Redescription and Morphometric Analysis of *Isorineloricaria* (Siluriformes: Loricariidae)

by

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Abstract

In this study, the genus *Isorineloricaria* Isbrücker 1980 is resurrected and redescribed. The complex history of the genus is reviewed. *Isorineloricaria* is diagnosed from *Hypostomus* by an elongated caudle peduncle, elongate hypertrophied breeding odontodes on nuptial males, central buccal papilla enlarged or multiple buccal papillae and from most *Hypostomus* by their lighter background coloration. The species of *Isorineloricaria* are redescribed and diagnosed; *Plecostomus annae* and *Hypostoma squalinum* are placed in the synonymy of *I. emarginata*; *Plecostomus biseriatus*, *P. scopularis*, and *P. virescens* are placed in the synonymy of *I. horrida*; *Plecostomus winzi* is placed in the synonymy of *I. tenuicauda*, and one new species is described from the Apure River basin of Venezuela. Speceis are largely allopatric and separated by color pattern. Species recognized as taxonomically valid are: *I. ammophila* from the Apure and Orinoco Rivers in Venezuela; *I. emarginata* from the lower Amazon River and it's tributaries; *I. gomesi* from Jaguaribe River, Ceará state, Brazil; *I. horrida* from the upper Amazon River, including the mainstem, Rio Napo, Rio Marañon, Rio Ucayali, Rio Juruá, Rio Purus, and Rio Madiera; *I. phrixosoma* from the Rio Ucayali, Peru; *I. spinosissima* from the Guayas River basin, Ecuador; *I. tenuicauda* from the Magdalena River basin in Colombia; *I. unicolor* from from upper Amazon tributaries of Bolivia, Brazil, Colombia, Ecuador, and Peru; *I. villarsi* from the Maracaibo basin in northwestern Venezuela and extreme eastern Colombia; *Isorineloricaria n. sp. 'Apure'* is described from the Apure and Orinoco Rivers in Venezuela. Photos of specimens and range maps are updated, and biogeorgaphic

patterns and their relationships with hypothesized geologic events across the South American continent are also discussed. During the middle to late Miocene, the vicariant events that divided the Magdalena and Maracaibo basins from the Amazonas and Orinoco rivers were very important in the evolution of *Isorineloricaria*, allowing for the rise of several of the taxa seen in the region. Furthermore, the rise of the Andes may have allowed the invasion of the piedmont areas by the smaller members of *Isorineloricaria*, such as *I. ammophila, I. phrixosoma*, and *I. unicolor*.

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Introduction

With just over 800 valid species, the family Loricariidae (suckermouth armored catfishes) is the largest catfish family in the world. Its members are restricted to freshwater habitats in Neotropical South America, Panama, and Costa Rica (Fig. 1) (Armbruster, 2004; Nelson, 2006). The genus *Hypostomus*, with over 130 valid species, is a complex group with a complex history. Currently, *Hypostomus* is recognized as either a single genus (Armbruster, 2004) or as six (Isbrücker, 2001). Three of Isbrücker's genera (*Aphanotorulus, Isorineloricaria, Squaliforma*) were recognized as the *H. emarginatus* species group by Armbruster (2004). Molecular data (Montoya-Burgos, 2003), and a more recent analysis of Armbruster's data (Armbruster, 2008), suggests that the *H. emarginatus* species group is monophyletic, and likely should be recognized as a genus separate from the rest of the Hypostomini, and I herein recognize *Isorineloricaria* as a valid genus. The species of *Isorineloricaria* are unusual in having a white to light tan background color with dark spots, the presence of hypertrophied odontodes on the bodies of nuptial males, relatively to extremely elongate caudal peduncles, and a large central or multiple buccal papilla.

Species of *Isorineloricaria* are generally found over sand or gravel in high gradient portions of piedmont streams. The range includes Trans-Andean streams such as the Magdalena and Guayas rivers and the Lake Maracaibo drainage, and major cis-Andean streams such as the Orinoco, Essequibo and Amazon basins.

Taxonomic History of Genera: The genus *Hypostomus* was most thoroughly reviewed by Boeseman (1968). In his work, he reviewed the generic name *Hypostomus*, tracing back the earliest descriptions of the members of this genus. Gronovius first published the generic name of *Plecostomus* in 1754. Its subsequent use continued until 1954, when it was determined that Gronovius' work often included the use of trinomials, thus making it invalid. Other authors, prior to Linnaeus, who also published the name *Plecostomus*, published it in invalid works based on our current system of nomenclature. Linnaeus incorrectly included *Plecostomus plecostomus* in the genus *Acipenser* (sturgeons), where it remained for some time. The next generic name used for any species in the genus was *Hypostomus* by Lacépède in 1803, making it the valid genus.

Isorineloricaria was described by Isbrücker (1980) for *Plecostomus festae* and *P. spinosissimus*, and Isbrücker suggested that the two species might be synonymous. Isbrücker did not provide a detailed diagnosis, suggesting that a future paper would provide more detail, but no further work was published. Isbrücker and Nijssen (1982) described the genus *Aphanotorulus* based on two specimens of a putatively new species *A. frankei*. *Aphanotorulus* was diagnosed based on the presence of numerous buccal papillae. *Squaliforma* was described by Isbrücker & Michels (2001; in *Isbrücker* et al., 2001), yet no objective diagnosis was provided for *Squaliforma*.

Armbruster (2004) found *Aphanotorulus, Isorineloricaria,* and *Squaliforma* to be nested within *Hypostomus*. He placed all three genera into the synonymy of *Hypostomus*, but suggested that the group could be found to be a single, distinct genus.

Taxonomic History of Species: *Hypostomus emarginatus* was the first described species, proposed by Valenciennes in Cuvier and Valenciennes (1840) from a dried

specimen obtained from the Amazon River (though the specific location was not recorded). The next species described was *Hypostoma squalinum* by Jardine in Schomburgk (1841), with the type locality in the Branco, Negro, and Essequibo rivers; however the type was lost and no records of it exist. Kner (1854) described *Hypostomus horridus* from the Rio Guapore in Brazil, and designated several dried specimens as syntypes. After the description of these species, there was a change at the generic identification of the species and subsequent authors used *Plecostomus* Gronovius 1754.

Before the invalidation of Gronovius' works, 17 species within *Isorineloricaria* were diagnosed within *Plecostomus*. Edward Drinker Cope was a prolific describer of fish, with three described species within this group: *P. biseriatus*, *P. scopularius*, and *P. virescens* all described by him from the upper Amazon River (Cope 1871, 1872, 1874). The syntypes of *P. virescens* and the holotype of *P. biseriatus* are all juveniles and of poor quality, but the holotype of *P. scopularius* is in excellent condition. *Plecostomus villarsi* was described by Lütken in 1874, and several syntypes were designated, yet the exact locality is unclear. It was originally noted as Caracas (Venezuela), yet that note was followed by a question mark, and I disagree with that locality identification based on examination of specimens from the Maracaibo basin and the lack of specimens of *Isorineloricaria* from the streams surrounding Caracas. Armbruster (2005) found that *Ancistrus mystacinus*, which also has a stated locality of "Caracas?" (Kner, 1854: 276), was from the Lake Maracaibo basin, and it appears as if this is also true for *P. villarsi*. Steindachner (1878, 1880, 1881, 1908) described *P. tenuicauda*, *P. spinosissimus*, *P. annae*, and *P. unicolor*, respectively. Fowler (1913, 1940a, 1940b, 1941, 1942, 1945) was the most prolific author of species descriptions within the group, describing *P. madeirae*, *P. phrixosoma*, *P. chaparae*, *P. iheringi*, *P. gomesi*, and

P. winzi respectively. Fowler (1942) objectively invalidated *P. iheringi* after learning that *P. iheringii* had already been used to describe another species of *Plecostomus,* and *P. gomesi* was chosen to replace *P. iheringi*.

