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A New Species of *Leporinus* (Characiformes: Anostomidae), from the Orinoco Basin, Venezuela

Michael D. Burns¹, Benjamin W. Frable¹, and Brian L. Sidlauskas¹

A new species of *Leporinus* in the *L. cylindriciformis* group is described from the Río Orinoco basin, Venezuela. This new species can be separated from congeners by the combination of an extremely dorsoventrally slender body, the presence of a prominent midlateral spot positioned ventral to the dorsal fin, and the absence of any other intense dark pigmentation. The new species is most similar to *L. aripuanaensis* from the Rio Aripuanã, Brazil, but can be most easily differentiated from that species by the absence (79% of specimens) or faint presence (21% of specimens) of a circular dark spot over the hypural plate in the new species, versus the presence of an intensely pigmented dark spot in that position, respectively. It can be further distinguished from *L. aripuanaensis* by the modal number of predorsal scales (12 versus 11). Small juveniles of the two species do not differ morphometrically, but their allometric growth trajectories differ. Above 70 mm SL, the new species differs from *L. aripuanaensis* in interorbital width (34–44% HL versus 30–34%) and eye diameter (29–34% HL versus 26–30% HL). This new species represents the most recent of a long series of newly discovered taxa within *Leporinus* and reinforces the Orinoco Basin as a region of high endemism.

LEPORINUS is the largest genus in the characiform family Anostomidae, with in excess of 90 valid species (Britski and Garavello, 2005; Britski and Birindelli, 2008; Dos Santos and Zuanon, 2008; Feitosa et al., 2011; Britski et al., 2012). The genus is widespread across much of South America with the highest species diversity occurring in the Amazon basin, which harbors roughly 45 species (Feitosa et al., 2011). Many species are still undescribed (Birindelli and Britski, 2009; Feitosa et al., 2011) and new species of *Leporinus* are discovered regularly (Birindelli et al., 2013; Britski and Birindelli, 2013).

Members of the genus are primarily omnivorous, and eat terrestrial insect larvae, aquatic invertebrates, plant material, and detritus (Goulding, 1980; Mérigoux and Ponton, 1998; Garavello and Britski, 2003; de Melo et al., 2004). Many species obtain relatively large sizes with some, such as *Leporinus muyscorum*, reaching 25 cm in total length (Garavello and Britski, 2003). As such, people across South America often exploit *Leporinus* as a food resource in subsistence fisheries (Bittencourt and Cox-Fernandes, 1990; Godinho, 1993).

The *Leporinus cylindriciformis* group includes species with a long slender body and a row of dark circular or horizontally elongate spots centered along the lateral-line scale row (Sidlauskas et al., 2011). The systematics of this group has been researched actively due to uncertainty as to the phenotypic and geographic range of several of the species, including *L. niceforoi* from the upper Amazon and *L. cylindriciformis* from the middle and lower Amazon (Sidlauskas et al., 2011). Two new species in this group were described recently (Dos Santos and Zuanon, 2008; Sidlauskas et al., 2011).

Examination of specimens of the *Leporinus cylindriciformis* group from the Río Orinoco basin in Venezuela revealed individuals with a slender long body similar to *L. cylindriciformis*, but an unusual color pattern. These Orinoco specimens display a single prominent dark spot centered along the lateral line at the midpoint of the body dorsal to the pelvic fin, rather than the two to four intense black spots along the lateral line typical of other members of the complex. Further examination revealed that some

specimens exhibit an additional faint spot along the lateral line over the hypural plate and another small spot posterior to the opercle proximate to the extrascapular. However, when these spots are present they are much smaller and less intense than the spot at the midpoint of the body. The absence or faintness of the hypural spot distinguishes these specimens from *L. aripuanaensis*, the most similar member in the species complex, which possesses a spot over the hypural plate of approximately equal size and intensity to the midlateral spot and inhabits the Rio Aripuanã and Rio Uatumã drainages of Brazil, the latter of which is a tributary of the Rio Madeira. Morphometric, meristic, and geographic analysis further revealed that the Orinoco specimens differ from *L. aripuanaensis* and all other known species within the *L. cylindriciformis* group, and thus represent a new species described herein.

MATERIALS AND METHODS

Specimens of the new species from the Orinoco basin were compared with other members of the *Leporinus cylindriciformis* complex including *L. amazonicus*, *L. aripuanaensis*, *L. apollo*, *L. cylindriciformis*, *L. cf. niceforoi*, *L. niceforoi*, *L. ortomaculatus*, and the similarly shaped but differently pigmented *L. brunneus*, which co-inhabits the Orinoco basin. Meristic counts follow Sidlauskas et al. (2011), which modified the methodology of other recent studies of taxonomy of *Leporinus* (Britski and Garavello, 2005; Britski and Birindelli, 2008), by reporting lower transverse scale counts at both the anal-fin origin and pelvic-fin origin and by counting the branched last dorsal- and anal-fin rays as single elements, a procedure which reflects the correspondence of external fin elements to their pterygiophores. Thirty-seven linear measurements follow Sidlauskas et al. (2011), except that measurements involving the landmark at the end of the vertebral column (e.g., standard length) were taken to the posterior midlateral margin of the hypural plate, as opposed to the midpoint of the terminal centrum as in Sidlauskas et al. (2011). That paper used a non-standard location of that landmark to maximize comparability with a concurrent geometric morphometric analysis, while the methodology used herein conforms to standard practice in characiform

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systematics. Data taken from specimens also examined by Sidlauskas et al. (2011), including specimens of *L. amazonicus*, *L. apollo*, *L. cylindriciformis*, *L. cf. niceforoi*, and *L. ortomaculatus*, were re-measured for all linear distances involving the posteriormost landmark. Cleared-and-stained specimens were prepared following Taylor and Van Dyke (1985).

Allometric differences among specimens were removed from 37 log-transformed measurements by the allometric Burnaby technique implemented in PAST (Hammer et al., 2001). These size-standardized data were then used in a Principal Components Analysis (PCA). The first three eigenvectors from the PCA were analyzed with a MANOVA implemented in PAST. The significances of differences between the means of putative species ($P \leq 0.05$) on each axis were tested with pairwise Tukey's *post-hoc* comparisons. Discriminant Function Analysis (DFA) was used to further discriminate the groups, and determine which of the 37 linear variables best separated the putative species. The untransformed variables that explained the highest proportion of variance in the DFA were regressed against standard length (SL) for each species to determine if the ontogenetic trajectories for these variables differed among species. This standardized-major-axis (Type II) regression, as well as tests of equality of slope and intercept, were done in the *smatr* package in R (Warton et al., 2012).

