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A new species of *Limatulichthys* Isbrücker & Nijssen (Loricariidae, Loricariinae) from the western Guiana Shield

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Abstract

Limatulichthys nasarcus n. sp. is described as a new species based on 15 specimens from the Ventuari and Caura Rivers in Southern Venezuela. The new species can be distinguished from its only congener, *L. griseus*, by the presence of anterior abdominal plates half the size of those at center of abdomen (vs. plates similar in size); distinct spots less than half of diameter of naris across entire dorsum, including snout and head (vs. indistinct dorsal spots larger or equal than diameter of naris); lateral portions of head and opercle with dark well-defined spots larger than those on dorsum (vs. spots on lateral portions of head and opercle equal in size to those on remainder of body); snout profile in dorsal view broadly rounded (vs. acutely triangular); head longer (21.4–24.2 SL vs. 17.7–21.0%); and anal fin longer (15.7–18.0 SL vs. 13.7–15.6%). Distinctiveness of the two species is further supported by their non-overlapping distribution in multivariate morphospace. The disjunct distribution of *L. nasarcus* across both the Caura and Ventuari rivers exclusive of the main Orinoco River channel contributes to a growing body of evidence supporting the historical connection between headwaters of these drainages. The hypothesized existence of a ‘proto-Berbice’ paleodrainage provides one explanation for such a connection.

Key words: *Limatulichthys*, Neotropics, taxonomy, Ventuari, Caura

Resumen

Limatulichthys nasarcus n. sp. es propuesta como una nueva especie a partir de 15 ejemplares provenientes de los ríos Ventuari y Caura al sur de Venezuela. La nueva especie puede ser distinguida de su único congénere, *L. griseus*, por la presencia de placas abdominales anteriores la mitad del tamaño que aquellas en el centro del abdomen (vs. placas de tamaño similar); manchas bien definidas, menos de la mitad del diámetro de las narinas, distribuidas en el dorso, incluyendo hocico y cabeza (vs. manchas grandes poco definidas en dorso, hocico y cabeza, más grandes o de igual tamaño al diámetro de las narinas); manchas oscuras bien definidas en las porciones laterales de la cabeza y opérculo más grandes que aquellas en el dorso (vs. manchas en las porciones laterales de la cabeza y opérculo del mismo tamaño a aquellas presentes en el dorso); perfil dorsal del hocico ancho, redondo (vs. extremadamente triangular); cabeza más larga (21.4–24.2 SL vs. 17.7–21.0%); y aleta anal más larga (15.7–18.0 SL vs. 13.7–15.6%). La diferenciación de ambas especies es soportada por su no superposición en la distribución en el morfoespacio multivariado. La distribución disyunta de *L. nasarcus* a lo largo tanto de los ríos Caura y Ventuari exclusivo del canal principal del río Orinoco contribuye a la creciente, y ya existente evidencia apoyando una conexión histórica entre las cabeceras de estos drenajes. La existencia hipotética de una paleocuenca “proto-Berbice” ofrece una explicación para dicha conexión.

Palabras clave: *Limatulichthys*, Neotrópico, taxonomía, Ventuari, Caura

Introduction

Isbrücker & Nijssen erected *Limatulichthys* and designated *Loricaria punctata* Regan as the type species (Isbrücker, 1979) with *Loricaria griseus* Eigenmann, *Rineloricaria petleyi* Fowler, and *Loricariichthys parnahybae* Fowler being treated as junior synonyms. Isbrücker *et al.* (2001) observed that the name *Loricaria punctata* was originally occupied by *Loricaria punctata* Kner (= *Pterygoplichthys punctatus*; Ferraris, 2007), and concluded that *Loricaria punctata* Regan should be treated as a junior homonym. Without providing justification, Isbrücker *et al.* (2001:24) recognized *Loricaria griseus* Eigenmann as a distinct species of *Limatulichthys*, and *Rineloricaria petleyi* Fowler as the senior synonym of *Loricaria punctata* Regan. Despite this, and also without providing justification, Ferraris (2003) regarded *Loricaria griseus* as the senior synonym of *Loricaria punctata* Regan and, therefore, as the type species of *Limatulichthys*, which he concluded was monotypic. Ferraris (2007), citing Isbrücker *et al.* (2001), later recognized *Limatulichthys petleyi* as a valid species. Covain & Fisch-Muller (2007) provided a more detailed taxonomic history of *Limatulichthys* and elaborated on justifications for the varying taxonomic conclusions of Isbrücker *et al.* (2001) and Ferraris (2003, 2007). They also concluded that *Limatulichthys* is monotypic and that *L. griseus* is its type species, as did Eschmeyer (2014).

The original description of *Limatulichthys* is brief. The authors (Isbrücker & Nijssen, in Isbrücker, 1979) mention only that the genus is similar to *Pseudoloricaria* Bleeker, with *Limatulichthys* being distinguished by having abdominal plates more similar to those found in the *Rineloricaria platyura* group (*sensu* Isbrücker) but lacking the enlarged odontodes of this group, whereas abdominal plates in *Pseudoloricaria* are more similar to those found in several species of *Loricaria* Linnaeus. Phylogenetic relationships of *Limatulichthys* to other loricariin genera have been examined using both morphological (Rapp Py-Daniel, 1997) and molecular data (Rodríguez *et al.*, 2011; Lujan *et al.*, 2014). All of these studies agree on its placement within tribe Loricariini, subfamily Loricariinae. Morphological data suggest that *Limatulichthys* is sister to a clade consisting of *Hemiodontichthys* Bleeker, *Reganella* Eigenmann, *Loricariichthys* Bleeker, and *Furcodontichthys* Rapp Py-Daniel, with *Pseudoloricaria* arising from the next most basal node (Rapp Py-Daniel, 1997), whereas molecular data suggest that *Limatulichthys* is sister to *Hemiodontichthys* (Rodríguez *et al.*, 2011).