Aphanotorulus frankei was described by Isbrücker and Nijssen (1982). Armbruster and Page (1996) described *A. ammophilus* and expanded *Aphanotorulus* to include *Plecostomus chaparae*, *P. madeirae*, *P. micropunctatus* (La Monte 1935), *P. popoi* (Pearson 1924), and *P. unicolor*. Armbruster's (1998) review of *Aphanotorulus* left the genus with just two valid species: *A. ammophilus* and *A. unicolor*; all the other members of *Aphanotorulus* were found to be junior synonyms of *A. unicolor*.

Squaliforma (Isbrücker and Michels; in Isbrücker et al. 2001) was described with little supporting evidence given to recognize the group at the time, and the genus' monophyly was not examined. Weber (in Reis et al. 2003) identified and placed other species in *Squaliforma,* but without comment. He also removed *Hypostomus watwata* from *Squaliforma*, hypothesizing that it belonged elsewhere in *Hypostomus*.

Phylogenetics: Species that conform to *Isorineloricaria* were first hypothosized to be a monophyletic group in Armbruster and Page (1996). Genetic studies by Montoya-Burgos et al. (2002) and Montoya-Burgos (2003) also suggest that these species form a monophyletic group. Both studies concluded that the inclusion of the *H. emarginatus* group in *Hypostomus* made *Hypostomus* polyphyletic, but gave no mention of elevating the group to a separate genus.

Armbruster (2004, 2008) provided the most complete phylogeny for loricariids to date, but focused on the Hypostominae. Armbruster's analysis confirmed Armbruster and Page's (1996) findings, and he diagnosed *Isorineloricaria* (his *H. emarginatus* group) by an

elongated first hypobranchial, seven or more infraorbital plates, contact between the metapterygoid and lateral ethmoid shifted anteriorly, an enlarged central papilla in the buccal cavity, and hypertrophied odontodes on the bodies of breeding males. He also recognized that the unique coloration of these species makes them readily identifiable from most other *Hypostomus*, and that future analyses might recognize the clade as a single genus distinct from *Hypostomus*.

Other than studies on the species ascribed to *Aphanotorulus*, there has been no detailed taxonomic work on *Isorineloricaria*, and no species described since 1945. In this paper, the species of *Isorineloricaria* are redescribed, *Plecostomus annae* and *Hypostoma squalinum* are placed in the synonymy of *I. emarginata*, *Plecostomus biseriatus*, *P. scopularis*, and *P. virescens* are placed in the synonymy of *I. horrida*, *Plecostomus winzi* is placed in the synonymy of *I. tenuicauda*, and one new species is described from the Apure River basin of Venezuela.

Materials and Methods

Counts and measurements follow Boeseman (1968) and Armbruster and Page (1996). Plate row terminology follows Schaefer (1997). Specimens were cleared and stained following methods of Taylor and Van Dyke (1985). Institutional abbreviations follow the American Society of Ichthyologist and Herpetologist Standard International Codes (http://www.asih.org). Other abbreviations listed below include: D. = distance, Dp. = depth, W.= width, L. = length.

Specimens were measured with digital calipers to the nearest 0.1 mm. Counts and measurements of bilaterally symmetric features were taken on the left side when possible. Measurements taken are labeled in Figures 2-4.

Morphometric data were analyzed using JMP (ver. 5.0.1.a, SAS Institute, 2002). Measurements were examined through the use of bivariate plots to search for any diagnostic characters. Diagnostic characters apply only to specimens greater than 100mm SL, unless otherwise noted. Measurements were also examined multivariately using principal component analysis (PCA). The first component of PCA was excluded because it represents overall size difference. The remainder of the principal components were plotted against standard length to show that they represent relative size differences (shape). Specimens of *Isorineloricaria ammophila* and *I. unicolor* were excluded from this analysis because they

were previously analyzed using the same data set (Armbruster 1998). Only specimens greater than 100mm SL were included in the analysis.

Isorineloricaria Isbrücker 1980

Type species: *Plecostomus spinosissimus* (Steindachner 1880)

Diagnosis: As a member of Hypostomini, (sensu (Armbruster, 2004) *Isorineloricaria* can be separated from the Corymbophanini by having an adipose fin (vs. adipose fin replaced by postdorsal ridge 13–17 azygous plates); from the Corymbophanini and Rhinelepini by having the iris operculum (vs iris operculum absent); from the Rhinelepini by lacking exposure of the coracoid strut (vs. coracoid strut exposed, supporting odontodes), and by having the anal fin I,4 (vs. I,6); from the Pterygoplichthini by having the stomach attached via the dorsal mesentery only (vs. connected to the lateral abdominal walls by a connective tissue sheet) and by usually having one plate between the suprapreopercle and opercle, rarely two (vs. two to three); from the Ancistrini (except *Spectracanthicus murinus* and some *Pseudancistrus*) and the Pterygoplichthini by having the cheek plates evertible to about 30° to the head and generally lacking hypertrophied odontodes on the cheek plates with the only exception nuptial males in a few species (vs. cheek plates evertible to 70° or more and hypertrophied odontodes usually present); from *Spectracanthicus* by having the dorsal and adipose fins separate (vs. connected by a posterior extension of the dorsal fin), and from *Pseudancistrus* without evertible cheek plates by lacking hypertrophied odontodes on the cheek and along the snout except in nuptial males of a few species (vs. odontodes present in males and females along the snout and on the cheek) and three plates between the head and dorsal fin (including the nuchal plate, vs. four or more).

Within the Hypostomini, *Isorineloricaria* can be separated from *Hypostomus* by an elongated caudle peduncle (vs. short caudle peduncle in *Hypostomus*), elongate hypertrophied breeding odontodes on nuptial males (vs. absence of hypertrophied odontodes in *Hypostomus*), central buccal papilla enlarged or multiple buccal papillae (vs. small or absent buccal papillae in *Hypostomus*) and from most *Hypostomus* by their lighter background coloration (vs. darker background coloration in *Hypostomus*).

Description: Member of the Loricariidae: Hypostominae: Hypostomini. Dorsoventrally flattened and elongate fishes, covered in plates. Head depth moderate to deep; suppraocipital crest from much higher than nape and posterior edge perpendicular to head, to greatly reduced, only slightly higher than nape and posterior edge level with nape. Nape flat to increasing in height posteriorly to dorsal fin. Dorsum sloped ventrally to procurrent fin rays and then elevating quickly to caudal fin.

Highly forked caudal fin with lower caudal lobe longer than upper caudal lobe. Pectoral-fin spines extend from just short of pelvic-fin insertion to just past pelvic-fin base. Pelvic fin spine reaches anal-fin insertion. Adipose fin present and triangular. Dorsal-fin spine not longer than first dorsal-fin ray; dorsal fin not reaching insertion of adipose fin when adpressed (more than one plate separating them).

Lips flat with short maxillary barbel on marginal edge. Buccal papilla present; buccal papillae range from multiple small papillae with central one enlarged to enlarged single papilla (Fig. 8). Teeth numerous, bicuspid, with long stalks.

Sexual Dimorphism: In breeding males, hypertrophied odontodes present on pectoral- and caudal-fin spines in increasing density and length distally. Slightly lengthened odontodes also found on edges of most plates and the adipose fin tip. Small odontodes

found on dorsal-fin spine, and sometimes randomly along paired fin rays. In peak spawning season, pectoral and pelvic spines of breeding males swollen. Hypertrophied odontodes may cover entire dorsal and lateral surfaces in some species including cheek and edge of snout.

Coloration: Light tan to white background, with brown to black spotting. Color in life similar to that in alcohol, yet some individuals show hints of orange and red in background colors. Dorsal surfaces and fins with spots; ventral surfaces with or without spots. Color patterns differ with ontogeny, and vary with species. In general, juveniles with proportionally larger spots than adults.

