



Redescription and expansion of the geographic distribution of *Phenacorhamdia nigrolineata* (Siluriformes: Heptapteridae)

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Phenacorhamdia nigrolineata is redescribed, and the expansion of its geographic distribution is presented based on abundant new records. Morphological analysis, meristic comparison and osteological description were performed. No one autapomorphy was identified for *P. nigrolineata*, but the species is identified by an exclusive combination of characters of coloration of the body, morphometric and meristic data (snout length, maxillary and outer mental barbels length; number of vertebrae). A discussion of its geographic distribution, coloration pattern of the body, the putative relationships among some species of the genus, and its conservation status are presented.

Keywords: Amazon basin, Coloration, South America, Small catfish, Taxonomy.

Phenacorhamdia nigrolineata é redescrita e a expansão de sua distribuição geográfica é apresentada com base em abundantes novos registros. Foram realizadas análises morfológicas, comparação merística e descrição osteológica. Nenhuma autapomorfia foi identificada para *P. nigrolineata*, mas a espécie é identificada por uma combinação exclusiva de caracteres de colorido do corpo, dados morfométricos e merísticos (comprimento do focinho, comprimento dos barbilhões maxilares e mentais externos; número de vértebras). Uma discussão dessa distribuição geográfica, padrão de coloração do corpo, as supostas relações entre algumas espécies do gênero e seu estado de conservação são apresentados.

Palavras-chave: América do Sul, Bacia Amazônica, Colorido, Pequeno bagre, Taxonomia.

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INTRODUCTION

Heptapteridae is a Neotropical group of catfishes currently with 233 valid species in 23 valid genera (Fricke *et al.*, 2023a). Among these genera, *Phenacorhamdia* Dahl, 1961 currently has 14 valid species (Fricke *et al.*, 2023b): *Phenacorhamdia anisura* (Mees, 1987), *P. macarenensis* Dahl, 1961, *P. provenzanoi* DoNascimento & Milani, 2008, and *P. taphorni* DoNascimento & Milani, 2008 from the Orinoco River basin; in the Amazon River basin, *P. boliviana* (Pearson, 1924) from the Beni River, *P. nigrolineata* Zarske, 1998 from the Ucayali River, and *P. somnians* (Mees, 1974) from the das Mortes River basin; *P. suia* Silva, Ochoa & Castro, 2022 from the Xingu River basin; *P. cabocla* Rocha, Ramos & Ramos, 2018 from the upper Parnaíba River basin; *P. hoehnei* (Miranda Ribeiro, 1914) from the Taquari River basin; *P. tenuis* (Mees, 1986) from Marowijne River basin; and in the Paraná River basin, *P. roxoi* Silva, 2020 from upper Paranapanema River basin, *P. tenebrosa* (Schubart, 1964) from lower Paraná River basin and *P. unifasciata* Britski, 1993 endemic to the São Bartolomeu River basin.

The latest hypotheses of phylogenetic relationships of Heptapteridae recovered *Phenacorhamdia* as monophyletic, using morphological (Bockmann, 1998) and molecular data (Silva *et al.*, 2021). The genus can be diagnosed by the osteological features proposed by Bockmann (1998:367) and DoNascimento, Milani (2008), and by a combination of non-unique characters that includes: body moderately to very elongate, uniformly brown, lacking dorsal bars, unpigmented regions, or a midlateral stripe (except *P. unifasciata*); mouth prognathous; first pectoral-fin ray mostly flexible (except for its basal third) and prolonged as a short filament; maxillary barbel usually reaching to the last third of the pectoral fin or slightly surpassing the posterior border of pectoral fin; origin of pelvic fin at vertical through the middle of dorsal-fin base or slightly anterior; adipose fin rectangular and moderately long, not confluent with caudal fin; anal fin short to moderately long, bearing 12–18 rays; and caudal fin deeply forked with the ventral lobe markedly longer than the dorsal lobe (Bockmann, Slobodian, 2018:246).

Phenacorhamdia nigrolineata was described based on three specimens captured in 1996 and 1997 during two expeditions in only one catchment area in Tierra Roja, near Pucallpa, Ucayali River basin, Peru. It was originally described having as main diagnostic feature a “narrow black line along the linea lateralis, a small adipose fin, no filamentous lobes of the caudal fin, small eyes, and an elongated body shape” (Zarske, 1998:27).

Dagosta, de Pinna (2019) compiled records of several fish species from the Amazon basin, recording the occurrence of *P. nigrolineata* in the Beni and Madre de Dios River basins, of southeast Peru; Barriga (2012:114) reported the occurrence of *P. nigrolineata* in Ecuador; and Maldonado-Ocampo *et al.* (2008:201) and DoNascimento *et al.* (2017:91) recorded its occurrence in southern Colombia.

In an extensive analysis of material of *Phenacorhamdia* from other sub-basins of the Amazon basin, several records of specimens with many characteristics similar to those of *P. nigrolineata* in a wide geographic distribution were recognized, confirmed by high-quality photographs and radiographs of the types. The redescription of the species can be justified since the original description has ambiguous characteristics given the current taxonomic knowledge of the genus *Phenacorhamdia* and few type specimens from only one locality. In the present work *P. nigrolineata* has its description expanded, accompanied by an overview of its osteology and the laterosensory system, based on the

examination of the holotype and paratypes. Additionally, its geographical distribution is extended to include much of the Amazon basin, supported by the examination of extensive comparative material. A discussion about coloration pattern of the body and the putative relationships between some species of *Phenacorhamdia* are presented.

MATERIAL AND METHODS

Morphometrics. Measurements were made using digital calipers with 0.1 mm precision, using a stereomicroscope. The measurements were taken on the left side whenever possible, following Lundberg, McDade (1986), Bockmann (1994), and DoNascimento, Milani (2008). Head length and body parts are given as proportions of standard length (SL); head parts are presented as proportions of head length (HL), except for measurements of barbels that were converted to proportions of SL.

Morphometric analysis. Our analyses are based on the morphometric data of 29 specimens of *P. nigrolineata* from different basins, 17 of *P. unifasciata*, and five of *P. boliviana*. Principal Component Analysis (PCA) was performed with PAST 4.03 statistical program (Hammer *et al.*, 2001). However, before performing the PCA analysis, a correlation was made between the morphometric variables, excluding only those that had a high correlation ($R^2 > 0.9$). The ANOVA test with Dunn's post hoc was also used, and the morphometric data, as they were not normal, had to be logarithmized.

Morphology and meristics. Counts include the number of fin rays, branchiostegals, 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 five associated with the Weberian complex (Lundberg, McDade, 1986), free vertebrae, and the compound caudal centrum (PU1+U1) (Lundberg, Baskin, 1969), counted as one element. Asterisks indicate counts for the holotype.

Osteological and morphological data of all *Phenacorhamdia* species were obtained from original descriptions, from Bockmann (1998), DoNascimento, Milani (2008), and from digital radiographs of *P. boliviana* available at CAS Ichthyology Primary Types Imagebase (<http://researcharchive.calacademy.org/research/ichthyology/types/index.asp>). Specimens were cleared and stained (c&s) followed Taylor, Van Dyke (1985). Additional data were obtained by photos and radiographs provided by the institutions NHMUK (*P. somnians*), MTD F (*P. nigrolineata*), RMNH.PISC (*P. tenuis*), and MNRJ (*P. hoehnei*). Osteological nomenclature and the laterosensory system follow Bockmann, Miquelarena (2008). Institutional abbreviations follow Sabaj (2022).