Limatulichthys griseus is putatively known from the Amazon, Tocantins, Essequibo, western Orinoco, and Parnaíba river basins in Brazil, Colombia, Ecuador, Guyana, Peru, and Venezuela (Ferraris, 2003), but to date no systematic revision of the species or comparative analysis of individuals from throughout its range has been published. In this study, we examined specimens of *Limatulichthys* from near the type locality of *L. griseus* in the Essequibo River basin, Guyana, and conduct a detailed comparison of these topotypes with congeners from the middle Ventuari River, a right (east) bank tributary of the upper Orinoco River, the Caura River, a right (south) bank tributary of the Orinoco River to the northwest of the Ventuari River, and the upper Orinoco River main channel, all in southern Venezuela. We describe the Ventuari and Caura river population as a species new to science, and discuss the biogeographical implications of its distribution.

Methods

Counts and measurements were made to the nearest 0.1 mm using digital calipers. Measurements were made on the left side of the body when possible. Morphometric data are given as percentages of standard length (SL) or head length (HL) and mostly follow Thomas & Rapp Py-Daniel (2008), with addition of the following measurements: distance from the anteriormost tip of the snout to the posteriormost margin of the naris (snout-naris distance); snout width at upper lip; snout width at anterior margin of nares; distance between nares at their posteriormost margin (internasal distance); maximum length of the premaxilla (premaxillary length); maximum length of the dentary (dentary length); rictal barbel length; distance from anteriormost to posteriormost margin of the lower lip (lower-lip length); distance from anterior border of orbit to posteriormost tip of opercle (post-orbit head length); maximum length of opercle (opercular length); ventral body width at insertion of pectoral spine (cleithral width); body width at pelvic-fin insertion (pelvic girdle width); body width at caudal-fin origin (posteriormost caudal-peduncle width); distance from pelvic-fin insertion to urogenital pore (pelvic-urogenital distance); distance from anal-fin origin to urogenital pore (anal-urogenital distance). Plate series nomenclature follows Paixão & Toledo-Piza (2009). We use the term spine for unbranched dorsal- and paired-fin rays and indicate the number of all unbranched rays with

Roman numerals, followed by Arabic numerals for branched rays. Institutional acronyms follow Sabaj Pérez (2012).

We performed a size-corrected principal component analysis (PCA) on linear measurements of the head region (see character list) by regressing the log-transformed values against the natural log of standard length in order to remove the potentially confounding effects of body size while maintaining body shape components (López-Fernández *et al.* 2012). These residuals were also used in a linear discriminant analysis (LDA), which found the linear combination of head morphometrics that best separated the species (calculated using the MASS package in R).

The holotype of *L. griseus* (FMNH 53077) was analyzed via images provided by the Field Museum of Natural History (Fig. 1).



FIGURE 1. Holotype of *Limatulichthys griseus*, FMNH 53077, 131 mm SL. Conawaruk (=Konawaruk), Guyana. Photos by M.W. Littman, reprinted from FMNH website with permission.

Results

Limatulichthys nasarcus, new species

(Fig. 2, Tables 1 and 2)

Holotype. MCNG 56560 (ex. AUM 39845), 150.9 mm SL, Venezuela, Orinoco River drainage, Ventuari River, beach below Raudales Tencua, 56 km ESE of San Juan de Manapiare, N 05°02'59", W 65°40'20", N.K. Lujan, O. Leon, R. Pajua, 19–20 April 2004.

Paratypes. Seven specimens, all from Venezuela, Amazonas State, Ventuari River drainage: AUM 39845, 1 alc., 122.5 mm SL, 1 cs, 130.7 mm SL, same data as holotype. AUM 39280, 1 alc., 112.2 mm SL, Parucito River at Raudales Salomon, 2.7 km NE of San Juan de Manapiare, N 05°20'46", W 66°02'00", N.K. Lujan, D.C. Werneke, O. León, 16 April 2004; ANSP 182816, 1 alc., 129.0 mm SL, Ventuari River, rapids below Salto Tencua, 227 km ESE of Puerto Ayacucho, 114 masl, N 05°03'03", W 65°37'28", N.K. Lujan, D.C. Werneke, M.H. Sabaj, T. Carvalho, 06 April 2010; MBUCV-V-35730, 1 alc., 137.6 mm SL, same data as AUM 39845. ROM 88302, 1 alc., 122.1 mm SL, same data as ANSP 182816. ANSP 191324, 1 alc., 134.9 mm SL, Ventuari River, downstream end

of extensive rocky rapids ca. 1 km below Salto Tencua, 227 km ESE of Puerto Ayacucho, N 05°03'03", W 65°37'28", M. Sabaj Pérez, N.K. Lujan, D.C. Werneke, T. Carvalho, S.V. Meza, O. Santaella, 16 April 2010.

TABLE 1. Comparative morphometrics for *Limatulichthys nasarcus* n. sp. and *L. griseus*. Holotype values not in percentages.