Etymology: Isbrücker (1980) derived the name *Isorineloricaria* from the Greek word *isos* "like" and *Rineloricaria*, a genus of the Loricariinae, which also have elongate caudal peduncles.

Isorineloricaria ammophila (Armbruster and Page 1996)

(Fig. 9)

Aphanotorulus ammophilus Armbruster & Page, 1996: 385, fig. 2 (middle). Type locality: Venezuela, Estado Cojedes, Río San Carlos, R. Portuguesa drainage at Caño Hondo, 2 km west of Las Vegas on the road from Las Vegas to Campo Allegre – 9º31'51"N, 68º39'39"W. Holotype: INHS 32035, 86.0 mm SL.

Diagnosis: *Isorineloricaria ammophila* is diagnosable from all other members of *Isorineloricaria*, except *I. unicolor*, by its numerous buccal papillae. *Isorineloricaria ammophila* is diagnosable from *I. unicolor* by the presence of ridges formed by the compound pterotics on the head (vs. ridges absent in *I. unicolor*); a pectoral fin that, when depressed, will reach well past the point of insertion of the last pelvic fin ray (vs. extending maximally to the insertion of the last pelvic fin ray in *I. unicolor*). See diagnosis of *I. unicolor* below for further diagnostic features for specimens greater than 75mm SL.

Description: Morphometric data given in Table 4. Head slightly compressed with raised supraoccipital crest; crest ending abruptly with posterior edge perpendicular to head. Sharp ridge present on compound pterotics. Large flap covering posterior opening of nare. Interorbital surface flat. Nape increasing in height posteriorly to dorsal fin.

Dorsal-fin spine slightly longer than or equal in length to first dorsal-fin ray. Pectoral-fin spine reaches past point of insertion on pelvic fin. Pelvic fin spine reaches insertion of the anal fin. Adipose-fin membrane extending to end of fourth adipose base plate (two plates separates adipose-fin membrane and first dorsal procurrent caudal-fin spine).

Lateral line plates 28-30 (mode 29; n= 93); dorsal-fin base plates six to 10 (mode seven; n= 93); folded dorsal plates 10-14 (mode 13; n= 90); plates between dorsal and adipose fins seven to 10 (mode eight; n= 93); adipose- fin plates three to four (mode three; n= 92); anal- fin base plates two to three (mode two; n= 93); plates from anal- fin insertion to last plate on caudal peduncle 13-16 (mode= 14; n= 93); plates in folded pectoral fin five to seven (mode six; n= 93); number of teeth on dentary 9-20 (mode= 14; n= 92); number of teeth on premaxilla 10-18 (mode= 14; n= 92).

Sexual Dimorphism: Breeding males with elongated odontodes on dorsal and lateral surfaces of body posterior to insertion of dorsal fin, increasing in length and density posteriorly. Odontodes also present on pectoral-fin spines and caudal-fin spines.

Color in alcohol: Light tan to white background. Ventral surface white. Dorsal and lateral surfaces with dark, round spots. Spots small to medium in size. Spots form longitudinal rows in some specimens, more random in other specimens. Spots on caudal fin create vertical bars when fin is compressed. On dorsal fin, two rows of spots lie between each fin ray. Juveniles with four brown saddles, a brown midlateral stripe, and a mottled head.

Range: (Fig. 20) Río Orinoco drainage in Venezuela, mainly from the Río Apure system. Possibly occurs in headwater streams of the Río Apure within Columbia.

***Isorineloricaria* n. sp. 'Apure'** New Species

Ray and Armbruster

(Fig. 10–11)

Holotype: INHS 35685, 269.1mm SL. Venezuela: Rio Portuguesa, 3 km northeast of El Barriero, Portuguesa. 09˚03'08"N, 069˚29'18"W. 1 January 1995. Collected by J.W. Armbruster, P.A. Ceas, M.H. Sabaj, C.A. Laird, S.M. Phelps, M.L. Manrique, F.T. Burbrink.

Paratypes: Venezuela: ANSP 134482, Rio Orituco, tributary of Rio Guarico, 15 km SSE of Calabozo on Cazorla Road; Orinoco drainage, Edo. Guarico, 25 November 1966, col. by N.R.Foster, J.Ramsey; ANSP 134519, Rio Orituco, tributary of Rio Guarico, 15 km SSE of Calabozo on Cazorla Road, Edo. Guarico, 26 November 1966, col. by N.R.Forster; ANSP 165834, Rio Orituco: ca. 15 km SE of Calabozo, Guarico, 2 November 1989, col. by S.Schaefer, et al.; ANSP166888, Rio Orinoco Basin: Caicara; L.Bartolico, Bolivar, 12 January 1988, col. by M. Rodriguez; FMNH 105992, Rio Suripa ca. 0.5 hrs by boat above confluence with Rio Caparo, Barinas, 07º40'00"N 070º28'00"W, 9 January 1991, col. by B. Chernoff, A. Machado, R. Royero, F. Gil; FMNH 105993, Playa Los Chicos in the Rio Suripa ca. 2.5 hrs. above Hato Mercedes, Barinas, 12 January 1991, col. by B. Chernoff, A. Machado, R. Royero, F. Gil; INHS 34432; INHS 35685; MCNG 34719; UF 80345; UF 80390 (XX), Rio Apure in Apurito, near chalana site., Apure, 7º56'0"N 68º28'50"W, D.C. Taphorn, C.R. Gilbert, L. Nico, 6 April 1984; USNM 348458, Rio Orituco where crossed by road from Calabozo, Guarico, 8.867, -67.300, 27 January 1983, col. by A. Machado-Allison et al.

Diagnosis: *Isorineloricaria* n. sp. 'Apure' can be diagnosed from *I. ammophila* and *I. unicolor* by a single, large buccal papillae (vs. multiple buccal papillae present in *I. ammophila* and *I. unicolor*); from *I. spinosissima* by having a larger caudal fin depth to head length ratio (see diagnosis of *I. spinosissima*); from *I. villarsi* by having a flattened compound pterotic (vs. sharp ridges present in *I. villarsi*); from *I. emarginata* by having a larger orbit diameter to interorbital width ratio (40.6–63.7% vs. 32.4–40.5%), which separates 96% of individuals; from *I. horrida* by having a supraoccipital crest with posterior edge perpindicular to head (vs. *I. horrida* with posterior edge gently sloping into nape); and from *I. tenuicauda* by having a larger caudal peduncle width to pectoral spine length ratio (59.6– 65.2% vs. 31.5– 56.2%), which separates 95% of individuals.

Description: Morphometric data given in Table 1. Head deep with tall supraoccipital crest; crest ending abruptly with posterior edge perpendicular to head. Rounded ridge forming on outer edge of each nare, rising dorsally over orbit, abrubtly ending postorbitally. Large flap covering posterior opening of nare. Interorbital surface flat. Nape flat.

Dorsal-fin spine not longer than first dorsal-fin ray. Pectoral-fin spine reaches past insertion of pelvic fin. Pelvic-fin spine just reaches insertion of anal fin. Adipose-fin membrane extending to end of third adipose base plate (one plate separates adipose-fin membrane and first dorsal procurrent caudal-fin spine).

Lateral line plates 27-30 (mode= 30; n= 23); dorsal-fin base plates seven to eight (mode= eight; n= 23); folded dorsal plates 11-13 (mode= 13; n= 23); plates between dorsal and adipose fins seven to 10 (mode= nine; n= 23); adipose fin plates two to four (mode= three; n= 23); anal fin base plates two to three (mode= two; n= 23); plates from anal fin

insertion to last plate on caudal peduncle 16-19 (mode= 19; n= 23); plates in folded pectoral fin five to eight (mode= six; n= 22); number of teeth on dentary 20-35 (mode= 24; n= 23); number of teeth on premaxilla 17-41 (mode= 24; n= 23).

