*. MZUSP 30809, 2, 38.3–48.9 mm SL, rio Itacaiunas, railway, 10 km east of the N-4, Pará. *Phenacorhamdia tenebrosa*. EEBP 197, 3 syntypes, 38.5–43.8 mm SL, rio Mogi Guaçu, Cachoeira de Emas, São Paulo. CICCAA 8618, 1 c&s, 40.8 mm SL, Porto Ferreira, rio Mogi Guaçu basin, São Paulo, 21°52'37"S 47°30'32"W. *Phenacorhamdia unifasciata*. MZUSP 36691, holotype, 60.2 mm SL, Ribeirao Santana (São Bartolomeu), Paranaíba basin, Distrito Federal. MZUSP 36692, 1 paratype, 43.8 mm SL, Ribeirão Mestre D'Armas (São Bartolomeu), Paranaíba basin, Distrito Federal. MZUSP 36693, 1 paratype, 46.6 mm SL, córrego Fumal (São Bartolomeu), Paranaíba basin, Distrito Federal. MZUSP 36694, 1 paratype, 53.0 mm SL, córrego Papua, tributary of rio São Bartolomeu, Paranaíba basin, Distrito Federal. MZUSP 36696, 1 paratype, 41.2 mm SL, córrego Quinze (São Bartolomeu), Paranaíba basin, Distrito Federal. MZUSP 36698, 1 paratype, 43.1 mm SL, rio Pipiripau (São Bartolomeu), Paranaíba basin, Distrito Federal. MZUSP 25051, 1 paratype, córrego Mestre D'Armas, tributary of rio São Bartolomeu, Planaltina, Goiás, 15°38'S 47°39'W. **Colombia.** *Phenacorhamdia anisura*. MHNU-I 1817, 1 c&s, 37.7 mm SL, Bocas del Guayuriba, Guayuriba River, Puerto López, Meta, 03°55'10.8"N 73°05'05.6"W. *Phenacorhamdia taphorni*. MHNU-I 2119, 1 c&s, 34.1 mm SL, bridge over Guayuriba River, 03°57'33.5"N 73°16'20.0"W, route Rincón de Pompeya-La Palmera, Villavicencio, Meta.

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The study complied with the animal welfare laws, guidelines, and policies of the Comité Nacional de Ética en la Ciencia y Tecnología, Argentina. Collection permits were granted by the Ministerio de Ambiente of Jujuy (permits' numbers: 1103-306 M/2016, Res. N° 137/2016-MA).

DATA AVAILABILITY STATEMENT

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

AI STATEMENT

The authors declare that ChatGPT (OpenAI) was used to assist with grammar correction, language polishing, and reference formatting. It was not used to generate or analyze data in this manuscript.

COMPETING INTERESTS

The authors declare no competing interests.

SUPPLEMENTARY MATERIAL

Supplementary material **S1**

Supplementary material **S2**

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