A taxonomic review of the Neotropical electric fish *Rhamphichthys* (Gymnotiformes: Rhamphichthyidae)

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The species diversity and taxonomy of *Rhamphichthys* is reviewed and seven species are considered valid: *Rhamphichthys apurensis* from the Orinoco and Cuyuni river basins; *R. drepanium* from the Amazon and Orinoco river basins; *R. hahni* from the Paraná-Paraguay River system; *R. heleios* and *R. lineatus* from the Amazon River basin; *R. pantherinus* from the upper Orinoco, Essequibo, Amazon and coastal rivers of North Brazil, and *R. rostratus* from the upper Orinoco, Amazon and coastal rivers of Guianas. Based on the examination of specimens from nominal species, from across their geographic ranges, including specimen types, the previous synonymization of four species (*R. blochii*, *R. reinhardtii*, *R. schomburgki*, and *R. schneideri*) with *R. rostratus*, and *R. marmoratus* with *R. pantherinus* is confirmed. Two other nominal species, *R. atlanticus* and *R. longior*, are proposed as junior synonyms of *R. pantherinus*. Species are redescribed and diagnosed based on color pattern, morphometric, meristic, and internal anatomy characters. Distribution maps and an identification key based on the examination of a comprehensive list of materials are also provided.

**Keywords:** Identification key, Ostariophysi, Species diversity, Taxonomy.

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A diversidade de espécies de *Rhamphichthys* é revisada e sete espécies são consideradas válidas: *Rhamphichthys apurensis* das bacias dos rios Orinoco e Cuyuni; *R. drepanium* das bacias dos rios Orinoco e Amazonas; *R. hahni* do sistema do rio Paraná-Paraguai; *R. heleios* e *R. lineatus* da bacia do rio Amazonas; *R. pantherinus* do alto rio Orinoco, Amazonas, Essequibo e rios costeiros do norte do Brasil; e *R. rostratus* do alto rio Orinoco, Amazonas e rios costeiros das Guianas. Baseado na revisão de material das espécies nominais cobrindo toda a distribuição geográfica, incluindo os espécimes tipos, confirma a sinonímia prévia de quatro espécies nominais (*R. blochii*, *R. reinhardti*, *R. schomburgki*, and *R. schneideri*) com *R. rostratus* e de *R. marmoratus* com *R. pantherinus*. Duas outras espécies nominais, *R. atlanticus* e *R. longior*, são propostas como sinonímia júnior de *R. pantherinus*. As espécies são redescritas e diagnosticadas baseando-se no padrão de colorido, morfometria, contagens e caracteres de anatomia interna. Mapas de distribuição e uma chave de identificação baseados em uma extensa revisão de material são fornecidos.

**Palavras-chave:** Chave de identificação, Diversidade de espécies, Ostariophysi, Taxonomia.

**INTRODUCTION**

The Rhamphichthyidae (Regan, 1911) is a monophyletic group of gymnnotiform electric fishes represented by five genera and 28 species (Carvalho et al., 2011; Carvalho, Albert, 2015; Tagliacollo et al., 2016; Ferraris et al., 2017; Fricke et al., 2022). Until recently (Albert, 2001; Ferraris, 2003; Carvalho, Albert, 2011), Rhamphichthyidae was restricted to three long–snouted genera *Rhamphichthys* Müller & Troschel, 1846, *Gymnorhamphichthys* Ellis, 1912 and the monotypic *Iracema* Triques, 1996, and more recently expanded to encompass the short-snouted genera *Hypopogus* Hoedman, 1962 and *Steatogenys* Boulenger, 1898, formerly placed in the family Hypopomidae (Tagliacollo et al., 2016; Ferraris et al., 2017; Alda et al., 2018).

Within the family Rhamphichthyidae, species of the subfamily Rhamphichthyinae are readily characterized by a long and tubular snout, and small oral jaws entirely lacking teeth, which they use in grasp–suction feeding on the substrates of river and lake bottoms, consuming a variety of small-bodied benthic and infaunal animals (Marrero, Winemiller, 1993; Winemiller, Adite, 1997). This group inhabits most water bodies in lowland tropical South America east of the Andes, ranging from the La Plata estuary in Argentina to the Orinoco basin of Venezuela (Ellis, 1913; Ferraris, 2003). Many *Rhamphichthys* grow to a large body size, sometimes reaching a meter of total length (Santos et al., 1984), thereby possessing one of the largest body length of gymnnotiform, together with some species of *Sternopygus* Müller & Troschel, 1846 and *Electrophorus* Gill, 1864 (Ellis, 1913; Albert, 2003; de Santana et al., 2019).

*Rhamphichthys* includes nine species (Ferraris et al., 2017; Fricke et al., 2022), which together extend throughout the entire geographic range of the family Rhamphichthyidae. *Rhamphichthys* inhabit deep (5–100 m) river channels or marginal habitats such as
oxbow lakes, being collected in relative abundance by bottom trawling in the Amazon and Orinoco basins (Cox Fernandes et al., 2004; Albert, Crampton, 2005; Crampton, Albert, 2006; Kim, Albert, 2018). Juveniles of some species exhibit an ontogenetic shift in habitats, moving from smaller rivers or marginal lakes to larger rivers (Crampton, 1998). There are reports of Rhamphichthys being consumed as food by some indigenous communities (Müller, Troschel, 1848; Ellis, 1913), however, they are not generally an important resource in most Amazonian fisheries; they are infrequently found in the fish markets (Santos et al., 1984) and are rarely encountered in the aquarium trade.

The name Rhamphichthys appeared for the first time in the literature as “Ramphichthys” in a footnote of Müller, Troschel (1846:194) lacking an “h,” a species description, or a justification (Albert, Campos-da-Paz, 1998; Ferraris, 2003 present as Müller, Troschel, 1844). The authorship and date of the genus Rhamphichthys is either credited to Müller, Troschel (1846) or to Müller, Troschel (1848) where it appeared as a new genus, with the correct spelling and a description (Albert, Campos-da-Paz, 1998; possibly M. T., 1949 according to Fricke et al., 2022). Rhamphichthys was described based on its toothless mouth, head and body laterally compressed, narrow gill slits, anus positioned before the eyes, and body completely scaled except for the head (Müller, Troschel, 1848). By monotypy the type-species was Gymnotus rostratus Linnaeus, 1766, one of the earliest gymnotiform to be formally described. Linnaeus (1766) description was based on Seba (1759; plate 32; Fig. 1A), from material probably originating from somewhere near Paramaribo in Suriname (Albert, Crampton, 2003; Campos-da-Paz, 2003). The known diversity of Rhamphichthys was greatly increased by the additions of Castelnau (1855) and Kaup (1856). Castelnau described three species: R. marmoratus Castelnau, 1855 (Fig. 1B) from the Araguaia River in Brazil; and R. pantherinus Castelnau, 1855 (Fig. 1D), and R. lineatus Castelnau, 1855, both from a lake on the Ucayali River in Peru. Castelnau’s species were diagnosed based mostly on color pattern differences and snout length. Kaup (1856) did the most comprehensive review to date of Rhamphichthys. He described six new species (two of this nominal species are currently placed in the monotypic genus Hypopomus Gill, 1864), examining material mostly from Guyana and French Guiana. Kaup’s diagnoses were based mostly on snout length, color pattern and the relative position of the anus. Several authors later criticized this last character due to ontogenetic variation (e.g., Günther, 1870).

After this early period of discovery, there was a trend towards synonymization in the genus. Steindachner (1868) considered only three species (R. lineatus, R. pantherinus, and R. marmoratus) of the genus to be valid. Günther (1870) regarded three species to be valid, and proposed R. marmoratus to be a junior synonym of R. pantherinus, which is interpreted as the principle of first reviewer by Ferraris et al. (2017). Later this decision was reversed by Eigenmann, Ward (1905) who considered R. marmoratus to be the senior synonym. Eigenmann, Ward (1905) and Ihering (1907) claimed that the many named species were simply different forms of a single highly variable Rhamphichthys rostratus. Other authors supported this interpretation of low species diversity for the group, with high variation within species. Lahille (1910) proposed that the Rhamphichthys inhabiting the La Plata basin was very similar to the species in the Amazon and Guianas. He considered that the genus comprised a single geographically widespread and phenotypically variable species. Ellis (1913) concurred, synonymizing all species of Rhamphichthys known at that date with the type–species R. rostratus.
Throughout much of the 20th Century there was no consensus regarding the diversity represented by *Rhamphichthys*, and the taxonomy of this genus remained poorly resolved. Adding to this confusion, later, two species of *Rhamphichthys* were described in other gymnotiform genera. *Sternarchorhamphus hahni* Meinken, 1937 based on superficial resemblance was originally described as a long-snouted apteronotid based on a single specimen from the Paraná River in Corrientes, Argentina. Campos-da-Paz, Paepke (1994) later transferred *Sternarchorhamphus hahni* to *Rhamphichthys*, but the authors expressed doubt about the validity of this species. Another *Rhamphichthys* species described in a different genus was *Gymnorhamphichthys apurensis* Fernández-Yépez, 1968, from a tributary of the Apure River in Venezuela. The generic allocation of *G. apurensis* was questioned by Nijssen et al. (1976) and Schwassmann (1989), who considered it an immature specimen of *Rhamphichthys*. Mago-Leccia (1994:41) considered *Rhamphichthys apurensis* a valid and probably endemic species of deep river waters in the Orinoco basin.

In his comprehensive review of Gymnotiformes, Mago-Leccia (1994) recognized seven valid species of *Rhamphichthys*, some however, of doubtful taxonomic status. Triques (1994, 1999) reviewed the diversity of Rhamphichthyidae, proposing three new species of *Rhamphichthys* in 1999 (*R. atlanticus*, *R. drepanium*, and *R. longior*), including eight valid species (Ferraris, 2003; Crampton, Albert, 2006; Crampton, 2011). The most recent species addition to *Rhamphichthys* was the description of *Rhamphichthys heleios* Carvalho & Albert, 2015 from the Amazon basin with the authors commenting on the species diversity of that basin and assigning *R. longior* as a junior synonym of *R. marmoratus* (Carvalho, Albert, 2015; Ferraris et al., 2017).
Rhamphichthys was first included in a phylogenetic analysis by Triques (1993), who found it to be the sister of Gymnorhamphichthys Ellis (1912). Albert, Campos-da-Paz (1998) and Albert (2001) diagnosed Rhamphichthys from other Gymnotiformes by the presence of four exclusive synapomorphies. In an analysis based on external morphology, Triques (2005a,b) proposed seven putative synapomorphies for Rhamphichthys, including several already proposed by previous studies within Gymnotiformes (Mago-Leccia, 1994; Albert, 2001). Currently, Rhamphichthys is regarded as a monophyletic group, and a sister clade to the monotypic Irracema (Carvalho, Albert, 2011; Tagliacollo et al., 2016).

Despite this extensive history of taxonomic work, the species diversity within Rhamphichthys remains poorly known and in need of revision (Campos-da-Paz, Paepke, 1994; Albert, Crampton, 2005). The goal of this paper is to review the diversity within this genus, document species distributions, review previously suggested synonyms, and propose new junior synonyms.

MATERIAL AND METHODS

Measurements were made to the nearest 0.1 mm with digital calipers or with rulers for larger specimens. The measurements follow those proposed by Carvalho et al. (2011) and Carvalho, Albert, (2011) except for the use of length to the end of anal fin (LEA) instead of standard length (SL; Mago-Leccia, 1976; Crampton et al., 2004). Morphometric data were expressed as percent of length to end of anal fin, except proportions of the head, which are expressed as percent of head length (HL). Osteological terminology follows Albert (2001). Damaged or incompletely regenerated specimens were not included in morphometric analyses, except for R. lineatus where individuals with almost complete regeneration were included due to a lack of fully intact specimens. The number of precaudal vertebrae includes the four of the Weberian apparatus. Caudal vertebrae were counted from the first vertebrae with a hemal spine to the last vertebrae in which the hemal spine is associated with an anal fin pterygiophore (Schwassmann, 1989; Lundberg, 2005). Numbers of vertebrae and displaced hemal spines were counted from radiographs and cleared and stained specimens prepared according to the method of Taylor, Van Dyke (1985). Most pictures were taken in a specially designed thin aquarium, following techniques explained by Sabaj-Pérez (2009), using a Panasonic Lumix DMC-FZ50 or a Nikon D90 digital SLR cameras. Drawings were made using a camera lucida attached to an Olympus SZX12 stereomicroscope. Material examined were listed into Freshwater Ecoregions of the World (FEOW) as proposed by Abell et al. (2008) located with the aid of the color scheme on the Google Earth® available at FEOW web site (feow.org). Material examined coordinates were presented in degrees minutes and seconds, typically georeferenced by GPS; or approximate coordinates shown in degrees and minutes, which are museum georeferenced or whenever possible by using Google Earth® or map charts and the distribution of Rhamphichthys species was mapped using ArcMap v. 10.6.1. Records include all material listed under Material Examined section. Museum acronyms follow Sabaj (2020).
Statistical analyses. Morphometric analyses were made using all measurements listed above, which are also used and explained in Carvalho et al. (2011) and Carvalho, Albert (2011), except for caudal peduncle depth and caudal appendage length which contains multiple missing entries. The ten measurements were adjusted for size variation. The Aitchinson (1982) log–ratio transformation was applied. In this method every individual is scaled based on the composite of all characters considered and thus does not eliminate the measurement that is adopted for size. The method has been used in size correction in fish morphometrics studies (Peres-Neto, Magnan, 2004; Leal, Sant-Anna, 2007; Delapieve et al., 2020). The size corrected data were then checked for normality using the Shapiro–Wilk test (Shapiro, Wilk, 1965; Shapiro et al., 1968). Outliers were removed after visual inspections of data plots. Principal component analysis (PCA) was used to assess overall differences in morphometric differences among species and within species. PCA on variances-covariances transformations was performed on groups delimited by species or within species by drainage basis. A simple Multivariate Analysis of Variance (MANOVA) was performed on PC1, PC2 and PC3 scores, which are the components that explain most data variation (<10%). MANOVA tests for possible differences between species and groups using the Wilks’ λ test of significance. Bonferroni adjustments were used when doing multiple comparisons to control for type I error (Rice, 1989). Statistical analyses were made using the program PAST v. 2.17 (Hammer et al., 2001).

RESULTS

Systematic accounts

Rhamphichthys Müller & Troschel, 1848

Rhamphichthys Müller & Troschel, 1848:640 (type-species: Gymnotus rostratus Linnaeus, 1766. Type by monotypy).

Altona Kaup, 1856:201 (type-species: Gymnotus rostratus Linnaeus, 1766. Type by monotypy).

Diagnosis. Rhamphichthys can be diagnosed from other rhamphichthyines by the following 10 characters: (1) absence of the Posterior Lateral Line (PLL) foramen in the hyomandibula, vs. foramen present in the posterior dorsal portion of hyomandibula (Carvalho, Albert, 2011: fig. 5); (2) presence of intermuscular bones in the levator operculi and protactor hyodei (Carvalho, Albert, 2011), vs. absence of intermuscular bones in these muscles; (3) anterior portion of the gas bladder covered in a bony capsule (Mago-Leccia, 1994:40; Albert, Campos-da-Paz, 1998: char. 216), vs. anterior portion of gas bladder membranous not enclosed in a bony capsule; (4) number of pectoral-fin rays 17–22 (Mago-Leccia, 1994:40; Carvalho, Albert, 2011), vs. 10–14 in Gymnorhamphichthys and 14–16 in Iracema; (5) presence of a skin fold inside the branchial opening (Triques, 2005a: char. 3), vs. skin inside the branchial opening smooth; (6) origin of anal fin anterior to vertical of branchial opening (Mago-Leccia, 1994:40), vs. origin of anal fin posterior to branchial opening vertical; (7) more than 300 anal-fin rays (Albert, Campos-da-Paz, 1998: char.197; Albert, 2001:196; Carvalho, Albert, 2011), vs. 260 or less anal-fin rays; (8) more than 90 caudal vertebrae, vs. less than 60 caudal vertebrae; (9) body entirely covered by scales as adult (Mago-Leccia, 1994:40; Albert, Campos-da-
Paz, 1998; Albert, 2001; Carvalho, Albert, 2011), vs. anterior portion of body scaleless; (10) presence of a subpectoral accessory electric organ (Giora, Carvalho, 2018), vs. absence of an accessory electric organ below pectoral fin.

**Common names.** The common or local names used for *Rhamphichthys* usually allude to its elongate snout or body form, often being referred to as the “beaked,” “sword,” or “machete” fish. In Argentina *R. hahni* may be called *bombilla* (Span. for a straw to drink Yerba Mate), *anguïya picuda* (pike eel), *morenita* (Span. little dark girl), or *señorita* (Span. girl) (Ringuelet et al., 1967). In Paraguay it is known variably as *morenita* or *piro-kysé* (Guaraní for knife–fish) (Neris et al., 2010). In the Paraná, Brazil, it may be called *espadão* (Port. big sword), *peixe-espada* (Port. swordfish), or *peixe-tatu* (Port. armadillo fish) (Godoy, 1986; Graça, Pavanelli, 2007). *Rhamphichthys rostratus* and *R. pantherinus* in the Tocantins basin of Brazil is called *itui-terçado* (Port. machete gymnotiform) (Santos et al., 1984). *Rhamphichthys drepanium* in Colombia (Arauca basin) is called *cuchillo ossa* or *caballo ossa* (Rugeles et al., 2007). In French Guyana, *R. rostratus* is commonly known by the Wayana Amerindian people as *mapalaine* (Fréry et al., 2001), and as *asa papi* by the Saramaka Marron people (Planquette et al., 1996). In Guyana the same species is called band fish or *wabri* (Ellis, 1913).

**Geographical distribution.** *Rhamphichthys* is known from most cis-Andean drainages of tropical South America, including the coastal drainages of Guianas, Orinoco, Essequibo, Amazon, Parnaiba basins; and the Paraná–Paraguay system (Fig. 2). The genus is present in nineteen of the Freshwater Ecoregions of the World (Abell et al., 2008; Tab. 1).