Sexual Dimorphism: Breeding males with hypertrophied odontodes on pectoral fin spine, which increase in density and length distally along spine. Paired-fin spines swell distally. Hypertrophied odontodes on caudal fin with largest spines occurring on caudal-fin spines and along the caudal-fin rays. Slightly hypertrophied odontodes present on distal end of adipose-fin spine. Hypertrophied odontodes covering posteromedial edge of most plates along body. Longest plate odontodes occur on mid-dorsal, median, and mid-ventral plate rows. Slightly hypertrophied odontodes also present on opercle, edge of snout, and cleithrum.

Color in alcohol: Body base color light brown or tan with large, dark, longitudinally oblong brown spots. Spots rarely circular on body. Spots cover entire body except abdomen; faint spots occur across ventral aspect of pectoral girdle in some specimens. Spots on paired fins combining to form bands, some separate spots distally. Dorsal-fin spine with dark spots anteriorly; interradial membrane of dorsal fin with two rows of spots. Caudal fin with spots that appear to form bands on upper lobe, and randomly distributed spots on lower lobe; lower lobe of caudal fin with dark brown background color in most specimens. Large spots sometimes visible on lower lobe of caudal fin when dark background absent or faded.

Spot patterning less concentrated in juveniles (more background color showing). Spotting pattern on fins becomes denser as fish ages. In juveniles one row of spots on interradial membranes of dorsal fin, bifurcating distally in larger specimens, eventually becoming two rows in adults.

Ecology: The holotype was collected in the Rio Portuguesa on a sandy run with moderate flow. The holotype is a nuptial male with breeding odontodes, suggesting that January is within the time of spawning as was suggested for *I. ammophila* (Armbruster and Page, 1996).

Range: (Fig. 21) This species is restricted to the Apure and middle Orinoco rivers and their tributaries in Venezuela. Only one specimen was from the main stem Orinoco River, just downstream of the mouth of the Apure.

Comments: The one specimen of *Isorineloricaria* n. sp. 'Apure' collected in the Orinoco River was also collected with a specimen of *I. emarginata*. This is the only known instance of the two being collected together. The waters where the two rivers connect may act as an extension of available habitat for each species, because the two are not known to occur downstream of the connection in either river. *Isorineloricaria* n. sp. 'Apure' appears to be restricted to white waters and *I. emarginata* to clear and blackwater rivers.

Isorineloricaria emarginata (Valenciennes 1840)

(Fig. 12)

Hypostomus emarginatus Valenciennes, in Cuvier & Valenciennes, 1840b: 500 (369 in Strasbourg deluxe edition). Type locality: Probablement or Xginaire du Brésil. Holotype: MNHN a-9447 (dry).

Plecostomus annae Steindachner, 1881c: 112, pl. 3 (figs. 2–2a). Type locality: Pará [= Belem, Brazil]. Holotype: NMW 44073. Listed as *Chaetostomus annae* in figure caption (p. 146).

Hypostoma squalinum Jardine, in Schomburgk, 1841: 142, pl. 2. Type locality: Rios Branco, Negro, and Essequibo. No types known.

Diagnosis: *Isorineloricaria emarginata* is diagnosable from *I. ammophila* and *I. unicolor* by the presence of a large buccal papillae (vs. multiple buccal papillae present in *I. ammophila* and *I. unicolor*); from *I. spinosissima,* and *I. tennuicauda,* and *I.villarsi* by having flat compound pterotics (vs. rounded ridge present in *I. spinosissima* and *I. tennuicauda* and a sharp ridge present in *I. villarsi* compound pterotics); from *I. villarsi* by lack of sharp ridge on compound pterotics (vs. sharp ridge present); from *Isorineloricaria* n. sp. ‘Apure’ by having a smaller orbit diameter to interorbital width ratio (32.4–40.5% vs. 40.6–63.7%), which separates 96% of individuals; also from *Isorineloricaria* n. sp. ‘Apure’ by having smaller, more circular spots on the head (vs. larger, oval spots in *Isorineloricaria* n. sp. ‘Apure’); from *I. horrida* by having a larger snout-nares distance to interorbit width ratio (98.0–175.4% vs. 70.5– 97.8%; Fig. 6); also from *I. horrida* by having circular spots

on the dorsal and paired fins which remain unfused across the length of the fin (vs. spots that fuse into bands across the dorsal and paired fins, mostly in adults).

Description: Morphometrics given in Table 1. Head moderately compressed. Supraoccipital crest not tall, with posterior edge sloping gently into nape. Interorbital surface flat. Nape increasing in depth posteriorly to dorsal fin. Pectoral fin reaches past point of insertion of pelvic fin. Depressed pelvic spine reaches point of insertion of the anal fin. Adipose fin triangular.

Lateral line plates 26-31 (mode= 29; n= 118); dorsal-fin base plates six to nine (mode= seven; n= 118); folded dorsal plates nine to 14 (mode= 12; n= 118); plates between dorsal and adipose fin seven to 12 (mode= nine; n= 118); adipose fin plates two to three (mode= three; n= 117); anal-fin base plates two to three (mode= two; n= 118); plates from anal fin insertion to last plate on caudal peduncle 14-19 (mode= 18; n =118); plates in folded pectoral fin five to eight (mode= six; n =116); number of teeth on dentary 10-45 (mode= 26; n =118); number of teeth on premaxilla 14-45 (mode= 29; n =118).

Sexual Dimorphism: Breeding males with hypertrophied odontodes on pectoral-fin spine, which increase in density and length distally along spine. Paired-fin spines swell and become larger distally. Odontodes also on caudal fin, with largest odontodes on spines and rays. Odontodes also covering posteromedial edge of most plates on lateral surface of body; most relatively short. Longest plate odontodes occur on mid-dorsal, median, and mid-ventral plate rows. Slightly lengthened odontodes present on cheek.

Color: Light tan to white background. Spotting pattern highly variable across range. Spots small to medium in size; can be very dense (less background color showing) to very sparse (more background color showing) across entire body. Ventral surface with some

spots across pectoral girdle or no spots. Spots on fin rays similar to those on body. Spots irregularly placed on paired-fin rays. Dorsal-fin membrane with two distinct rows of spots between each fin ray. Lower caudal fin lobe dark in color, almost black in some specimens.

Range: (Fig. 22) A wide-ranging species, *I. emarginata*'s range includes the upper Orinoco River (except the Rio Apure); the Essequibo River and it tributaries; the lower Amazon River including the Rio Negro, the Rio Tapajos, and the Rio Xingu.

Isorineloricaria gomesi (Fowler 1941)

(Fig. 13)

Plecostomus iheringi Fowler, 1941a: 150, figs. 50–52. Type locality: Ceará [Brazil]. Holotype: ANSP 69409. Preoccupied by *Plecostomus iheringii* Regan, 1908; replaced by *Plecostomus gomesi* Fowler, 1942.

Plecostomus gomesi Fowler, 1942: [1]. Type locality: Ceará [Brazil]. Holotype: ANSP 69409. Replacement name for *Plecostomus iheringi* Fowler, 1941; preoccupied by *Plecostomus iheringii* Regan, 1908.

Diagnosis: Known only from holotype. *Isorineloricaria gomesi* is diagnosed from *I. ammophila* and *I. unicolor* by a single, large buccal papillae (vs. multiple buccal papillae); from all other *Isorineloricaria* only by its distribution (thought to be found only in the Jaguaribe River, Ceará state, Brazil).

Description: Morphometrics given in Table 5. Head moderately compressed. Suppraoccipital crest not tall, with posterior edge sloping gently into nape. Interorbital surface flat. Nape slightly increasing in depth posteriorly. Pectoral fin reaches past point of insertion of pelvic fin. Depressed pelvic spine reaches point of insertion of the anal fin.

Lateral line plates 29; dorsal-fin base plates eight; folded dorsal plates 12; plates between dorsal and adipose fin seven; adipose fin plates two; anal-fin base plates two; plates from anal fin insertion to last plate on caudal peduncle 16; plates in folded pectoral fin five; number of teeth on dentary 24; number of teeth on premaxilla 25.