	Holotype	<i>L. nasarcus</i>			<i>L. griseus</i>		
	150.9	Min	Max	Mean	Min	Max	Mean
Percentages in SL							
Head length	36.4	21.4	24.2	23.4	17.7	21.0	19.2
Predorsal length	47.9	30.9	33.4	31.7	30.0	34.4	32.0
Posdorsal length	87.3	56.8	62.4	58.1	58.0	63.6	60.6
Posanal length	74.1	48.1	50.9	50.0	49.4	52.8	51.7
Abdominal length	24.1	16.0	18.0	16.8	14.5	18.0	17.0
Thoracic length	20.7	12.9	14.2	14.1	12.5	14.5	13.4
Dorsal fin length	29.8	19.7	21.4	21.2	17.2	22.8	19.8
Pectoral fin length	24.0	15.9	17.5	16.4	14.0	16.8	15.7
Pelvic fin length	21.1	14.0	15.9	14.7	12.0	15.1	13.9
Anal fin length	24.0	15.7	18.0	16.2	13.7	15.6	14.6
Head depth at supraoccipital tip	12.0	6.4	8.0	6.8	5.9	7.8	7.2
Body depth at dorsal fin origin	12.9	7.4	8.8	8.4	7.7	9.1	8.4
Caudal peduncle depth	2.6	1.2	1.9	1.5	1.2	1.7	1.5
Cleithral width	22.8	12.6	16.4	14.7	11.4	13.8	12.2
Distance between origin of pelvic fin and urogenital pore	10.8	6.0	7.4	6.6	6.0	7.1	6.8
Distance between origin of anal fin and urogenital pore	17.0	10.8	12.0	11.3	10.9	12.3	11.5
Body width at dorsal fin origin	21.1	12.8	15.3	14.0	11.9	15.3	12.9
Body width at pectoral fins origin	25.4	16.6	17.6	16.8	13.6	18.3	16.0
Body width at pelvic fins origin	21.8	13.3	15.2	14.3	11.7	15.6	13.0
Body width at anal fin origin	18.9	10.9	13.4	12.5	10.2	13.0	11.6
Body width at caudal fin origin	4.5	2.4	3.0	2.8	2.0	3.2	2.3
Percentages in HL							
Head width	26.0	69.8	80.8	73.6	73.8	88.9	83.2
Interorbital distance	5.2	14.1	15.7	15.3	12.1	18.2	13.7
Internasal distance	2.4	6.3	9.0	6.6	5.3	9.7	6.8
Orbital diameter	6.3	17.3	25.4	21.6	21.6	32.6	26.6
Distance from border of orbit to opercle	9.4	24.9	29.9	27.0	26.2	39.4	28.5
Opercular length	25.5	70.1	84.4	73.7	81.9	99.6	89.8
Snout length	15.3	42.0	51.6	43.5	48.7	58.0	53.8
Distance from tip of snout to nasal	11.8	32.3	40.1	34.8	36.5	47.1	42.3
Rictal barbel length	2.2	5.4	10.5	6.8	6.2	12.8	7.3
Premaxillary length	2.7	5.2	10.3	6.3	5.3	8.8	6.7
Dentary length	3.4	7.2	10.0	8.0	6.8	10.8	9.4
Lower lip width	11.2	30.8	50.4	38.1	33.0	47.4	41.2
Snout width at anterior margin of nares	20.2	52.4	65.3	55.5	50.0	65.7	58.7
Width of head at upper lip	15.2	38.2	45.2	41.5	32.2	49.7	40.6

Non-types: Seven specimens, all from Venezuela, Bolivar State, Caura River drainage: ANSP 135884, 2 alc., 104.5 and 119.5 mm SL, sandbar along Caura River some 400 m upstream from Cano Barranca-Rio Caura junction, N 07°08'00", W 65°04'00", J.E. Bohlke and W.G. Saul, 30 January 1977. ANSP 135900, 1 alc., 80.5 mm SL, sandbar along Caura River at junction of Caño Chuapo and Caura River, N 07°07', W 65°00', J.E. Bohlke and W.G. Saul, 29 January 1977. ANSP 135755, 1 alc., 60.0 mm SL, Urbana (Urbani) River on Maripa-Las Trincheras road, N 07°18', W 65°00', J. E. Bohlke, W.G. Saul, and E. Ferrer-Veliz, 20 January 1977. ANSP 135883, 3 alc., 22.2–92.9 mm SL, sandbar 0.80 km upstream from Jabillal on Caura River, N 06°56', W 64°50', J.E. Bohlke, W.G. Saul, E. Ferrer-Veliz, and local boys, 27 January 1977.

TABLE 2. Comparative meristics for *Limatulichthys nasarcus* n. sp. and *L. griseus*.

Counts	Holotype	<i>L. nasarcus</i>			<i>L. griseus</i>		
		Min	Max	Mode	Min	Max	Mode
Lateral plates of median series	17	17	18	18	17	18	18
Lateral plates of mid-ventral series	20	19	20	20	19	20	20
Coalescent plates	11	10	11	11	10	11	11
Ventrolateral thoracic plates	5	5	6	6	5	6	6
Premaxillary teeth	8	5	8	7	6	13	9
Dentary teeth	10	6	10	8	7	14	11
Dorsal fin rays	i-7	i-7	i-7		i-7	i-7	
Pectoral fin rays	i-6	i-6	i-6		i-6	i-6	
Pelvic fin rays	i-5	i-6	i-5		i-6	i-5	
Anal fin rays	i-5	i-5	i-5		i-5	i-5	
Caudal fin rays	i-10-i	i-10-i	i-10-i		i-10-i	i-10-i	



FIGURE 2. Holotype of *Limatulichthys nasarcus* n. sp., MCNG 56560, 150.9 mm SL, Venezuela, Orinoco River drainage, Ventuari River, beach below Raudales Tencua, 56 km ESE of San Juan de Manapiare, latitude 05°2'59"N, 065°40'20"W, N.K. Lujan, O. Leon and R. Pajua, 19–20 April 2004 (photo by NKL).

Diagnosis. *Limatulichthys nasarcus* can be diagnosed from *L. griseus* by having: anterior abdominal plates half the size of those at center of abdomen (vs. plates similar in size); spots across the entire dorsum, including snout and head, less than half of diameter of naris (vs. indistinct spots larger or equal than diameter of naris); dark well-defined spots on lateral portions of head and opercle, larger than those on dorsum (vs. spots on lateral portions of head and opercle equal in size to those on remainder of body); profile of snout in dorsal view broadly rounded (vs. acutely triangular); head longer (21.4–24.2 SL vs. 17.7–21.0%); and longer anal fin (15.7–18.0 SL vs. 13.7–15.6%).