RESULTS

Phenacorhamdia nigrolineata Zarske, 1998

(Figs. 1–7; Tab. 1)

Phenacorhamdia nigrolineata Zarske, 1998:27 (original description). —Bockmann, Guazzelli, 2003:416 (catalog). —Zarske, 2003:23 (list of types). —Ferraris, 2007:189 (catalog). —DoNascimento, Milani, 2008:165 (comparison). —Maldonado-Ocampo *et al.*, 2008:201 (list of the Colombia). —Barriga, 2012:114 (list of the Ecuador). —DoNascimento *et al.*, 2017:91 (list of the Colombia). —Rocha *et al.*, 2018:355 (comparison). —Dagosta, de Pinna, 2019:118 (list of the Amazon). —Silva *et al.*, 2022:2 (comparison).
Phenacorhamdia sp. —Bockmann, Slobodian, 2013:54, photo (catalog of the Madeira River).

Diagnosis. *Phenacorhamdia nigrolineata* is distinguished from congeners, except *P. cabocla*, *P. macarenensis*, and *P. roxoi*, by having a homogeneously dark brown body, without a true, darkly pigmented midlateral stripe (*vs.* usually light brown in *P. anisura*, *P. boliviana*, *P. hoehnei*, *P. taphorni* or yellowish in *P. somnians*, *P. suia*, *P. tenebrosa*, *P. provenzanoi*, and *P. tenuis*; *P. unifasciata* has a longitudinal dark brown stripe along the dorsal half of the body). Additionally, *P. nigrolineata* differs from all congeners by having a shorter snout (33.2–33.6% *vs.* 34.3–43.0% HL in *P. anisura*, *P. hoehnei*, *P. macarenensis*, *P. roxoi*, *P. somnians*, *P. suia*, *P. taphorni*, *P. tenebrosa*, and *P. unifasciata*). In *P. nigrolineata* the maxillary barbel reaches the end of distal margin of the pectoral fin when adpressed to body (*vs.* reaching the origin of the pectoral fin in *P. cabocla*, *P. somnians*, *P. suia*, and *P. unifasciata*; reaching $\frac{3}{4}$ of the pectoral fin length in *P. anisura*; reaching half the length of pectoral fin in *P. tenuis*; reaching the origin of the pelvic fin in *P. macarenensis*). The caudal-peduncle depth in *P. nigrolineata* is 5.3–8.2% SL (*vs.* 4.3–5.1% SL in *P. provenzanoi*). In *P. nigrolineata* the outer mental barbel reaches the origin of the pectoral fin (*vs.* not reaching in *P. anisura* and *P. taphorni*). *Phenacorhamdia nigrolineata* is distinguished from congeners by having 40–41 total vertebrae (*vs.* 39 in *P. taphorni*; 43 in *P. boliviana*; 44 in *P. cabocla*; 43 or 45 in *P. suia*; 45 in *P. somnians*; 45 or 46 in *P. roxoi*; 46 or 47 in *P. unifasciata*; 47 or 48 in *P. provenzanoi*; and 53 or 55 in *P. tenuis*).

Description. Morphometric data in Tab. 1. Small catfish with elongated body (maximum 47.6 mm SL). Body elliptical in cross section through dorsal-fin origin, progressively more compressed laterally in posterior half. Dorsal profile straight from origin of snout to occipital region, slightly convex from this region to dorsal-fin origin, markedly convex from end of dorsal fin to end of adipose fin base, and straight along caudal peduncle. Ventral profile of head convex, straight along abdomen, then slightly convex at end of anal-fin base and straight along ventral portion of caudal peduncle (Fig. 1).

Head depressed. Snout short, straight in lateral view. Body shallow before dorsal-fin origin and before adipose-fin origin. Mouth prognathous. Anterior and posterior nares forming square in dorsal view. Maxillary barbel moderately long, reaching end of distal margin of pectoral fin when adpressed to body. Outer mental barbel reaching origin of pectoral fin. Inner mental barbel reaching branchiostegal membrane. Eyes small and without free margin, dorsally oriented, and located slightly anterior to medial portion of head.



FIGURE 1 | *Phenacorhamdia nigrolineata*, MTD F 20728, holotype, 37.6 mm SL, Peru, Departamento de Ucayali, Tierra Roja, near Pucallpa: **A.** Dorsal, **B.** Left lateral, and **C.** Ventral views. Photographed by Mario Richter.

Pectoral fin rounded with one unbranched and six* (4) branched rays. Simple pectoral-fin ray mostly flexible, except for its basal third, not prolonged by a short filament. Dorsal fin long and rounded with one unbranched and six* (4) branched rays, branched rays gradually shorter. Pelvic fin long and rounded, with one unbranched and five* (4) branched rays, originating slightly anterior to vertical line through origin of dorsal fin. Shallow adipose fin, rectangular, and short, with posterior lobe free and not confluent with caudal fin. Origin of anal fin anterior to origin of adipose fin. Origin of adipose fin vertically aligned to origin of second branched anal-fin ray. Anal fin with one (1) or two* (3) anteriormost rays embedded in thick skin fold, and iv,9*(4) rays (Figs. 2–3).

Caudal fin bifurcated, lobes pointed, ventral lobe slightly longer than dorsal; Dorsal lobe with 13*(3) or 14(1) procurrent rays and one unbranched and five (1) or seven* (3) branched principal rays. Ventral lobe with 13(3) or 15*(1) procurrent rays and one unbranched and eight* (4) branched principal rays.

TABLE 1 | Morphometric data of *Phenacorhamdia nigrolineata* (data of types not included in the range of non-types). N: Number of non-types; SD: Standard deviation.