***Leporinus arimaspi*, new species**

Figures 1–6; Tables 1, 2

Holotype.—MBUCV-V-35695, 1, 117.5 mm SL, Venezuela, Amazonas, Río Casiquiare, 152.92 km NE of San Carlos de Río Negro, 2°47'56"N, 66°0'23"W, N. K. Lujan et al., 24 March 2005.

Paratypes.—Venezuela: Amazonas: ANSP 159370, 4, 54.7–77.4 mm SL (2 specimens, 62.4 and 64.6 mm SL CS), Río Orinoco, Raudales de Alturas at Culebra, ca. 7 km S of Puerto Ayacucho, 5°23'N, 67°31'W, W. G. Saul et al., 11 November 1985; ANSP 182644, 4, 59.3–79.9 mm SL (1 specimen, 72.3 mm SL CS), Río Orinoco, Pasaganado, 38 km N of San Fernando de Atabapo, 4°23'4"N, 67°46'28"W, M. H. Sabaj et al., 1 March 2005; ANSP 182651, 1, 189.5 mm SL, Río Orinoco, bedrock outcrop, 52.9 km SE of San Antonio, 102 km W of La Esmeralda, 3°6'1"N, 66°27'46"W, M. H. Sabaj et al., 4 March 2005; ANSP 182663, 1, 57.4 mm SL, Río Casiquiare, left bank, upstream from mouth of Río Siapa, 2°9'21"N, 66°27'50"W, N. K. Lujan et al., 19 March 2005; ANSP 182664, 2, 52.3–83.7 mm SL, Caño Grulla, tributary of Río Orinoco, near comunidad Cipuana, 76.7 km N of San Fernando de Atabapo, 4°43'48"N, 67°49'8"W, M. H. Sabaj et al., 1 March 2005; ANSP 182667, 2, 56.6–62.5 mm SL, Río Orinoco, beach and bedrock outcrop, 50 km E of San Fernando de Atabapo, 3°58'13"N, 67°15'18"W, M. H. Sabaj et al., 2 March 2005; ANSP 182679, 2, 126.5 and 158.8 mm SL, Río Manapiare, Ventuari, Orinoco drainage, 20 km NW of San Juan de Manapiare, 5°27'10"N, 66°10'37"W, N. K. Lujan et al., 12 April 2004; AUM 41346, 1, 58.7 mm SL, Río Orinoco at Manaka, 70 km E of San Fernando de Atabapo, 3°57'29"N, 67°5'1"W, D. C. Werneke et al., 3 April 2004; AUM 41452, 1, 85.1 mm SL, Río Manapiare, at mouth of Caño Yutaje, 14 km NW of San Juan de Manaka, 5°26'12"N, 67°5'1"W, M. H. Sabaj et al., 11 April 2004; AUM 43085, 1, 54.6 mm SL, Caño Grulla, 76.7 km N of San Fernando de

Atabapo, comunidad Cipuana, 4°43'48"N, 67°49'7"W, N. K. Lujan et al., 1 March 2005; AUM 43124, 1, 81.4 mm SL, Pasaganado, on Río Orinoco, 38 km N of San Fernando de Atabapo, 4°23'3"N, 67°46'27"W, N. K. Lujan et al., 1 March 2005; AUM 43125, 5, 70.0–90.8 mm SL, Pasaganado, on Río Orinoco, 38 km N of San Fernando de Atabapo, 4°23'3"N, 67°46'27"W, N. K. Lujan et al., 1 March 2005; AUM 43801, 2, 107.2–151.3 mm SL, Río Casiquiare, 153 km NE of San Carlos de Río Negro, 2°47'55"N, 66°0'23"W, N. K. Lujan et al., 24 March 2005; CAS 20129, 1, 135.9 mm SL, Río Casiquiare, Caracol, above rapids, C. Tementz, 25 February 1925; CAS 20130, 1, 176.2 mm SL, Río Casiquiare, Laja Solomoni, C. Tementz, 10 March 1925; MBUCV-V-35701, 4, 55.5–68.3 mm SL, Río Orinoco, Raudales de Alturas at Culebra, ca. 7 km S of Puerto Ayacucho, 5°23'N, 67°31'W, W. G. Saul et al., 11 November 1985; OS 18903, 2, 60.0–65.6 mm SL, Río Orinoco, Raudales de Alturas at Culebra, ca. 7 km S of Puerto Ayacucho, 5°23'N, 67°31'W, W. G. Saul et al., 11 November 1985; OS 18904, 3, 63.6–75.5 mm SL (1 specimen, 72.28 mm SL CS), Río Orinoco, Pasaganado, 38 km N of San Fernando de Atabapo, 4°23'4"N, 67°46'28"W, M. H. Sabaj et al., 1 March 2005. Venezuela: Bolívar: ANSP 159340, 1, 50.5 mm SL, Río Caura near Puerto Las Majadas, 4°38'18"N, 64°50'24"W, W. Saul et al., 23 November 1985; ANSP 159361, 1, 65.3 mm SL, Río Caura at Maripa ferry crossing, 7°27'N, 65°12'W, B. Chernoff et al., 19 November 1985; ANSP 159376, 3, 61.4–73.6 mm SL, confluence of Río Orinoco and Río Caura, Las Piedras, 7°38'36"N, 64°50'W, W. Saul et al., 23 November 1985; ANSP 160294, 9, 52.6–94.2 mm SL, Caño (possibly Caño Curimo) drawing into Río Caura near confluence of Río Caura, Río Orinoco, 7°37'48"N, 64°50'42"W, B. Chernoff et al., 22 November 1985; ANSP 165817, 1, 79.5 mm SL, confluence of Río Orinoco and Río Caura at Las Piedras, 7°38'36"N, 64°50'W, W. Saul et al., 23 November 1985; OS 18905, 3, 62.4–77.0 mm SL, Caño (possibly Caño Curimo) feeding Río Caura near confluence of Río Caura, Río Orinoco, 7°37'48"N, 64°50'42"W, B. Chernoff et al., 22 November 1985.