Description. Head and body strongly depressed. Dorsal profile sloped upward from snout to supraoccipital tip, slightly concave or straight from supraoccipital to caudal peduncle. Ventral profile straight. Snout broad, rounded in dorsal view (see Diagnosis; Fig. 2), with rounded anterior margin and convex sides; snout covered with plates. Orbits oriented dorsally, internares space narrower than interorbital space. Orbital notch poorly developed, dorsal margin of orbit not raised.

Upper lip with fringe of usually five triangulate papillae increasing in size laterally, papillae not extending past premaxillary teeth. Row of triangulate papillae extending along margins of lower lip to base of maxillary barbel. Maxillary barbel short, thin, and attached to lower lip via fleshy membrane. Lower lip divided by median furrow with lateral lobes expanded posteriorly to create an emarginated posterior profile. Ventral surface of lower lip having scarce hemispherical papillae. Teeth bilobed, slender. All teeth having medial cuspid larger than lateral. Premaxillary teeth 5–8 per ramus (mode = 7), dentary 6–10 per ramus (mode = 8).

Abdomen covered with contiguous plates from cleithrum to insertion of pelvic fins, plates not organized into distinct patterns. Ventral surface between cleithrum and oral disk having few poorly developed plates in both small and large specimens, with a small region totally lacking plates around the lower lip. Plates missing around pectoral-fin insertion. Anterior abdominal plates smaller than central abdominal plates (see Diagnosis; Fig. 3) Three preanal plates surrounding urogenital pore. Predorsal region in both juvenile and adult specimens lacking well-developed keels. Two predorsal plates.

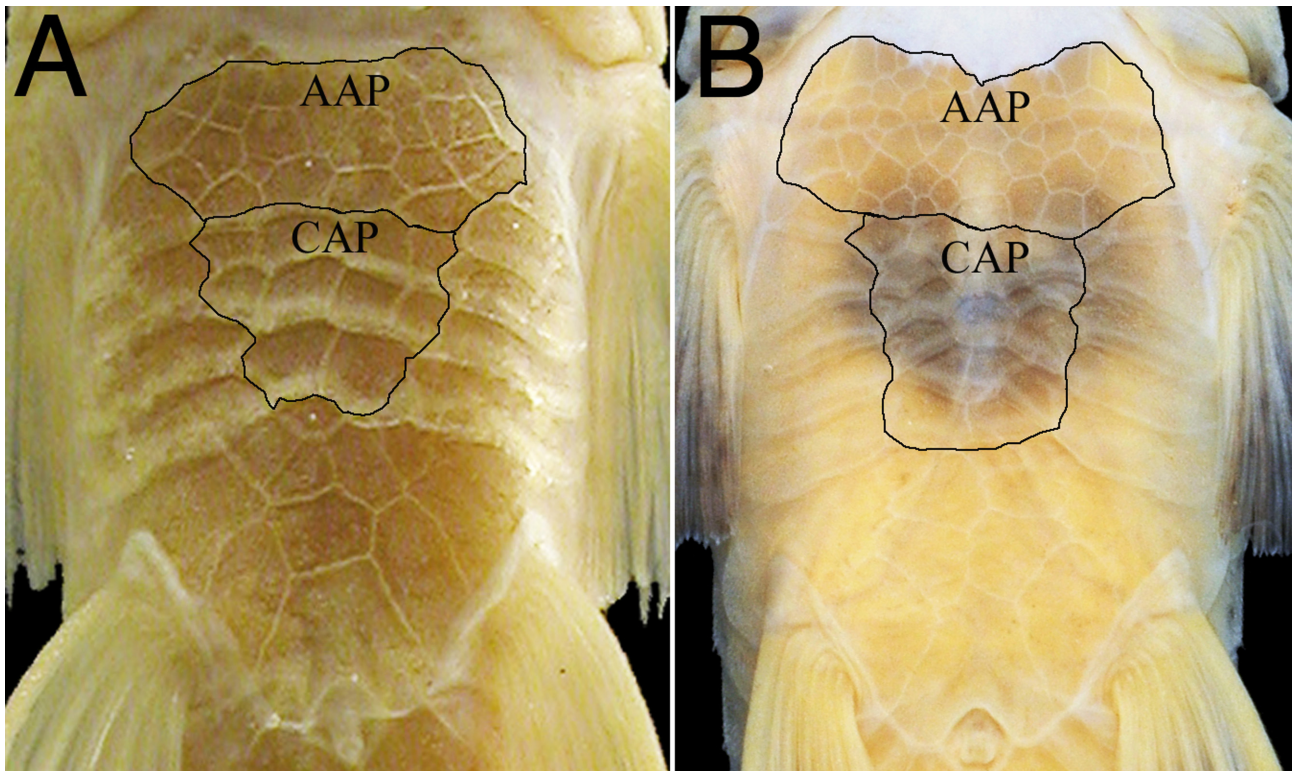


FIGURE 3. Abdominal plates pattern in (A) *Limatulichthys griseus* and (B) *Limatulichthys nasarcus* n. sp. AAP= Anterior abdominal plates; CAP= Central abdominal plates.