**Taxonomic account.** In this review we recognized seven valid species of *Rhamphichthys*. Principal component analysis (PCA) was used to investigate morphometric variation of the seven species of *Rhamphichthys* using 10 linear measurements. Results show that the first three principal components (PC1, PC2 and PC3) account for approximately 70% of the variance (Tab. S1). Scores were plotted for PC1 vs. PC2 and PC1 vs. PC3 that represent 38.49, 16.44 and 15.13% of the total variances, respectively (Figs. 3A–B). The PCA of 10 morphometric measurements indicates three morphologically distinct groups within *Rhamphichthys* (Fig. 3B). Group (1), formed by *R. pantherinus*, *R. lineatus*, and *R. heleios*, has strong loadings of eye diameter and interorbital distance on component 3 (Tab. S2). Group (2), formed by *R. drepanium* and *R. hahni*, has strong loadings of branchial opening and postorbital length on PC1 (Fig. 3; Tab. S2). Group 3, formed by *R. rostratus* and *R. apurensis*, is composed of *Rhamphichthys* with the most elongate snouts, and has strong loadings of head length (HL) and preorbital length (PR) on PC1 (Fig. 3; Tab. S2). A Multivariate Analysis of Variance (MANOVA) was performed using the PC scores of the first three and most important components of the PCA. There were no statistically significant differences in morphometrics between *R. hahni* and *R. drepanium* (G1 species) and between *R. apurensis* and *R. rostratus* (G3 species; Tab. S1). Within G2 of species there were no statistically significant differences between *R. heleios* and *R. lineatus* and *R. pantherinus* (Tab. S1). The MANOVA fails to support a distinction of species within the three proposed morpho groups of *Rhamphichthys* (G1, G2, and G3) and shows statistical significance of species in different groups *Rhamphichthys* (Tab. S3; Wilks’ λ: 0.1061; P < 0.001; F18,410.6 = 27.61).
FIGURE 2 | Map showing the geographic distribution of *Rhamphichthys* in South America based on museum examined lots.
**FIGURE 3** | Scatter plots of principal component scores of 10 measurements. **A.** PC1 vs. PC2. **B.** PC1 vs. PC3. All seven species of *Rhamphichthys*: red = *R. apurensis*; blue *R. drepanium*; pink = *R. hahni*; yellow = *R. heleios*; pale green = *R. lineatus*; brown = *R. pantherinus*; and grey = *R. rostratus*. Grey circles in **B** represent the three putative morpho groups (G 1–3).
TABLE 1 | Distributional data of species of *Rhamphichthys* in cis-Andean drainages of South America. Numbers corresponds to FEO of Abell et al. (2008): Orinoco Llanos-307; Orinoco Guiana Shield-308; Orinoco Delta-309; Essequibo-310; Guianas-311; Negro-314; Amazonas Guiana Shield-315; Amazonas Lowlands-316; Mamoré-318; Guaporé-Itenez-319; Xingu-322; Amazonas estuary and coastal drainages-323; Tocantins-Araguaia-324; Parnaíba-325; Lower Uruguay-332; Chaco-342; Paraguay-343; Upper Paraná-344; and Lower Paraná-345. Asterisk (*) indicate the type-locality. Asterisks (**) indicates that *Rhamphichthys hahni* is allochthonous in the Upper Paraná (344) ecoregion.

<table>
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<tr>
<th>Orinoco</th>
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<th>NE Brazil</th>
<th>Paraná-Paraguay</th>
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<tr>
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<td>X*</td>
<td>X</td>
<td>X</td>
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<td>X</td>
<td>X*</td>
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**Key to the species of *Rhamphichthys***.

A summary of variable characters within *Rhamphichthys* is given in Tab. 2.

1a. Snout long (58.4–65.1% of HL); caudal vertebrae to end of anal fin 101–117 ........ 2
1b. Snout short (46.4–59. % of HL); caudal vertebrae to end of anal fin 90–100......... 3
2a. Anal fin usually clear or hyaline, caudal vertebrae to end of anal fin 101–109 ........ *Rhamphichthys apurensis* (Orinoco basin and Cuyuni River).
3a. Dorsal saddles sickle shaped and paired not contacting each other at middorsal line ................................................................. 4
3b. Dorsal saddles absent or unpaired and intercalated ........................................ 5
4a. Posterior gas bladder always membranous, large, and not reduced; 19–21, rarely 19 (mode 20) precaudal vertebrae; 90–93 (mode 90) caudal vertebrae.....................................................*Rhamphichthys hahni* (Paraná-Paraguay system).
4b. Posterior gas bladder reduced thick–walled or large and membranous; 18–20, rarely 20 (mode 19) precaudal vertebrae, 92–94 caudal vertebrae.................................*Rhamphichthys drepanium* (Amazon and Orinoco basins).
5a. Dorsal saddles in an intercalated pattern, extending ventrally to lateral line ...............................................................*Rhamphichthys pantherinus* (Amazon, upper Orinoco, Tocantins, Parnaíba, and Essequibo basins).
5b. Dorsal saddles absent ........................................................................................................ 6
6a. Body coloration mostly light, sometimes with scattered dark chromatophores in the dorsum, inconspicuous diagonal bands, and dark blotches in the anal fin .............................................*Rhamphichthys lineatus* (Amazon basin).
6b. Body coloration mostly brown, with no saddles in the darker dorsum and series of blotches over lateral line and series of spots in the anal fin ..........................................................*Rhamphichthys heleios* (Amazon basin).
Rhamphichthys apurensis (Fernández-Yepéz, 1968)

(Figs. 4–6, 7A; Tab. 3)


Diagnosis. Rhamphichthys apurensis differs from its congeners, except from R. rostratus and R. pantherinus by the larger snout (58.4–63.7% of HL; Figs. 5, 7), vs. shorter snout (46.4–59.1% of HL); larger caudal appendage (23.2–36.8% of LEA), vs. shorter caudal appendage (5.8–20.3% of LEA). Rhamphichthys apurensis differs from R. rostratus by having a lower number of caudal vertebrae to end of anal fin (106–109), vs. higher number of caudal fin vertebrae (109–115; rarely 109); and by having a clear anal fin membrane, vs. anal fin membrane usually distally pigmented forming a longitudinal dark stripe. Rhamphichthys apurensis differs from R. pantherinus by the relatively larger snout (58.4–63.7% of HL), vs. shorter snout (51.4–59.1% of HL); and by the large number of caudal vertebrae to end of anal fin (101–109), vs. lower number of caudal vertebrae (91–100).
**Description.** Morphometrics and meristics given in Tab. 3. Adult body size moderate to large as compared with other congeners, maximum size 520 mm LEA. Mouth subterminal. Snout relatively long, more than half of head length (Fig. 5). Dorsal profile of snout strongly concave in front of eye, head profile slightly convex posteriorly. Anterior nares positioned terminally, posterior nares located closer to snout than eyes, at about one fourth of head length. Body profile almost straight to slightly concave dorsally. Ventral body profile slightly concave from anal–fin origin to end of anal fin. Greatest body depth slightly posterior to end of body cavity. Body tapering posterior to mid body. Eyes relatively large and positioned laterally, about seven times contained in postorbital length. Urogenital papilla developed and anteriorly positioned below eyes in specimens larger than 480 mm LEA. Urogenital papilla relatively small. Posterior gas bladder absent. Caudal appendage laterally compressed, its depth about three times its width.


![Image of Rhamphichthys apurensis](image-url)
**FIGURE 5** | Detail of the head of *Rhamphichthys apurensis*, ANSP 166484, 390 mm LEA, Laguna Mamo at Nuevo Mamo, Anzoátegui, Venezuela.

**TABLE 3** | Morphometric and meristic of *Rhamphichthys apurensis*. SD = standard deviation, n = number of specimens.

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<th>n</th>
<th>Range</th>
<th>Mean</th>
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<td><strong>Percents of LEA</strong></td>
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<td>Caudal filament depth</td>
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<td><strong>Percents of head length</strong></td>
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<tr>
<td>Interorbital distance</td>
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<td>0.5</td>
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<tr>
<td>Snout length</td>
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<td>60.9</td>
<td>1.6</td>
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<td>34.4–38.1</td>
<td>36.3</td>
<td>1.1</td>
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<td>Eye diameter</td>
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<td>14.8</td>
<td>1.1</td>
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<td>Branchial Opening</td>
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<td>1.4</td>
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<td>Anal-fin rays</td>
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<td>Pectoral-fin rays</td>
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<td>17–21</td>
<td>18.4</td>
<td>1.2</td>
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Coloration in alcohol. Ground color of dorsal and lateral surfaces of head and body pale yellow (Figs. 4–6). Head surface covered with scattered dark-brown blotches of about eye size; snout mostly dark, ventral head margin less pigmented. Epaxial body surface with many intercalated and dark pigment saddles across the mid-dorsum extending ventral to the lateral line. Hypaxial body surface with many dark pigment bands oriented at a slight diagonal to the long axis, sometimes contacting dorsal saddles, generally diffuse over pterygiophores region, and extending to proximal portion of anal-fin rays. Anal-fin membrane mostly clear or hyaline (Figs. 4, 7A), except for ventral extensions of lateral bands and some scattered dark round pigment blotches (Fig. 6). Pectoral fin clear or hyaline in most specimens, sometimes with scattered dark pigment blotches. Caudal appendage with dark vertically elongate pigment blotches.

Geographical distribution. *Rhamphichthys apurensis* is distributed throughout the Orinoco basin and its larger tributaries and in the Cuyuni drainage of Essequibo (Fig. 8; Tab. 1). *Rhamphichthys apurensis* inhabits mostly the deep waters of the main channel of Orinoco River and large size tributaries (Mago-Leccia, 1994).

Material examined. Orinoco Llanos: ANSP 160251, 1, Venezuela, Bolívar, Río Guariquito at confluence of Río Orinoco, 07°39’36”N 66°20’W. ANSP 162300, 60 (12 specimens measured in Tab. 3, 330–520 mm LEA; 1 cs), Venezuela, Bolívar, Río Orinoco

![Figure 6](https://ni.bio.br/scielo.br/ni)
FIGURE 7 | Coloration pattern of the lateral portion of body at about midlenght of LEA in *Rhamphichthys*. A. *Rhamphichthys apurensis*, ANSP 162300, 390 mm LEA. B. *Rhamphichthys drepanium* from Orinoco Basin, ANSP 181071, 320 mm LEA. C. *Rhamphichthys drepanium*, INPA 17682, 375 mm LEA. D. *Rhamphichthys hahni*, MZUSP 59297, 355 mm LEA. E. *Rhamphichthys lineatus*, MCP 26374, 340 mm LEA. F. *Rhamphichthys pantherinus*, MCP 24814, 405 mm LEA. G. *Rhamphichthys rostratus*, ANSP 187120, 520 mm LEA. H. *Rhamphichthys heleios*, INPA 42308, 335 mm LEA. Anterior portion towards left.
near mouth of Río Caura, 07º38’N 64º52’W. ANSP 162707, 3, Venezuela, Bolivar, Río Orinoco about 50 m above mouth of Río Cuchivero, 07º40’N 65º57’W. ANSP 166845, 9, Venezuela, Bolivar, Laguna Castillero at Caicara del Orinoco, 07º38’20”N 66º09’00”W. ANSP 166484, 3, Venezuela, Anzoátegui, Laguna Mamo at Nuevo Mamo, 08º28’N 63º02’W. ANSP 188936, 1, Venezuela, Apure, Río Apure Isla Playa del Medio, near mouth of Río Portuguesa, 07º55’47”N 67º31’12”W. ANSP 190968, 1, Venezuela, Anzoátegui, Río Orinoco deep channel upstream Los Baranacos, 08º21’N 62º43’W. AUM 53707, 4, Venezuela, Bolivar, Río Orinoco at Caicara del Orinoco ferry boat landing, 07º38’44”N 66º10’46”W. CUMV 72365, 2, Venezuela, Apure, San Fernando de Apure, Río Apure east of San Fernando Bridge, 07º54’N 67º28’W. CUMV 82347, 2, Venezuela, Apure, San Fernando de Apure, Río Apure east of San Fernando Bridge, 07º54’N 67º28’W. FMNH 85503, 1, Venezuela, Apure, Río Arauca 32.5 km south of Biruaca, 07º34’N 67º38’W. IAvH-P 1021, 1, Colombia, Meta, Puerto Gaitán, Estero el Carrizal, Río Manacancas, 4º23’N 72º04’N. IAvH-P 17554, 1, Colombia, Casanare, Paz de Ariporo, Tapa El Venado, 05º39’14”N 71º00’31”W. IAvH-P 17587, 1, Colombia, Casanare, Paz de Ariporo, Tapa El Venado, 05º36’49”N 71º05’44”W. IAvH-P 17558, 2, Colombia, Casanare, Paz de Ariporo, Caño la Hermosa, 05º42’20”N 71º01’11”W. IAvH-P 18415, 2, Colombia, Casanare, Pore Caño Curimina, 05º35’09”N 71º50’19”W. IAvH-P 19994, 1, Colombia, Casanare, Orocué, Caño Aguaverde, Reserva Paralmarito-Casambá, 04º52’09”N 71º38’27”W. IAvH-P 24332, 4, Venezuela, Río Orinoco near mouth of Río Caura, 07º38’N 64º52’W. IAvH-P 25042, 1, Colombia, Meta, Caño Carrestilar. IAvH-P 25726, 3, Colombia, Vichada, Puerto Carreño, Caño Charapa, 06º05’33”N 67º30’03”W. IAvH-P 25784, 1, Colombia, Vichada, Puerto Carreño, Río Orinoco, 05º59’58”N 67º25’18”W. IAvH-P 28420, 2, Colombia, Vichada, Puerto Carreño, Río Orinoco, upstream Caño D’agua, 05º45’04”N 67º37’14”W. IAvH-P 28482, 1, Colombia, Vichada, Puerto Carreño, REserva Natural Bojonawi, 06º07’04”N 67º30’37”W. IAvH-P 28484, 1, Colombia, Vichada, Puerto Carreño, Laguna El Pañuelo, 06º07’04”N 67º30’32”W. ICNMCN 3456, 1, Colombia, Meta, Puerto Lopez, Laguna de Menegua. ICNMCN 5359, 1, Colombia, Vichada, Río Orinoco. LBP 10226, 1, Venezuela, Guárico, Río Apure at Cabruta, 07º37’24”N 66º24’48”W. MCNG 5985, 1, Venezuela, Apure, Hato El Frio, 07º53’N 68º52’W. MCNG 13143, 1, Venezuela, Apure, Río Apure at San Fernando. MCNG 20360, 1, Venezuela, Apure, Río Apure at Isla del Medio. MCNG 26351, 1, Venezuela, Apure, Muñoz, borrow pit at Módulo Fernando Corrales, 07º32’N 69º42’W. MCNG 31124, 1, Venezuela, Bolivar, Laguna Maldonado, 08º06’N 63º46’W. MCNG 31232, 1, Venezuela, Anzoátegui, Laguna de Tineo, 08º11’N 63º28’W. MCNG 33241, 13, Venezuela, Bolivar, Laguna Bartolico 07º38’N 66º06’W. MCNG 37462, 2, Venezuela, Apure, Río Arauca at El Yagual, 07º28’N 68º25’W. MCNG 51559, 5, Venezuela, Apure, right margin of Río Apure at Piedral. MPUJ 6564, 3, Colombia, Casanare, Caño Orosio. MPUJ 11697, 1, Colombia, Casanare, Caño La Hermosa, 05º42’20”N 71º01’11”W, MPUJ 12007, 1, Colombia, Casanare, Paz de Ariporo, Tapa Las Matas, 05º39’14”N 71º00’31”W. Rorinoco Guiana Shield: MCNG 36173, 2, Venezuela, Bolivar, Río Caura at Salto Pará, 06º18’N 64º30’W. Orinoco Delta and coastal drainages: ANSP 149461, 1, Venezuela, Monagas, inlet on Isla Chivera below Barrancas 145 nautical miles from sea bouy 08º40’12”N 62º12’W. ANSP 188934, 1, Venezuela, Delta Amacuro, Río Orinoco just downstream los Castillos, 08º31’N 62º22’W. ANSP 192671, 1, Venezuela, Delta
Amacuro, Río Orinoco, Brazo Imataca near S shore, 08°21’N 62°43’W. CAS 51077, 1, Venezuela, Delta Amacuro, Río Orinoco at El Toro, 08°31’N 61°29’W. MZUSP 44495, 2 (2 specimens measured in Tab. 3, 252–282 mm LEA), Venezuela, Delta Amacuro, Río Orinoco at Isla Tres Caños, 08°38’N 61°59’W. UMMZ 211324, 2, Venezuela, Delta Amacuro, Shallow channel of Río Orinoco across from Isla Tres Caños, 08°40’N 62°01’W. USNM 228767, 1, Venezuela, Delta Amacuro, Río Orinoco first small caño on W side of La Paloma 100 m above its mouth 92 nautical miles upstream of sea Buoy, 08°29’N 61°25’W. USNM 228768, 1, Venezuela, Monagas, Isolated lagoon on Isla Tapatapa at Río Orinoco 163 nautical miles from sea buoy, 08°31’36”S 62°26’42”W. USNM 233796, Venezuela, Delta Amacuro, Río Orinoco downstream Isla Portuguesa about 116.5 nautical miles from sea buoy, 08°36’12”N 61°46’24”W. USNM 388748, 1, Venezuela, Río Orinoco. 

Essequibo: USNM 404246, 1, Guyana, Cuyuni River, Cuyuni River about 15 km upstream from Waikuni mountains in Vicinity of mouth of Toropaur River, 06°41’31”N 59°34’38”W. USNM 402687, 1, Guyana, Cuyuni-Mazaruni, sand beach in the Cuyuni River immediately downstream Kanaima falls, 06°52’28”N 60°14’54”W. USNM 402688, 1, Guyana, Cuyuni-Mazaruni, Cuyuni River about 15 km upstream from Waikuni mountains in Vicinity of mouth of Toropaur River, 06°41’31”N 59°34’38”W.

**FIGURE 8** | Distribution of *Rhamphichthys apurensis* based on examined museum specimens. Red dot represents the approximate type-locality.
**Rhamphichthys drepanium** Triques, 1999

(Figs. 7B–C, 9–14; Tab. 4)


*Rhamphichthys* sp. —Lavoué *et al*., 2012: fig. 2 (illustrated and EOD description).