Color in alcohol: Dark tan background. Spots small to medium in size; moderately dense (less background color showing) on head. Few if any spots visible along dorsal and

lateral sides of body. Ventral surface with no spots. Spots on fin rays similar to those on body. No patterns on paired-fin rays. Dorsal-fin membrane with two distinct rows of spots between each fin ray. Caudal fin with spots in vertical bands. Lower caudal fin lobe dark in color.

Range: (Fig. 21) *Isorineloricaria gomesi* is only known from its type locality. No other specimens are known.

Isorineloricaria horrida (Kner 1854)

(Fig. 14)

Hypostomus horridus Kner, 1854: 259, pl. 1 (fig. 1). Type locality: Forte do Principe am Rio Guaporé, Brazil. Syntypes (3): NMW 16325 (1), NMW 86604 (1). Originally proposed as *Hyp. horridus*.

Plecostomus biseriatus Cope, 1872a: 285. Type locality: the Amazon, between the mouth of the Rio Negro and the Peruvian Amazon or Ucayale River. Holotype: ANSP 8279.

Plecostomus scopularius Cope, 1871a: 55. Type locality: the Amazon above the mouth of the Rio Negro. Lectotype: ANSP 8081, designated by Fowler (1915: 233); illustrated in Cope (1872a: pl. 16, no. 1).

Plecostomus virescens Cope, 1874b: 137. Type locality: not explicitly given [Upper Amazon]. Syntypes: ANSP 21280 (4).

Diagnosis: *Isorineloricaria horrida* can be diagnosed from *I. ammophila* and *I. unicolor* by a single, large buccal papillae (vs. multiple buccal papillae); from *I. spinosissima* and *I. tenuicauda* by having flat compound pterotics (vs. rounded ridges on the compound pterotics in *I. spinosissima* and *I. tenuicauda* and sharp ridge present in *I. villarsi*); from *I. emarginata* by having a smaller snout-nares distance to interorbit width ratio (70.5– 97.8% vs. 98.0– 175.4%), which separates 92% of individuals (Fig.6); from *I. spinosissima* by having a larger caudal fin depth to head length ratio (see diagnosis of *I. spinosissima*); from *I. phrixosoma* by having fewer elongate hypertrophied covering the dorsal and ventral surfaces of body except the head (vs. many hypertrophied odontodes present- see *I. phrixosoma* description); from *Isorineloricaria* n. sp. ‘Apure’ by having a

supraoccipital crest with posterior edge gently sloping into nape (vs. *Isorineloricaria* n. sp. 'Apure' with posterior edge perpindicular to head).

Description: Morphometric data given in Table 2. Head moderately deep with tall supraoccipital crest; supraocipital crest taller than nape and posterior edge of crest gently sloping into nape. Nape flat.

Pectoral-fin spine reaches posterior to insertion of pelvic fin. Pelvic-fin spine reaches insertion of anal-fin spine. Two plates separate adipose-fin membrane and first dorsal procurrent caudal fin spine.

Lateral line plates 27-30 (mode 28; n= 73); dorsal-fin base plates six to eight (mode seven; n= 73); folded dorsal plates 10-14 (mode 12; n= 72); plates between dorsal and adipose fin six to 11 (mode nine; n= 73); adipose fin plates one to four (mode three; n= 73); anal fin base plates one to three (mode two; n= 73); plates from anal fin insertion to last plate on caudal peduncle 13-19 (mode =17; n =73); plates in folded pectoral fin four to eight (mode six; n =72); number of teeth on dentary 10-42 (mode =27; n =73); number of teeth on premaxilla nine to 37 (mode =22; n =73).

Sexual dimorphism: Breeding males with short hypertrophied odontodes on ventral surfaces of body except the head. Odontodes on body short; only on posterior edges of plates. Odontodes present on pectoral- and caudal-fin spines; odontodes increase in density and length distally on each fin spine. Hypertrophied odontodes absent from pelvic, dorsal, and adipose fin spines.

Color in alcohol: Light tan background color with brown spots. Small spots covering head, increasing in size and becoming more elongate posteriorly along the body. In adults, spots begin to fuse together on head to create lines with reticulated patterns; largest

specimens with mostly reticulated lines present, few spots remaining. Some specimens with small spots on ventral side of body along pectoral girdle. Paired fins with elongate spots, usually forming bands on fins. Dorsal fins in adults with elongate spots forming bands. Small, random spotting pattern apparent on adipose fin. Lower half of caudal fin rays darker in color than base color, dark coloration not extending to lower caudal spine.

Range: (Fig. 23) *Isorineloricaria horrida* is found in the upper Amazon River, including the mainstem, Rio Napo, Rio Marañon, Rio Ucayali, Rio Juruá, Rio Purus, and Rio Madiera.

Isorineloricaria phrixosoma (Fowler 1940)

(Fig. 15A–C)

Plecostomus phrixosoma Fowler, 1940a: 233, figs. 21–23. Type locality: Ucayali River basin, Contamana, Peru. Holotype: ANSP 68650.

Diagnosis: *Isorineloricaria phixosoma* is diagnosable from *I. ammophila* and *I. unicolor* by a single, large buccal papillae (vs. multiple buccal papillae in *I. ammophila* and *I. unicolor*); from all other *Isorineloricaria* by the presence of hypertrophied odontodes covering all lateral and ventral surfaces except the head in breeding males (vs. covering all dorsal and lateral surfaces including the head in *I. spinosissima* and vs. covering portions of dorsal and lateral surfaces in all other *Isorineloricaria*). This species is known only from its holotype, which is a breeding male.

Description: Morphometric data given in Table 5. Head moderately deep. Interorbital surface flat; nape of unknown shape due to damage.

Pectoral-fin spine reaches past point of insertion on the pelvic fin. Pelvic-fin spine reaches past the point of insertion of the anal fin. Caudal fin highly forked with lower lobe longer than upper lobe.

Lateral line plates 28; dorsal fin base plates seven; folded dorsal plates 12; plates between dorsal and adipose fin seven; adipose fin plates two; anal fin base plates two; plates from anal fin insertion to last plate on caudal peduncle 15; plates in folded pectoral fin six; number of teeth on dentary 21; number of teeth on premaxilla 15.

Sexual Dimorphism: Although small, holotype breeding male. Entire dorsal and lateral surfaces of body covered with hypertrophied odontodes. Dorsal surface of head without odontodes.

Color in alcohol: Body background color light, almost white. Spots on head small and circular; densely packed. Dorsal-fin membranes with two rows of spots. Few spots visible on body due to hypertrophied odontodes.

Range: (Fig. 21) Rio Ucayali, near Contamana, Peru. Known only from type locality.

Comments: I hypothesize that his species is actually a hybrid. This specimen was collected in an area where both *I. horrida* and *I. unicolor* are sympatric. It should be noted that the specimen does not share the multiple buccal papillae or the unicuspid teeth of nuptial *I. unicolor*, yet it is the smallest breeding male (with hypertrophied odontodes) collected of any species of *Isorineloricaria*, other than *I. ammophila* and *I. unicolor*. Given these combination of characters and the high sampling effort in the drainages around the type localityresuting in no more specimens of the species, hybridation is a very ; however, given the poor condition of the specimen and lack of other speimens

Isorineloricaria spinosissima (Steindachner 1880)

(Fig. 16)

Plecostomus spinosissimus Steindachner, 1880b: 98, pl. 5 (figs. 1, 1a). Type locality: Guayaquil [Ecuador]. Holotype: NMW 55027.

Plecostomus festae Boulenger, 1898c: 11. Type locality: Rio Vinces and Rio Peripa, Equateur. Syntypes: BMNH 1898.11.4.32 (1), ZMUT 1518 (1).