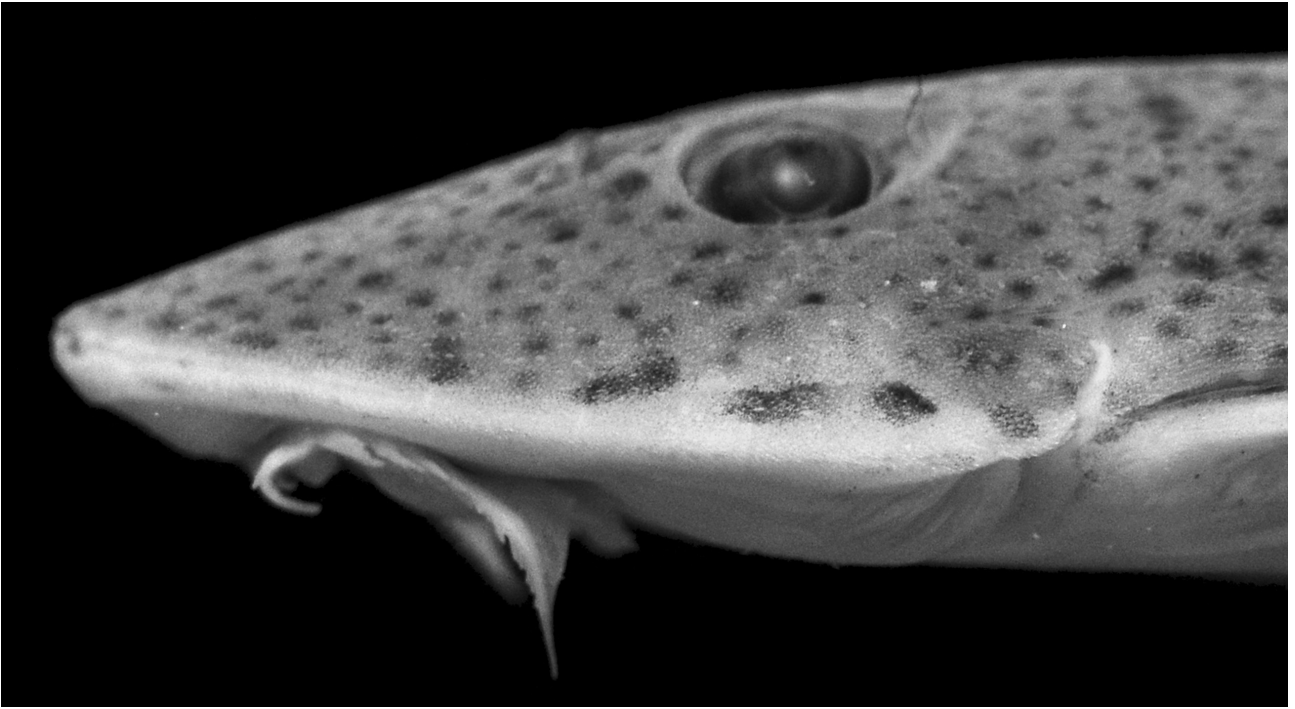


FIGURE 4. Lateral view of head of *Limatulichthys nasarcus* n. sp. (holotype) showing characteristically dark and large spots along the lateral margin (photo by NKL).