	Holotype	Paratypes		Non-types				
	MTD F 20728	MTD F 20739	MTD F 17472	Min	Max	Mean	SD	N
Standard length (mm)	37.6	32.0	33.2	19.5	47.6	32.3	-	25
Percentages of standard length								
Body depth	8.9	8.4	9.3	6.8	10.6	9.0	1.3	25
Predorsal length	43.2	40.4	45.2	38.9	45.4	42.7	2.0	25
Dorsal-fin base	11.1	10.6	11.4	8.6	13.2	10.7	1.6	25
Dorsal-fin to adipose-fin	29.3	29.1	29.2	17.2	29.2	20.7	3.9	25
Preadipose length	69.0	72.8	72.9	65.8	73.8	70.9	2.8	25
Adipose-fin length	11.6	10.6	11.5	18.3	25.5	20.1	2.5	25
Adipose-fin depth	2.4	2.2	2.4	2.4	4.4	3.2	0.7	25
Prepectoral length	21.3	21.3	21.1	16.8	25.1	21.6	2.8	25
Prepelvic length	41.0	37.7	43.4	36.9	42.7	39.7	2.0	25
Preanal length	64.8	60.9	66.8	61.2	70.2	65.8	2.6	25
Pectoral-fin length	12.5	12.5	12.3	12.5	17.3	14.6	1.6	25
Dorsal-fin length	14.4	13.8	15.0	12.7	21.5	17.4	2.8	25
Pelvic-fin length	13.8	13.8	13.9	13.8	16.1	14.5	0.9	25
Anal-fin length	11.2	10.9	11.1	10.0	12.5	11.4	0.8	25
Anal-fin base	14.2	13.8	14.7	15.1	22.1	16.6	2.3	25
Caudal-peduncle length	19.2	17.8	21.0	12.3	18.6	16.3	2.1	25
Caudal-peduncle depth	6.3	5.8	6.9	5.3	8.2	6.3	1.1	25
Upper caudal-fin lobe length	19.2	18.1	19.8	17.6	23.1	20.0	2.3	25
Lower caudal-fin lobe length	23.3	21.3	25.6	19.4	30.6	24.5	3.5	25
Maxillary-barbel length	30.8	27.6	34.0	20.0	36.7	26.9	4.0	25
Outer mental-barbel length	15.4	15.1	15.4	12.8	19.9	16.8	2.4	25
Inner mental-barbel length	12.0	11.9	11.7	8.5	14.1	10.9	2.0	25
Head length	19.4	17.5	20.5	19.9	24.7	22.5	2.0	25
Percentages of head length								
Head width	71.3	77.4	70.1	65.0	80.5	70.8	3.3	25
Head depth	50.7	50.0	50.0	32.3	50.7	38.8	3.6	25
Snout length	33.2	33.4	33.6	33.3	37.5	35.7	1.4	25
Eye diameter	10.5	8.9	11.8	7.8	12.2	9.6	1.7	25
Fleshy interorbital	29.2	30.4	30.5	21.1	27.2	24.8	2.1	25
Mouth gape	40.0	39.1	39.4	37.2	53.7	42.6	3.2	25

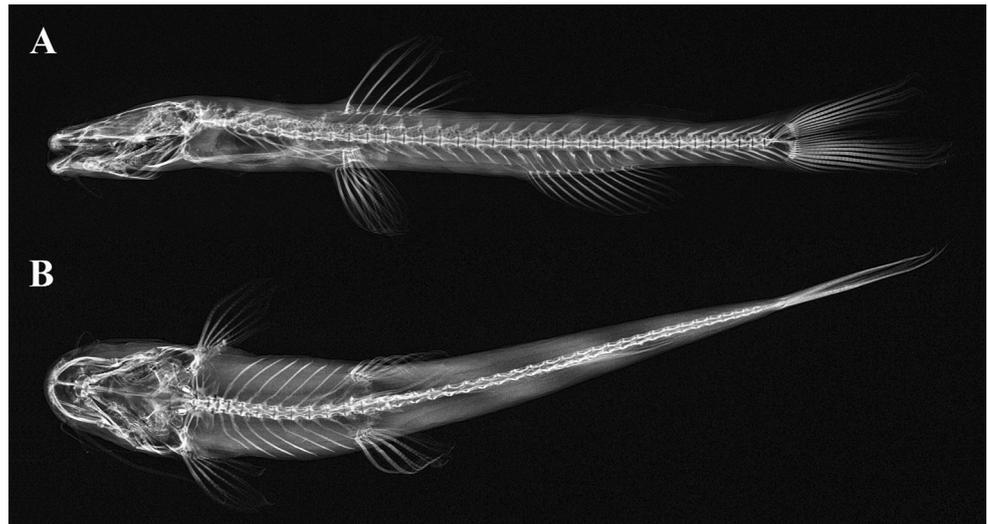


FIGURE 2 | Radiographic images of *Phenacorhamdia nigrolineata*, MTD F 20728, holotype, 37.6 mm SL: **A.** Left lateral and **B.** Ventral views. Photographed by Mario Richter.

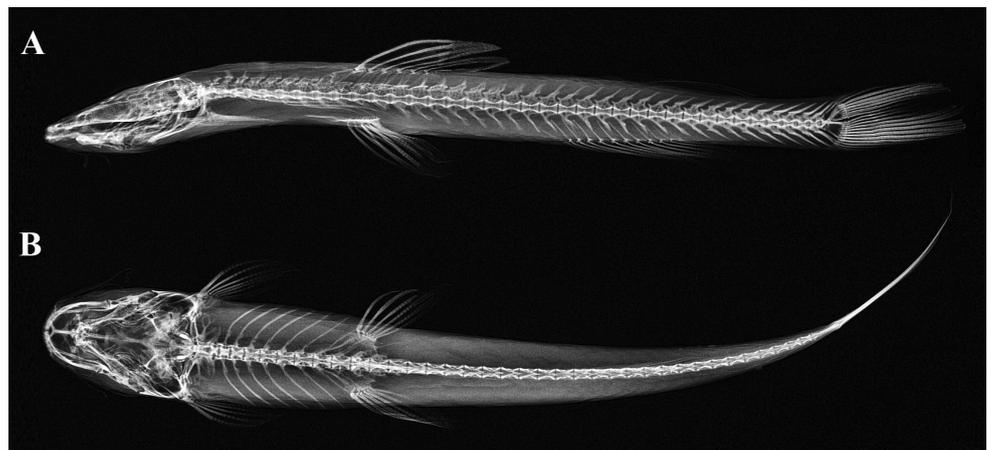


FIGURE 3 | Radiographic images of *Phenacorhamdia nigrolineata*, MTD F 17472, paratype, 33.2 mm SL: **A.** Left lateral and **B.** Ventral views. Photographed by Mario Richter.

Osteological characters. In dorsal and ventral views of mesethmoid, anterior edge bifurcates and forms conspicuous cornua (Fig. 4). In dorsal view, central area of posterior edge constitutes anterior margin of anterior cranial fontanel; laterally, posterior edge articulates with frontals. Posterior to cornuas, bone widens and shows lateral projections approximately equal to cornuas, with a mesial process in anterior portion of posteroventral expansion of mesethmoid. Anterior cranial fontanel is elliptical, about one-third of its length extends through mesethmoid, and extending for about 20% of length of neurocranium. Posterior cranial fontanel elongated, elliptical, and extending about one-third of length of neurocranium.

Premaxillary tooth plate retangular-shaped, its distal border slightly wider and without posterior projection. Elongated dental plate, larger than premaxillary plate. Both premaxillary and dentary plates with conical teeth.

Frontal bone connects anterior with mesethmoid and posteriorly to parieto-supraoccipital, defining lateral and posterior border of posterior cranial fontanelle. Frontal form triangle anteriorly. Epiphyseal bar located slightly posteriorly, aligned with posterolateral process of frontal. Parieto-supraoccipital U-shaped in dorsal view, articulating anteriorly with frontal, sphenotic, pterotic and with epiotic posteriorly, and continues posteriorly as process, elongated and pointed, not bifurcate.