**FIGURE 9** | Holotype of *Rhamphichthys drepanium*, MZUSP 6893, 372 mm LEA, lago Janauari at confluence of rio Negro and rio Solimões, Amazonas, Brazil.

**FIGURE 10** | Detail of the head of holotype of *Rhamphichthys drepanium*, MZUSP 6893, 372 mm LEA, lago Janauari at confluence of rio Negro and rio Solimões, Amazonas, Brazil.
Diagnosis. *Rhamphichthys drepanium* differs from all congeners except *R. hahni* by having paired sickle-shaped saddles along the middorsum interrupted at the midline (Figs. 15B–C), vs. absence of saddles or intercalated saddles on the middorsum (Figs. 15A, D–G). It differs from *R. hahni* by the shape of the posterior gas–bladder, which is usually reduced with thickened walls, vs. always membranous and balloon like in *R. hahni* (Fig. 16D). Also, *R. drepanium* differs from *R. hahni* by the number of precaudal vertebrae usually 18–20, rarely 20 (mode 19), vs. 19–21, rarely 19 (mode 20; Tab. 5); and by the number of caudal vertebrae 92–94, vs. 90–93 (mode 90; Tab. 5).

Description. Morphometrics and meristic given in Tab. 4. Adult body size moderate to large compared with other congeners, maximum size 604 mm LEA. Mouth subterminal. Snout relatively short and robust, about half of head length. Dorsal profile of snout strongly concave in front of eye, head profile slightly convex posteriorly. Anterior nares positioned terminally; posterior nares located closer to snout than eyes at about one third of length. Body profile almost straight to slightly concave dorsally. Ventral body profile slightly concave from anal–fin origin to end of anal fin. Greatest body depth slightly posterior to end of body cavity. Body tapering posterior to mid body.

**Coloration in alcohol.** Ground color of dorsal and lateral surfaces of head and body light to dark brown (Figs. 9–14). Individuals from the Amazon River basin are overall generally darker (Figs. 9–12) than individuals from the Orinoco River basin (Figs. 13–14). Head mostly dark brown except for scattered, light, irregular small blotches, smaller than eye size; ventral portion of head lighter than dorsal portion. Dorsum of body presenting sickle–shaped dark saddles, these reaching ventrally to lateral line. Presence of lateral darkish lateral bands, slightly diagonally located from anteroventral to posterodorsal axis. Lateral bands sometimes with a light central area. Lateral bands often

| TABLE 4 | Morphometrics and meristic of *Rhamphichthys drepanium*. H = holotype, SD = standard deviation, n = number of specimens. |
| --- | --- | --- | --- | --- |
| **Length to end of anal fin (LEA)** | H | n | Range | Mean | SD |
| Anal-fin length | 92.7 | 24 | 82.8–92.7 | 88.9 | 2.2 |
| Body depth | 9.3 | 24 | 8.8–12.1 | 10.1 | 0.9 |
| Pectoral-fin rami | 5.1 | 24 | 4.5–7.2 | 5.7 | 0.6 |
| Head length | 13.6 | 24 | 12.2–17.6 | 14.0 | 1.1 |
| Caudal filament length | – | 20 | 5.8–20.3 | 11.9 | 3.6 |
| Caudal filament depth | – | 20 | 1.4–2.4 | 1.8 | 0.2 |
| **Percents of head length** | | | | | |
| Interorbital distance | 10.9 | 24 | 9.3–15.0 | 11.7 | 1.4 |
| Snout length | 50.9 | 24 | 49.5–54.6 | 51.6 | 1.2 |
| Postorbital length | 44.3 | 24 | 43.4–48.1 | 45.6 | 1.4 |
| Eye diameter | 3.8 | 24 | 3.9–6.5 | 5.1 | 0.6 |
| Post. nares length | 18.1 | 24 | 13.2–18.6 | 16.3 | 1.2 |
| Branchial opening | 20.7 | 24 | 17.2–27.4 | 21.9 | 2.7 |
| **Meristic** | | | | | |
| Anal-fin rays | 390 | 23 | 310–390 | 349.0 | 22.8 |
| Pectoral-fin rays | 17 | 24 | 16–19 | 17.5 | 0.8 |
contacting the dorsal saddles; forming a contiguous band; these usually not contacting the ventrolateral bands over pterygiophores region, which are contiguous with the dark areas of the proximal region of the anal fin. Specimens larger than 500 mm of LEA uniformly dark, with inconspicuous saddles and bands. Anal fin mostly dark with clear and vermiculous areas proximally, and clear spots distally. Pectoral fin mostly clear or hyaline, with dark vertical bars. Caudal appendage with dark vertically elongate bands.

**Geographical distribution.** *Rhamphichthys drepanium* is distributed in the Amazon and Orinoco basins (Fig. 17; Tab. 1). In the Amazon basin it is frequently collected in lentic waters, e.g., floodplain oxbow and ria lakes. In the Orinoco basin it is commonly collected in lotic habitats, including flooded savannas and barrow pits in the Llanos, sometimes being found in the main channel of small to medium sized, slowly flowing rivers.

**Electric organ discharge.** A tetraphasic discharge according to Lavoué *et al.* (2012, fig. 2d) identified as *Rhamphichthys* sp.

**Comments.** *Rhamphichthys drepanium* has been often erroneously identified as *R. marmoratus* (currently junior synonym of *R. pantherinus*) in the Orinoco River basin (e.g., Mago-Leccia, 1994 and see also synonym list). *Rhamphichthys pantherinus* has a relatively restricted distribution in the Orinoco, occurring only in the Ventuari, Guaviare and Metica river basins.

**Geographic variation.** Specimens from the Orinoco basin (Figs. 14–15) are overall less pigmented and relatively clearer than specimens collected in the Amazon basin (Figs. 9–13). Despite their disjunct distribution, the populations in the Amazon and Orinoco basins exhibit relatively little morphological differences. A PCA was conducted using 11 morphometric characters to compare both geographic groups of *R. drepanium* (Amazon and Orinoco) and the allied species *R. hahni* from Paraná-Paraguay system. The first three principal components (PC1, PC2 and PC3) explain most of the variance (69.1%; Tab. S4). Scores were plotted for PC1 vs. PC2 and show large morphometric

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**TABLE 5** Number of specimens observed for precaudal vertebrae (PCV) and caudal vertebrae (CV) counts in *Rhamphichthys*.

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<th>19</th>
<th>20</th>
<th>21</th>
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<th>90</th>
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FIGURE 13 | *Rhamphichthys drepanium*, FMNH 102111, LEA not measured, Río Suripa between pumping station of Hato Mercedes and mouth in Río Anaro, Barinas, Venezuela.

overlap of populations of *R. drepanium* in the Amazon *R. drepanium* in the Orinoco and *R. hahni*. Strong loadings separating these groups are the interorbital diameter (IO), eye diameter (ED), and branchial opening (BO; Fig. 18; Tab. S5). A Multivariate Analyses of Variance (MANOVA) was done using the PC scores of the first three axis of the PCA. There are no statistically significant differences between morphometrics between *R. hahni* and *R. drepanium* from the Amazon and the comparison between other groups are marginally significant except when comparing the Orinoco population of *R. drepanium* with *R. hahni* (Tab. S6; Wilks’ λ: 0.4475; P< 0.001; F6,90 = 7.424).

Material examined. Orinoco Llanos: ANSP 128227, 2 (2 specimens measured in Tab. 4, 430–432 mm LEA), Colombia, Meta, Caño Rico at La Defensa NW of Laguna Mozambique. ANSP 165186, 1 (1 specimens measured in Tab. 4, 365 mm LEA),
Venezuela, Guárico, Esteros de Camaguan, 6 km N of Camaguan on road between Calabozo and San Fernando de Apure, 08°09'N 67°36'W. ANSP 166566, 2 (2 specimens measured in Tab. 4, 325–532 mm LEA), Venezuela, Bolivar, Almacén, Laguna Maldonado, 08°06'N 63°45'W. ANSP 181071, 2 (2 specimens measured in Tab. 4, 315–320 mm LEA), Venezuela, Apure, Río Apure along right bank of channel near María Nieves bridge at vicinity of San Fernando de Apure, 07°53'N 67°28'W. ANSP 188935, 5, Venezuela, Apure, Río Apure Isla playa del Médio at mouth of Río Portuguesa, 07°55'N 67°31'W. AUM 22668, 2, Venezuela, Portuguesa, Río Portuguesa in El Mamón 24 km E of Guanare, 09°04'N 69°30'W. CAS 64326, 1 (1 specimen measured in Tab. 4, 320 mm LEA), Venezuela, Portuguesa, Río Maria at bridge on Guanaré–Acarigua highway, 09°10'N 69°35'W. CAS 64425, 1 (1 specimen measured in Tab. 4, 232 mm LEA), Venezuela, Portuguesa, Caño Maracá at highway between Guanarito–Guanare km 60. CUMV 72364, 4, Venezuela, Apure, Esteros de Camaguán farm pond about 35 km N of San Fernando, 08°07'N 67°36'W. CUMV 72371, 3, Venezuela, Apure, San Fernando de Apure, Río Apure east of San Fernando Bridge, 07°54'N 67°28'W. CUMV 82360, 2, Venezuela, Apure, Río Apure near mouth of Portuguesa, west of San Fernando, 07°55'N 67°30'W. CUMV 90146, 1, Venezuela, Portuguesa, Río Las Marias. FMNH 102111, 1 (1 specimen measured in Tab. 4, 267 mm LEA), Venezuela, Barinas, Río Suripia between pumping station of Hato Mercedes and mouth in Río Anaro. FMNH 105141, 1, Venezuela, Barinas, Río Anaro about 10 minutes from mouth in Río Suripia, 07°49'N 70°18'W. FMNH 105142, 8 (2 specimens measured in Tab. 4, 295–315 mm LEA), Venezuela Barinas, Cano Socopo about 3.5 hours upstream from boat of Hato Mercedes in Río Suripia, 07°47'N 69°56'W. FMNH 105143, 1, Venezuela, Barinas, Playa Los Chicos in the Río Suripia 2.5 hours above Hato Mercedes. IAvH–P 9241, 4, Colombia, Arauca, Tame, Caño El Rucio 2 km via Arauca–Tame, 06°40’N 70°30’W. IAvH–P 17545, 1, Colombia, Casanare, Paz de Ariporo, Tapa el Venado, 05°36’49’N 71°05’44’W. IAvH–P 17555, 1, Colombia, Casanare, Paz de Ariporo, Tapa las Matas, 05°39’14’N 71°00’31’W. IAvH–P 17559, 1, Colombia Casanare, Caño la Hermosa, 05°42’20’N 71°01’11’W. IAvH–P 17972, 1, Colombia, Arauca, Arauquita, confluence of stream, río Arauca and brazo Bayonero. IAvH–P 22115, 1, Colombia, Arauca, Arauquita, Río Aguas de Limón. ICNMCN 1321, 1, Meta Puerto Lopez, Laguna de Menegua. ICNMCN 1727, Colombia Arauca, Cravo Norte, Caño Negro, Caño Ormedillo on the road to Arauca. ICNMCN 3333, 1, Colombia Arauca, Cravo Norte, Caño Negro, Caño Armadillo on the road to Arauca. ICNMCN 5568 1, Colombia, Casanare, Canno Carupana tributary to Río Gachiria. LBP 3040, 1, Venezuela, Bolivar, Río Orinoco upstream Caicara del Orinoco, 07°38’11’N 66°19’04’W. MCNG 2149, 1, Venezuela, Barinas, borrow pit 1.2 km south of Bruzual, 08°01’N 69°20’W. MCNG 3110, 3, Venezuela, Barinas, flooded area bridge at Bruzual, 08°03’N 69°20’W. MCNG 5256, 2, Venezuela, Apure, Río Sarare, 07°10’N 71°15’S. MCNG 5343, 1, Venezuela, Portuguesa/Barinas, Río Bocono, 08°43’N 69°34’W. MCNG 5984, 6, Venezuela, Apure, Hato El Frio, 07°53’N 68°52’W. MCNG 12848, 6, Venezuela, Barinas, Río Guasimito, 08°13’N 68°25’W. MCNG 14405, 1, Venezuela, Portuguesa, stream E of Guayabal. MCNG 14521, 1, Venezuela, Guárico, river between Cazorla and Guayabal, 07°57’N 67°09’W. MCNG 15771, 1, Venezuela, Apure, creek south to Bruzual. MCNG 19525, 2, Venezuela, Guárico, highway Calabozo to Camaguan km 271. MCNG 20694, 1, Venezuela, Apure, Río Apure 200 m upstream Maria Nieves bridge, 07°53’N.
FIGURE 15 | Coloration pattern of the dorsum in *Rhamphichthys*.  
A. *Rhamphichthys aprurensis*, ANSP 162300, 390 mm LEA.  
B. *Rhamphichthys drepanium*, ANSP 181071, 313 mm LEA.  
C. *Rhamphichthys halmi*, FMNH 108548, 370 mm LEA.  
D. *Rhamphichthys lineatus*, FMNH 114685, 290 mm LEA.  
E. *Rhamphichthys marmoratus* MCP 39982, 320 mm LEA.  
F. *Rhamphichthys rostratus*, ANSP 187120, 520 mm LEA.  
G. *Rhamphichthys heleios*, INPA 42308, 335 mm LEA. Anterior portion towards right.
67°28’W. MCNG 24076, 3, Venezuela, Apure, Laguna El Pozón. MCNG 25434, 1, Venezuela, Apure, Via Arichuna 4 km from Boquerone. MCNG 25520, 4, Venezuela, Guárico, Via Arichuna 4 km from the bridge. MCNG 25533, 1, Venezuela, Apure, Río Lagero, Isla Apurito. MCNG 26246, 1, Venezuela, Barinas, Río Ticoporo, 07°47’N 69°56’W. MCNG 26648, Venezuela, Portuguesa, Caño San José between Guanaritico and La Capilla, 08°41’09”N 68°56’49”W. MCNG 27371, 1, Venezuela, Portuguesa, Caño Ignes tributary to Río Portuguesa. MCNG 28621, 2, Venezuela, Apure, Módulos del Apure borrow pit 49, 07°30’N 69°30’W. MPUJ 6563, 2, Casanare, Caño Orosio, 05°12’11”N 71°01’56”W. MPUJ 8493, 1, Casanare, Trinidad, Caño Varajuste, bridge on main road, 05°24’22”N 71°37’56”W. MPUJ 11694, Colombia, Casanare, Paz de Ariporo, Tapa el Venado, 05°36’49”N 71°05’44”W. MPUJ 11695, 1, Colombia Casanare, Paz de Ariporo, Tapa Las Matas, 05°39’14”N 71°00’31”W. MPUJ 11696, 1, Colombia, Casanare, Paz de Ariporo, Tapa la Guayabera, 05°38’41”N 71°13’47”W. UF 37025, 3 (2 specimens measured in Tab. 4, 171–207 mm LEA; 1 cs), Venezuela, Apure,
Hato El Frio borrow pit near Río Guaritico, 07°52′N 69°19′W. UF 78066, 2 (2 specimens measured in Tab. 4, 247–257, mm LEA, 1 cs), Venezuela, Guárico, borrow pit in palm savannah 2.3 km N of San Fernando de Apure, 07°52′S 68°55′W. UF 80303, 1 (1 specimen measured in Tab. 4, 277 mm LEA, 1 cs), Venezuela, Portuguesa, old Río Guanare about 12 km S of Arismendi, 08°22′N 68°19′W. USNM 200243, 1, Venezuela, Apure, Río Apure 5 km W of San Fernando de Apure, 07°53′N 67°29′W. USNM 260245, 1, Venezuela, Apure, Río Apure about 2 km E of bridge at San Fernando de Apure, 07°53′N 67°29′W. USNM 270259, 4, Venezuela, Apure, side channel of Río Apure about 3 km W of center of San Fernando de Apure, 07°53′S 67°29′W. ZMB 10015, 1, Venezuela, Apure. **Orinoco Delta and coastal drainages:** USNM 228821, 1, Venezuela, Delta Amacuro, Río Orinoco first small caño on W side of Caño Paloma 100 m above its mouth 92 nautical miles upstream from sea buoy, 08°29′N 62°25′W. **Rio Negro:** INPA 27613, 1, Brazil Amazonas, rio Negro at Praia Grande, 03°02′S 60°32′W. **Amazonas lowlands:** INPA 4805, 4 (3 specimens measured in Tab. 4, 360–485 mm LEA), Brazil, Amazonas, Autazes, lago do Castanho, 03°33′S 59°13′W. INPA 4848, 1, Brazil, Amazonas, lago do Camaleão at ilha da Marchantaria. INPA 13036, 2 (1 specimen measured in Tab. 4, 473 mm LEA), Brazil Amazonas, Manaquiri, lago Janauacá, 03°23′S 60°16′W. INPA 13037, 4 (2 specimens measured in Tab. 4, 420–500 mm LEA), Brazil Amazonas, Manaquiri, lago Janauacá, 03°23′S 60°16′W. INPA 17682, 6 (2 specimens measured in Tab. 4, 382–395 mm LEA, 1 cs), Brazil, Amazonas, Manaus,
Costa do Catalão, 03°10'S 59°56'W. INPA 18324, Brazil, Amazonas, Alvarães, lago Amanã at mouth of igarapé Baré, 02°29'S 64°41'W. INPA 27602, 1 (1 specimen measured in Tab. 4, 372 mm LEA), Brazil, Amazonas, Manaus, paraná do Xiborena, 03°09'S 59°55'W. INPA 27603, 1 (1 specimen measured in Tab. 4, 207 mm LEA), Brazil, lago do Padre. MCP 45526, 1, Brazil, Amazonas, rio Tefé in ilha do Martelo at lago do Martelo, 03°46'49"S 64°59'29"W. MPEG 10075, 2, Brazil, Pará, Juruti, lago da Piranha, 02°12'S 56°06'W. MZUSP 6893, holotype (1 specimen measured in Tab. 4, 372 mm LEA), Brazil, Amazonas, Manaus, lago Janauari at confluence of rio Negro and rio Solimões, 03°12'S 60°01'W. MZUSP 48509, 2 paratypes (2 specimens measured in Tab. 4, 325–390 mm LEA), collected with holotype. MZUSP 36144, 2 (1 specimen measured in Tab. 4, 385 mm LEA), Brazil, Amazonas, lago Amanã mouth of rio Japurá, 02°30'S 64°42'W. USNM 306734, 1, Brazil, Amazonas, lago Janauari near its mouth. USNM 306766, 1, Brazil, Amazonas, São José, lago do Castanho at Janauacá. USNM 306876, 1 paratype of *R. drepanium*, Brazil, Amazonas, lago Janauari at first brick plant. **Mamoré–Madre de Dios Piedmont.** MNHN 1988–1028, 1, Bolívia, Puerto Almacén, Río Ibaré tributary to Río Mamoré, 14°52'S 64°58'W.
**Rhamphichthys hahni** (Meiken, 1937)

(Fig. 19–24; Tab. 6)


*Rhamphichthys marmoratus* non Castelnau, 1855. —Bertoni, 1939:57 (listed).