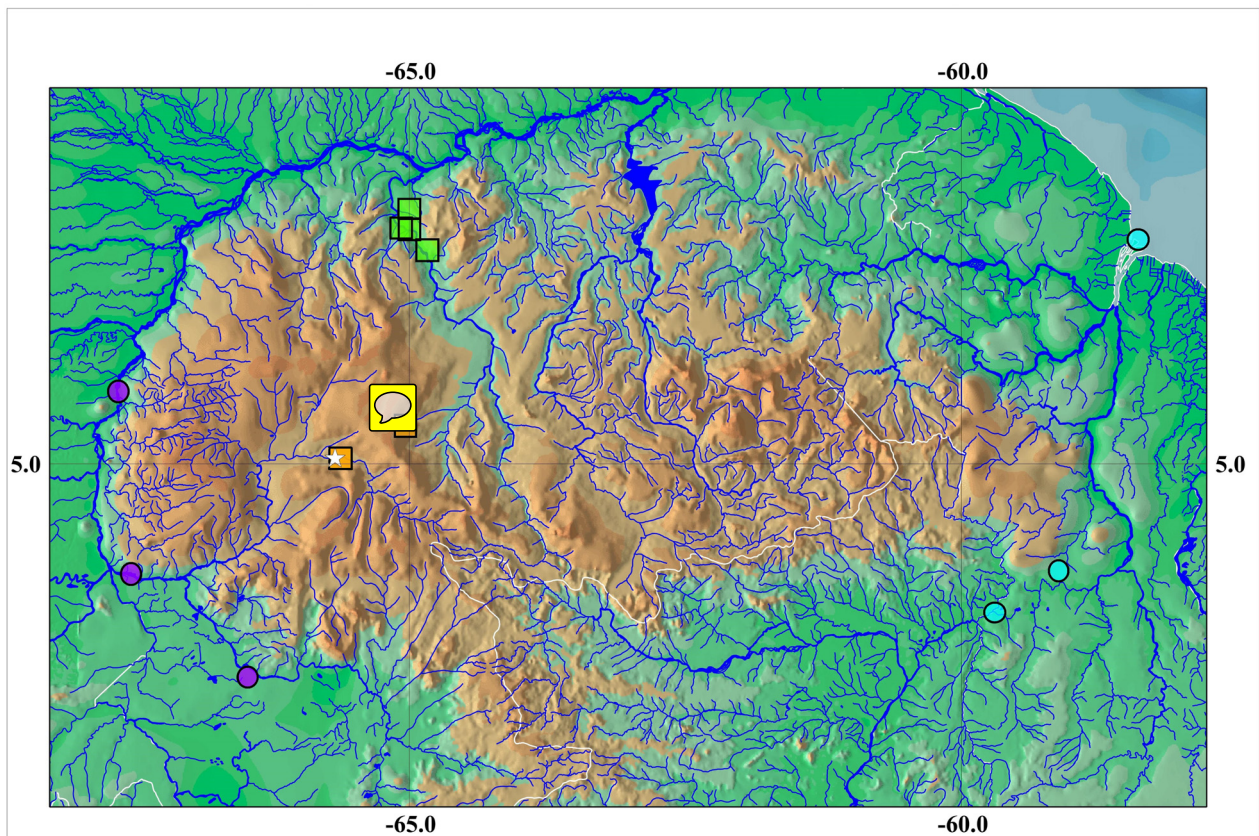


FIGURE 5. Map of southern Venezuela and western Guiana shield showing type locality (white star) and distribution of *Limatulichthys nasarcus* n. sp. (orange squares represent type specimens, whereas non-type specimens are represented by green squares); *Limatulichthys griseus* (blue circles); and *Lim. cf. griseus* (purple circles).

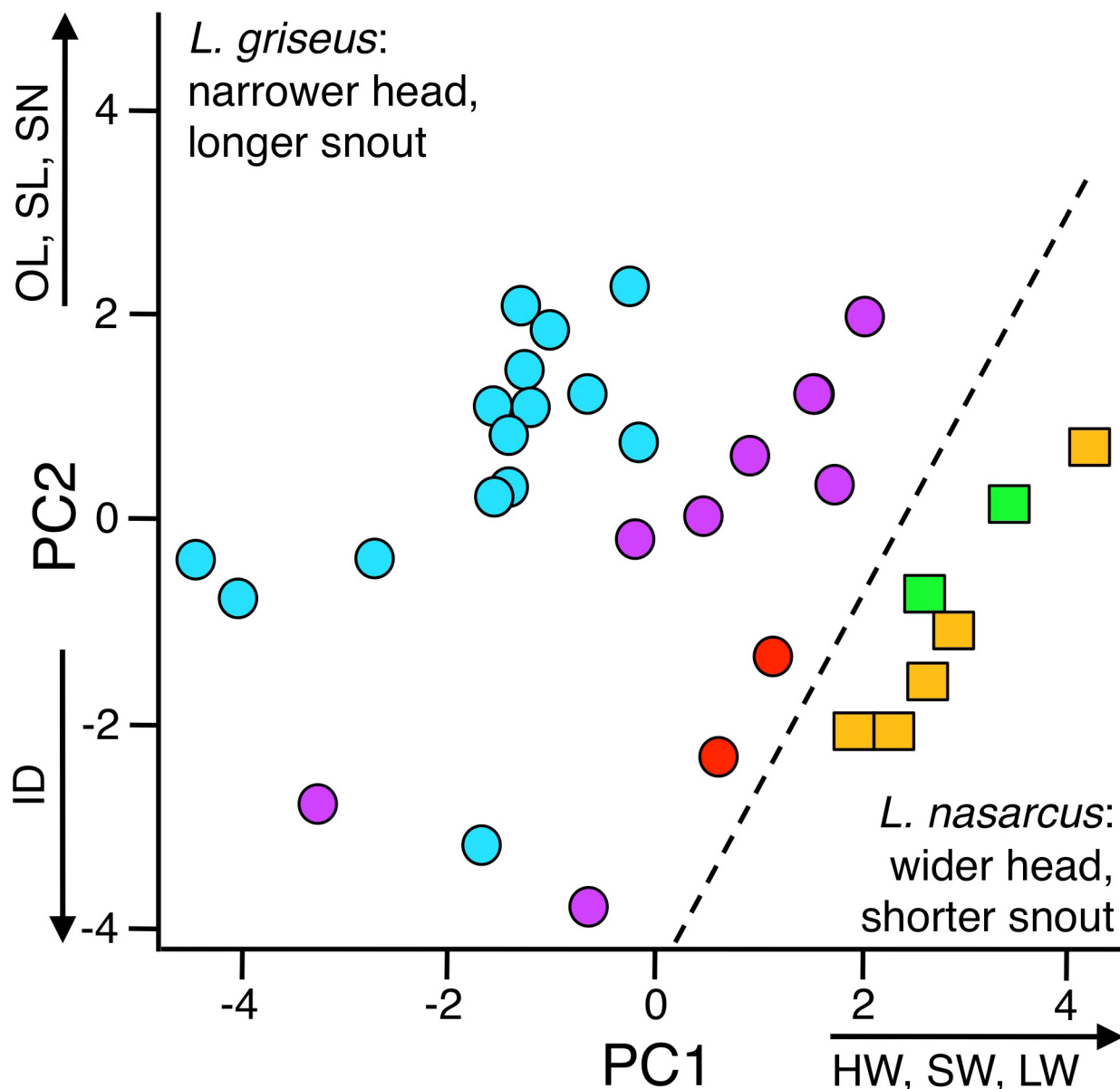


FIGURE 6. Size-corrected PCA for components 1 and 2, showing differentiation between morphological characters of the head region. On PC1: head width (HW), snout width at anterior margin of nares (SW), and width of head at upper lip (LW) loaded most positively. PC2: Opercular length (OL), snout length (SL), and distance from tip of snout to nasal loaded most positively (SN), while interorbital distance (ID) loaded most negatively. Symbols as in Figure 5; *Limatulichthys* cf. *griseus* “Beni” (red circles).

Pectoral fin I,6; first branched ray extending posteriorly slightly beyond pelvic-fin origin, first branched ray longer than spine and all other branched rays; posterior margin concave. Pelvic fin I,5; spine shorter or equal in length to branched rays; posterior margin either straight or oblique. Anal fin I,5; origin posterior to vertical through posteriormost dorsal-fin insertion; first three branched rays longer than others; posterior margin convex. Dorsal fin I,7; spine and first branched ray longer than others; spine extended as filament almost twice as long as branched rays; posterior margin obliquely convex. Caudal fin i,10,i; upper caudal ray extended as a filament almost twice as long as branched rays; posterior margin concave.