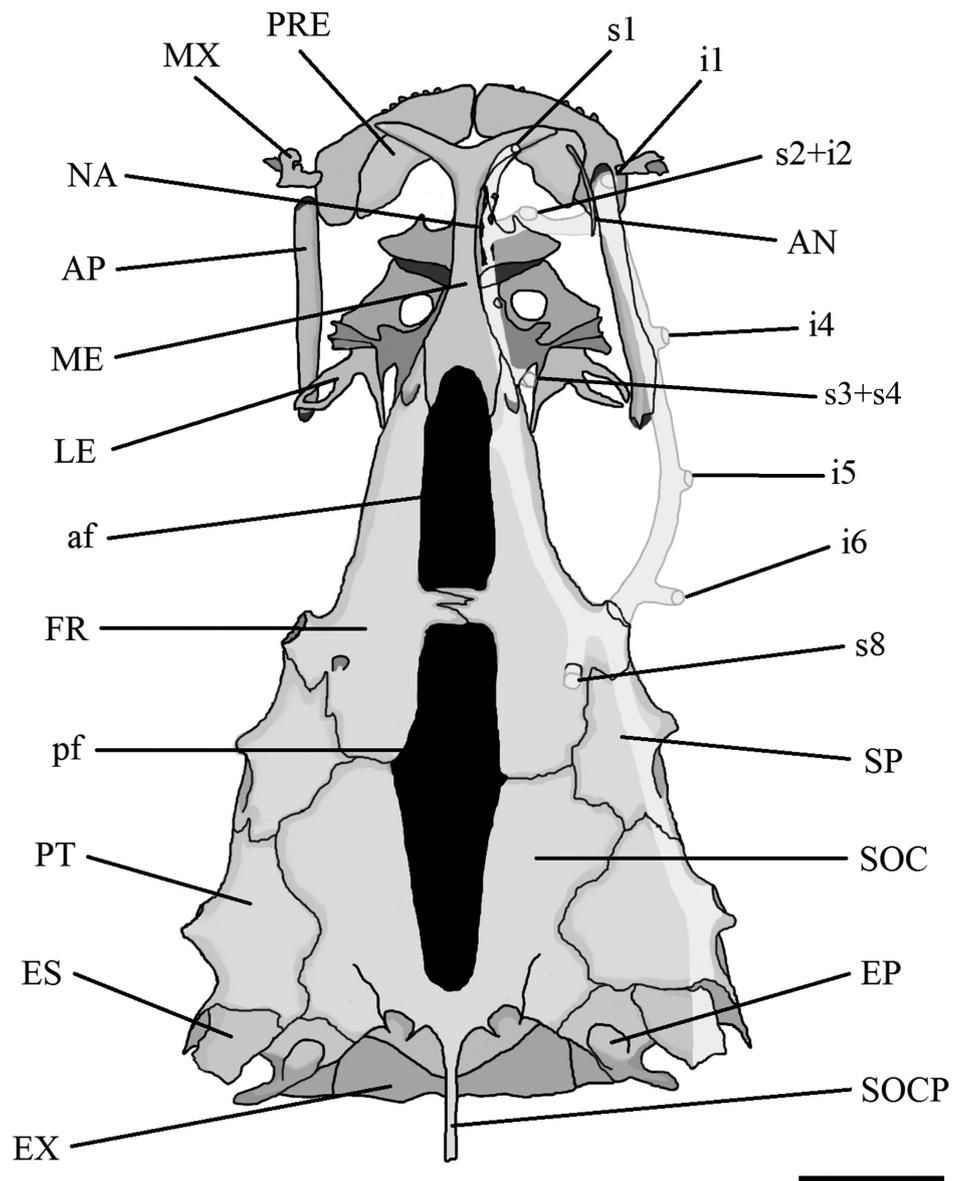


FIGURE 4 | Illustration of the cranium of *Phenacorhamdia nigrolineata*, dorsal view, MCP 53512, 40.0 mm SL. Abbreviations: af, anterior fontanel; AN, antorbital; AP, autopalatine; EP, epioccipital; ES, extrascapula; EX, exoccipital; FR, frontal; i1–6, infraorbital sensory branches 1 to 6; LE, lateral ethmoid; ME, mesethmoid; MX, maxilla; NA, nasal; pf, posterior fontanel; PRE, premaxilla; PT, pterotic; s1–8, supraorbital sensory branches 1 to 8; s2+i2) supraorbital sensory branch 2 + infraorbital sensory branch 2; SP, sphenotic; SOC, supraoccipital; SOCP, supraoccipital process. Scale bars = 1 mm.

Branchial arches with basibranchials 2 and 3 and hypobranchials 1 and 2 ossified. Five ceratobranquials and pharyngobranchials 3 and 4. Four small and conical gill rakers in first ceratobranquial. Seven branchiostegals.

Pre-caudal vertebrae 17*(4) and caudal vertebrae 23(1) or 24*(3), totaling 40(1) or 41*(3) vertebrae. Nine*(4) pleural ribs (Figs. 2–3). First hemal spine at 18th*(4) vertebrae. Neural spines bifids from vertebrae one to 17*(4), including Weberian complex; neural spine of 13th vertebra reduced to small spiniform process. Seven*(4) pterygiophores of dorsal fin, first inserted anterior to neural spine of 13th*(4) vertebra. Anal fin pterygiophores 12(2) or 13*(2); first pterygiophore of anal fin anterior to hemal spine of 22th* vertebrae; posterior pterygiophores extend to 29th* vertebrae. Hemal spine bifid between vertebrae 23*(2), 24(1), or 25(1) to 29*(2), 30(1), or 32(1) associated to anal fin pterygiophores (Figs. 2, 3, 5A). Configuration of neural and hemal spines of the three last caudal vertebrae inclined at 30° in relation to the axis of the vertebral column (Figs. 2, 3, 5B).