Non-type material.—Venezuela: Amazonas: ANSP 191183, 1, 96.3 mm SL, Río Ventuari, Orinoco Dr., along wooded shoreline just downstream of beach at mouth of Caño Marujeta, 4°17'53"N, 66°17'58"W, M. H. Sabaj et al., 2 April 2010; AUM 42998, 1, 54.1 mm SL, Río Orinoco at Puerto Venado, 4.3 km S of Samariapo, 56.4 km SSW of Puerto Ayacucho, 6°12'38"N, 67°48'17"W, N. K. Lujan et al., 26 February 2005; AUM 54179, 1, 102 mm SL, Caño Maco, at San Francisco de Maco community, 157.5 km ESE of Puerto Ayacucho, 5°57'21"N, 66°21'2"W, J. Birindelli, 14 April 2010; AUM 54422, 1, 146 mm SL, Río Manapiare, at Manapiare landing, 173.8 km ESE of Puerto Ayacucho, 5°19'43"N, 66°3'2"W, J. Birindelli, 13 April 2010. Venezuela: Bolívar: ANSP 169624, 1, 70.1 mm SL, Río Orinoco at El Burro, 6°12'N, 67°26'W, B. Chernoff et al., 26 November 1985; AUM 22343, 1, 102.8 mm SL, Río Orinoco at El Burro across from Puerto Paez at mouth of Río Meta, 6°12'53"N, 67°25'32"W, J. W. Armbruster, 25 December 1999.

Diagnosis.—*Leporinus arimaspi* can be distinguished from all other valid members of *Leporinus* except *L. aripuanaensis*, *L. amazonicus*, *L. apollo*, *L. cylindriciformis*, *L. niceforoi*, and *L. ortomaculatus* by the combination of an extremely dorsoventrally slender body (body depth immediately anterior to

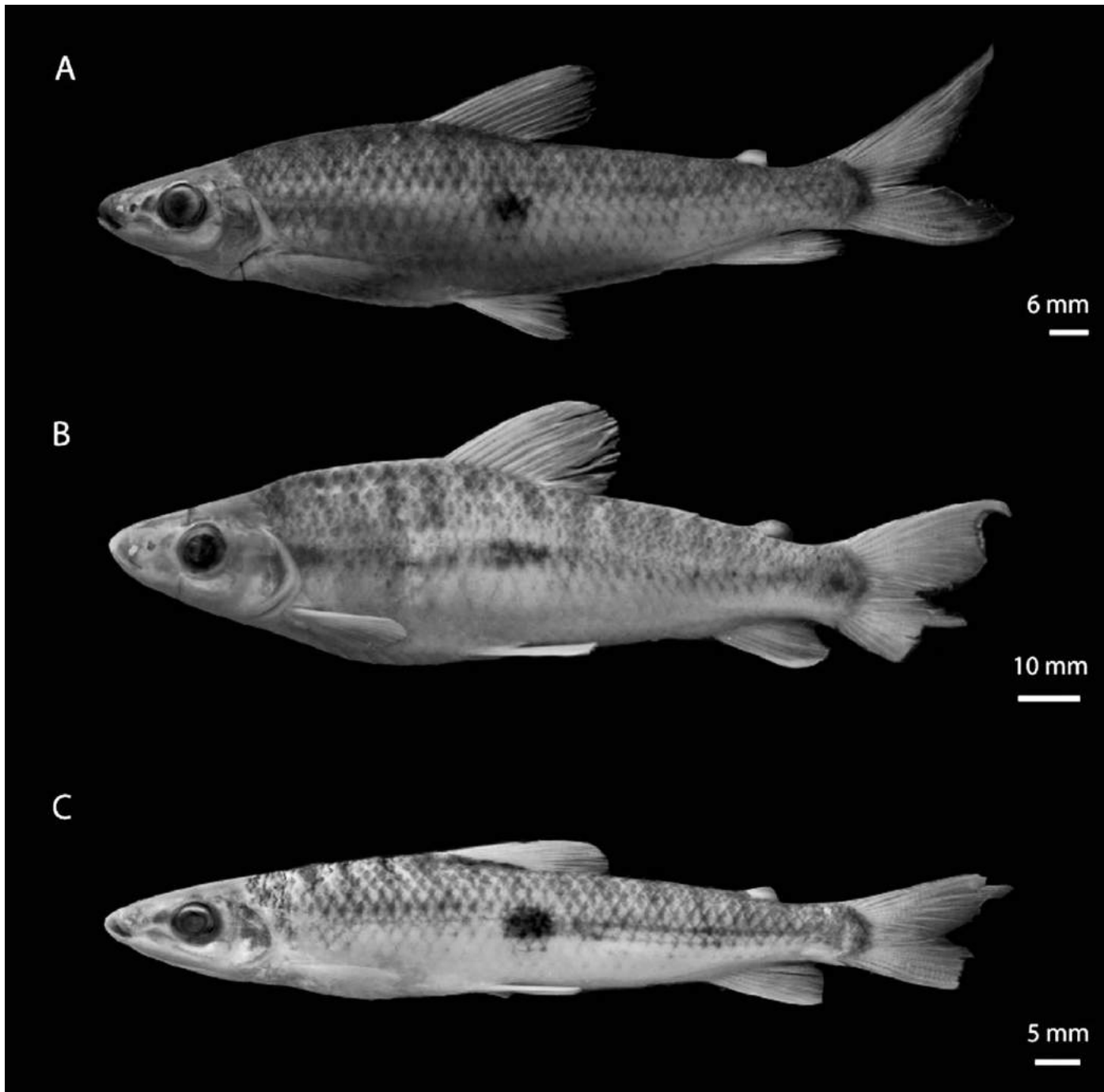


Fig. 1. (A) *Leporinus arimaspi*, holotype, MBUCV-V-35695, 117.5 mm SL, Venezuela, Amazonas, Río Casiquiare, 152.92 km NE of San Carlos de Río Negro, 2°47'56"N, 66°0'23"W. (B) *Leporinus arimaspi*, alternative color morph showing faint pigmentation over hypurals, collected with the holotype. (C) *Leporinus arimaspi*, alternative color morph with faint posterior midlateral stripe, AUM 22343, 102.8 mm SL, Venezuela, Bolivar, Río Orinoco at El Burro across from Puerto Paez at mouth of Río Meta, 6°12'53"N, 67°25'32"W.

the dorsal-fin origin of 19–27% SL, versus 29% SL or greater) and the pigmentation pattern (one or more dark spots centered along the lateral-line scale row). *Leporinus arimaspi* can be distinguished from *L. apollo*, *L. cylindriformis*, *L. niceforoi*, and *L. ortomaculatus* by the absence of the dark spot along the lateral-line posterior to the dorsal-fin insertion and anterior to the adipose-fin origin, versus the presence of an intense dark spot in that position. It can be further distinguished from *L. apollo* and *L. cylindriformis* by possession of five upper transverse scale rows (versus six in most specimens), and four lower transverse scale rows (versus five in most specimens), and from *L. ortomaculatus* by the

absence of rows of spots dorsal and ventral to the lateral-line scale row (versus the presence of such spots). *Leporinus arimaspi* can be distinguished from *L. amazonicus* by the possession of 37 to 40 total lateral-line scales (versus 43–45), 38 vertebrae (versus 41), and four lower transverse scale rows at the pelvic-fin insertion (versus 5 in most specimens). *Leporinus arimaspi* can be most easily distinguished from the most similar species, *L. aripuanaensis*, by the absence (or faint presence) of a circular dark spot over the hypural plate, versus the presence of an intensely pigmented dark spot in that position. It can be further distinguished from *L. aripuanaensis* by the modal number of predorsal scales (12

Table 1. Meristic counts summarized as ranges followed by the mean ± 1 standard deviation in parentheses. Single values in a cell indicate invariant counts among the examined specimens for a given species.