Color in alcohol. Dorsal base color sandy brown; small, distinct, unorganized black spots distributed across entire dorsum. Three or four conspicuous black spots on lateral margins of the head below the eye, spots larger than those on dorsum (Fig. 4). Five indistinct transversal bands that are similar in color to spots: anteriormost margin of first band at dorsal-fin origin, anteriormost margin of second band at posteriormost tip of dorsal-fin rays when adpressed, anteriormost margin of third band six plates posterior from posteriormost insertion of dorsal fin,

anteriormost margin of fourth band four plates posterior to the third band, and anteriormost margin of fifth band two plates anterior to caudal-fin origin. All fins except anal fin with black dots. Pectoral fins with spots both on membrane and rays, while on other fins spots only present on rays. Anal fin hyaline. Caudal fin with a noticeable horizontal black band across posterior half of the lower branched rays (Fig. 2). Ventrums uniformly pale yellow. Sexual dimorphism: None observed.

Distribution. Known from the middle Ventuari and lower Caura rivers, Orinoco River drainage, Venezuela (Fig. 5).

Etymology. The specific epithet *nasarcus* is a combination of the Latin *nasus* meaning snout, and *arcus* meaning bow-shaped, in reference to the rounded snout of the species when compared to its congener *Limatulichthys griseus*.

Remarks. As part of our comparative analysis, we examined two *Limatulichthys cf. griseus* specimens from the Beni River, Amazon Basin, Bolivia (AUM 28353) that were morphologically similar to *L. nasarcus*. According to the PCA analysis (Fig. 6), though, *Limatulichthys cf. griseus* ‘Beni’ can still be separated from *L. nasarcus* by presenting a narrower head and longer snout—characters that are shared with *L. griseus*. We therefore tentatively identify these specimens as *L. cf. griseus* ‘Beni’ due to the limited number of specimens available and the tremendous geographic distance between the populations analyzed here.

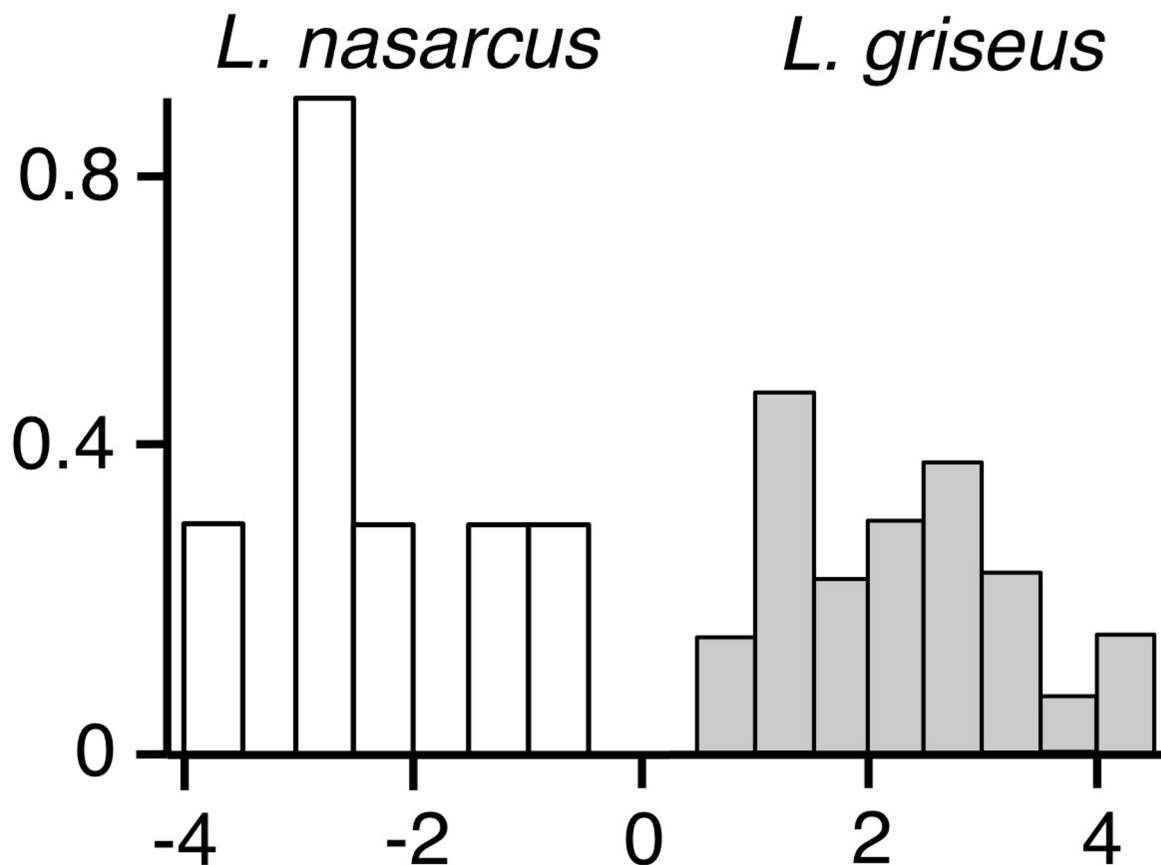


FIGURE 7. Results of discriminant analysis, which show whether linear measurements of the head region (see Table 1), could be discriminated between *Limatulichthys nasarcus* n. sp. and *Limatulichthys griseus*. Values of the discriminant scores for each species are plotted.