*Rhamphichthys reinhardti* non Kaup, 1856. —Bertoni, 1939:57 (listed).


**Diagnosis.** *Rhamphichthys hahni* differs from its congeneres, except *R. drepanium* by having sickle shaped saddles on the dorsal midline, vs. absence of saddles or intercalated saddles on the dorsum. It differs from *R. drepanium* by the shape of the posterior gas-bladder, which is always membranous and ballon like, vs. a posterior gas bladder usually reduced with thickened walls (Fig. 17). It also tentatively differs from *R. drepanium* by the number of precaudal vertebrae 19–21 rarely, 19 (mode 20), vs. 18–20 rarely 20 (mode 19; Tab. 5); and by the number of caudal vertebrae 90–93 (mode 90), vs. 92–94 (Tab. 5).

**Description.** Morphometrics and meristic given in Tab. 6. Adult body size moderate to large compared with other congeners, maximum size 615 mm LEA. Mouth subterminal. Snout relatively short and robust about half of head length. Dorsal profile of
snout strongly concave in front of eye, head profile slightly convex posteriorly. Anterior naires positioned terminally; posterior naires located closer to snout than eyes at about one third of length. Body profile almost straight to slightly concave dorsally. Ventral body profile slightly concave from anal–fin origin to end of anal fin. Greatest body depth slightly posterior to end of body cavity. Body tapering posterior to mid body. Eyes relatively small and positioned laterally, about nine times contained in postorbital length. Urogenital papilla developed and anteriorly positioned below eyes in specimens larger than 360 mm LEA. Urogenital papilla large in adults. Posterior gas bladder large not reduced, membranous (Fig. 16d). Caudal appendage laterally compressed, its depth about three times its width.

**TABLE 6 | Morphometric and meristic data for *Rhamphichthys hahni*. H = holotype, SD = standard deviation, n = number of specimens.**

<table>
<thead>
<tr>
<th></th>
<th>H</th>
<th>n</th>
<th>Range</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length to end of anal fin (LEA)</td>
<td>253</td>
<td>27</td>
<td>230–600</td>
<td>383</td>
<td>–</td>
</tr>
<tr>
<td>Percents of LEA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anal-fin length</td>
<td>88.9</td>
<td>27</td>
<td>72.7–90.7</td>
<td>86.1</td>
<td>4.4</td>
</tr>
<tr>
<td>Body depth</td>
<td>10.1</td>
<td>27</td>
<td>8.0–12.2</td>
<td>10.3</td>
<td>1.2</td>
</tr>
<tr>
<td>Pectoral-fin length</td>
<td>6.1</td>
<td>27</td>
<td>4.2–6.4</td>
<td>5.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Head length</td>
<td>14.6</td>
<td>27</td>
<td>11.8–15.3</td>
<td>14.0</td>
<td>0.8</td>
</tr>
<tr>
<td>Caudal filament length</td>
<td>–</td>
<td>22</td>
<td>7.3–15.4</td>
<td>10.2</td>
<td>1.7</td>
</tr>
<tr>
<td>Caudal filament depth</td>
<td>1.8</td>
<td>25</td>
<td>1.3–2.2</td>
<td>1.7</td>
<td>0.2</td>
</tr>
<tr>
<td>Percents of head length</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Interorbital distance</td>
<td>10.5</td>
<td>27</td>
<td>8.5–13.6</td>
<td>10.3</td>
<td>1.1</td>
</tr>
<tr>
<td>Snout length</td>
<td>51.7</td>
<td>27</td>
<td>46.4–54.3</td>
<td>51.3</td>
<td>1.9</td>
</tr>
<tr>
<td>Postorbital length</td>
<td>44.7</td>
<td>27</td>
<td>42.7–48.6</td>
<td>45.8</td>
<td>1.7</td>
</tr>
<tr>
<td>Eye diameter</td>
<td>7.0</td>
<td>27</td>
<td>4.6–7.0</td>
<td>5.5</td>
<td>0.6</td>
</tr>
<tr>
<td>Post. nares length</td>
<td>17.0</td>
<td>27</td>
<td>14.4–20.2</td>
<td>16.7</td>
<td>1.3</td>
</tr>
<tr>
<td>Branchial opening</td>
<td>17.0</td>
<td>27</td>
<td>17.1–25.0</td>
<td>21.0</td>
<td>2.3</td>
</tr>
<tr>
<td>Meristic</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anal-fin rays</td>
<td>328</td>
<td>24</td>
<td>310–360</td>
<td>339.6</td>
<td>14.5</td>
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<tr>
<td>Pectoral-fin rays</td>
<td>17</td>
<td>25</td>
<td>16–19</td>
<td>17.7</td>
<td>0.8</td>
</tr>
</tbody>
</table>

**FIGURE 19 | *Rhamphichthys hahni*, holotype of *Sternarchorhamphus hahni*, ZMB 33367, 253 mm LEA, Río Paraná near Corrientes, Corrientes, Argentina.**

**FIGURE 20** | *Rhamphichthys hahni*, detail of head of holotype of *Sternarchorhamphus hahni*, ZMB 31367, Río Paraná near Corrientes, Corrientes, Argentina.

**FIGURE 21** | *Rhamphichthys hahni*, MZUSP 59927, 355 mm LEA, rio Novo at Brejo de Santa Sofia, Mato Grosso do Sul, Brazil.
Coloration in alcohol. Ground color of dorsal and lateral surfaces of head and body light brown to pale yellow (Figs. 19–24). Head presenting scattered dark brown blotches of about eye size; snout mostly dark, ventral margin less pigmented. Dorsum of body presenting sickle shaped saddles, these reaching ventrally to lateral line. Presence of lateral darkish lateral bands, slightly diagonally located from anteroventral to posterodorsal axis. Lateral bands sometimes contacting the dorsal saddles; ventrolateral bands diffuse over pterygiophore region, extending to the proximal region of the anal–fin rays and not contiguous with the lateral bands. Anal fin mostly dark with clear vermiculous areas proximally and light spots distally. Pectoral fin almost completely dark except for transverse rows of light spots; these contacting each other sometimes forming clear bars. Caudal appendage with dark vertically elongate bands.

Karyotype: *Rhamphichthys hahni* has 50 chromosomes and a formula comprised of 20m+24sm+6a (FN = 94; Mendes *et al*., 2012).

Geographical distribution. *Rhamphichthys hahni* is the single species of the genus known from the Paraná-Paraguay river system (Fig. 25). It is known from the southern La Plata River in Argentina to the northern Paraguay River in Brazil and Paraguay. Is also known from the Uruguay River and Upper Paraná River in Brazil. The presence of this species in the Upper Paraná is due to the construction of Itaipu Dam, which by elevating a portion of the Lower Paraná eliminated the Sete Quedas falls as a barrier for dispersal (Langeani *et al*., 2007; Júlio Jr. *et al*., 2009). Another species of the genus was cited for this system (i.e., *R. rostratus* in Caputi *et al*., 1994; Shibatta, 2006; Neris *et al*., 2010, and others), however the only *Rhamphichthys* species occurring in this system is *R. hahni*. This species inhabits rivers and lakes, feeding on insect larvae and oligochaetes in the muddy bottom.

**FIGURE 22** | Detail of head of *Rhamphichthys hahni*, MZUSP 59297, rio Novo at Brejo de Santa Sofia, Mato Grosso do Sul, Brazil.
(Ringuelet et al., 1967, Hahn et al., 2004). Willink et al. (2000) reports *R. hahni* living under water hyacinths in swamps of the lowlands of Brazilian Pantanal. Presents paternal care and offspring from October to February in the upper Paraná, gonads mature at 444 mm SL in females and 368 mm SL in males (Suzuki et al., 2004).

From the La Plata River region some specimens exhibited an asymmetrical position of the eyes, similar but in a minor degree to what was reported for the apteronotid *Orthosternarchus tamandua* by Hilton et al. (2007). As for example MACN 6386 (330 mm LEA) which has a preorbital distance of 46.4% of head length on the left side and 53.3% on the right side.

Also, from the La Plata region a specimen of *R. hahni* (MPL 6556, 325 mm LEA) was being parasitized by the copepod genus *Lernaea*. The parasite had about 40 mm found attached inside its gill chamber leaving its posterior body by the opercula. The relationship between Gymnotiformes and this parasite is apparently rare (Takemoto et al., 2009).

**FIGURE 23 | *Rhamphichthys hahni*, FMNH 108066, 280 LEA, Río Paraguay at Estância Voluntad in Puerto Voluntad, Alto Paraguay, Paraguay.**

**FIGURE 24 | Detail of the head of *Rhamphichthys hahni*, FMNH 108066, Río Paraguay at Estância Voluntad in Puerto Voluntad, Alto Paraguay, Paraguay.**
Electric organ discharge. According to Caputi et al. (1994), *R. hahni* (identified as *R. rostratus*) has a tetraphasic discharge with 2.5 ms duration (50±0.2 Hz). Caputi and collaborators studied specimens collected in the Río Uruguay at the gate for migrating fish of Salto Grande Dam (Salto, Uruguay; Caputi et al., 1994:634) and identified as *Rhamphichthys rostratus* (see Caputi et al., 1994, 1999 for more details on EOD and the EO).

Material examined. Lower Uruguay: MCP 38709, 1 (1 specimen measured in Tab. 6, 280 mm LEA), Brazil, Rio Grande do Sul, Itaqui, rio Ibicuí, 29°24’S 56°42’W. Chaco: MACN 8034, 1, Argentina, Formosa, Parque Nacional del Pilcomayo, 25°04’S 57°58’W. Paraguay: FMNH 108066, 1 (1 specimen measured in Tab. 6, 280 LEA), Paraguay, Alto Paraguay, Río Paraguay at Estância Voluntad in Puerto Voluntad, 20°42’S 57°57’W. FMNH 108548, 2 (2 specimens measured in Tab. 6, 360–370 LEA), Brazil, Mato Grosso do Sul, rio Negro at road between Nhecolandia and highway BR-262, 19°17’10”S 57°03’23”W. MZUSP 24736, 1 (1 specimen measured in Tab. 6,
Taxonomic review of *Rhamphichthys*

480 mm LEA), Brazil, Mato Grosso, Coxipó da Ponte, rio Coxipó da Ponte, 18°38'S 56°03'W. MZUSP 24862, 1 (1 specimen measured in Tab. 6, 560 mm LEA), Brazil, Mato Grosso, Barão de Melgaço, rio Cuiabá at Bocaiúva, 16°11'S 55°57'W. MZUSP 26918, 1 (1 specimen measured in Tab. 6, 360 mm LEA), Brazil, Mato Grosso, fazenda Jofre at Transpantaneira highway 17°21'S 56°46'W. MZUSP 27739, 1 (1 specimen measured in Tab. 6, 470 mm LEA), Brazil, Mato Grosso do Sul, Coixim, rio Taquari, 18°30'S 54°45'W. MZUSP 52514, 1 (1 specimen measured in Tab. 6, 290 mm LEA), Brazil, Mato Grosso do Sul, rio Piquiri at Pantanal de Piau guas at fazenda Santo Antônio. MZUSP 59297, 2 (2 specimens measured in Tab. 6, 230–345 mm LEA, 1 cs), Brazil, Mato Grosso do Sul, Aquidauana, rio Novo at brejo de Santa Sofia, 19°36'S 56°27'W. NUP 2206, 3, Brazil, Mato Grosso, Chapada dos Guimarães, Manso reservoir, 14°41'S 55°32'. NUP 3162, 5, Brazil, Mato Grosso, Barão do Melgaço, baia Sinhá Mariana tributary to rio Cuiabá, 16°20'S 55°44'W. NUP 3482, 1, Brazil, Mato Grosso, Santo Antônio do Leverger, rio Cuiabá, 15°51'S 56°05'W. NUP 4137, 1, Brazil, Mato Grosso, rio Cuiabá. NUP 9892, 1, Brazil, Mato Grosso do Sul, Porto Murtinho, rio Amonguijá tributary to rio Paraguai, 21°41'10"S 57°52'53"W. UMMZ 208107, 10 (4 specimens measured in Tab. 6, 335–410 mm LEA), Paraguay, Central, rio Paraguay overflow at 1 km downstream Puente Remanso, 25°11'S 57°33'W. ZMB 19570, 2, Paraguay.

**Upper Paraná:** LBP 3096, 1, Brazil, Mato Grosso do Sul, Baitapora, rio Bahia, 22°43'19"S 53°17'11"W. LBP 9623, 1, Brazil, Mato Grosso do Sul, Angélica, riacho de Engano, 22°02'37"S 53°43'38"W. MZUSP 44062, 4 (4 specimens measured in Tab. 6, 420–600 mm LEA), Brazil, São Paulo, Rosana, rio Paranapanema at Rosana hydroelectric power plant, 22°35'S 52°52'W. NUP 356, 2, Brazil, Parana, Porto Rico, mouth of riacho Caracu in the rio Paraná, 22°45'S 53°15'W. NUP 417, 1, Paraná, Porto Rico, island in rio Paraná, 22°45'S 53°16'W. NUP 1708, 3, Brazil, Paraná, Formosa do Oeste, rio Piquiri, 24°11'S 53°19'W. NUP 3367, 1, Brazil, Mato Grosso do Sul, Taquaruçu, lagoa dos Patos, 22°49'S 53°33'W. NUP 9623, 2, Brazil, Mato Grosso do Sul, Taquaruçu, rio Samambaia tributary to rio Paraná, 22°39'14"S 53°11'52"W. **Lower Paraná:** MACN 1003, 1, Argentina, Buenos Aires, Río de La Plata, Dársena Norte at Buenos Aires, 34°35'S 58°21'W. MACN 4837, 1, Argentina, Buenos Aires, Río de La Plata. MACN 5941, Argentina, Buenos Aires, Pallermo. MACN 5943, 1, Argentina, Santa Fé, Maciel, Río Maciel, 32°27'S 60°50'W. MACN 5971, 1, Argentina, Chaco, Río Paraná Guazu, close to Arroyo Gutiérrez. MACN 5983, 4 (2 specimens measured in Tab. 6, 395–410 mm LEA), Santa Fé, Argentina, Rosario, Río Paraná at Rosario, 32°56'S 60°37'W. MACN 6184, 10, Argentina, Buenos Aires, Río de La Plata OSN. MACN 6386, 2 (1 specimen measured in Tab. 6, 330 mm LEA), Argentina, Buenos Aires, Río de La Plata OSN. MACN 6722, 4, Argentina, Buenos Aires, Río de La Plata at SEGBA filters. MLP 259, 1, Argentina, Buenos Aires, Río de La Plata. MACN 7228, 2, Argentina, Corrientes, Corza–Cuey. MHNG 2600.077, 1, Paraguay, Canendiyu, Salto Guairá, Río Paraná at Itaipu reservoir, 24°05'S 54°18'W. MLP 48, 1, Argentina, Buenos Aires, Magdalena, Río de La Plata at Punta Atalaya, 35°00'S 57°31'W. MLP 363, 1, Argentina, Buenos Aires, Río de La Plata. MLP 550, 1, Argentina, Buenos Aires, Río de La Plata. MLP 2850, 1, Argentina, Buenos Aires, Ensenada, Río de La Plata at Punta Lara, 34°49'S 57°55'W. MLP 3313, 1, Argentina, Buenos Aires, Ensenada, Río de La Plata at Punta Lara, 34°49'S 57°55'W. MLP 656, 1, Argentina, Buenos Aires, La Plata, Río Santiago, 34°51'S 57°52'W. MZUSP 23133, 1 (1 specimen measured in Tab. 6, 260 mm LEA),
Argentina, Buenos Aires, Río de La Plata (OSN Buenos Aires), 34°33’S 58°23’W. NUP 1515, 1, Brazil, Paraná, Santa Helena, rio Paraná Itaipu reservoir. NUP 1871, 1, Brazil, Paraná, Guairá, rio Paraná Itaipu reservoir. NUP 4664, Brazil, Paraná, Guairá, Rio São Francisco Verdadeiro, tributário do rio Paraná, 24°06’37’S 54°18’28”W. NUP 7890, 1, Brazil, Paraná, Candido Rondon, rio Paraná Itaipu reservoir. ZMB 31367, holotype of *Sternarchorhamphus hahni*, Argentina, Corrientes, Río Paraná near Corrientes.

*Rhamphichthys heleios* Carvalho & Albert, 2015

(Fig. 26–29; Tab. 7)


**Diagnosis.** *Rhamphichthys heleios* differs from all congeners by the presence of irregular dark rounded blotches along the lateral body surface over the lateral line, sometimes connected forming an irregular longitudinal dark stripe, vs. diagonally displaced dark bands on the ventrolateral surface of the body over this region sometimes faded in *R. lineatus*. It differs from *R. lineatus* by an overall dark, vs. light color pattern of the body. It differs from *R. rostratus* and *R. apurensis* by a short snout (50.5–55.1% of HL), vs. long snout (58.4–65.1% of HL); by low number of anal-fin rays (320–345), vs. high number of anal-fin rays (347–455). It differs from *R. drepanium*, *R. hahni*, *R. rostratus*, *R. apurensis*, and *R. pantherinus* by the absence of dark transversal saddles on the mid dorsum.