	<i>Leporinus arimaspi</i> (holotype)	<i>Leporinus arimaspi</i>	<i>Leporinus aripuanaensis</i>
Number of specimens		58	17
Unbranched dorsal-fin rays	ii	ii	ii
Branched dorsal-fin rays	10	10	10
Unbranched anal-fin rays	ii	ii	ii
Branched anal-fin rays	8	8	8
Unbranched pectoral-fin rays	i	i	i
Branched pectoral-fin rays	15	15–16 (15.5 \pm 0.7)	15–17 (15.7 \pm 0.7)
Unbranched pelvic-fin rays	i	i	i
Branched pelvic-fin rays	8	8	8
Upper principal caudal-fin rays	10	10	10
Lower principal caudal-fin rays	9	9	9
Lateral line scales to anterior margin of hypural plate	35	34–35 (34.3 \pm 0.5)	33–35 (34.1 \pm 0.6)
Scales over hypural plate	4	4–5 (4.3 \pm 0.5)	3–5 (4.4 \pm 0.6)
Total lateral line scales	39	37–40 (38.5 \pm 0.7)	37–39 (38.4 \pm 0.6)
Upper transverse scales at dorsal-fin origin	5	5	5
Lower transverse scales at pelvic-fin origin	4	4	4
Lower transverse scales at anal-fin origin	4	4	4
Circumpeduncular scales	16	16	15–16 (15.94 \pm 0.2)
Predorsal scales	11	11–13 (11.9 \pm 0.5)	10–11 (10.73 \pm 0.5)
Premaxilla teeth	4	3–4 (3.9 \pm 0.3)	4
Dentary teeth	4	3–5 (3.9 \pm 0.3)	3–4 (3.92 \pm 0.3)
Vertebrae	38	38	38

versus 11), as well as the following morphometrics in specimens between 70 and 92 mm SL: interorbital width 34–44% HL versus 29–34% HL and eye diameter 29–34% HL versus 25–30% HL. These measurements may also distinguish the two species at larger body sizes; but no specimens of *Leporinus aripuanaensis* larger than 92 mm SL were available.

Description.—Meristic values for holotype and paratypes in Table 1, morphometrics in Table 2. Body fusiform and very slender (Fig. 1). Head elongate and triangular in lateral view. Greatest body depth and width located at dorsal-fin origin. Profile of predorsal region of body nearly straight with slight convexity. Body constricted ventrally posterior to adipose fin and anterior to hypural plate. Adipose-fin origin located at vertical through base of fourth branched anal-fin ray. Pelvic-fin insertion located at vertical through origin of second branched dorsal-fin ray.

Head profile forming rounded point in anterior view; mouth slightly subterminal, upper and lower jaws meet on horizontal plane that is slightly dorsal to the ventral margin of the orbit. Upper lip thick and weakly grooved across lips, overhanging lower jaw slightly, lip angled posteroventrally and curving around posterior margin of maxilla. Lower lip moderately grooved across lips, covering dentary teeth when jaw closed. One row of typically four teeth on each dentary (range 3–5) and premaxilla (range 3–4), with largest near symphysis and teeth decreasing in size laterally (Fig. 2). Fifth dentary tooth occasionally present and fourth premaxillary or dentary tooth occasionally lacking. Premaxillary teeth multicuspid, usually with three cusps, central cusp largest, symphyseal and adjacent two teeth angle anteroventrally with concave interior surface, most posterior tooth small and flat. Dentary teeth spoon-shaped with rounded cusps; symphyseal teeth concave interiorly, lateral teeth

wider and flat. Premaxillary teeth overhanging dentary teeth when jaw closed.

Pectoral fins elongate, with second and third unbranched rays longest. Adipose fin slightly elongate with convex upper margin and straight ventral margin. Caudal-fin lobes distinctly pointed, with longest rays immediately ventral to dorsalmost rays and immediately dorsal to ventralmost rays. Body fully scaled. Fins unscaled, except for sheath of small scales on base of anal fin and few scale rows extending onto basal portions of caudal-fin rays.

Coloration in alcohol.—Overall drab brown, darker dorsally and fading to lighter tan on ventral surface (Fig. 1). Transverse dark bars present along dorsum and continuing ventrally, ventral portion of bars much fainter than dorsal portion. Portion of bars below lateral line absent or very faint in larger specimens (>100 mm SL). Faint stripe running along posterior half of lateral line in less than 5% of specimens (Fig. 1C).

Distinct, dark, large spot centered along lateral line at midportion of body dorsal to pelvic-fin origin (Fig. 1A). Midlateral spot darker and more circular in smaller individuals (<100 mm SL), with the spot fading slightly, shrinking in size, and having more horizontally ellipsoid shape in larger individuals. Small, faint black spot located along lateral line over hypural plate in only 21% of specimens, absent in other 79% of specimens (Fig. 1B). Small dark spot located just posterior to the opercle proximate to the extrascapular; spot faint in the same previous 21% of specimens and absent in the other 79% of specimens.

Melanophores present along fin-ray margins, but rarely on interradiation membranes. Pigmentation on dorsal, anal, and caudal fins outlining segmentation and branching of rays; densest from midpoint to distal portion of rays. Pigmentation on fins and rays absent in all specimens. Adipose fin

Table 2. Linear morphometrics for all examined species summarized as observed ranges, with mean \pm standard deviation in parentheses. Standard length (SL) appears in millimeters. Measures 1 to 29 are percentages of SL, measures 30–37 are percentages of head length.