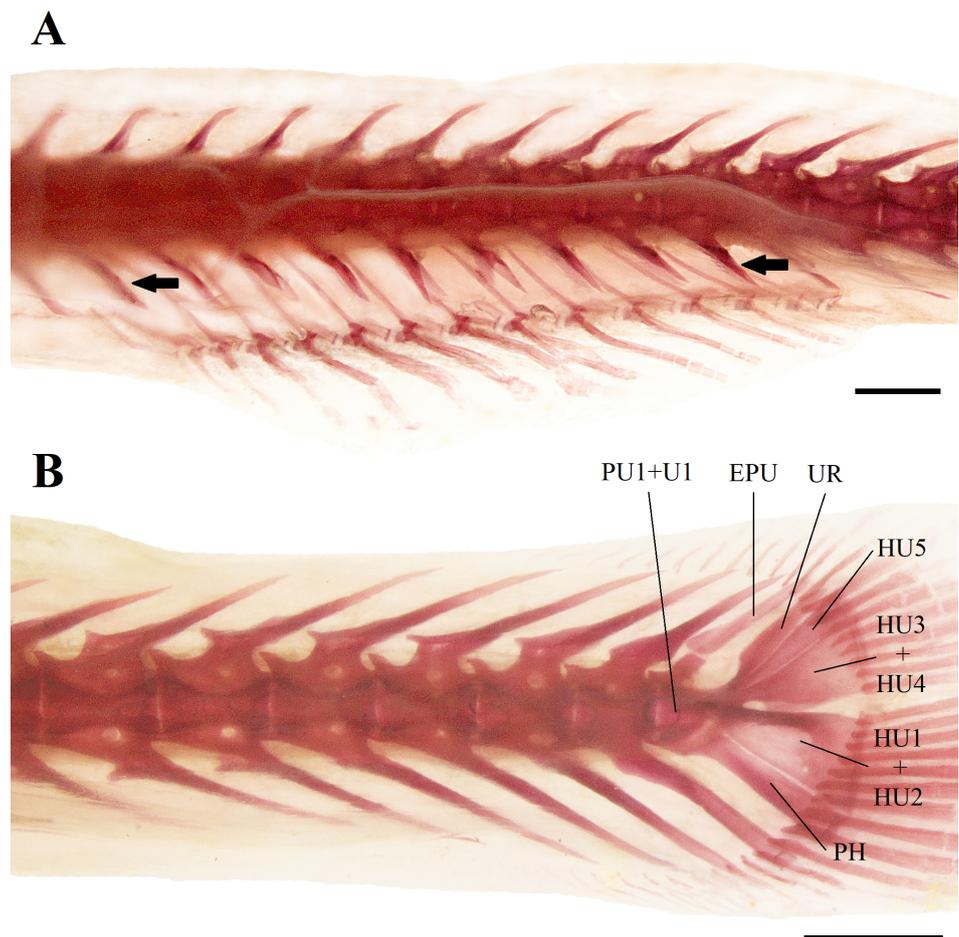


FIGURE 5 | Lateral view of caudal vertebrae of *Phenacorhamdia nigrolineata*, MCP 53512, 40.0 mm SL: **A**. Hemal spines bifids between vertebrae 24 and 32 (arrows) associated with pterygiophores of the anal fin; **B**. Posterior vertebrae and caudal skeleton. Abbreviations: EPU, epural; HU1+HU2, ventral hypural plate formed by coossification of hypurals 1 and 2; HU3+HU4, dorsal hypural plate formed by co-ossification of 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. Scale bars = 1 mm.

Caudal skeleton formed by ossified parhypural, fused to PU1+U1 complex in anterior portion; hypural 1 and 2 co-ossified as plate, fused to PU1+U1 complex centrum previously; hypural 3 and 4 co-ossified as plate, not fused to PU1+U1 complex centrum and without contact to HU1+HU2; hypural 5 ossified and free, not fused to PU1+U1 complex centrum, without contact with HU3+HU4. Uroneural ossified and fused to PU1+U1 complex centrum (Figs. 2, 3, 5B).

Laterosensory system. Head with supraorbital pore s1 medially adjacent to anterior nostril, dorsal to cornuas of mesethmoid; s2+i2 halfway between anterior and posterior nares; s3+s4 very close to edge of posterior nares, dorsal to lateral ethmoid; s6 (in the middle of anterior fontanel) absent; s7 absent; s8 in frontal, posterior to eyes. Infraorbital pore i1 adjacent to anterior nares and opposite to pore s1, next to maxilar; i3 absent; i4 ventral and anterior to ocular border, next to posterior extremity of autopalatine; i5 and i6 pores posterior to eyes (Fig. 4). Preoperculomandibular pores pm1–pm4 located between lower lip and base of mental barbels; pm5 and pm6 just posterior to edge of mouth, and dorsal to base of outer mental barbels, ventral to maxilar; pm7, pm8, pm9 just posterior to base of inner mental barbel. Preopercle with two pores, pm9 and pm10. Postotic pore po1 associated with pm11, forming po1+pm11 complex pore; po2 and po3 dorsally to beginning of opercular membrane. Branch of lateral line originating between po2 and po3, running laterally and posterior to end of head. Conspicuous groove along body, from height of end of pectoral fin retracted to end of caudal peduncle.

Coloration in alcohol. Body homogeneously light brown. Dorsal region of head and occipital region brown. Ventral region pale. Pectoral, dorsal, pelvic, and caudal fin-rays light brown, with inter-radial membranes hyalines. Distal margin of adipose fin hyaline (Figs. 1, 6). Dark groove or shadow along almost entire length of lateral line of the body.

Coloration in life. Body homogeneously dark brown, with ventral region slightly lighter tone. Fin rays dark brown, with inter-radial membranes hyalines. Base of the adipose fin dark brown (Fig. 7).

Geographical distribution. *Phenacorhamdia nigrolineata* is distributed across Brazil, Colombia, and Peru (western Amazon basin), and Guyana. Its northernmost record is found in Branco River basin and the easternmost in the middle Tapajós River basin (Fig. 8).

Comparative morphometry. Principal component analysis showed better separation of groups with components 1 and 2 (Fig. 9). The first component retained the highest change (91.2%), followed by the second component (5.6%). In component 1, the population of *P. boliviana* from the Beni River basin differs from the others (positive loadings, Tab. 2), with the other groups being more similar, while in component 2, the population of *P. unifasciata* from the Upper Paraná River basin is more distant from the other groups (negative loadings, Tab. 2).

The ANOVA test showed that no significant morphometric differences were found between the evaluated populations of *P. nigrolineata* of the Amacayacu, Madeira, Tapajós, and Ucayali River basins with the variables analyzed, indicating that these populations



FIGURE 6 | *Phenacorhamdia nigrolineata*. **A.** MTD F 17472, paratype, 33.2 mm SL, Peru, Ucayali departament, Tierra Roja, Ucayali River basin (Photographed by Mario Richter). **B.** IAvH-P 10948, 45.0 mm SL, Colombia, Amazonas River basin, Leticia, PNN Amacayacu (Photographed by Juan Gabriel A. Garzón). **C.** MCP 53512, 40.0 mm SL, Brazil, Tapajós River basin, Itapacurazinho river. **D.** AUM 36000, 24.8 mm SL, Guyana, Rupununi River, tributary of the Branco River basin (Photographed by Jonathan Armbruster). Scale bars = 1 cm.

FIGURE 7 | Unpreserved aquarium specimen supposedly of *Phenacorhamdia nigrolineata* (approximately 60 mm SL) from Madre de Dios River basin, Peru, showing its color in life. Photographed by Steven Grant.



may be the same species. However, the same test revealed that the populations of *P. boliviana* from the Beni River basin and *P. unifasciata* from the Upper Paraná River basin are significantly different ($F = 2.719$, $df = 55.98$, $p = 0.02867$). When subjected to Dunn's post hoc test, populations of *P. boliviana* from the Beni River basin showed greater differentiation with populations of *P. nigrolineata* than with *P. unifasciata* from the Upper Paraná River basin ($p < 0.05$).

Conservation status. The type locality of the *P. nigrolineata*, which has suffered from deforestation of native forest cover, mining, and road constructions (Cañas, 2019:147), is outside the area of the nearest national parks such as Cordillera Azul, Sierra del Divisor, Reserva Nacional Tambopata, and El Sira in Peru. The species, hitherto known as endemic to a single location in western Peru (Zarske, 1998), is broadly distributed across the western Amazon basin in relatively little disturbed areas, and it is considerably abundant in some places. *Phenacorhamdia nigrolineata* should be categorized as Least Concern (LC), according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2022).