**Description.** Morphometrics and meristics given in Tab. 7. Adult body size small to moderate compared with other congeners, maximum size 400 mm LEA. Mouth subterminal. Snout relatively short and robust, size about half of head length. Dorsal profile of snout strongly convex from snout tip to nares; concave from this point to

---

**FIGURE 26** | Holotype of *Rhamphichthys heleios*, INPA 42309, 375 mm LEA, confluence of rio Amazonas and Solimões at Costa do Catalão, Amazonas, Brazil.
eye and convex from this point to supraoccipital. Anterior nares positioned terminally; posterior nares located closer to snout than eyes at about one third of length. Body profile almost straight to slightly concave dorsally. Ventral body profile slightly concave from anal–fin origin to end of anal fin. Greatest body depth slightly at vertical of posterior end of anal fin or posterior to end of body cavity. Body tapering posterior to mid body. Eyes relatively large and positioned laterally. Urogenital papilla developed and anteriorly positioned below eyes in specimens larger than 330 mm LEA. Urogenital papilla large. Posterior gas bladder reduced with thickened walls. Caudal appendage laterally compressed, its depth about three times its width.

**FIGURE 27** | Detail of the head of holotype of *Rhamphichthys heleios*, INPA 42309, 375 mm LEA, confluence of rio Amazonas and Solimões at Costa do Catalão, Amazonas, Brazil.

**FIGURE 28** | Paratype of *Rhamphichthys heleios*, juvenile, MCP 45545, 133 mm LEA, ilha do Martelo, Tefé, Amazonas, Brazil. Picture of the right side (figure horizontally inverted).

**Coloration in alcohol.** Ground color of dorsal and lateral surfaces of head and body light brown to pale yellow (Figs. 26–29). Head with scattered large dark brown blotches of about eye; snout mostly dark, ventral margin less pigmented. Dorsum of body dark, presenting darker irregular marks laterally displaced not forming saddles. Presence of large dark blotches over the midlateral surface of body running from humeral region to a vertical of the end of anal fin; blotches sometimes coalescent forming an irregular longitudinal stripe. Lateral line clearer forming an inconspicuous light longitudinal stripe. Two pairs of whitish stripes running on the lateral surface of body, one over and another below the midlateral region presenting the dark blotches. Lateroventral region brownish with darker rounded or vermiculous blotches over pterygiophores region. Anal fin mostly clear or hyaline, with scattered chromatophores, these forming round blotches on the proximal and posterior regions. Pectoral fin clear with darkish irregular bars. Caudal appendage light brown with scattered darker blotches.

**Geographical distribution.** *Rhamphichthys heleios* is known from the Solimões and Amazon Rivers in Brazil upstream of the mouth of the Madeira River (Fig. 30; Tab. 1). It is also known from a single locality in the Guaporé River in Brazil. It inhabits mostly lakes in the floodplain of large rivers.
**TABLE 7** | Morphometric and meristic data for *Rhamphichthys heleios*. H = holotype, SD = standard deviation, n = number of specimens.

<table>
<thead>
<tr>
<th></th>
<th>H</th>
<th>n</th>
<th>Range</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length to end of anal fin (LEA)</td>
<td>333</td>
<td>5</td>
<td>320–400</td>
<td>355.3</td>
<td>–</td>
</tr>
<tr>
<td><strong>Percents of LEA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anal-fin length</td>
<td>90.1</td>
<td>6</td>
<td>88.0–90.1</td>
<td>89.1</td>
<td>0.8</td>
</tr>
<tr>
<td>Body depth</td>
<td>7.8</td>
<td>6</td>
<td>7.5–8.8</td>
<td>8.2</td>
<td>0.5</td>
</tr>
<tr>
<td>Pectoral-fin length</td>
<td>4.8</td>
<td>6</td>
<td>4.3–5.1</td>
<td>4.8</td>
<td>0.2</td>
</tr>
<tr>
<td>Head length</td>
<td>12.0</td>
<td>6</td>
<td>11.4–13.0</td>
<td>12.4</td>
<td>0.6</td>
</tr>
<tr>
<td>Caudal filament length</td>
<td>16.9</td>
<td>3</td>
<td>12.7–16.9</td>
<td>14.5</td>
<td>2.2</td>
</tr>
<tr>
<td>Caudal filament depth</td>
<td>1.7</td>
<td>5</td>
<td>1.5–2.0</td>
<td>1.8</td>
<td>0.1</td>
</tr>
<tr>
<td><strong>Percent of head length</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Interorbital distance</td>
<td>12.3</td>
<td>6</td>
<td>10.3–14.9</td>
<td>12.2</td>
<td>1.7</td>
</tr>
<tr>
<td>Snout length</td>
<td>52.8</td>
<td>6</td>
<td>50.5–55.1</td>
<td>52.5</td>
<td>1.5</td>
</tr>
<tr>
<td>Postorbital length</td>
<td>45.9</td>
<td>6</td>
<td>41.1–45.9</td>
<td>44.1</td>
<td>1.7</td>
</tr>
<tr>
<td>Eye diameter</td>
<td>5.4</td>
<td>6</td>
<td>5.1–6.5</td>
<td>5.8</td>
<td>0.5</td>
</tr>
<tr>
<td>Post. nares length</td>
<td>19.0</td>
<td>6</td>
<td>16.2–19.0</td>
<td>17.9</td>
<td>0.9</td>
</tr>
<tr>
<td>Branchial opening</td>
<td>22.4</td>
<td>6</td>
<td>16.5–24.4</td>
<td>21.8</td>
<td>2.7</td>
</tr>
<tr>
<td><strong>Meristics</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anal-fin rays</td>
<td>342</td>
<td>5</td>
<td>320–345</td>
<td>357.8</td>
<td>15.0</td>
</tr>
<tr>
<td>Pectoral-fin rays</td>
<td>17</td>
<td>6</td>
<td>16–19</td>
<td>17.1</td>
<td>0.7</td>
</tr>
</tbody>
</table>

**FIGURE 30** | Distribution of *Rhamphichthys heleios* based on examined museum specimens. Red dot represents the type-locality.
Material examined. Amazonas lowlands: INPA 42309, holotype, 375 mm LEA, Brazil, Amazonas, Iranduba, confluence of rio Amazonas and Solimões at Costa do Catalão, 5 Feb 1998. INPA 17683, 1, paratype, 270 mm LEA, Brazil, Amazonas, Iranduba, ilha da Marchantaria, 19 Nov 1998. INPA 18321, 1, paratype, 370 mm LEA, Brazil, Amazonas, Alvarães, rio Japurá at comunidade Caborini, 24 Feb 2000. INPA 18323, 1, paratype, 530 mm LEA, Brazil, Amazonas, Alvarães, rio Japurá mouth of Lago Caxinguba at Reserva Mamirauá, 3 Feb 1999. INPA 18331, 1, paratype, 330 mm LEA, Brazil, Amazonas, rio Japurá at paraná Maiana, W. G. R. Crampton. INPA 18332, 1, paratype, 250 mm LEA, Brazil, Amazonas, Alvarães, rio Solimões at Vila Alencar at reserva Mamirauá, 9 Jul 2000. INPA 27611, 1, paratype, 235 mm LEA, Brazil, Amazonas, Manaus, rio Solimões at paraná do Xiborena, 12 Mar 1998. INPA 42308, 4 (4 specimens measured in Tab. 7, 333–400 mm LEA, 1 cs), paratype, 303–400 m LEA, collected with the holotype. MZUSP 115347, 1, 450 mm LEA, collected with holotype. INPA 42306, 1 (1 specimen measured in Tab. 7, 367 mm LEA), Brazil, Rondônia, Guarajá-Mirim, rio Mamoré downstream Surpresa, 11°43’S 65°05’W.

**Rhamphichthys lineatus** Castelnau, 1855

(Fig. 31–34; Tab. 8)

*Rhamphichthys lineatus* Castelnau, 1855:87 (original description, type-locality: Lake of Ucayali River, Peru).


*Iracema* sp. C. Albert, 2001:117 (Listed).

**Diagnosis.** *Rhamphichthys lineatus* differs from congeners, except *R. heleios*, by the absence of clearly marked saddles, *vs*. presence of sickle shaped or intercalated saddles. It differs from *R. heleios* by the absence of rounded dark lateral blotches over the lateral line region these sometimes coalescent forming a longitudinal stripe.

**Description.** Morphometrics and meristic given in Tab. 8. Adult body size moderate to large compared with other congeners, maximum size 530 mm LEA. Mouth subterminal. Snout relatively short and robust about half of head length. Dorsal profile of snout strongly concave in front of eye, head profile slightly convex posteriorly. Anterior nares positioned terminally; posterior nares located closer to snout than eyes at about one third of length. Body profile almost straight to slightly concave dorsally. Ventral body profile slightly concave from anal–fin origin to end of anal fin. Greatest body depth about midbody, tapering posterior to this portion. Caudal appendage short, rarely intact.
Eyes relatively small and positioned laterally, about nine times contained in postorbital length. Urogenital papilla developed and anteriorly positioned below eyes in specimens larger than 400 mm LEA. Urogenital papilla large in adults. Posterior gas bladder absent. Caudal appendage laterally compressed, its depth about three times its width.


Coloration in alcohol. Ground color of dorsal and lateral surfaces of head and body light brown to pale yellow (Figs. 31–34). Head with scattered dark chromatophores mostly in dorsal region, ventral region less pigmented. Dorsum of body darker lacking conspicuously formed saddles. Lateral region with scattered chromatophores, clear areas forming white stripes in the lateral line and one or two above the line of the anal fin pterygiophores. Faint dark bands sometimes present in the body. Anal fin mostly clear sometimes presenting dark irregular vermiculous areas, especially in juveniles (Fig. 34). Pectoral fin almost entirely clear or hyaline, sometimes with dark pigments forming irregular bars.
Geographical distribution. *Rhamphichthys lineatus* is known only from the Ucayali, Solimões, and Amazon rivers in Peru and Brazil, apparently not found in the Amazon River downstream mouth of Tapajós River in Brazil (Fig. 35). It is typically found in the main channel of these rivers or tributary lakes.

Electric organ discharge. The electric organ discharge of *Rhamphichthys lineatus* generates short-pulse-type EOD with a tetraphasic discharge varying in duration 1.5–2 ms mid-high range rates of 40–100 Hz (1.8 kHz) with little day night variation in the EOD rates (Crampton, Albert, 2006).

Material examined. Amazonas Lowlands: ANSP 189537, 1 (1 specimen measured in Tab. 8, 300 mm LEA), Brazil, Amazonas, rio Amazonas upstream Itacoatiara, 03°15'33"S 58°58'42"W. ANSP 189532, 1 (1 specimen measured in Tab. 8, 310 mm LEA), Brazil, Amazonas, rio Solimões below mouth of rio Purus, 03°38'41"S 61°27'48"W. CAS 36688, 1, Peru, Loreto, Caño Chancho near Pebas, 03°20'S 71°51'W. FMNH 114685, 4 in part (1 cs), Brazil, Amazonas, rio Amazonas between rio Madeira and paraná do Serpa, 03°16'36"S 58°35'09"W. INPA 4725, 1, Brazil, Amazonas, Lago do Castanho, Janauacá, 03°49'38"S 60°21'57"W. INPA 9381, 1, Brazil, Amazonas, Iranduba, rio Solimões Lago Comprido at ilha da Marchantaria, 03°14’S 59°56’W. INPA 15827, 3 (1 cs), Brazil, Amazonas, Alvarães, rio Japurá paraná Maiana at reserva
do Mamirauá, 02°16’S 66°23’W. INPA 27606, 1 (1 specimen measured in Tab. 8, 515 mm LEA), Brazil, Amazonas, Manaus, paraná do Xiborena at ilha do Catalão, 03°12’S 59°36’W. INPA 27607, 1 (1 specimen measured in Tab. 8, 430 mm LEA), Brazil, Amazonas, Manaus, Careiro da Várzea, Paraná do Rei, 03°09’S 59°36’W. INPA 27608, 2 (2 specimens measured in Tab. 8, 500 mm LEA), Brazil, Amazonas, Manaus, paraná do Curari, 03°14’S 59°56’W. MCP 33456, 1, Brazil, Amazonas, Alvarães, praia Caborini at confluence of rio Japurá and rio Solimões, 03°07’08”S 64°47’18”W. MCP 33457, 3 (1 cs), paraná Maiana at lago Mamirauá system. MNHN 3982, holotype of *Rhamphichthys lineatus*, Peru, lake near Río Ucayali. MUSM 6639, 1, Peru, Loreto, market at Iquitos, 03°42’S 73°14’W. MZUSP 102703, 1, Brazil, Amazonas, rio Solimões downstream mouth of rio Purus, 03°36’16”S 61°21’12”W. UF 116566, 1, Peru, Loreto, Maynas, Rio Nanay. USNM 320022, 2, Brazil, Amazonas, creek connecting rio Solimões and rio Tefé with a black water lake about 15 miles E of Coari.

**TABLE 8** | Morphometric and meristic data for *Rhamphichthys lineatus*. H = holotype, SD = standard deviation, n = number of specimens.

<table>
<thead>
<tr>
<th></th>
<th>H</th>
<th>n</th>
<th>Range</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length to end of anal fin (LEA)</td>
<td>530</td>
<td>7</td>
<td>265–530</td>
<td>407</td>
<td>–</td>
</tr>
<tr>
<td><strong>Percents of LEA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anal-fin length</td>
<td>90.5</td>
<td>7</td>
<td>87.1–92.0</td>
<td>89.2</td>
<td>1.7</td>
</tr>
<tr>
<td>Body depth</td>
<td>7.4</td>
<td>8</td>
<td>7.4–10.6</td>
<td>9.3</td>
<td>1.0</td>
</tr>
<tr>
<td>Pectoral-fin length</td>
<td>5.0</td>
<td>8</td>
<td>4.7–6.2</td>
<td>5.3</td>
<td>0.4</td>
</tr>
<tr>
<td>Head length</td>
<td>10.9</td>
<td>8</td>
<td>10.3–13.1</td>
<td>11.8</td>
<td>1.0</td>
</tr>
<tr>
<td>Caudal filament length</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Caudal filament depth</td>
<td>–</td>
<td>1</td>
<td>1.7–1.7</td>
<td>1.7</td>
<td>–</td>
</tr>
<tr>
<td><strong>Percents of head length</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Interorbital distance</td>
<td>12.4</td>
<td>8</td>
<td>11.2–15.3</td>
<td>12.7</td>
<td>1.4</td>
</tr>
<tr>
<td>Snout length</td>
<td>53.1</td>
<td>8</td>
<td>52.1–56.0</td>
<td>54.2</td>
<td>1.2</td>
</tr>
<tr>
<td>Postorbital length</td>
<td>42.4</td>
<td>8</td>
<td>41.8–46.9</td>
<td>43.0</td>
<td>1.6</td>
</tr>
<tr>
<td>Eye diameter</td>
<td>5.5</td>
<td>8</td>
<td>4.5–6.9</td>
<td>5.3</td>
<td>0.7</td>
</tr>
<tr>
<td>Post. nares length</td>
<td>15.5</td>
<td>8</td>
<td>15.3–19.0</td>
<td>17.0</td>
<td>1.1</td>
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<tr>
<td>Branchial opening</td>
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<td>8</td>
<td>17.5–24.6</td>
<td>21.0</td>
<td>2.4</td>
</tr>
<tr>
<td><strong>Meristic</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anal-fin rays</td>
<td>381</td>
<td>6</td>
<td>341–381</td>
<td>354.7</td>
<td>15.5</td>
</tr>
<tr>
<td>Pectoral-fin rays</td>
<td>17</td>
<td>8</td>
<td>17–19</td>
<td>18</td>
<td>0.7</td>
</tr>
</tbody>
</table>
**FIGURE 35** | Distribution of *Rhamphichthys lineatus* based on examined museum specimens. Red dot represents the approximate type-locality.

*Rhamphichthys pantherinus* Castelnau, 1855

(Fig. 36–47; Tab. 9)

*Rhamphichthys pantherinus* Castelnau, 1855:86 (original description, type-locality: d'un lac pres du Ucayali).
—Günther, 1870:5 (as senior synonym of *R. marmoratus*).
—Cope, 1878:682 (listed).
—Ferraris, 2003:496 (listed as junior synonym).
—Ortega *et al*., 2011:41 (listed).
—Ferraris *et al*., 2017:28 (listed as senior synonym of *R. marmoratus*).
—Meza-Vargas *et al*., 2021:21 (listed).

*Rhamphichthys marmoratus* Castelnau, 1855:86 (original description, type-locality: l’Araguay (Araguaia River), Brazil.
—Günther, 1870:5 (as a junior synonym of *R. pantherinus*).
—Eigenmann, Ward, 1905:168 (listed).
—Santos *et al*., 1984:19 (illustrated and briefly described).
—Santos *et al*., 2004:105 (illustrated and briefly described).
—Ferraris, 2003:496 (listed).
—Camargo *et al*., 2004:139 (listed).
—Lucinda *et al*., 2007:81 (listed).
—Anjos *et al*., 2008:204 (listed).
—Montrag *et al*., 2009:246 (listed).
—Ferreira *et al*., 2011:6 (listed).
—Ortega *et al*., 2011:41 (listed).
—Carvalho, Albert, 2015:40 (comparative material examined).
—Crampton *et al*., 2016: (outgroup comparison).
—Tagliacollo *et al*., 2016:29, fig. 5 (phylogenetic relationships).
—Giora, Carvalho, 2018:1060 (accessory electric organ anatomy).
—DoNascimento *et al*., 2017:66 (listed).
Taxonomic review of *Rhamphichthys*


**Diagnosis.** *Rhamphichthys pantherinus* differs from its congeners, except *R. apurensis* and *R. rostratus* by a color pattern with intercalated dark saddles on the mid dorsum, not paired at the midline, *vs.* sickle–shaped saddles (*R. drepanium* and *R. hahni*) or no saddles (*R. lineatus* and *R. heleios*). It differs from *R. rostratus* and *R. apurensis* by the relatively shorter snout 51.4–59.1% of HL, *vs.* 58.4–62.7 of HL (Fig. 47); and by the number of caudal vertebrae 94–100, *vs.* 101–115 (Tab. 5).