Diagnosis: *Isorineloricaria spinosissima* can be diagnosed: from *I. ammophila* and *I. unicolor* by the presence of a single, large buccal papillae (vs. multiple buccal papillae present in *I. ammophila* and *I. unicolor*); from all other *Isorineloricaria* by having a smaller caudal fin depth to head length ratio (16.5–19.1% vs. 20.6–30.1%).

Description: Morphometric data given in Table 2. Head moderately deep; tall supraoccipital crest with posterior edge level with nape. Interorbital surface flat. Nape with increasing height from posterior edge of the supraoccipital to the insertion of the dorsal-fin spine. Extremely elongate caudal peduncle in adults; caudal peduncle circular in cross-section.

Pectoral-fin spine does not reach insertion of pelvic fin. Pelvic-fin spine does not reach point of anal fin insertion.

Lateral line plates 31-33 (mode 32; n= 11); dorsal fin base plates seven to eight (mode seven; n= 11); folded dorsal plates 10-14 (mode 13; n= 11); plates between dorsal and adipose fin nine to 11 (mode 10; n= 11); adipose fin plates three to four (mode four; n= 11); anal fin base plates two to three (mode two; n= 11); plates from anal fin insertion to last plate on caudal peduncle 19-21 (mode =20; n =11); plates in folded pectoral fin four to

seven (mode four; n =11); number of teeth on dentary 19-31 (mode =19; n =11); number of teeth on premaxilla 17-34 (mode =29; n =11).

Sexual dimorphism: Breeding males with hypertrophied odontodes on all surfaces of body except ventral surface of head and abdomen. Odontodes present on pectoral, dorsal, adipose, and caudal- fin spines; odontodes increase in density and length distally on each fin spine.

Color in alcohol: Body background white to light tan. Spots numerous on dorsal and lateral surfaces. Spots dark brown; not uniform in shape and moderate to very dense, especially on head. Random spotting on paired fins. Dorsal fin with two rows of spots between each ray. Spots difficult to view in breeding males due to distortion caused by presence of breeding odontodes. Ventral surfaces without spots.

Juveniles with much lighter base color and very large dark spots. Spots randomly distributed on dorsal and lateral surfaces and all fins.

Range: (Fig. 21) Endemic to the Guayas River basin, Ecuador.

Comments: Large ontogenetic shape change between juveniles and adults. Isbrücker (1980) suggested *Plecostomus festae* be recognized as a separate species from *I. spinosissima* due to their wide variation in shape and size; however, Weber (in Reis et. al 2003) recognized *P. festae* as a junior synonym of *I. spinosissima*. The ontogenetic shifts in shape most likely explain the wide variation in counts and measurements.

Isorineloricaria tenuicauda (Steindachner 1878)

(Fig. 17)

Plecostomus tenuicauda Steindachner, 1878a: 90. Type locality: Magdalenen-Stromes [Colombia]. Syntypes: MSNG 8856 (1), NMW 42596 (1), NMW 44263 (1), NMW 44264 (1), NMW 44265 (1), NMW 44266 (3), NMW 44268 (1), NMW 44294 (1), ZMUC P 30172 (1). One syntype illustrated in Steindachner (1879d: pl. 6).

Plecostomus winzi Fowler, 1945b: 9, figs. 4–7. Type locality: Honda, Colombia. Holotype: ANSP 71623. Distribution: Magdalena River basin, Colombia, known only from holotype (Weber, 2003).

Diagnosis: *Isorineloricaria tenuicauda* can be diagnosed from *I. ammophila* and *I. unicolor* by a single, large buccal papillae (vs. multiple buccal papillae present in *I. ammophila* and *I. unicolor*); from *I. villarsi*, *I. emarginata*, and *I. horrida* by a rounded ridge present on the compound pterotics (vs. sharp ridge present on *I. villarsi* and ridge absent on *I. emarginata* and *I. horrida*); from *I. spinosissima* by having a larger caudal fin depth to head length ratio (see diagnosis of *I. spinosissima*); from *Isorineloricaria* n. sp. 'Apure' by having a smaller caudal peduncle width to pectoral spine lenth ratio (31.5–56.2% vs. 59.6–65.2%), which separates 95% of individuals.

Description: Morphometric data given in Table 3. Head moderately deep with tall supraoccipital crest; crest often ending sharply. Ridges formed on compound pterotics rounded in most specimens (lack a sharp ridge). Nape slightly increasing in height posteriorly.

Pectoral-fin spine reaches posterior to insertion of pelvic fin. Pelvic-fin spine reaches insertion of anal-fin spine. Adipose-fin spine triangular, adipose-fin membrane extending to third adipose fin plate (two plates separate adipose-fin membrane and first dorsal procurrent caudal fin spine).

Lateral line plates 28-29 (mode 28; n = 12); dorsal fin base plates seven to nine (mode eight; n = 12); folded dorsal plates 13-15 (mode 13; n = 12); plates between dorsal and adipose fins six to nine (mode eight; n = 12); adipose fin plates three to four (mode three; n =12); anal-fin base plates two to three (mode two; n =12); plates from anal fin insertion to last plate on caudal peduncle 15-17 (mode =17; n =12); plates in folded pectoral fin five to nine (mode seven; n =12); number of teeth on dentary 20-35 (mode =29; n =10); number of teeth on premaxilla 20-35 (mode =30; n =12).

Sexual Dimorphism: Breeding males with hypertrophied odontodes on pectoral-, adipose-, and caudal-fin spines, which increase in length and density distally. Small hypertrophied odontodes on the dorsal-fin spine. Hypertrophied odontodes also on the pectoral- and caudal-fin rays. Paired-fin spines swollen. Hypertrophied odontodes covering posteromedial edge of most plates along body, cheek plates, opercle, along snout, and cleithrum.

Color in alcohol: Background light brown or tan. Covered in small brown spots over entire body. Some specimens lack spots on abdomen. Spots small and uniform in size all over body, except abdomen and paired-fin rays. Spots on abdomen vary from small single spots to large fused spots with open centers (circles and semicircles). Some elongate (fused) spots on paired-fin rays. Two rows of spots between fin rays on paired fins. One row of spots between rays on caudal fin. Dorsal-fin membranes with randomly placed spots.

Juveniles without abdominal spots. Smallest spots on head, with increasing size posteriorly. Spots form bands in paired fins, dorsal fin and caudal fin.

Range: (Fig. 21) *Isorineloricaria tenuicauda* is restricted to the Río Magdalena basin, Colombia.

Isorineloricaria unicolor (Steindachner 1908)

(Fig. 18)

Plecostomus unicolor Steindachner, 1908f: 164. Type locality: Rio Purús. Lectotype: NMW 44271: 2, designated by Armbruster (1998b: 254).

Plecostomus madeiræ Fowler, 1913: 571, fig. 23. Type locality: Madeira River, about 200 miles east of W. long. 63º54'W, Brazil. Holotype: ANSP 39312.

Plecostomus popoi Pearson, 1924: 20, pl. 3 (fig. 2). Type locality: Popoi River, Upper Río Beni, Bolivia. Holotype: CAS 77346.

Plecostomus micropunctatus La Monte, 1935: 1, fig. 1. Type locality: Rio Purus: [...] in the vicinity of the mouth of Rio Macauhan, a tributary of Rio Iaco which, in turn, is a tributary of Rio Purus (70º15'W, 7º30'S). Holotype: AMNH 12598.

Plecostomus chaparae Fowler, 1940c: 81, figs. 38–40. Type locality: Boca Chapare, Río Chimore, Cochabamba, Bolivia. Holotype: ANSP 69067.

Aphanotorulus frankei Isbrücker & Nijssen, 1983a: 108, figs. 1–2. Type locality: [...] du Pérou, Dept. Ucayali, Prov. Coronel Portillo, système du Rio Aguaytia. Rio Neshua (environ 08º36'S, 74º50'W), 60 km S.O. de Pucallpa, le long de la route de Tingo Maria. Holotype: ZMA 116.640.