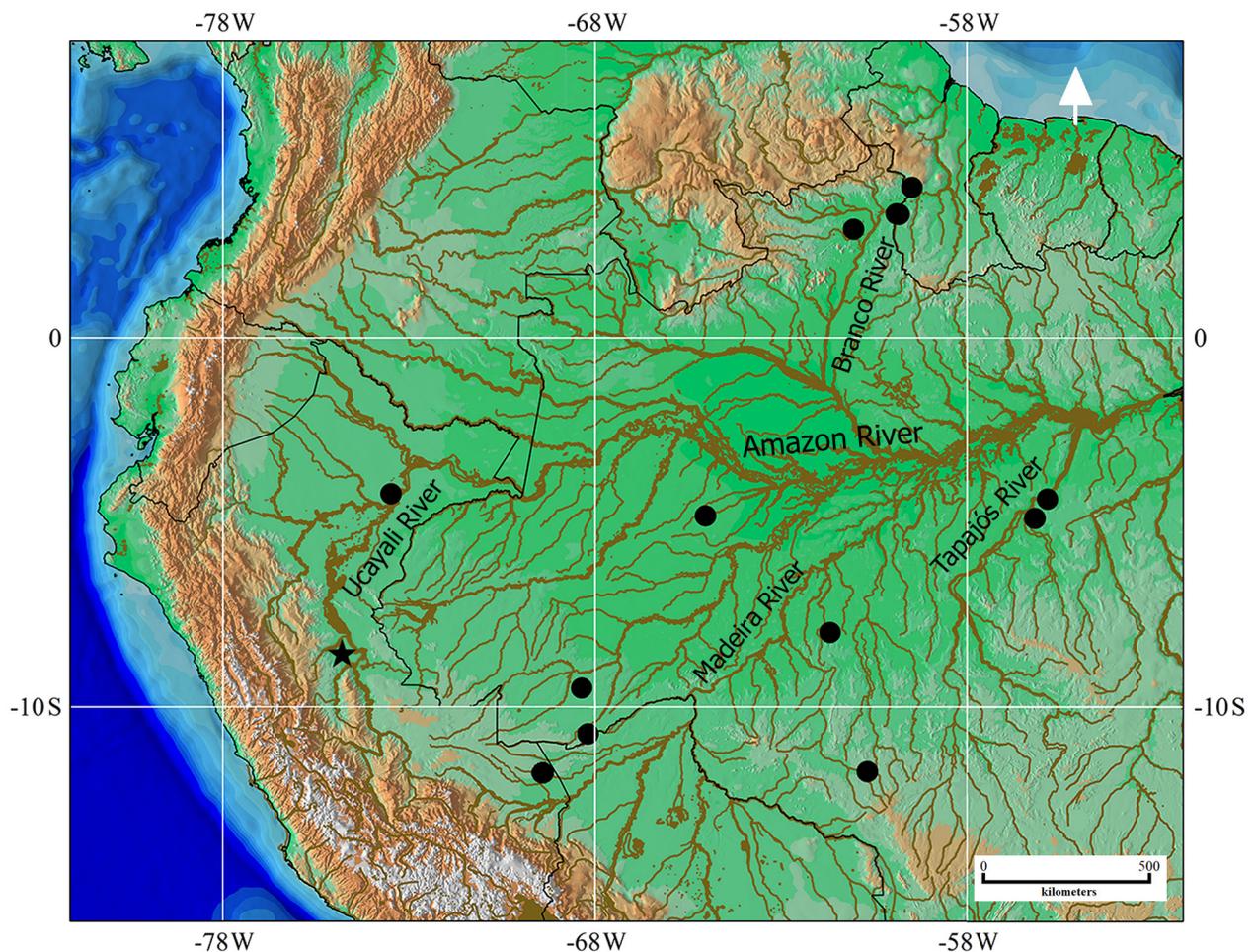


FIGURE 8 | Geographical distribution of *Phenacorhamdia nigrolineata* in the western Amazon basin. Black star represents the type locality in Peru; black dots represent remaining known localities. One dot may represent more than one lot.

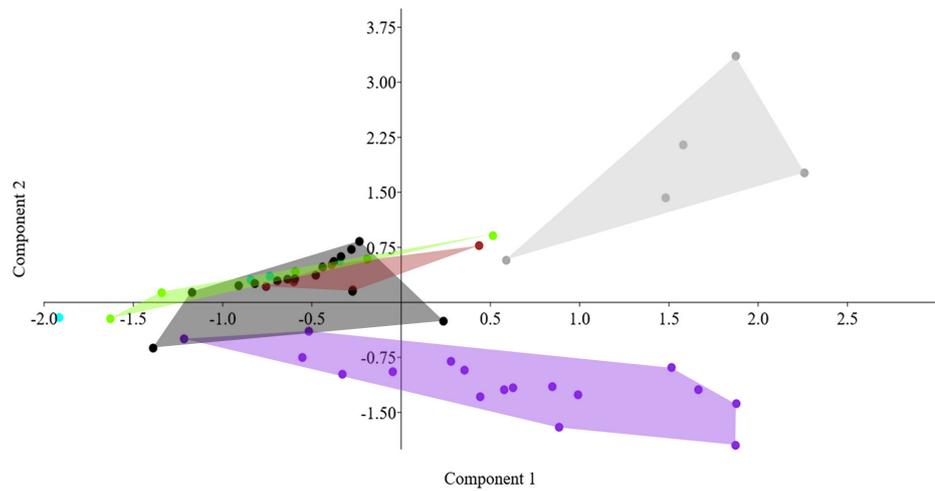


FIGURE 9 | Dispersion of individual scores of first two principal component analysis of four populations of *Phenacorhamdia nigrolineata* (blue dots = Ucayali River basin; brown dots = Amayacu River basin; green dots = Madeira River basin; black dots = Tapajós River basin), *P. boliviana* (gray dots = Beni River basin), and *P. unifasciata* (purple dots = Upper Paraná River basin).

TABLE 2 | Variables loadings on first two principal components axis of combined samples of populations of *Phenacorhamdia nigrolineata*, *P. boliviana*, and *P. unifasciata*.

	PC 1	PC 2
Standard length (mm)	0.84244	-0.21118
Body depth	0.089675	-0.0061115
Prepectoral length	0.14127	0.12426
Adipose-fin length	0.22804	-0.26398
Adipose-fin depth	0.034949	0.0015475
Pectoral fin length	0.11747	0.17017
Dorsal fin length	0.10038	0.15841
Pelvic fin length	0.095642	0.12949
Anal fin length	0.10331	0.055195
Anal-fin base	0.10076	-0.030776
Caudal-peduncle depth	0.067091	-0.015436
Upper caudal-fin lobe length	0.17855	0.10836
Lower caudal-fin lobe length	0.23735	-0.033882
Maxillary-barbel length	0.14556	0.85182
Outer mental-barbel length	0.093924	0.19238
Inner mental-barbel length	0.089318	0.11619
Head width	0.096252	0.050351
Head depth	0.075541	0.023925
Snout length	0.063192	0.035825
Mouth gape	0.067426	-0.033748
Fleshy interorbital	0.031838	0.025651
Eigenvalue	182.78	11.3929
% variance	91.2	5.6

Ecological notes. Two specimens supposedly belonging to *P. nigrolineata* were photographed in Peru in April 2017. Both were collected in shallow streams, cloudy and slow, and are not preserved (Steven Grant, 2021, pers. comm.). The first, measuring approximately 10 cm SL was found in a small tributary on the Las Piedras River (12°11'35.7"S 69°09'48.4"W) and the second, approximately 6 cm SL, was found in a tributary of the Gamitana River, both tributaries in the Madre de Dios River basin (12°16'19.2"S 69°04'37.9"W). The adult specimens in aquarium (Fig. 7) have coloration pattern in life and many characteristics compatible with the species *P. nigrolineata* (Zarske, 1998: fig. 2), although they are larger than the other specimens analyzed up to 47.6 mm SL, including the holotype.