![FIGURE 36](image1.png) Holotype of *Rhamphichthys pantherinus*, MNHN 3993, 730 mm LEA, lake near Río Ucayali, Peru.

![FIGURE 37](image2.png) Detail of the head of holotype of *Rhamphichthys pantherinus*, MNHN 3993, 730 mm LEA, lake near Río Ucayali, Peru.
FIGURE 38 | Holotype of *Rhamphichthys marmoratus*, MNHN 3959, Rio Araguaia, Brazil.

FIGURE 39 | Detail of the head of holotype of *Rhamphichthys marmoratus*, MNHN 3959, rio Araguaia, Brazil.

FIGURE 40 | *Rhamphichthys pantherinus*, ANSP 182785, 410 mm LEA, Río Manapiare at mouth of Caño Yutaje 14 km NW of San Juan de Manapiare, Amazonas, Venezuela.
Description. Morphometric and meristic given in Tab. 9. Adult body size large compared with other congeners, maximum size 850 mm LEA. Mouth subterminal. Snout relatively short about half of head length. Dorsal profile of snout strongly concave in front of eye, head profile slightly convex posteriorly, some specimens with almost straight profile from snout to end of head. Anterior nares positioned terminally; posterior nares located closer to snout than eyes at about one third of length. Body profile almost straight to slightly concave dorsally. Ventral body profile slightly concave from anal-fin origin to end of anal fin. Greatest body depth slightly posterior to end of body cavity. Body tapering posterior to mid body. Eyes small. Urogenital papilla developed and anteriorly positioned below eyes in specimens larger than 440 mm LEA. Urogenital papilla relatively small in adults. Posterior gas bladder reduced, presenting thin membranous walls. Caudal appendage laterally compressed, its depth about three times its width, relatively short.


Coloration in alcohol. Ground color of dorsal and lateral surfaces of head and body pale yellow to dark brown (Figs. 36–47). Head with scattered dark brown blotches of about eye size; snout mostly dark dorsally, its ventral margin less pigmented. Body with dark intercalated saddles reaching ventral to the lateral line. Presence of lateral dark lateral bands, slightly diagonally placed along the long body axis. Bands sometimes contacting
the dorsal saddles; bands diffuse over pterygiophores region, extending to the proximal region of the anal fin rays. Anal fin mostly clear or hyaline except for scattered pigments these forming longitudinal stripes; sometimes presenting no pigments or scattered dark spots limited to the posterior end of anal fin. Pectoral fin clear or hyaline with broad dark bars. Caudal appendage with dark vertically elongate blotches.

**Geographical distribution.** *Rhamphichthys pantherinus* is the most widespread and common species of the genus, known from the Amazon and several of its tributaries, upper Orinoco, Tocantins, Essequibo, and coastal northern drainages of Brazil from the Turiaçu to Paranaiba drainages (Fig. 48; Tab. 1). In the Orinoco River basin is restricted to its upper portions on the Guiana Shield of Venezuela and in the upper Meta and Guaviare River basins (Fig. 48). This species inhabits a variety of habitats including channels and flood plain lakes of medium to large-sized rivers.

**TABLE 9** | Morphometric and meristic data for *R. pantherinus*. H = holotype of *R. pantherinus*; H1 = holotype of *R. marmoratus*; H2 = holotype of *Rhamphichthys atlanticus*; H3 = *Rhamphichthys longior*. SD = Standard deviation; n = number of specimens.

<table>
<thead>
<tr>
<th></th>
<th>H</th>
<th>H1</th>
<th>H2</th>
<th>H3</th>
<th>n</th>
<th>Range</th>
<th>Mean</th>
<th>SD</th>
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<tbody>
<tr>
<td><strong>Length to end of anal fin (LEA)</strong></td>
<td>730</td>
<td>–</td>
<td>690</td>
<td>850</td>
<td>52</td>
<td>285–850</td>
<td>452.5</td>
<td>–</td>
</tr>
<tr>
<td><strong>Percents of LEA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Anal-fin length</td>
<td>92.8</td>
<td>–</td>
<td>89.8</td>
<td>89.4</td>
<td>52</td>
<td>74.6–101.4</td>
<td>89.7</td>
<td>3.9</td>
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<tr>
<td>Body depth</td>
<td>8.4</td>
<td>–</td>
<td>7.6</td>
<td>5.9</td>
<td>52</td>
<td>4.8–10.8</td>
<td>8.6</td>
<td>1.2</td>
</tr>
<tr>
<td>Pectoral-fin length</td>
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<td>–</td>
<td>4.2</td>
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<td>52</td>
<td>3.6–6.5</td>
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</tr>
<tr>
<td>Head length</td>
<td>10.7</td>
<td>–</td>
<td>12.2</td>
<td>9.1</td>
<td>53</td>
<td>9.2–15.2</td>
<td>12.6</td>
<td>1.3</td>
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<td>Caudal filament length</td>
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<td>–</td>
<td>–</td>
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<td><strong>Percents of head length</strong></td>
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<td>53</td>
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<td>52.6</td>
<td>58.1</td>
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<td>51.4–59.1</td>
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<td>40.0</td>
<td>43.3</td>
<td>53</td>
<td>37.5–46.7</td>
<td>41.9</td>
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<td>15.5</td>
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<td>53</td>
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<td>53</td>
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<td>Anal-fin rays</td>
<td>369</td>
<td>381</td>
<td>430</td>
<td>395</td>
<td>32</td>
<td>360–455</td>
<td>396.7</td>
<td>23.3</td>
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<td>Pectoral-fin rays</td>
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<td>18</td>
<td>19</td>
<td>19</td>
<td>32</td>
<td>17–22</td>
<td>18.4</td>
<td>1.3</td>
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Remarks on synonymy. *Rhamphichthys pantherinus* is proposed here to have three junior synonyms: *R. marmoratus* (Figs. 38–39), *R. atlanticus* (Figs. 42–43), and *R. longior* (Figs. 44–45). *Rhamphichthys pantherinus* is the senior synonym as Günther (1870) serves as first reviser treating. Later, starting with Eigenmann, Eigenmann (1891:62), *R. marmoratus* was treated as valid over *R. pantherinus*, perhaps due to page precedence. This was perpetuated for a long time in the taxonomic history of *Rhamphichthys* (see synonym list above). Apparently, this case does not fit the *nomen oblitum* ICZN’s rule since *R. pantherinus* was cited as valid in at least two publications (of which we aware) since 1899 (Oliveira, 1988; Ortega *et al.*, 2011). These species have been considered

**FIGURE 42** | *Rhamphichthys pantherinus*, holotype of *Rhamphichthys atlanticus*, MZUSP 43612, 690 LEA, lago Viana tributary to Pindare-Mearim System, Maranhão, Brazil.

**FIGURE 43** | Detail of the head of *Rhamphichthys marmoratus*, holotype of *Rhamphichthys atlanticus*, MZUSP 43612, 690 LEA, lago Viana tributary to Pindare-Mearim system, Maranhão, Brazil.
FIGURE 44 | *Rhamphichthys pantherinus*, holotype of *Rhamphichthys longior*, MZUSP 48507, 850 mm LEA, lago Paru at confluence of rio Trombetas and rio Paru-do-Oeste, Pará, Brazil.

FIGURE 45 | Detail of the head of *Rhamphichthys pantherinus*, holotype of *Rhamphichthys longior*, MZUSP 48507, 850 mm LEA, lago Paru at confluence of rio Trombetas and rio Paru-do-Oeste, Pará, Brazil.
synonyms in the past by several authors (Mago-Leccia, 1994; Triques, 1999; Ferraris, 2003). After examining an extensive quantity of material and types of both species we confirm and agree with these synonymizations. Rhamphichthys atlanticus was diagnosed by Triques (1999:3) by a uniform light brown anal fin without dark marks and a membranous swim bladder overlapped by visceral organs. The first character is highly variable within R. pantherinus throughout its distribution and does not diagnose the R. atlanticus allopatric population as separate from the others. The anal-fin coloration character is shared by R. pantherinus, R. apurensis, and R. rostratus, and does not diagnose R. atlanticus from R. pantherinus. Rhamphichthys longior was also described by Triques (1999:4) based on two measurements: a shallower body depth and a shorter head length. Under an extensive review of material these characters seem to represent the end of a cline in variation observed in very large specimens (Fig. 49; Tab. 9), and do not support a diagnosis for R. longior. In addition, large specimens are frequently stored coiled in jars, impairing accurate measurement of overall body size such as LEA or anal-fin length. A PCA was done using populations of R. pantherinus including types of R. pantherinus, R. marmoratus, R. longior (Trombetas), and R. atlanticus (Mearim). No morphological differences were found to support the existence of distinct species within this group. Despite their disjunct distribution, the populations in the Amazon and Northeastern Brazil basins exhibit relatively little morphological differences. A PCA was conducted using 11 morphometric characters to compare geographic groups of R. pantherinus, including types of the putative R. atlanticus and R. longior species. The first three principal components (PC 1, PC 2 and PC 3) explain most of the variance (69.5%; Tab. S7). Scores were plotted for PC 1 vs. PC 2 and PC 1 vs. PC 3 show large morphometric overlap of geographic populations of R. pantherinus. Strong loadings separating some of these groups are the interorbital standard length (SL), anal fin length; preorbital length (PR), distance to posterior nares (PN); branchial opening (BO) and body depth (BD) (Fig. 50; Tab. S8). A Multivariate Analyses of Variance (MANOVA) was done using the PC scores of the first three axes of the PCA. Populations of Rhamphichthys from Trombetas drainage are statistically different from most populations of Rhamphichthys pantherinus except from Negro basin and Mearim system (Tab. S9; Wilks’ λ: 0.1946; P< 0.001; F15,105.3 = 5.681).