Diagnosis: *Isorineloricaria unicolor* is diagnosable from all other members of *Isorineloricaria*, except *I. ammophila*, by its numerous buccal papillae (vs. single, large papilla). *Isorineloricaria unicolor* is diagnosable from *I. ammophila* by the absence of a ridge on the compound pterotic (vs. ridge present in *I. ammophila*). The urohyal is also uniquely modified in *I. unicolor*. The urohyal in *I. unicolor* has arms, which are thin and

elongate, that overlap with the anterohyal (vs. short lateral arms of the urohyal that do not overlap the anterohyal in most other Loricariids) (Armbruster 1998). In specimens larger than 75mm SL, *I. unicolor* has a larger orbit diameter to snout length ratio (28.0–42.2% vs. 18.5–27.9%), a larger caudal depth to pectoral spine length ratio (25.6–35.1% vs. 19.8–25.5%), and a smaller pectoral spine length to thorax length ratio (99.3–116.9% vs. 117.0–136.3%) than *I. ammophila* (Armbruster 1998).

Description: Morphometric data given in Table 4. Head slightly compressed with raised supraoccipital crest; crest ending abruptly with posterior edge perpendicular to head. Large flap covering posterior opening of nare. Interorbital surface flat. Nape increasing in height posteriorly.

Dorsal-fin spine slightly shorter than or equal in length to first dorsal-fin ray. Pectoral-fin spine even with point of insertion on pelvic fin. Pelvic fin spine comes even to insertion of the anal fin. Adipose-fin membrane extending to end of fourth adipose base plate.

Lateral line plates 28-32 (mode 29; n = 307); dorsal fin base plates six to nine (mode seven; n = 306); folded dorsal plates 10-13 (mode 12; n = 300); plates between dorsal and adipose fins six to 10 (mode eight; n = 305); adipose fin plates two to four (mode three; n =305); anal-fin base plates two to three (mode three; n =307); plates from anal fin insertion to last plate on caudal peduncle 13-16 (mode =14; n =307); plates in folded pectoral fin four to seven (mode five; n =302); number of teeth on dentary four to 18 (mode =12; n =302); number of teeth on premaxilla four to 17 (mode =12; n =304).

Sexual dimorphism: Breeding males have elongate, unicuspid teeth. Hypertrophied odontodes also present on the posterior dorsal and lateral plates. Odontodes also present on the adipose- fin spine and upper caudal- fin spine.

Color in alcohol: Light tan to white background. Ventral surface white. Dorsal and lateral surfaces with dark, round spots. Spots small to medium in size. Spots form longitudinal rows in some specimens, more random in other specimens. Spots on caudal fin create vertical bars when fin is compressed. Spots on dorsal fin lie anterior to each dorsal fin ray.

Range: (Fig. 20) A wide-ranging species, with populations known from upper Amazon tributaries of Bolivia, Brazil, Colombia, Ecuador, and Peru.

Isorineloricaria villarsi (Lütken 1874)

(Fig. 19)

Plecostomus villarsi Lütken, 1874a: 211. Type locality: Caracas. Syntypes: ZMUC P 30149 (1), ZMUC P 30150 (1).

Diagnosis: *Isorineloricaria villarsi* can be diagnosed from *I. ammophila* and *I. unicolor* by a single, large buccal papillae (vs. multiple buccal papillae present in *I. ammophila* and *I. unicolor*); from all other members of *Isorineloricaria* by having distinct raised ridges on the compound pterotics (vs. rounded ridges on *I. spinosissima* and *I. tenuicauda* and ridges absent in all other *Isorineloricaria*).

Description: Morphometric data given in Table 3. Head moderately deep with prominent supraoccipital crest; crest often ending abruptly, with posterior edge perpendicular to head. Ridges formed on compound pterotics; compound pterotic ridges align with keel of mid-dorsal plate row to form continuous series. Nape flat.

Caudal fin highly forked with lower lobe longer than upper lobe. Pectoral-fin spine reaches past point of insertion on the pelvic fin. Pelvic-fin spine comes even to the insertion of the anal fin. Adipose fin spine pointed; adipose-fin membrane extending to end of third adipose base plate (two plates separate adipose-fin membrane and first dorsal procurrent caudal-fin spine).

Lateral line plates 28 (mode 28; n= 15); dorsal-fin base plates seven to nine (mode eight; n= 15); folded dorsal plates 12-13 (mode 12; n= 15); plates between dorsal and adipose fins seven to nine (mode eight; n= 15); adipose fin plates two to four (mode three; n= 15); anal-fin base plates two (mode two; n= 15); plates from anal fin insertion to last

plate on caudal peduncle 16-18 (mode =17; n= 15); plates in folded pectoral fin five to seven (mode six; n =151); number of teeth on dentary 24-36 (mode =36; n= 15); number of teeth on premaxilla 20-38 (mode =26; n= 15).

Sexual Dimorphism: Breeding males with hypertrophied odontodes on pectoral fin spines, which increase in length and density distally. Adipose-fin spine and caudal-fin spines also covered with hypertrophied odontodes. Caudal-fin rays also with odontodes in the same manner, though not as large as on caudal-fin spines. Hypoertrophied odontodes also covering posteromedial edge of most plates along body. Longest plate odontodes occur on mid-dorsal, median, and mid-ventral plate rows. Hypertrophied odontodes also present on opercle, along snout, cleithrum, posterior edges of head, and dorsal-fin spine.

Color in alcohol: Body base color light brown or tan. Base color darkens in largest specimens (breeding males). Spots oblong (not perfectly circular) on head and body. Greatest density occurs on head, with spots increasing in size posteriorly. Spots on head centered on anterior end of supraoccipital crest and radiate outward. Abdominal spots observed in some specimens and range from small spots with random distributions to large spots in columns. Paired fin spines with bands, with paired fins having random spots that are often fused together. Dorsal-fin spine with dark spots anteriorly; interradial membrane of dorsal fin with two rows of spots between each fin ray. Caudal fin with random spotting. Lower caudal fin lobe with dark coloration in large adults, with spots apparent.

Juveniles have no spots on abdomen. Spots appear to form bands on paired fins and caudal fin when the fins are depressed in juveniles.

Ecology: Unknown, however habitat degradation within the Maricaibo basin is a threat to this species.

Distribution: (Fig. 21) *Isorineloricaria villarsi* is restricted to the Maracaibo basin in northwestern Venezuela and extreme eastern Colombia.

Comments: There are two color morphs in the Maracaibo basin, one with small spots on the abdomen, and the other with large spots.

Results and Discussion

Hypostomus tenuis, which was originally included in the *H. emarginatus* group, has been removed from *Isorineloricaria* after examination of the type specimens. Its position elsewhere in *Hypostomus* needs to be evaluated. Weber's (Reis et al. 2003) removal of *H. watwata* was in agreement with the phylogeny of Montoyo-Burgos (2003), where it was found to be nested within *Hypostomus* and not *Isorineloricaria*. These conclusions suggest it not be included in this study.

The PCA (Fig. 5) placed the species into three partially overlapping distributions. *Isorineloricaria spinosissima* was separate from all other species in the analysis, differing mainly along PC2, which was strongly effected by measurements associated with their long, narrow caudal peduncles. The remainder of the species are in two overlapping groups separating largely along PC3: an Amazon/Essequibo/Orinoco group of *I. emarginata* + *I. gomesi* + *I. horridus* + *I. phrixosoma* and a trans-Andean/Orinoco group of *Isorineloricaria* n. sp. 'Apure' + *I. tenuicauda* + *I. villarsi*. PC3 also separated *I. spinosissima* from the Amazon/ Essequibo/ Orinoco group. Within each group, there was a lot of overlap. *Isorineloricaria* n. sp. 'Apure' has the smallest range on the graph, and was nested within the distribution of *I. villarsi*, with which I assume it to share a sister relationship.