Material examined. Peru: Ucayali River basin: MTD F 20728, holotype (photo and radiograph), 37.6 mm SL, Ucayali departament, Tierra Roja, Ucayali River, in the road between Campoverde and Tournavista, 08°51'50.6"S 74°48'05.8"W. MTD F 17472, 1 paratype, 33.2 mm SL (photo and radiograph), MTD F 20739, 1 paratype, 32.0 mm SL, same data of the holotype. **Amazonas River basin:** ANSP 179013, 1, 19.5 mm SL, Loreto, Itaya River, tributary of the Amazonas River, under the bridge in the highway Iquitos–Nauta, about 25 miles southwest of Iquitos, 04°13'31.2"S 73°28'57.4"W. **Brazil: Purus River basin:** MCP 35986, 1, 22.3 mm SL, Acre, Sena Madureira, Antomari River, between Branco and Sena Madureira Rivers, in the BR-364, 09°29'27"S 68°21'29"W. **Madeira River basin:** LIRP 10035, 2, 34.9–39.6 mm SL, Rondônia, São Miguel do Guaporé, Piranhas stream, tributary of the São Miguel River, 11°45'12.5"S 60°40'51.8"W. MCP 35989, 1, 24.8 mm SL, Acre, Xapuri, Iná River, tributary of the Xipamanu River, at the rear of Uberaba farm, about 6 km from BR-317, 10°44'13.0"S 68°11'16.0"W. MNRJ 15691, 1, 43.1 mm SL (x-ray), Rondônia, Ouro Preto do Oeste, Urupá River, tributary of the Machado River, 10°46'02.2"S 62°07'07.8"W. MZUSP 121769, 5, 28.3–47.6 mm SL, Rondônia, Manicoré, second stream after the restaurant of the km 150 in the Transamazônica highway, BR-230, towards Apuí, 07°59'00"S 61°41'00"W. **Tapajós River basin:** MCP 53512, 14 (1 c&s) 24.6–45.8 mm SL, Pará, Itaituba, Itapacurazinho River, Transamazônica road, 04°22'12.9"S 55°50'14.9"W. MCP 53473, 5, 25.2–42.9 mm SL, Pará, Trairão, tributary of the Taburari River, BR-163, between Trairão and Caracol, 04°53'38.6"S 56°10'43.8"W. MPEG 28510, 1, 24.2 mm SL, Pará, Jacareacanga, Vila Rato, 05°13'49.8"S 56°55'22.8"W. **Amazonas River basin:** MPEG 11750, 1, 35.3 mm SL, Amazonas, Coari, tributary of the Tartaruga River, tributary of the Urucu River, 04°53'55.3"S 65°19'18.8"W. MPEG 12195, 2, 32.6–35.7 mm SL, Amazonas, Coari, IMT stream, Solimões River, 04°49'28.92"S 65°01'50.16"W. **Solimões River basin:** MPEG 12331, 2, 25.5–28.4 mm SL, Amazonas, Coari, IMT stream, 04°49'38.6"S 65°01'56.6"W. **Colombia: Amazon River basin:** IAvH-P 10948, 1 of 5, 45.0 mm SL, Amazonas, Leticia, PNN Amacayacu, 03°00'47.6"S 70°00'01.9"W. **Guyana: Branco River basin:** AUM 36000, 24.8 mm SL, Rupununi River, 03°56'02.0"N 59°16'21.1"W.

DISCUSSION

Phenacorhamdia nigrolineata is known from its type locality in Tierra Roja, near Pucallpa, in the Beni and Madre de Dios River basins, of southeastern Peru, in the Napo–Pastaza (NP) drainages in Ecuador, and from the Amazon River basin (Amz), in southern Colombia (Barriga, 2012; Dagosta, de Pinna, 2019; Zarske, 1998). Maldonado–Ocampo *et al.* (2008:201) and DoNascimento *et al.* (2017:91) recorded *P. nigrolineata* for Amazon River basin (Amz) (voucher IAvH-P 10948, Fig. 6B). Barriga (2012:114) reported the occurrence of this species to the Napo–Pastaza (NP) River drainage, but it was not possible to analyze material of the species mentioned in Ecuador (which does not have a known voucher number), although we consider this record to be very likely due to its proximity to the type locality. In addition to the already known occurrence in the Ucayali River basin, Dagosta, de Pinna (2019:118) also reported the presence of *P. nigrolineata* for the Purus and Beni–Madre de Dios basins.

The species now has its geographic distribution greatly expanded to include much of the western portion of the Amazon basin, including Brazil. Its easternmost known record is in the Tapajós River basin (Fig. 6C) and the southernmost in the Guaporé River basin (Fig. 8). The holotype of *P. nigrolineata* shares with the specimen of the Tapajós River the presence of an anterior process at the base of the neural spine of the last caudal vertebrae, but not the presence of a similar process at the base of the hemal spines (Figs. 2A, 5B). However, this character seems to be variable in this species, since this process at the base of the hemal spines of the last caudal vertebrae can be found in the paratype (MTD F 17472), collected at the same type-locality (Fig. 3A). Unfortunately, it was not possible to obtain morphometric data from the material of *Phenacorhamdia* from Branco River basin (Ferreira *et al.*, 2007:157, photo) in order to confirm its identity as *P. nigrolineata*.

In the original description of *Phenacorhamdia nigrolineata*, Zarske (1998) drew attention to what he considered to be a narrow dark line running longitudinally along the lateral line. The presence of this feature in its blackish-colored body, considered unique in *Phenacorhamdia*, gave rise to the etymology of the species [*nigro* (Latin): black; *lineata* (Latin): line, with a dark line]. This dark brown color and the “dark line” in the body are present in specimens from the analyzed lots. Together with the other diagnostic characters, they justify the identification of the material as *P. nigrolineata* and its wide distribution throughout the western Amazon basin.

Zarske (1998) made a brief discussion about this “dark line” along the body, comparing it with the stripe pattern still uncommon for the *Phenacorhamdia*, present only in *P. unifasciata*, a species of very elongated body endemic of the São Bartolomeu River basin, in the Federal District region, State of Goiás, Brazil. The condition present in this species is a true, wide band along the dorsal half of the body (not exactly above the lateral line), running from the snout to the end of the caudal peduncle, although there is still a darker groove along the side of the body (Britski, 1993:49, fig. 1). A similar condition, that is, a well-defined stripe along the body, is also present in many species of the genera *Brachyrhamdia* Myers, 1927, *Imparfinis* Eigenmann & Norris, 1900, *Pimelodella* Eigenmann & Eigenmann, 1888, *Rhamdia* Bleeker, 1858, and *Rhamdella* Eigenmann & Eigenmann, 1888.