Material examined. Orinoco Guiana Shield: ANSP, 182785, 1, Venezuela, Amazonas, Río Manapiare at mouth of Caño Yutaje 14 km NW of San Juan de Manapiare, 05°26’11"N 66°06’45"W. AUM 41505, 1, same collection site of ANSP 182785. Orinoco Llanos. IavH-P 19414, 2, Colombia, Meta, La Macarena, Lake at left margin of río Guayabero, 02°17’35"N 73°52’32"W. Essequibo: AUM 48696, 1, Guyana, Upper Takutu-Upper Essequibo, Aruwa falls on Rupununi river 15 miles upstream of Yupukari, 03°30’06"N 59°20’22"W. AUM 44834, 1, Guyana, Upper Takutu-Upper Essequibo, Rupununi river at Yupukari, 03°39’53"N 59°20’36"W. AUM 49772, 1, Guyana, Upper Takutu-Upper Essequibo, Aruwa creek, 03°30’N 59°20’W. AUM 49650, 1, Guyana, Upper Takutu-Upper Essequibo, Rupununi river at Kwatamang landing, 03°55’03”N 59°06’01”W. AUM 49885, 2, Guyana, Upper Takutu-Upper Essequibo, borrow pit 12 km S of Annai, Rupununi River, 03°56’36”N 59°13’40”W. Rio Negro: ANSP 199237, Brazil, Amazonas, rio Jauaperi 10.3 km upriver of São Francisco, 01°35’08”S 61°28’35”W. ANSP 199238, 1, Brazil, Amazonas,
rio Negro 3 km upriver from paraná das Onças, 13 km downriver of Novo Caioe, 01°50'S 61°24'W. FMNH 114684, 1, Brazil, Amazonas, rio Branco between tributary rio Viruá and mouth in the rio Negro, 01°16'45"S 61°50'33"W. INPA 4429, 1 (1 specimen measured in Tab. 9, 495 mm LEA), Brazil, Amazonas, Manaus, rio Negro, 03°08'S 60°03'W. MCP 26375, 5 (4 specimens measured in Tab. 9, 308–355 mm LEA, 1 cs), Brazil, Amazonas, rio Negro 15.0 miles downstream Moura, 01°33'28"S 61°34'15"W. MCP 26304, 1, Brazil, Amazonas, rio Jauaperi 9.6 km upstream São Francisco, 01°34'46"S 61°28'38"W. MZUSP 44823, 1, Brazil, Amazonas, rio Negro at Anavilhanas, 02°42'S 60°45'W. Amazon Guiana Shield: AUM 35507, 1, Upper Takutu–Upper Essequibo, Pirara River tributary of the Ireng River at Pirara, 03°37'17"N 59°40'29"W. MCP 46090, 1, Brazil, Roraima, rio Anauá tributary to rio Branco near Rorainópolis, MNRJ 14447, 1, Brazil, Roraima, rio Jatapu, 00°45'N 59°17"W. Western Amazon Piedmont: IAvH-P 6062, 1, Colombia, Caquetá, Araracuara, Río Caquetá, 00°35'S 72°26'W. FMNH 103361, 2, Ecuador, Napo, tributary to Rio Cuyabeno about 3 km upstream Laguna Grande, 00°00'N 76°12'W. FMNH 103362, 1, Ecuador, Napo, Rio Águas Negras about 2 km S of Marian, 00°02'S 76°18'W. Amazonas lowlands: ANSP 120347, 2, Peru, Pucallpa, 08°23'S 74°32"W. ANSP 178359, 1, Peru, Loreto, Río Yanayacu downstream from Emerald Forest 25 miles S of Iquitos, 04°14'54"S 73°17'54"W. ANSP 178463, 1, Peru, Loreto, Río Nanay at Pampa Chica village about 4.5 km W of Iquitos, 03°45'09"S 73°17'00"W. ANSP 189536, 2, Brazil, Amazonas, rio Amazonas 24.1 km upriver of Itacoatiara, 21.3 km downriver of mouth of Madeira 03°16'42"S 58°35'18"W. ANSP 189557, 1, Brazil, Pará, rio Trombetas 30.5 km downstream of Porto Trombetas 6.2 km upstream vila Aracuá, 01°31'17"S 56°08'47"W. ANSP 199236, 1, Brazil, Amazonas, rio Juruá, 10 km downriver of Pauapixuna, 18.6 km upriver of Tamanicoa, 02°37'59"S 65°45'08"W. ANSP 199239, 1, Brazil, Pará, rio Trombetas, 7.6 km downstream of Santa Cecilia 17.8 km upstream of Orixinimá, 01°38'04"S 55°58'48"W. ANSP 199241, 1, Brazil, Amazonas, rio Japurá, 14 km upriver of rio Solimões, 10 km upriver of Serraria, 02°58'21"S 64°48'56"W. ANSP 199242, 1, Brazil, Amazonas, rio Solimões 21.3 km downriver of Tamanicoa, 15.2 km upriver of Pallheta, 02°35'21"S 65°30'46"W. FMNH 54704, 1, Brazil, Pará, rio Tapajós at Santarém, 02°24'S 54°46"W. FMNH 111592, 1, Peru, Loreto, Río Yanayacu sobre 2.3 km north its mouth in the Río Maranón, 04°40'0'S 73°50"W. FMNH 114687, 2, Brazil, Amazonas, rio Purus upstream from rio Solimões, 04°03'48"S 61°33'50"W. FMNH 114686, 1, Brazil, Pará, rio Trombetas between tributaries Cuminá and lago Arixica, 01°32'40"S 56°01'07"W. FMNH 115522, 3 in part (2 specimens measured in Tab. 9, 445–445 mm LEA), Brazil, Pará, rio Trombetas between tributaries lago Bacabal and lago Arixica, 01°31'10"S 56°08'59"W. ICNMCN 5220, 1, Colombia, Amazonas, Leticia, Quebrada Yaguaraca km 8 on road to Leticia. ICNMCN 16424, 1, Colombia Amazonas, Puerto Nariño, Río Loreto Yacu. INPA 685, 1 (1 specimen measured in Tab. 9, 415 mm LEA), Brazil, Pará, rio Trombetas between tributaries lago Bacabal and lago Arixica, 01°31'10"S 56°08'59"W. ICNMCN 5220, 1, Colombia, Amazonas, Leticia, Quebrada Yaguaraca km 8 on road to Leticia. ICNMCN 16424, 1, Colombia Amazonas, Puerto Nariño, Río Loreto Yacu. INPA 685, 1 (1 specimen measured in Tab. 9, 415 mm LEA), Brazil, Pará, rio Trombetas between tributaries lago Bacabal and lago Arixica, 01°31'10"S 56°08'59"W. ICNMCN 5220, 1, Colombia, Amazonas, Leticia, Quebrada Yaguaraca km 8 on road to Leticia. ICNMCN 16424, 1, Colombia Amazonas, Puerto Nariño, Río Loreto Yacu. INPA 685, 1 (1 specimen measured in Tab. 9, 415 mm LEA), Brazil, Pará, Santarém, rio Curuá–Una 80 km downstream Curuá–Una Dam. INPA 4815, 1 (1 specimen measured in Tab. 9, 632 mm LEA), Brazil, Amazonas, Careiro da Várzea, ilha do Careiro at paraná do Rei, 03°09'S 59°36"W. INPA 5077, 1 (1 specimen measured in Tab. 9, 615 mm LEA), Pará, Orixinimá, rio Trombetas at lago do Salgado, 01°28'55°58"W. INPA 6497, 1 (1 specimen measured in Tab. 9, 400 mm LEA), Brazil, Pará, Tucuruí, rio Tocantins at lago Tãuá. INPA 9349, 1 (1 specimen measured in Tab. 9, 375 mm LEA), Brazil, Para, Tucuruí, rio Tocantins at Lagoinho. INPA 9363, 1 (1
specimen measured in Tab. 9, 495 mm LEA), Brazil, Pará, Rio Tocantins at Icangui. INPA 15825, 2 (1 specimen measured in Tab. 9, 615 mm LEA), Brazil, Amazonas, rio Tefé at Toco Preto. INPA 17684, 2, Brazil, Amazonas, Manaus, rio Solimões at Costa do Catalão. INPA 18329, 1 (1 specimen measured in Tab. 9, 350 mm LEA), Brazil, Amazonas, rio Janauacá, 03°23’S 60°16’W. MCP 24814, 2 (2 specimens measured in Tab. 9, 310–405 mm LEA), Brazil, Amazonas, rio Madeira. MCP 33380, 4, Brazil, Amazonas, canal do lago Mamirauá at the comunidade Boca do Lago Mamirauá, 03°06’37’S 64°47’49”W. MCP 33392, 1, Brazil, Amazonas, rio Tefé at ilha do Martelo, 03°46’49”S 64°59’29”W. MCP 33450, 1, Brazil, Amazonas, praia Caborini at confluence of rio Solimões and rio Jaquirá, 03°07’08”S 64°47’18”W. MCP 33454, 4 (4 specimens measured in Tab. 9, 303–352 mm LEA), Brazil, Amazonas, Alvaraes, rio Telfé at west margin between mouth of lago Mamirauá and mouth of raraná Jaquirá, 03°07’34”S 64°47’18”W. MCP 33458, 1, Brazil, Amazonas, Tefé, rio Tefé 1 km downstream mouth of rio Curupira, 03°41’53”S 65°00’57”W. MCP 33459, 1, Brazil, Amazonas, Tefé, lago Tefé at comunidade Nogueira, 03°17’58”S 64°46’21”W. MCP 39982, 1 (1 specimen measured in Tab. 9, 322 mm LEA), Brazil, Acre, Bujari, rio Riozinho do Andirá at highway CR–364 between rio Branco and Sena Madureira, 09º43’21”S 68°07’45”W. MNHN 3993, holotype of *Rhamphichthys pantherinus*, Peru, lake near Rio Ucayali. MPEG 5373, 1, Brazil, Pará, Monte Alegre, Lago Grande de Monte Alegre, 02°14’S 54°09’W. MPEG 5565, 1, Brazil, Amazonas, Tefé, rio Solimões at Costa Capivara. MPUJ 6012, 1, Colombia, Meta, Casibare, Lake at río Manacacá, 03°14’50”N 72°58’18”W. MUSM 571, 1, Peru, Ucayali, Pucallpa, Río Ucayali at Masisea 08°33’S 74°20’W. MUSM 1645, 5, Peru, Ucayali, Río Ucayali, Ucayilla. MUSM 6813, 2, Peru, Loreto, Río Huallaga at Yurimaguas, 05°53’S 76°06’W. MUSM 6640, 2, Peru, Loreto, Iquitos, market at Iquitos. MUSM 13433, 3 (2 specimens measured in Tab. 9, 285–296 mm LEA), Peru, Laguna Cachibococha at Coronel Portillo, 08°19’S 74°34’W. MUSM 14239, 1 (1 specimen measured in Tab. 9, 315 mm LEA), Peru, Loreto, Maynas, Río Aguaro at Puesto de Vigilância Castana, 00°48’14”S 75°14’26”W. MZUSP 9515, 1, Brazil, Pará, rio Tapajós at Aveiro. MZUSP 22155, 1, Brazil, Amazonas, rio Madeira at Humaitá. MZUSP 23373, 1, Brazil, Amazonas, Fonte Boa, igarapé Manduaçu at paraná de Iupiá NW of Fonte Boa, 02°31’S 66°06’W. MZUSP 48507, holotype of *Rhamphichthys longior*, Brazil, Pará, Oriximiná, lago Paru on confluence with rio Trombetas and rio Paru do Oeste, 01°31’S 56°01’W. MZUSP 5630, 3 paratypes of *Rhamphichthys longior* (3 specimens measured in Tab. 9, 710–760) collected with holotype. MZUSP 44492, Brazil, Pará, Belo Monte, rio Xingu near rapids at rocky pools, 03°07’S 51°42’W. UFAM uncatologued, 1, Brazil, Amazonas, rio Jurumá upstream Carauari. UMMZ 230841, 1, Peru, Loreto, rio Momón near Bora Village, 03°40’S 73°16’W. USNM 284578, 2, Peru, Loreto, Yarina Cocha side cano, 08°16’S 74°36’W. USNM 284579, 1, Peru, Loreto, creek entering rio Manite about 10 km upriver from junction of río Manite and Amazonas, 03°32’S 72°40’W. USNM 29914, 1, Brazil, Amazonas, São José, lago do Castanho at Janauacá. **Mamoré-Madre de Dios piedmont:** MNHN 1988–1028, 1, Bolivia, Puerto Almacén, Rio Ibare tributary to río Mamoré, 14°52’S 64°58’W. **Guaporé-Itenez:** FMNH 54702, 3, Bolivia, San Joaquin, 13°02’S 64°38’W. INPA 9370
(1 specimen measured in Tab. 9, 435 mm LEA), Brazil, Rondônia, rio Guaporé at Surpresa. INPA 9371, 1 (1 specimen measured in Tab. 9), Brazil, Rondônia, Guarajá-Mirim, rio Mamoré downstream Surpresa, 11°43'S 65°05'W. Xingu: MNRJ 33653, 2 (2 specimens measured in Tab. 9, 335–353 mm LEA), Brazil, Mato Grosso, Cumaru do Norte, rio Trairão tributary to rio da Ponte 15 km S of Cumaru do Norte, 07°56'S 50°47'W. MNRJ 33659, 1 (1 specimen measured in Tab. 9, 341 mm LEA), Brazil, Pará, Tucuma, small creek tributary to igarapé Carapaná on highway PA-279, 06°44'S 51°09'W. MNRJ 33661, 1, Brazil, Pará, São Felix do Xingu, Igarapé Magoarizinho tributary to rio Fresco, 06°42'00"S 51°33'51"W. MZUSP 36016, 1, Brazil, Pará, São Felix do Xingu, rio Fresco at aldeia Gorotire, 07°46'S 51°08'W. Tocantins-Araguaia. INPA 9364, 2 (2 specimen measured in Tab. 9, 375–595 mm LEA), Brazil, Pará, rio Tocantins between Itupiranga and Nova Ipixuna, 05°07'24"S 49°19'02"W. MNHN 3959, holotype of Rhamphichthys marmoratus, Brazil, rio Araguaia. MZUSP 22809, 1, Brazil, Mato Grosso, rio Araguaia at Santa Terezinha, 10°35'S 50°34'W. MZUSP 44680, 1, Brazil, Tocantins, rio Tocantins upstream Itaguatins, 05°46'S 47°31'W. Amazonas estuary and coastal drainages: MNRJ 12177, 3 (1 specimen measured in Tab. 9, 430 mm LEA), Brazil, Amapá, rio Aporema tributary to rio Araguari at fazenda Modelo do Aporema, 01°08'N 50°50'W. MPEG 2798, 5, Brazil, Pará, Cachoeira do Arari, mouth of rio Goiapi. MPEG 2969, 1, Brazil, Pará, Cachoeira do Arari, rio Goiapi, Consuelo, fazenda Santa Maria. MPEG 3036, 1, Brazil, Pará, Muana, iguarape Maguari Grande tributary to rio Anajás at Fazenda Campo Limpo. MPEG 3009, 1, Brazil, Maranhão, rio Turiaçu 1 km upstream posto Indígena Guajá, 03°07'S 46°02'W. MPEG 4504, 1, Brazil, Pará, rio Guamá at Ourém, 01°33'S 47°06'W. MPEG 4684, 2, Brazil, Pará, Ponta de Pedras, rio Pará, 01°24'S 48°48'W. MPEG 5466, 1, Brazil, Pará, Castanhal, rio Apei at Boa Vista do Apeu, 01°18'S 47°59'W. MPEG 6489, 1, Brazil, Pará, Caxianã, Estação Científica Ferreira Penna, 01°46'S 51°25'W. MPEG 6491, 2, Brazil, Pará, Caxianã, baía de Caxianã, 01°38'S 51°19'W. MPEG 7540, 2, Brazil, Pará, Ponta de Pedras, rio Quia–Paraná, at igarapé Baiano, 01°21'12"S 48°57'04"W. MPEG 8234, 1, Brazil, Pará, Ipixuna do Pará, 02°53'21"S 47°47'30"W. MPEG 8833, 1, Brazil, Pará, Portel, rio Anapu, 01°54'51"S 51°22'36"W. MPEG 9121, 1, Brazil, Pará, Paragominas, rio Capim, 03°19'27"S 48°35'53"W. MPEG 11388, 1,
Brazil, Pará, Melgaço, igarape Curuá tributary to Caxiuanã, 01°43'59"S 51°27'08"W. MPEG 18347, 2, Brazil, Pará, Almeirim, mouth of rio Paru, 01°32'5"S 52°37"W. MPEG 18688, Brazil, Pará, Santa Cruz do Arari, lago Arari, 00°39'9"S 49°09'W. MPEG 18690, 1, Brazil, Pará, Cachoeira do Arari, lago do Tatu. MPEG 18691, 2, Brazil, Pará, Cachoeira do Arari, rio Arari, 01°00'0"S 48°57"W. MPEG 18695, 1, Brazil, Pará, Cachoeira do arari, lago de Santa Cruz at headwaters of rio Goiapi. MPEG 18698, 2, Brazil, Pará, Cachoeira do Arari, lago Recreio. MZUSP 22272, 1, Brazil, Pará, igarapé Pacui in the highway BR-010 at km 97. MZUSP 43612, holotype of *Rhamphichthys atlanticus*, Brazil, Maranhão, lago do Viana Pindaré-Mearim system, 03°14'3"S 45°01'W. MZUSP 48508, paratype of *Rhamphichthys atlanticus*, collected with the holotype (1 specimen measured in Tab. 9, 650 mm LEA). MZUSP 44493, 2 (1 cs), Brazil, Pará, Castanhal, rio Apeu at Boa Vista do Apeu, 01°18'8"S 47°59'W. MZUSP 44686, 1, Brazil, Amapá, rio Araguari at Ferreira Gomes. MZUSP 44689, 1, Brazil, Pará, lake at igarapé Muru tributary to rio Tocantins downstream Tucurui, 03°46'0"S 49°41'W. MZUSP 104578, 1 (1 specimen measured in Tab. 9, 550 mm LEA), Maranhão, Caxias, rio Itapecuru, 05°02'44"S 43°24'45"W. MZUSP 104599, 2 (1 specimen measured in Tab. 9, 590 mm LEA), Brazil, Maranhão, Governador Eugenio Barros, rio Itapecuru, 05°26'37"S 43°52'03"W. Parnaíba. ANSP 88270, 1, Brazil, Piauí, rio Parnaíba at Teresina, 05°05'5"S 42°49'W. MZUSP 51112, 1, Brazil, Piauí, Teresina market.

**FIGURE 47** | Head of juveniles of *Rhamphichthys pantherinus*, UMMZ 230841, 125 mm LEA (above), and *Rhamphichthys rostratus*, UMMZ 216489, 110 mm LEA (below), showing the snout size differences early on development.
**Rhamphichthys rostratus** (Linnaeus, 1766)

(Fig. 49–60; Tab. 10)


**FIGURE 48** | Distribution of *Rhamphichthys pantherinus* based on examined museum specimens. Red dot represents the approximate type-locality. Yellow dot is *Rhamphichthys atlanticus* type-locality; blue dot is *Rhamphichthys longior* type-locality.
**Taxonomic review of Rhamphichthys**


**Rhamphichthys schneideri** Kaup, 1856:136, fig. 11 (original description: type-locality: Cayenne. Holotype: MNHN 3957).


**Diagnosis.** *Rhamphichthys rostratus* differs from all congeners by a greater number of caudal vertebrae (111–117), vs. lower number of vertebrae (90–109). *Rhamphichthys rostratus* also differs from all congeners, except from *R. apurensis*, by a longer snout (58.8–65.1% of HL), vs. shorter snout (46.4–59.1% of HL), and a longer caudal appendage (18.4–35.6% of LEA), vs. shorter caudal appendage (5.8–20.3% of LEA; except in *R. pantherinus*, 9.1–28.8 %). *Rhamphichthys rostratus* further differs from all congeners except *R. apurensis* and *R. pantherinus* by the intercalated pattern of the saddles on the mid dorsum, vs. a sickle shaped or absence of saddles. *Rhamphichthys rostratus* typically has darkly pigmented distal ends of the anal fin rays, forming a longitudinal stripe (Fig. 61), vs. anal fin varying in pigmentation but not forming a distal darkened stripe.

**Description.** Morphometrics and meristics given in Tab. 10. Adult body size large as compared with other congeners, maximum size 850 mm LEA, maturing at about 420–460 mm LEA. Mouth subterminal. Snout very long, more than half of head length. Dorsal profile of snout strongly concave in front of eye, head profile slightly convex posteriorly. Anterior nares positioned terminally; posterior nares located closer to snout than eyes at about one fourth of length. Body profile almost straight to slightly concave dorsally. Ventral body profile slightly concave from anal–fin origin to end of anal fin. Greatest body depth slightly posterior to end of body cavity. Body tapering posterior to mid body. Eyes small, positioned laterally. Urogenital papilla developed and anteriorly positioned below eyes in specimens larger than 400 mm LEA. Urogenital papilla small. Posterior gas bladder small and membranous in between viscera. Caudal appendage long, laterally compressed, its depth about three times its width.

![Figure 49](image-url) **Figure 49** | Linear regression of *Rhamphichthys pantherinus* populations. Blue circles = Amazon Basin (open circle = holotype of *R. pantherinus*); red circles = Mearim System (open circle = holotype of *R. atlanticus*); black circles = Trombetas basin (open circle = holotype of *R. longior*).
**FIGURE 50** | Scatter plots of PCA scores. A. PC 1 vs. PC 2; B. PC 1 vs. PC 3. PCA of *Rhamphichthys pantherinus* geographic populations: Red = Amazon; blue = Mearim (including *R. atlanticus* holotype); pink = Negro; golden = Tocantins (type-locality of *R. marmoratus*); brown = Tombetas (including types of *R. longior*); yellow = western Amazon (including *R. pantherinus* holotype) and grey = Xingu.
Taxonomic review of *Rhamphichthys*


**Coloration in alcohol.** Ground color of dorsal and lateral surfaces of head and body yellow to dark brown (Figs. 51–62). Head with scattered dark brown blotches of about eye size; snout mostly dark, ventral margin less pigmented. Body presenting dark intercalated saddles, these reaching ventrally the lateral line. Presence of dark lateral pigment bands, slightly diagonally placed along the long axis of the body. Bands sometimes contacting the dorsal saddles; bands diffuse over the pterygiophore region, extending to the proximal region of the anal fin rays. Anal fin mostly clear except for distal portion dark. Pectoral fin clear with broad dark bars. Caudal appendage with dark vertically elongate blotches.

**TABLE 10** Morphometric and meristic data for *Rhamphichthys rostratus*. H1 = holotype of *Rhamphichthys reinhardtii*; H2 = holotype of *R. schneideri*; H3 = holotype of *R. schomburgki*; H4 = holotype of *R. blochii*; SD = standard deviation; n = number of specimens.

<table>
<thead>
<tr>
<th></th>
<th>H1</th>
<th>H2</th>
<th>H3</th>
<th>H4</th>
<th>n</th>
<th>Range</th>
<th>Mean</th>
<th>SD</th>
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<tr>
<td><strong>Length to end of anal fin (LEA)</strong></td>
<td>600</td>
<td>630</td>
<td>700</td>
<td>510</td>
<td>32</td>
<td>270–700</td>
<td>446.9</td>
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<td><strong>Percents of LEA</strong></td>
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<td></td>
<td></td>
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<tr>
<td>Anal-fin length</td>
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<td>88.9</td>
<td>87.5</td>
<td>94.1</td>
<td>32</td>
<td>80.6–94.1</td>
<td>88.2</td>
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<td>Body depth</td>
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<td>8.9</td>
<td>8.1</td>
<td>8.6</td>
<td>32</td>
<td>6.1–8.9</td>
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<tr>
<td>Pectoral-fin length</td>
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<td>4.7</td>
<td>3.6</td>
<td>5.3</td>
<td>32</td>
<td>3.7–5.6</td>
<td>4.8</td>
<td>0.5</td>
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<tr>
<td>Head length</td>
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<td>14.0</td>
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<td>15.9</td>
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<td>12.4–15.9</td>
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<td>Caudal filament length</td>
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<td>–</td>
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<td>21</td>
<td>32</td>
<td>17–39</td>
<td>62.9</td>
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</table>
FIGURE 51 | *Rhamphichthys rostratus*, ANSP 187120, 520 mm LEA, Lawa Lawa River Cataract west of base camp 8 km W of Anapaiake, Sipaliwini, Suriname.

FIGURE 52 | Detail of head of *Rhamphichthys rostratus*, ANSP 187120, 520 mm LEA, Lawa Lawa River Cataract west of base camp 8 km W of Anapaiake, Sipaliwini, Suriname.

FIGURE 53 | *Rhamphichthys rostratus*, holotype of *Rhamphichthys blochii*, ZMB 4089, 510 mm LEA, South America.
FIGURE 54 | *Rhamphichthys rostratus*, holotype of *Rhamphichthys blochii*, ZMB 4089, 510 mm LEA, South America.

FIGURE 55 | *Rhamphichthys rostratus*, holotype of *Rhamphichthys reinhardtii*, MNHN 3956, 600 mm LEA, Brazil.

FIGURE 56 | Detail of the head of *Rhamphichthys rostratus*, holotype of *Rhamphichthys reinhardtii*, MNHN 3956, 600 mm LEA, Brazil.
**FIGURE 57** | *Rhamphichthys rostratus*, holotype of *Rhamphichthys schneideri*, MNHN 3957, 700 mm LEA, Cayenne, French Guiana.

**FIGURE 58** | Detail of the head of *Rhamphichthys rostratus*, holotype of *Rhamphichthys schneideri* MNHN 3957, 700 mm LEA, Cayenne, French Guiana.

**FIGURE 59** | *Rhamphichthys rostratus*, holotype of *Rhamphichthys schomburgki*, MNHN 3958, 700 mm LEA, Demerara, Guyana.
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**FIGURE 60** | Detail of the head of *Rhamphichthys rostratus*, holotype of *Rhamphichthys schomburgki* MNHN 3958, 700 mm LEA, Demerara, Guyana.

**FIGURE 61** | *Rhamphichthys rostratus*, ANSP 182428, 445 mm LEA, fisherman catch purchased from canoe in Belen, Iquitos, reportedly from Lower Río Itaya, Loreto, Peru.

**FIGURE 62** | Detail of the head of *Rhamphichthys rostratus*, ANSP 182428, 445 mm LEA, fisherman catch purchased from canoe in Belen, Iquitos, reportedly from lower Río Itaya, Loreto, Peru.
Geographical distribution. *Rhamphichthys rostratus* is known from the Amazon, Essequibo, Tocantins, and coastal river of Guianas basins (Fig. 63; Tab. 1). It inhabits river channels of medium to large size rivers. It is also found in flooded forest and oxbow lakes.