	<i>Leporinus arimaspi</i> (holotype)	<i>Leporinus arimaspi</i> (paratypes)	<i>Leporinus aripuanaensis</i>
Standard length	117.53	43.2–189.53 (75.19 \pm 26.79)	47.72–90.78 (72.64 \pm 11.23)
1 Snout to dorsal-fin origin	45.87	44.20–48.52 (45.84 \pm 0.9)	45.94–49.62 (47.41 \pm 0.9)
2 Snout to adipose-fin origin	85.84	79.93–88.18 (84.85 \pm 1.3)	83.91–86.22 (85.04 \pm 0.7)
3 Snout to anal-fin origin	82.94	75.38–84.10 (80.63 \pm 1.7)	78.99–84.10 (81.52 \pm 1.5)
4 Snout to pelvic-fin insertion	49.22	29.72–56.72 (49.49 \pm 2.9)	50.15–54.73 (51.88 \pm 1.3)
5 Snout to pectoral-fin insertion	25.7	25.10–28.28 (27.30 \pm 0.7)	25.82–31.62 (28.36 \pm 1.4)
6 Dorsal-fin origin to pectoral-fin insertion	27.39	23.28–28.17 (26.02 \pm 1.1)	24.55–29.04 (25.99 \pm 1.1)
7 Dorsal-fin origin to pelvic-fin insertion	24.73	19.99–25.48 (23.12 \pm 1.2)	19.81–23.23 (21.92 \pm 0.9)
8 Dorsal-fin origin to anal-fin origin	42.98	39.96–45.11 (41.72 \pm 1.3)	36.77–41.52 (39.51 \pm 1.4)
9 Dorsal-fin origin to anal-fin insertion	50.61	44.97–50.92 (47.05 \pm 1.5)	44.33–50.06 (46.82 \pm 1.7)
10 Dorsal-fin origin to posterior margin of hypurals	57.68	54.20–59.16 (56.78 \pm 1.1)	52.45–57.84 (54.67 \pm 1.5)
11 Dorsal-fin origin to adipose-fin origin	42.08	38.26–42.40 (40.65 \pm 1.1)	36.18–41.29 (38.63 \pm 1.6)
12 Length of dorsal-fin base	15.7	14.01–16.11 (14.75 \pm 0.5)	13.04–15.61 (14.05 \pm 0.7)
13 Dorsal-fin insertion to pelvic-fin origin	22.94	17.71–24.84 (21.49 \pm 1.5)	17.75–23.26 (20.35 \pm 1.6)
14 Dorsal-fin insertion to adipose-fin origin	27.27	24.02–27.75 (25.7 \pm 1.0)	23.32–27.18 (25.47 \pm 1.1)
15 Dorsal-fin insertion to anal-fin origin	29.82	26.11–30.34 (27.92 \pm 1.3)	25.11–29.81 (26.81 \pm 1.3)
16 Dorsal-fin insertion to anal-fin insertion	35.66	33.00–36.31 (34.24 \pm 0.8)	30.51–34.69 (32.71 \pm 1.4)
17 Adipose-fin origin to anal-fin origin	13.74	12.59–15.96 (14.05 \pm 0.7)	13.31–15.36 (14.61 \pm 0.6)
18 Adipose-fin origin to anal-fin insertion	11.03	9.76–13.52 (11.22 \pm 0.8)	9.22–11.65 (10.59 \pm 0.7)
19 Adipose-fin origin to posterior margin of hypurals	16.85	15.01–18.09 (16.21 \pm 0.8)	13.12–18.62 (15.62 \pm 1.3)
20 Length of anal-fin base	8.61	7.46–9.81 (8.54 \pm 0.5)	7.94–10.05 (8.75 \pm 0.6)
21 Anal-fin insertion to posterior margin of hypurals	10.68	10.28–12.44 (11.54 \pm 0.4)	10.78–13.00 (11.72 \pm 0.7)
22 Pelvic-fin insertion to anal-fin origin	35.16	31.29–35.39 (33.28 \pm 1.0)	26.98–33.23 (30.60 \pm 1.6)
23 Pelvic-fin insertion to adipose-fin origin	41.74	34.73–41.74 (37.61 \pm 1.7)	33.64–40.02 (37.90 \pm 1.5)
24 Pelvic-fin insertion to posterior margin of hypurals	54.81	50.03–55.17 (51.76 \pm 1.2)	49.05–53.1 (50.89 \pm 1.2)
25 Pelvic-fin insertion to pectoral-fin insertion	24.89	22.14–28.98 (24.92 \pm 2.0)	21.66–26.42 (24.61 \pm 1.3)
26 Greatest body depth	24.84	19.42–26.85 (23.35 \pm 1.5)	19.24–23.92 (21.93 \pm 1.2)
27 Greatest body width	12.27	9.51–16.02 (12.25 \pm 1.4)	9.07–12.43 (10.75 \pm 0.7)
28 Caudal-peduncle depth	7.89	7.25–10.00 (8.68 \pm 0.6)	8.05–9.25 (8.74 \pm 0.4)
29 Head length	23.6	22.90–28.39 (25.57 \pm 1.2)	23.66–27.60 (25.31 \pm 1.0)
30 Preopercle length	77.13	75.05–85.60 (78.19 \pm 2.2)	74.17–81.24 (77.59 \pm 2.0)
31 Snout to anterior margin of eye	38.38	34.29–45.17 (38.65 \pm 2.9)	36.60–41.69 (38.72 \pm 1.7)
32 Head depth	77.39	66.10–78.26 (70.49 \pm 3.4)	63.02–73.34 (67.66 \pm 4.0)
33 Snout depth	46.67	40.34–49.23 (44.73 \pm 2.8)	37.43–45.18 (41.10 \pm 2.0)
34 Jaw length	19.1	17.23–24.61 (21.17 \pm 1.6)	16.86–23.23 (20.07 \pm 1.8)
35 Eye diameter	33.31	28.27–34.79 (31.31 \pm 1.6)	26.47–30.26 (28.60 \pm 1.2)
36 Interorbital width	36.31	29.64–44.16 (36.79 \pm 3.3)	30.73–34.41 (32.53 \pm 1.0)
37 Snout to supraoccipital crest	87.93	82.41–91.92 (89.65 \pm 1.9)	87.24–99.71 (91.42 \pm 2.74)

with diffuse bar halfway between fin origin and fin margin in some specimens. Melanophores concentrated at adipose-fin margin in other specimens.

Preserved specimens with considerable variation in overall color intensity. Some pale; with stripes hardly noticeable and no pigmentation on fins. Others with darker background and more intense stripes and spots (Fig. 1B). Smaller specimens typically have more intense striping and spots.

Distribution.—Occurring throughout the Río Orinoco drainage in Venezuela, including the ríos Caura, Pamoni, Casiquiare, Manapiare, and Ventuari (Fig. 3). Some specimens collected near bedrock outcroppings and banks.