This brown “dark line” in *Phenacorhamdia nigrolineata* is not a true pigmented line, but instead, a dark groove or shadow where the lateral line of the body is located, separating

the epaxial and hypaxial muscles. This pattern appears to occur in *P. macarenensis*, the type species of the genus with color “rather dark and faintly mottled brown, with the lower parts somewhat paler”, according to the original description and drawing in Dahl (1961:505, 507). A similar condition occurs in some *Phenacorhamdia* species that have a furrow, easily visualized in alcohol, as in *P. tenuis* and *Phenacorhamdia* sp. n. “Juruená”. In *P. tenebrosa* and in the dark brown species *P. roxoi* this dark groove occurs in some small specimens (Silva, 2020:276, figs. 4a–f), but not in larger ones [Silva, 2020: fig. 1, middle photo (MZUSP 125819, holotype) and topotypes of *P. tenebrosa* (MZUSP 22940 and MNRJ 21499)]. This feature is common in other species of *Phenacorhamdia* and heptapterids due to the fixation process. Therefore, we conclude that the dark brown line in *P. nigrolineata* is not a valid character to distinguish it from other congeners.

Other characteristics cited by Zarske (1998) concern the length of the maxillary barbel in *P. nigrolineata*, reaching the end of the pectoral fin adpressed to body. The length of maxillary barbel is shared by *P. boliviana* (type locality in Huachi, Bolivia), a species relatively closer geographically to the Peruvian species. However, the latter features a color pattern that is grayish in life, densely covered by spots or melanophores (AUM 51212), unlike *P. nigrolineata* (Fig. 7). On the other hand, in *P. somnians* and *P. unifasciata* the maxillary barbel may or may not reach the origin of the pectoral fin, while in *P. macarenensis*, known from just a single specimen in Caño Lozada, near the Sierra de La Macarena, Colombia, the maxillary barbel reaches the origin of the pelvic fin. Furthermore, another character that differentiates *P. nigrolineata* is its long anal fin with 13 (iv+9) rays and eight pleural ribs, while *P. somnians* has only 10 (iv+6) rays and nine pleural ribs. In his count, Zarske (1998) described *P. nigrolineata* as having “Vertebrae: (4) + 34 to 35 = 38 to 39”, although he did not clarify the counting methodology used for the Weber complex and the compound caudal centrum counted as one element. Thus, we arrived at the count of 40 or 41 total vertebrae [(5) + 34 to 35 + (1)] for the holotype (Fig. 2) and the paratype of the species (Fig. 3).

Phenacorhamdia nigrolineata can be included in the supposed monophyletic clade called “short-snouted” group, formed by *P. provenzanoi*, *P. tenuis*, and *Phenacorhamdia* sp. n. A *aff. P. tenuis* (*sensu* Bockmann, 1998), species with snout lengths between 31.5–34.3% HL. This hypothesis is supported by the configuration of the neural and hemal spines of the posterior vertebrae in relation to the vertebral column inclined in 30° or less (Bockmann, 1998:367), which is present in *P. nigrolineata* (Figs. 2A, 3B, 5B). On the other hand, the monophyletic “long-snouted” group would be formed by the species *P. anisura*, *P. hoehnei*, *P. macarenensis*, *P. somnians*, *P. tenebrosa*, and *P. unifasciata* (Bockmann, 1998:368), in addition to *P. taphorni* and *P. provenzanoi*. The inclusion of these species in this group is based on the supposed presence of nine synapomorphies detailed by DoNascimento, Milani (2008:175), species which have the snout length between 34.3–40.0% HL.

Through the analysis of the x-ray of the type and non-type specimens of *P. boliviana*, the configuration of the neural and hemal spines of the last caudal vertebrae of this species is at an angle less than 30° and the range of the snout length not overlap that of *P. nigrolineata* (37.8–39.3% in *P. boliviana* vs. 33.2–33.6% HL in *P. nigrolineata*). Thus, *P. boliviana* cannot be assigned to any of the groups mentioned, since it was not possible to analyze in detail the nine synapomorphies listed by Bockmann (1998:335), which still needs to be corroborated through a broader phylogenetic analysis of *Phenacorhamdia*, which is already in progress.

Comparative material examined. *Phenacorhamdia boliviana*: **Bolivia**: CAS 63632, 47.0 mm SL (photo and x-ray of the syntype). AUM 51212, 1, not measured (photo). MZUSP 27813, 5, 45.2–66.4 mm SL. **Peru**: MUSM 7787, 1, 47.0 mm SL. *Phenacorhamdia hoehnei*: **Brazil**: MNRJ 787, 29.7 mm SL (x-ray of the lectotype). ZUFMS (photo), material uncatalogued and not measured. *Phenacorhamdia roxoi*: **Brazil**: MZUSP 125819 (photo of the holotype), 63.8 mm SL. MZUEL 20009, 58.0 mm SL. MZUEL 10405, 2, 48.8–51.2 mm SL. *Phenacorhamdia somnians*: **Brazil**: BMNH 1971.7.29.4, 55.0 mm SL (photos and x-ray of the holotype). *Phenacorhamdia tenebrosa*: MZUSP 22940, topotype, 46.3 mm SL. *Phenacorhamdia tenuis*: **Guyana**: RMNH 29422 (photos of holotype), 71.0 mm SL. RMNH 29288, 45.3 mm SL (photos and x-ray of the paratype). *Phenacorhamdia unifasciata*: **Brazil**: MZUSP 36691, holotype, 61.5 mm SL. MZUSP 25051, 1 paratype, 49.30 mm SL. MZUSP 36692, paratype, 45.5 mm SL. MZUSP 36693, 1 paratype, 48.4 mm SL. MZUSP 36694, paratype, 53.9 mm SL. MZUSP 36695, 1 paratype, 27.4 mm SL. MZUSP 36696, paratype, 41.8 mm SL. MZUSP 36697, 1 paratype, 38.7 mm SL. MZUSP 36698, paratype, 49.4 mm SL. MZUSP 36700, 2 paratypes, 36.5–54.4 mm SL. *Phenacorhamdia* sp. n. “Jurueña”: **Brazil**: MZUEL 7881, 6, 23.3–58.5 mm SL. MZUEL 9027, 1, 28.8 mm SL. MZUEL 9117, 7, 26.2–45.0 mm SL. MNRJ 29551, 5 of 11, 25.0–28.5 mm SL. *Phenacorhamdia* sp.: **Brazil**: LIRP 10921, 6, 20.6–28.6 mm SL. LIRP 10922, 3, 23.4–26.9 mm SL. LIRP 10923, 7, 22.5–38.8 mm SL. **Brazil**: *Pimelodella cristata*: MPEG 22484, 1, 72.2 mm SL. *Pimelodella humeralis*: MPEG 15712, 3, not measured. MPEG 15744, 6, not measured. **Colombia**: *Phenacorhamdia anisura*, IAvH (photos), material uncatalogued and not measured.

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AUTHORS' CONTRIBUTION

Íthalo da Silva Castro: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing.

Wolmar Benjamin Wosiacki: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing.

ETHICAL STATEMENT

Not applicable.

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The author declares no competing interests.

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