Ecological notes. Adult specimens of Wismar Guyana are reported to feed on mud-inhabiting worms and insects, including annelids, dipteran larvae, and gyrinid amphipods (Ellis, 1913:173).

Remarks on synonym and geographic variation. The synonyms of *Rhamphichthys rostratus* were proposed by several authors (see introduction) and were established by Mago-Leccia (1994). After examining Kaup’s (1856) *Rhamphichthys* type material we concur to this extensive synonymization. A PCA was done using geographic populations of *R. rostratus* and little geographic variation on morphometrics was observed between Amazon, Negro and Guianas populations. The first three principal components (PC 1, PC 2 and PC 3) explain most of the variance (75.3%; Tab. S10). Scores were plotted for PC 1 vs. PC 2 and show large morphometric overlap of geographic populations of *R. rostratus* (Fig. 62). Strong loadings separating some of these groups are the interorbital standard length (SL), anal fin length; preorbital length (PR), pectoral–fin length (PFL); branchial opening (BO) and Eye diameter (BD) (Tab. S11). A Multivariate Analyses of Variance (MANOVA) was done using the PC scores of the first three axes of the PCA. Populations of *R. rostratus* from Amazon marginally differs statistically from Guianas and Negro basin (Tab. S12; Wilks’ λ: 0.3435; P < 0.001; F6,48 = 5.651).

Remarks. The type of *Gymnotus rostratus* is lost (Mago-Leccia, 1994; Ferraris, 2003). Although Linnaeus’ 1766 description of *R. rostratus* is very brief and too superficial to distinguish between different species of the genus, *R. rostratus* is the only species in the genus inhabiting Surinamese rivers (Mol *et al*., 2012), the likely type–locality of this species (Albert, Crampton, 2003).

Material examined. ZMB 4089 holotype of *Rhamphichthys blochii* America. MNHN 3956, holotype of *Rhamphichthys reinhardtii*, cabinet d’ajuda, probably Amazon basin in Brazil. Essequibo: UMMZ 216489, 1, Guyana, Essequibo River at opposite side of Bartica, 06°24’N 58°35’W. Guianas: ANSP 187119, 1 (1 specimen measured in Tab. 10, 580 mm LEA), Suriname, Sipaliwini, Lawa Lawa river Cataract west of base camp 8 km west of Anapaiake, FMNH 53293, 1, Guiana, Demerara River at Wismar. ANSP 187120, 1 (1 specimen measured in Tab. 10, 520 mm LEA), Suriname, Sipaliwini, Lawa Lawa river, Cataract west of base camp 8 km W of Anapaiake, 03°19’31”N 54°03’48”W, 18 Apr 2007. J. Lundberg, M. Sabaj, P. Willink, J. Mol *et al*. MHNG 2316.17, 1, French Guiana, Antecome Pata upper Maroni. MHNG 2117.007, 1, Suriname, Sipaliwini, Tapahony River Kumaru Konde Sula, 03°21’N 55°25’W. MNHN 3957, holotype of *Rhamphichthys schneideri*, French Guyana, Cayenne. MNHN 3958, holotype of *Rhamphichthys schomburgkii*, Guyana. MNHN 1998.1569, 1, Suriname, Oulemoni, 03°08’N 54°26’W. MNHN 2000.5923, 1 (1 specimen measured in Tab. 10, 270 mm LEA), French Guyana, Maroni, St. Laurent du Maroni, Antecume Pata, camp nivree, rapids in the main channel upstream the village, 03°18’N 54°05’W. MNHN 2001.2291,
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1 (1 specimen measured in Tab. 10, 420 mm LEA), French Guiana, Litany, Saint Laurent du Maroni, port of d'antecume pata. MNHN 2002.816, 1 (1 specimen measured in Tab. 10, 670 mm LEA, French Guiana, Litany, St. Laurent du Maroni, Waterfall Almina–Emen. USNM 225654, 1, Suriname, Nickerie, Mataway creek approximately 8 km from its intersection with Corantijn River, 04°47'N 57°45'W. ZMB 6433, 1, Suriname, Maroni. **Rio Negro**: ANSP 189560, 1, Brazil, Amazonas, rio Jauaperi 9.2 km above confluence with rio Negro, 01°35'08"S 61°28'35"W. AUM 43333, 1, Venezuela, Amazonas, Rio Casiquiare at mouth of Caño Caripo 36 km WSW of La Esmeralda, 03°06'48"N 65°52'40"W. FMNH 115524, 1, Brazil, Amazonas, Manaus, rio Negro between tributaries igarapé Taruma–Mirim and rio Solimões, 03°07'36"S 60°07'55"W. INPA 4428, 2 (2 specimens measured in Tab. 10, 480–510 mm LEA) (Brazil, Amazonas, Manaus, rio Negro near Manaos. MCP 26285, 1, Brazil, Amazonas, rio Negro 9.6 miles upstream São Francisco, 01°34'46"S 61°28'38"W. MCP 26286, 2, Brazil, Amazonas, rio Negro about 9.6 miles downstream Novo Caioe, 01°41'13"S 61°29'02"W. MCP 27756, 23 (5 specimens measured in Tab. 10, 380–450 mm LEA, 1 cs), Brazil, Amazonas, rio Negro 15 miles downstream Moura, 01°33'28"S 61°34'15"W. MCNG 37875, 1, Venezuela, Amazonas, Rio Casiquiare at Isla Cuamate downstream Caño Solano, 02°00'N 66°57"W. MZUSP 32217, 1, Brazil, Amazonas, rio Negro downstream mouth of rio Daraá, 00°28'3S 64°46"W. MZUSP 32220, 1, Brazil, Amazonas, rio Ariara tributary to rio Negro, 00°31'S 63°33"W. MZUSP 32223, 1, MZUSP 32230, 1, Brazil, Amazonas, rio Negro at Anavilhanas, 02°42'S 60°45"W. MZUSP 32231, 1, Brazil, Amazonas, rio Negro at mouth of rio Urubaxi, 00°31'S 64°50"W. MZUSP 32232, 1, Brazil, Amazonas, rio Negro in flooded forest at São Gabriel da Cachoeira, 00°07'S 67°05"W. MZUSP 32233, 1, Brazil, Amazonas, flooded forest near confluence of rio Negro and rio Marauíá, 00°24'S 65°12"W. MZUSP 91650, 1, Brazil, Amazonas, rio Uapés. MZUSP 92251, 1 (1 specimen measured in Tab. 10, 330 mm LEA), Brazil, Amazonas, São Gabriel da Cachoeira, igarapé Curuni 500 m below port of comunidade São José II, tributary to rio Tiquié, 00°13'N 69°36"W. MZUSP 93446, 1 (1 specimen measured in Tab. 10, 530 mm LEA), Brazil, Amazonas, São Gabriel da Cachoeira, rio Tiquié near comunidade Serra do Mucura, 00°10'S 69°07"W. USNM, 373070, 1, Brazil, Amazonas, rio Negro 5.6 km below São Francisco, 01°42'22"S 61°24'27"W. **Amazonas Lowlands**: ANSP 182428, Peru, Loreto, fisherman catch purchased from canoe in Belen, Iquitos, reportedly from lower Rio Itaya, 03°45'S 73°25"W. ANSP 189533, 1, Brazil, Amazonas, rio Amazonas, 162 km downriver Manaos, 31 km upstream Itacoiatiara, 03°15'36"S 58°34'12"W. ANSP 189552, 2, Brazil, Amazonas, rio Madeira 4.7 km downstream from Rosarinho and 17.9 km from vila Urucurituba 03°39'17"S 59°03'27"W. ANSP 189565, 1 (1 specimen measured in Tab. 10, 370 mm LEA), Brazil, Amazonas, rio Solimões downstream rio Juruá mouth 21.5 km downstream Tamanicoa, 02°34'38"S 65°30'11"W. ANSP 189556, 1, Brazil, Amazonas, rio Solimões 9 km upstream Santa Antonio do Içá, 03°08'53"S 67°53'29"W. ANSP 189558, 1, Brazil, Amazonas, rio Juruá 9.2 km of Pauapixuna, 02°40'54"S 65°48'57"W. ANSP 189559, 1 (1 specimen measured in Tab. 10, 375 mm LEA), Brazil, Amazonas, rio Solimões 45.9 km downstream of Codajás and 18.2 km upstream of Anori, 03°52'21"S 61°42'49"W. CAS 36690, 1, Peru, Loreto, Caño del Chancho near Pebas, 03°20'S 71°51"W. FMNH 114680, 1 (1 specimen measured in Tab. 10, 340 mm LEA), Brazil, Amazonas, rio Solimões between tributaries rio Japurá and lago Caimbe, 03°19'32"S 64°32'18"W. FMNH 114682, 3, Brazil, Amazonas, rio
Madeira between Paraná do Canuma and rio Amazonas, 03°40'14"S 59°04'12"W. FMNH 114683, Brazil, Amazonas, rio Solimões between tributaries rio Japurá and lago Caimbé, 03°18'30"S 64°35'25"W. FMNH 115521, 1 (1 specimen measured in Tab. 10, 370 mm LEA), Brazil, Pará, rio Trombetas between tributaries lago Bacabal and lago Samauma, 01°31'03"S 56°09'57"W. FMNH 115523, 1 (1 specimen measured in Tab. 10, 443 mm LEA), Brazil, Pará, rio Trombetas between tributaries lago Bacabal and lago Aracuazinho, 01°31'10"S 56°08'59"W. IA-vH-P 3192, 2, Colombia, Amazonas, Leticia, PNN Amacayacu, 03°00'47"S 70°00'01"W. IA-vH-P 5342, 2, Colombia, Amazonas, La Chorrera, Lago Grande at rio Igará-Paraná, 00°44'S 73°01W. ICNMCN 6671, 1, Colombia, Guiania, San Felipe, Río Negro at San Felipe. INPA 9360, 1 (1 specimen measured in Tab. 10, 640 mm LEA), Brazil, Amazonas, Presidente Figueiredo, igarapé Nazaré tributary to rio Uatumá. INPA 17645, 2 (1 cs), Amazonas, Careiro da Varzea, paraná do Rei at ilha do Careiro, 03°09'S 59°43"W. INPA 27621, 2 (2 specimens measured in Tab. 10, 330–365 LEA), Brazil, Amazonas, Manaus, rio Solimões at Costa do Catalão. MNHG 2552.17, 1, Brazil, Pará, rio Tapajós at Aveiro, 03°36'S 55°19"W. MCP 26455, 2, Brazil, Pará, rio Trombetas 6.25 miles upstream vila Aracuá, 01°31'13"S 56°09'20"W. MCP 33444, 1, Brazil, Amazonas, Alvarães, rio Japurá near mouth of lago Mamirauá, 03°07'40"S 64°46'26"W. MCP 33446, 1, Brazil, Amazonas, Alvarães, rio Japurá paraná Maiana. MCP 33447, 1, Brazil, Amazonas, rio Tefé at Toco Preto. MPEG 1299, 1, Brazil, Pará, rio Amazonas at Óbidos, 01°54'S 55°31"W. USNM 52552, 1, Brazil, rio Amazonas. Mamoré-Madre de Dios: FMNH 54701, 1, Bolivia, Río Mamore. MNHN 1988–1029, 1, Bolivia, mouth of Río Ibare. Madeira Brazilian Shield. MZUSP 13957, 1, Brazil, Rondônia, rio Machado at igapó Paraíso. Tocantins-Araguia. MCN 18986, 2, Brazil, Tocantins, Ananás, ribeirão Curicacas left margin tributary of rio Araguaia, 06°09'30"S 48°16'21"W. MCN 18987, 1, Brazil, Pará, Marabá, rio Taurizinho left margin tributary of rio Tocantins, 05°22'40"S 49°00'54"W. MCN 18988, 2, Brazil, Tocantins, rio Tocantins between Vila Nova dos Martírios and Buriti do Tocantins, 05°16'06"S 48 06'52"W. Amazonas estuary and coastal drainages: ANSP 189541, 1, Brazil, Pará, rio Acarai upstream from confluence with rio Xingu and Porto de Moz, 02°04'34"S 52°20'42"W. MPEG 2300, 1, Brazil, Pará, Gurupá, rio Amazonas downstream Gurupá near Estreito, 01°21'S 51°36"W. MPEG 5466, 1, Brazil, Pará, Castanhal, rio Apeu at Boa Vista do Apeu. MPEG 18693, 3, Brazil, Pará, Cachoeira do Anari, rio Arari. MZUSP 32225, 3, Brazil, Amapá, rio Araguari.
FIGURE 63 | Distribution of *Rhamphichthys rostratus* based on examined museum specimens.

FIGURE 64 | Scatter plots of scores factored on principal component I and II. PCA of *Rhamphichthys rostratus* allopatric populations: Amazon (Red, not including the rio Negro basin; Coastal rivers of Guianas (Blue, type-locality) and rio Negro (Grey).
DISCUSSION

*Rhamphichthys* is one of the less studied genera with respect to alpha taxonomy within Gymnotiformes. The last published taxonomic review of the genus was the one made by Kaup, 1856 and has been used as literature for species identifications. Triques (1999) described three new species but did not comment on previously described species. The taxonomy of this genus dates from an era when the typological species concept was used, and when the studies were based on a small number of specimens, often no more than the single type specimen. After examining a comprehensive set of materials, including types of the species and materials throughout their geographic ranges, we conclude that diversity within *Rhamphichthys* is lower than previously thought.

*Rhamphichthys rostratus* is the species of the genus with the largest number of junior synonyms. Kaup (1956) published most of these names, based on variation in the position of the anus with respect to a vertical through the eye, and on gross body proportions. Subsequent studies have shown the anus changes position with growth (Schawassmann, 1989), thus invalidating the use of anal position as a diagnostic species-level trait (e.g., Mago-Leccia, 1994). We therefore synonymized several nominal species with type-species *R. rostratus*, supporting suppositions of previous authors (Mago-Leccia, 1994; Ferraris, 2003). After examining holotypes of *R. reinhardti*, *R. blochi*, *R. schnederi*, and *R. schomburgki*, we conclude that all these nominal species are junior synonyms of *R. rostratus*.

*Rhamphichthys pantherinus* also has many junior synonyms. The synonym of this species with *R. marmoratus* was already proposed (Günther, 1870; Eigenmann, Eigenmann, 1891; Mago-Leccia, 1994; Triques, 1999; Ferraris, 2003), which has been confirmed here after examining the holotypes and a large number of specimens of this species. According to Castelnau (1855), *R. marmoratus* differs from *R. pantherinus* by “gorge vert” translated as “green neck” meaning the posteroventral region of the head green (Fig. 1). None of the *Rhamphichthys* specimens examined exhibits green coloration on any portion of the body, and this description may be an artifact of old preservation or fixation methods. It is noticeable in the original drawings and in the type specimen the relative overall darker coloration of *R. marmoratus* as compared to *R. pantherinus*. These differences in coloration were observed within specimens of *R. pantherinus* with noticeably darker specimens present in some localities of the lower reaches of the eastern Amazon basin. Also noticeable in these darker specimens is the presence of darker pigment bands, saddles, and spots in the dorsal region of the head, however presenting less contrast with the generally darker brown pigmented body. Kaup (1856) considered *R. pantherinus* nearest to *R. marmoratus*, but proposed the position of the anus and snout length to distinguish the two species. The position of the anus is long known to change with ontogeny (Mago-Leccia, 1994), reflected by the difference in size between the two specimens and the snout length of both falls within the range of the species (Tab. 9).

Additional new junior synonyms are proposed here for *R. pantherinus* with *R. longior* and *R. atlanticus*. *Rhamphichthys atlanticus* does not differ from *R. marmoratus* in any of the morphological traits measured and examined. The proposed clearer pattern (lacking markings or spots) for the anal fin as diagnostic for *R. atlanticus* (Triques, 1999) was observed in several other specimens throughout the Amazon basin and therefore does not diagnose *R. atlanticus* from *R. pantherinus*. Also, other populations examined from
regions near the type-locality of *R. atlanticus*, such as the Parnaíba River and Coastal drainages of the Maranhão State in Brazil, do not present any differences from *R. marmoratus*. Therefore, until more data are available to test if these disjunct geographic group/groups are distinct evolving lineages, we propose a synonym in the absence of morphological diagnostic characters. *Rhamphichthys longior* presents no diagnostic characters as compared to *R. pantherinus*. The population examined from Trombetas River (type-locality of *R. longior*) presents a relatively more slender body shape in lateral view and a longer caudal appendage. However, these traits are also observed in *R. pantherinus* from the Negro River drainage, and they are not diagnostic in the sense that the ranges of these morphometric characters overlap substantially. Also, there are no geographical physical barriers between the lower Trombetas River and other populations in the Amazon basin that could justify characterizing these two species as allopatric. We here consider these species as synonyms until further observations based on additional data (e.g., molecular) are available. This newly delimited *R. pantherinus* increases considerably the geographic distribution of this species, making it one of the most widespread species of Gymnotiformes. This species is the most widespread of the genus and, despite the large distribution *R. pantherinus*, shows a relatively homogeneous morphology throughout its range.

*Rhamphichthys drepanium* from the Amazon and Orinoco basins is morphologically very similar to *R. hahni* from the Paraguay–Paraná basin, being putatively differentiated by vertebral counts and gas bladder morphology. Triques (1999) diagnosed *R. drepanium* based on the presence in adults of a highly reduced swim-bladder, a thick-walled body cavity, and a characteristic color pattern with sickle-shaped pigment bars interrupted dorsally that do not cross or reach the dorsal midline (Fig. 15). *Rhamphichthys drepanium* shares all these characters with *R. hahni*, although the posterior gas bladder is more variable in *R. drepanium*, being sometimes membranous (Figs. 16A–C).

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AUTHORS’ CONTRIBUTION

Tiago P. Carvalho: Conceptualization, Data curation, Formal analysis, Project administration, Writing-original draft, Writing-review and editing.

James S. Albert: Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Writing-review and editing.

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COMPETING INTERESTS

The author declares no competing interests.

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