Etymology.—We name the species *arimaspi* after the mythical Arimaspi people of northern Scythia in Greek mythology. The large black spot on the midlateral portion of the

body in this new species is reminiscent of the single, pronounced, centrally located eye that the Arimaspi people were said to possess. A noun in apposition.

DISCUSSION

Morphometric differentiation from *L. aripuanaensis*.—PCA of size-standardized variables indicates that *Leporinus arimaspi* and *L. aripuanaensis* differ in body shape (Fig. 4). The two most important eigenvectors index 21.75% ($\lambda_1 = 5.150$) and 14.65% ($\lambda_2 = 3.468$) of the total variance, respectively (see Table 3 for loadings). PC1 exhibits differences in dorsal-fin position, body width, body depth, and head depth. PC2 exhibits differences in the snout to anal-fin origin length, snout to supraoccipital crest length, dorsal-fin and pelvic-fin position, and head length. The MANOVA for the first three Principal Components revealed statistically significant

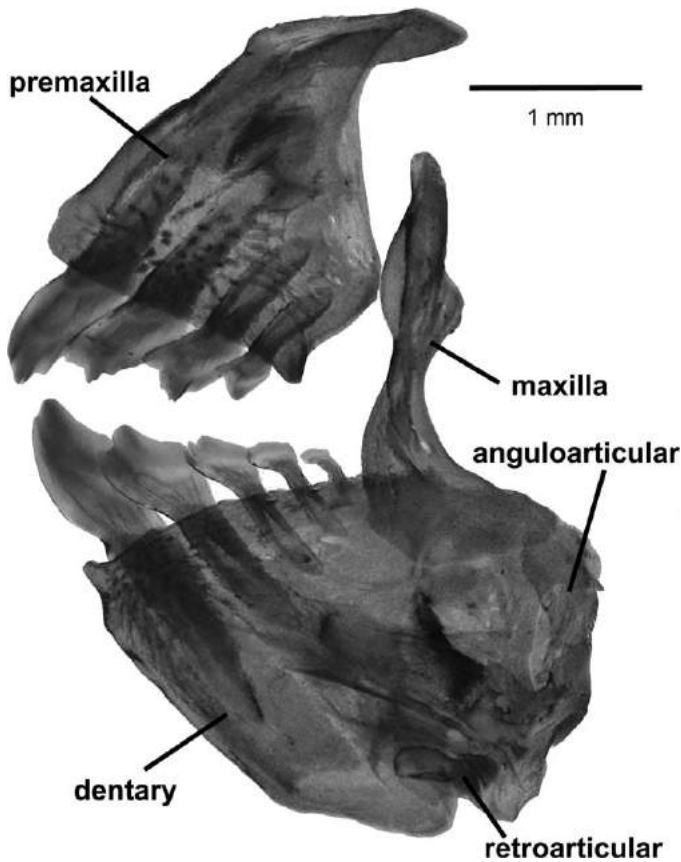


Fig. 2. Right upper and lower jaws of *Leporinus arimaspi*, paratype, ANSP 182644, in lateral view. Image reversed to standard left-facing orientation.

differences between the two species ($P < 0.0001$). The Tukey HSD tests showed which axes are responsible for the overall significance of the MANOVA. PC1 ($P < 0.0001$) and PC2 ($P < 0.05$) had significant differences between species; however, PC3 had no significant differences and was not considered further. The DFA revealed complete separation

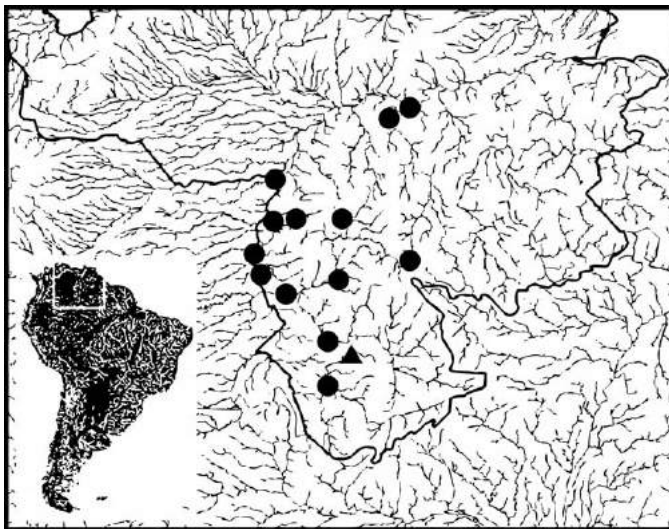


Fig. 3. Geographic distribution of examined specimens of *Leporinus arimaspi*. Triangle represents holotype locality. Some symbols represent more than one collection locality. Black outline represents political demarcation of Venezuela.

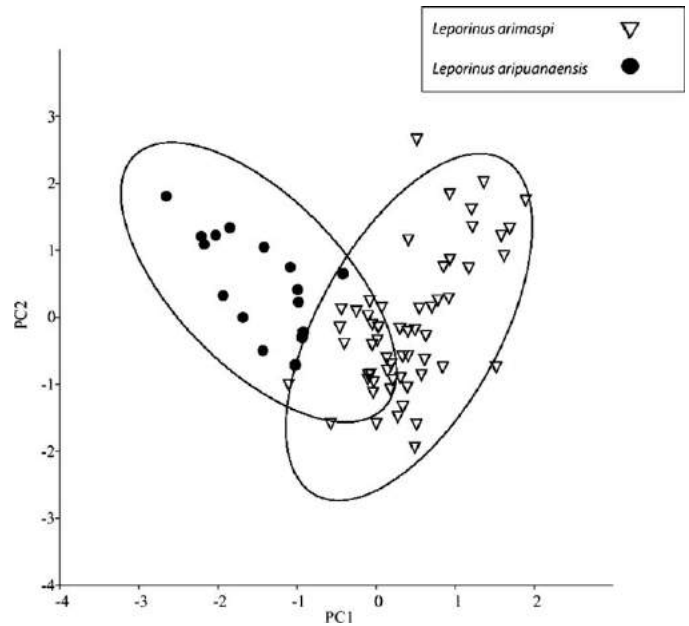


Fig. 4. Scatterplot of principal component 1 (PC1) vs. principal component 2 (PC2) for *Leporinus arimaspi* (gray triangles) and *L. ariapuaensis* (black dots) showing slight separation between two species. Ellipses represent 95% confidence intervals.

between the two species with correct classification occurring 100% of the time (Fig. 5). The DFA found two measurements (eye diameter and interorbital width) to exhibit the most variation between the two species (Table 3).