Discussion

Limatulichthys nasarcus is assigned to the genus *Limatulichthys* based on abdominal plate arrangement, abdominal plate size, and lip morphology being largely shared with *L. griseus*. In their original description of *Limatulichthys*, Isbrücker & Nijssen (in Isbrücker, 1979:91) provided only one diagnostic character: arrangement of the abdominal

plates similar to those occurring on the *Rineloricaria platyura* group. The authors also stated that *Limatulichthys* is similar to *Pseudoloricaria* but can be differentiated from the latter by abdominal plate arrangement. Our observations do not support those in the original description. We did not observe any clear difference in abdominal plate arrangement between *Limatulichthys* and *Pseudoloricaria* and we did not observe separate, relatively sparse plates like those observed in members of the *Rineloricaria platyura* group. Nevertheless, male dimorphism related to the hypertrophy of odontodes on lateral portions of the head was lacking in both *Limatulichthys* and *Pseudoloricaria*, as reported in Isbrücker (1979).

Limatulichthys nasarcus is the second member of the Loricariinae, and the third member of the Loricariidae distributed through portions of the Caura and Ventuari Rivers but absent from intervening main channel habitats of the Orinoco River. This distribution is all the more striking in that a different species of *Limatulichthys* (*L. cf. griseus*) is known from intervening main river channel habitats (Fig. 5), suggesting that the disjunct modern distribution of *L. nasarcus* reflects an historical headwater connection between the Caura and Ventuari and not just the absence of intervening habitat. *Harttia merevari* was described by Provenzano *et al.* (2005) from the upper Caura River, around the same time as *H. merevari* was also discovered by one of us (NKL) in the upper Ventuari River above Salto Tencua. *Harttia merevari* remains the only species of its genus known from the Orinoco River basin, with all of its congeners distributed further to the south and east. Likewise *Pseudolithoxus anthrax* Armbruster & Provenzano is known only from the Caura and Ventuari Rivers and the Orinoco River main channel upstream of the Ventuari, but is not known from intervening Orinoco River habitats (Lujan & Birindelli, 2011).

A fourth, unrelated loricariid genus, *Lithoxus* Eigenmann, is not yet known from the Caura River, but also has a curiously disjunct distribution: *Lithoxus jantjiae* Lujan is only known from headwaters of the Ventuari River in Venezuela and *Lit. lithoides* Eigenmann from main channel habitats of the Essequibo River to the east in Guyana (Lujan, 2008). Lujan (2008) and Lujan & Armbruster (2011) suggested that the phylogenetic relationships and geographic distributions of *Lithoxus* were consistent with geologic evidence of an ancient river basin (the proto-Berbice) that connected headwaters of the Caura and Ventuari with a main river channel that flowed south and east to join with portions of the modern Essequibo and Berbice rivers. Recent molecular phylogenetic data (Lujan *et al.*, 2014) provide further support for such a biogeographical pattern. Relatively recent geological uplift of the Guiana Shield combined with northward, headwater expansion of the Branco River drainage in the Amazon Basin led to breakup of the proto-Berbice starting in the Late Pliocene (~2–3 million years ago; Lujan & Armbruster, 2011). The modern distribution of *Limatulichthys nasarcus* may, as with other taxa listed above, be a relict of the breakup of headwaters of the proto-Berbice.

Material examined. *Limatulichthys griseus*: GUYANA, Essequibo River drainage: ROM 85937, 10 alc., Pirara River, approx. 40.2 km N of Lethem at Pirara; ROM 64779, 1 alc., Kurupukari, channel at South end of Cowhead Island; AUM 44405, 5 alc., Rupununi River at Kwatamang.

Limatulichthys cf. griseus: COLOMBIA, Orinoco River drainage: AUM 28763, 1 alc., Meta River basin, Manacías River, sandbar on left (W) bank 7 km SSE Puerto Gaitan, Meta Department; VENEZUELA, Orinoco River drainage: ANSP 162170, 1 alc., Playa Guacamaya on the Orinoco ca. 20–30 km upstream from San Fernando de Atabapo, N 04°00'00", W 67°31'00", B. Chernoff, O. Castillo, J. Moreno, 7 March 1987; ANSP 182989, 1 alc., Orinoco River at beach near Puerto Ayacucho, N 05°39'23", W 67°37'52", N.K. Lujan, M. Arce Hernandez, T.E. Wesley, 13 April 2005; ANSP 162344, 2 alc., Orinoco River at beach approx. ½ hr. upstream from Isla Temblador, N 03°04'00", W 66°28'00", W.G. Saul, H. Lopez, J. Fernandez, O. Castillo, M.E. Antonio, J. Moreno, 9 March 1987; PERU, Ucayali River drainage: ROM 55678, 1 alc., Lullapichis River, 300 m E of Panguana Camp, in Panguana Station Vicinity, Huanuco department, Pachitea River, E. Holm and B. Alvarado; ROM 55679, 1 alc., Lullapichis River, approximate 2 km upstream from mouth (at Pachitea River), Huanuco department, E. Holm, B. Alvarado, and H. Sisniegas; ROM 55680, 1 alc., Pachitea River, vicinity of Lullapichis Mouth, Huanuco department, E. Holm, B. Alvarado, and H. Sisniegas.

Limatulichthys cf. griseus "Beni": BOLIVIA, Beni drainage: AUM 28353, 2 alc., Purus River drainage, Acre River at Cobija.

Pseudoloricaria laeviuscula: GUYANA, Essequibo River drainage: ROM 85928, 10 alc., Rupununi River at Dadanawa; ROM 85924, 15 alc., Rupununi River at Yapukari, right bank; ROM 86215, 9 alc., Sawariwau River, Potarinao at road crossing.

Rineloricaria fallax: GUYANA, Essequibo River drainage: AUM 47876, 10 alc., Rupununi River at Kwatamang landing, Reg 9 (Up. Takutu-Up. Essequibo).

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