The Type II regression analysis for eye diameter and interorbital width against SL revealed statistically distinct slopes between the two species ($P = 0.0005$; $P < 0.0001$). The difference between the two species becomes apparent at around 70 mm SL and increases at larger sizes (Fig. 6), indicating that the species begin life with similar shapes, then diverge as they grow.

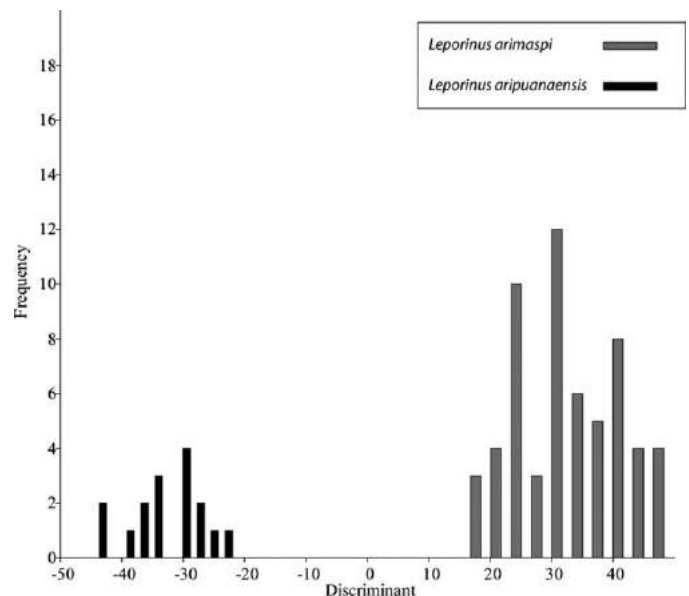


Fig. 5. Discriminant function analysis showing complete separation between *Leporinus arimaspi* (gray) and *L. ariapuaensis* (black) and 100% correct classification.

Table 3. Principal component (PC) loadings from the morphometric analysis. Loadings larger than 0.2 are in bold.

	PC1	PC2	PC3	DFA scores
Snout to dorsal-fin origin	-0.1914	0.1417	0.0297	-3.658
Snout to adipose-fin origin	-0.1513	0.0932	-0.1448	-1.405
Snout to anal-fin origin	-0.1741	0.2461	-0.0753	-3.659
Snout to pelvic-fin insertion	-0.5129	-0.1481	0.2565	-2.178
Snout to pectoral-fin insertion	-0.1579	0.1682	0.0476	-4.614
Dorsal-fin origin to pectoral-fin insertion	-0.0879	-0.088	0.1623	1.583
Dorsal-fin origin to pelvic-fin insertion	0.0843	-0.1287	0.2244	5.844
Dorsal-fin origin to anal-fin origin	0.2613	-0.0843	0.0767	9.403
Dorsal-fin origin to anal-fin insertion	0.0722	-0.1313	-0.1049	-6.828
Dorsal-fin origin to posterior margin of hypurals	0.1529	-0.2826	-0.239	0.979
Dorsal-fin origin to adipose-fin origin	0.1968	-0.2103	-0.1905	7.003
Length of dorsal-fin base	0.0723	-0.1072	0.0372	1.382
Dorsal-fin insertion to pelvic-fin origin	0.1546	0.1531	0.1345	8.151
Dorsal-fin insertion to adipose-fin origin	-0.022	-0.2237	-0.1084	-12.95
Dorsal-fin insertion to anal-fin origin	0.1177	-0.1185	0.0155	0.161
Dorsal-fin insertion to anal-fin insertion	0.0847	-0.2649	-0.0698	1.08
Adipose-fin origin to anal-fin origin	0.0297	0.0589	0.1719	-9.658
Adipose-fin origin to anal-fin insertion	0.0928	0.0095	0.1396	-0.2984
Adipose-fin origin to posterior margin of hypurals	-0.0111	-0.1146	0.0737	2.222
Length of anal-fin base	-0.06	-0.0217	-0.0496	-2.782
Anal-fin insertion to posterior margin of hypurals	-0.0364	0.0111	0.012	0.208
Pelvic-fin insertion to anal-fin origin	0.2919	-0.1771	-0.0142	2.843
Pelvic-fin insertion to adipose-fin origin	-0.0066	0.025	-0.1887	-1.364
Pelvic-fin insertion to posterior margin of hypurals	0.0247	-0.1859	-0.0394	-0.127
Pelvic-fin insertion to pectoral-fin insertion	0.1843	0.5053	-0.52	-3.484
Greatest body depth	0.2338	0.0781	0.2523	-6.091
Greatest body width	0.263	-0.0162	0.132	-3.976
Caudal-peduncle depth	0.0381	0.0519	0.1459	-8.699
Head length	0.1198	0.2071	0.2542	-14.66
Preopercle length	0.1153	0.182	0.1005	7.287
Snout to anterior margin of eye	-0.0081	-0.0137	0.2123	0.989
Head depth	0.2041	0.0878	0.16	-1.787
Snout depth	0.1638	0.0746	0.0502	7.482
Jaw length	0.0612	0.038	0.0702	2.211
Eye diameter	0.1432	0.0818	-0.0246	21.11
Interorbital width	0.1846	-0.003	0.1379	14.98
Snout to supraoccipital crest	0.0832	0.2696	0.2034	-2.297

Historical comments.—In 1882, Steindachner apparently recognized the distinctiveness of *L. arimaspi* based on overall body shape and coloration, and labeled specimens in the Vienna ichthyology collection (NMW 68054 and NMW 68149) with this morphology as *Leporinus orinocensis* Steind (Birindelli, pers. comm., 2013). However, he never published his description, and we learned of the existence of the specimens only during review of this current paper. If the Vienna specimens are in fact *L. arimaspi* (as they appear to be from photographs shared with us by Dr. Birindelli), more than 130 years will have passed between the recognition of *L. arimaspi* as a new species, and its formal description!

Biogeographic implications.—The morphological similarity between *L. arimaspi* and *L. aripuanaensis*, coupled with their large geographic separation, suggests an interesting evolutionary history for these two taxa. This morphological resemblance could indicate convergence or may result from a vicariant event during the uplift of the Andes, which separated the Orinoco from the Amazon basin (Lundberg et al., 1998). Many groups of Neotropical fishes, including

representatives from Siluriformes, Beloniformes, and Characiformes, show separation of sister clades between the Orinoco and Amazon Basins because of this geologic event (Arratia, 1987; Azpelicueta, 1994; Lovejoy and de Araújo, 2000; Sivasundar et al., 2001). However, *L. aripuanaensis* is currently only known from two localities, the Rio Aripuanã and the Rio Uatumã, with both populations of *L. aripuanaensis* being closer to populations of *L. arimaspi* than they are to each other. If the two species are not sister taxa, either the morphology represents the ancestral condition or convergence occurred between the two species. If it is the former, then other undiscovered populations with morphology similar to *L. aripuanaensis* and *L. arimaspi* may await discovery. Completion of the in-depth phylogenetic analysis on which we are working with several collaborators will help test these hypotheses.

Color polymorphisms.—Although all specimens of *L. arimaspi* possess the diagnostically distinct, dark, large spot centered along the lateral-line scale row dorsal to the pelvic-fin origin, other aspects of coloration vary within the species.

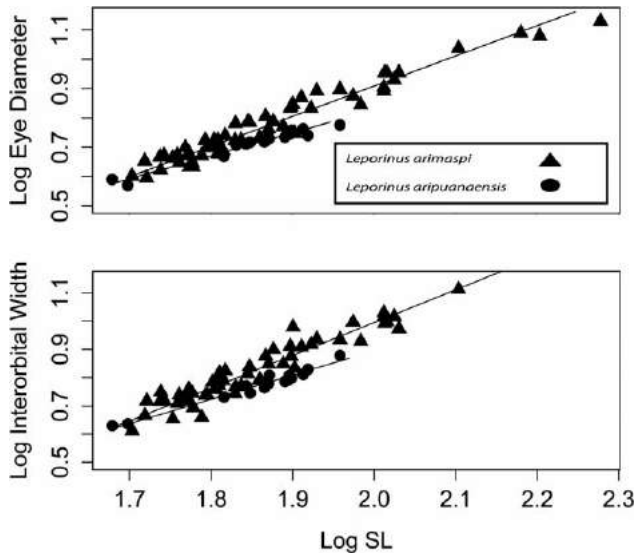


Fig. 6. Regressions of natural logarithm of eye diameter and interorbital width against natural logarithm of SL for *Leporinus arimaspi* (gray triangles) and *L. aripuanaensis* (black dots) showing different slopes.

Six specimens (21%) had a small, faint black spot located along the lateral line over the hypural plate and a small dark spot located just posterior to the opercle (Fig. 1B), while one specimen had an additional faint stripe running along the posterior half of lateral line (Fig. 1C). Though morphometric and meristic measurements group all three color morphs together, with such low sample sizes and without genetic samples it is difficult to determine if the color morphs represent color plasticity or additional undescribed species. Because of this difficulty, we included all three color morphs in our concept of *Leporinus arimaspi*, but excluded the specimens with additional faint spots and the specimen with the lateral stripe from the type series. An in-depth phylogenetic and biogeographic analysis of this group is needed to fully understand the amount of species diversity and morphological plasticity in the region.

MATERIAL EXAMINED

Leporinus amazonicus: UF 162283, 1, 171.5 mm SL, Peru, Loreto, Río Ucayali drainage, Caño Yarina, Pacaya Samira National Reserve, flooded forest, 5°22'0"S, 74°30'48"W; USNM 305164, 1, 64.6 mm SL, Peru, Loreto.

Leporinus aripuanaensis: INPA 15371.0, 18, 46.2–91.8 mm SL, Brazil, Amazonas, Amadio Presidente Figueiredo, 2°2'3"S, 60°1'29"W.

Leporinus brunneus: ANSP 159365, 1, 109.5 mm SL, Venezuela, Amazonas, Río Orinoco at El Burro, 6°12'N, 67°26'W; ANSP 166762, 1, 74.8 mm SL, Venezuela, Bolivar, Río Orinoco Basin, Río Aro, Salto El Pajaro; ANSP 182672, 1, 67.9 mm SL, Venezuela, Amazonas, Río Orinoco, Pasaganado, 38 km N of San Fernando de Atabapo, 4°23'4"N, 67°46'28"W; ANSP 190763, 1, 60.6 mm SL, Venezuela, Amazonas, Río Ventuari, Orinoco drainage, at Raudales Chipirito, 88.5 km E of San Fernando de Atabapo, 4°4'7"N, 66°17'13"W; AUM 43122, 1, 86.0 mm SL, Venezuela, Amazonas, Pasaganado, on Río Orinoco, 38 km N of San Fernando de Atabapo, 4°23'3"N, 67°46'27"W.

Leporinus cylindriciformis: MCZ 20430, holotype, 195.3 mm SL, Brazil, Pará, Río Xingu at Porto de Moz, 1°45'S, 52°10'W.

Leporinus niceforoi: ANSP 40492, 1, 117.1 mm SL, Colombia, Caqueta, Florencia, Río Ortegusa basin, Amazon watershed; ANSP 70491, 1, 128.0 mm SL, Colombia, Caqueta, Florencia, Río Ortegusa basin, Amazon watershed.

Leporinus cf. *niceforoi*: FMNH 102150, 2, 33.6–75.3 mm SL, Ecuador, Napo, Río Yasuni, 1–2 km downstream from confluence with Río Jatuncocha, 0°59'6"S, 75°25'36"W; FMNH 102153, 6, 35.4–101.9 mm SL, Ecuador, Napo, Río Tiputini, near mouth in Río Napo and quebradas, 0°49'S, 75°31'W; FMNH 102156, 5, 117.8–158.9 mm SL, Ecuador, Napo, upper Río Tiputini, upstream from bridge, 0°44'30"S, 76°53'W; FMNH 111343, 1, 54.5 mm SL, Peru, Loreto, Punto Caño, about 7 km above mouth of Río Chambira in Río Marañon, 5°0'S, 74°53'W; FMNH 111344, 2, 40.6–46.4 mm SL, Peru, Loreto, Río Chambira and small tributaries above mouth in Río Marañon, 5°0'S, 74°53'W; FMNH 111608, 1, 81.3 mm SL, Peru, Loreto, Río Amazonas drainage, upstream from Iquitos; USNM 311303, 1, 58.5 mm, Ecuador, Napo, Estero Trinita, 45 min by boat from Rocafuerte on left margin of Río Yasuni.

Leporinus ortomaculatus: ANSP 159346, 5, 50.2–78.0 mm SL, Venezuela, Bolivar, Caño (possibly Caño Curimo) draining into Río Caura near confluence of Río Caura and Río Orinoco, 7°37'48"N, 64°50'42"W; ANSP 160346, 2, 42.0–47.3 mm SL, Venezuela, Bolivar, confluence of Río Orinoco and Río Caura at Las Piedras, 7°38'36"N, 64°50'0"W; ANSP 182671, 6, 54.9–74.2 mm SL, Venezuela, Amazonas, Río Orinoco, 117 km E of La Esmeralda, 3°17'24"N, 66°36'W.

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