Biogeography: A discussion of biogeography within this group is limited without a current phylogenetic hypothesis; however, there are patterns that occur amongst the

distributions of the members of *Isorineloricaria* that mirror hypothesized geological events that occurred within the last 70my across the South American continent. The rise of the Andes in present day Ecuador led to a vicariant event that isolated the Guayas drainage from the rest of the western basins on the continent, and the ancestors of *I. spinosissimus*. This was the site of the Marañon Portal, which is thought to have been a connection to the Pacific Ocean for the Late Cretaceous drainages on the South American continent (Lundberg, 1998). Recent evidence does not suggest that it was a link to the Pacific Ocean, suggesting that the present fauna may have been the result of stream capture during the rise of the Andes.

During the middle to late Miocene, the vicariant events that divided the Magdalena and Maracaibo basins from the Amazonas and Orinoco rivers were very important in the evolution of *Isorineloricaria*. The further rise of the Andes in Colombia isolated the Magdalena, which began ~11mya. The isolation of the Maracaibo basin began ~8mya with the rise of the Mérida Andes, Sierra de Perijá, and the Eastern Cordillera (Lundberg, 1998). This separated the Maracaibo basin from the Apure River, and the rest of the Orinoco system. These vicariant events led to the isolation of populations of *I. tenuicauda* in the Magdalena, *I. villarsi* in the Maracaibo, and *Isorineloricaria* n. sp. 'Apure' in the Apure. This pattern of distribution suggests that *I. spinosissima, I. tenuicauda, I. villarsi,* and *Isorineloricaria* n. sp. 'Apure' would form a monophyletic group, and the pattern of isolation would suggest the following relationships: *I. spinosissima* + (*I. tenuicauda* + (*I. villarsi,* and *Isorineloricaria* n. sp. 'Apure')). These four species do separate from the Amazon/Essequibo/Orinoco group in the PCA providing some support for the group as monophyletic.

The Amazon/ Essequibo/ Orinoco group may also form a clade together with *Isorineloricaria ammophila* and *I. unicolor*. This group may have had an origin in the Guiana and/or Brazilian Shields. *Isorineloricaria emarginatus* is found in both the Brazilian and Guiana Shields, and this is likely the main area of South America that had appropriate habitat for *Isorineloricaria* prior to the uplift of the Andes. The rise of the Andes may have allowed the group to invade the piedmont, where the smaller species (*I. ammophila, I. phrixosoma*, and *I. unicolor*) evolved. It should also be noted that the approximate dividing point of the ranges of *I. horrida* and *I. emarginata* is the Purus arch, though no conclusions of its importance can be made here.

The distribution of *Isorineloricaria ammophila* and *I. unicolor* are unique and represent more recent vicariant events (Armbruster and Page 1996). These sister taxa have a distribution which is suggestive of a distribution following the drainage patterns of the Late Miocene (10.8–8mya) which was characterized by a large river flowing along the base of the Andes and draining into the Caribbean at the present day mouth of Lake Maracaibo. The dichotomy between the taxonomies of Armbruster (2004) and Isbrücker (2001) are glaring in terms of the number of genera recognized within the Hypostomini. Although the most recent published support is for recognizing a single genus as in Armbruster (2004, 2008), this has largely not been accepted as is obvious from Ferraris' (2007) recognition of *Aphanotorulus, Isorinelorica*, and *Squaliforma*, which are clearly monophyletic, monotypic, and paraphyletic genera respectively. With 130 species, the taxonomy of the Hypostomini is complex. It is clear that *Isorineloricaria* as recognized herein is a well-diagnosed, monophyletic clade. What is unknown is whether recognizing it as such will make *Hypostomus* paraphyletic, and I leave this question to future researchers.

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Material Examined

Isorineloricaria emarginata: Brazil: ANSP 187270 (3); MCZ 7805 (1); MCZ 7807 (2); MCZ 7824 (1); MCZ 7840 (2); MCZ 7860 (1); MCZ 7992 (1); MNRJ 12710 (1), rio Passa Três, afluente esquerdo rio Maranhão, alto Tocantins, Uruaçu, Goias, 14°30'S, 49º9'W, G.W. Nunan, D.F. Moraes Jr., 26 October 1996; MNRJ 12781 (1), Rio Bagagem, à montante da foz do córrego Barriguda, afluente direito Rio Maranhão, alto Tocantins, Niquelândia, Goiás, 14º5'S 48º14'W, col. by G.W. Nunan & D.F. Moraes Jr., 15 October 1985; MNRJ 12932 (1), Rio Tocantins, em Porto do Garimpo, mun. Minaçu/Cavalcante, Minaçu, Goiás, 13º34'5"S 48º6'4"W, col. by D.F. Moraes Jr., 13 January 1988; MNRJ 12944 (1), Afluente do córrego Lageado (afluente margem esquerda Rio Tocantins) na estrada para Porto Rubião, Minaçu, Goiás, 13º38'85"S 48º19'12"W, col. by D.F. Moraes Jr., 16 January 1988; MNRJ 18360 (1), poças formadas por riacho da margem esquerda do Rio Tocantins, a montante de Ponte Rubão durante enchimento, Colinas do Sul, Goiás, col. by D.F. Moraes, D.A. Habolth, O.T. Oyakawa et al., 28 October 1996; MNRJ 19338 (1), Rio Tocantins, próximo da cidade de Tucuruí, Tucuruí, Pará, col. by L.C. Alvarenga; MNRJ 29536 (1); MNRJ 31177 thru 31196= Same locality data; MZUSP 24064 (1), Rio Tocantins, entre Mocajuba e Baião, Baião, Pará, 2º40'S 49º42'W, col. by Expedição Permanente à Amazônia, 9 September 1970; MZUSP 24086 (1), Lago às margens do igarapé Espírito Santo, entre Baiao e Tucuruí, Rio Tocantins, Baião/Tucuruí, Pará, 3º46'S 49º41'W, col. by

Expedição Permanente à Amazônia, 11 September 1970; MZUSP 27637 (1), Rio Negro, Pedra do Gavião, Moura, Amazonas, 1º28'S 61º38'W, col. by L.P.S. Portugal, 13 November 1982; MZUSP 34550 (1), Igarapé do Cujobim, Rio Branco, em frente da ilha de Maracá, Roraima, 3º25'N 60º20'W, col. by M. Goulding, 13 November 1984; MZUSP 40478 (1), Rio Paranã (cachoeira), fazenda Olho d'Água, Flores de Goiás, Goiás, 14º26'S 47º3'W, col. by J.C. Oliveira & W.J.M. Costa, 12 September 1988; MZUSP 52308 (1), Rio Araguaia, Rio Tocantins, Mato Grosso; MZUSP 52327 (1), Rio Araguaia, Bandeirantes, Rio Tocantins, Mato Grosso, 13º40'S 50º48'W; MZUSP 52342 (1), Rio Araguaia, Araguaiana, Rio Tocantins, Mato Grosso, 15º43'S 51º51'W; MZUSP 54208 (1), Rio Araguaia, Ilha do Bananal, GO, Mato Grosso; MZUSP 54539 (1), Rio Araguaia, s/ dados de localidade, Rio Tocantins; MZUSP 86893 (2); MZUSP 87081 (3); MZUSP 87082 (4); MZUSP 89734 (1); MZUSP 92720 (1); MZUSP 94085 (1); MZUSP 94415 (1); MZUSP 95627 (5); MZUSP 96132 (1); MZUSP 96598 (1); MZUSP 97217 (2); NMW 44073 (1) (Holotype: Plecostomus annae Steindachner 1881), Pará [=Belem, Brazil]; USNM 191582 (1), Rio Araguaia, Near Aruana, -14.967 -51.400, col. by H.R. Axelrod, 1960. Columbia: ANSP 146867 (1), Rio Negrito at bridge on road joining Puerto Lopez and Villavicencio; 200-400 yd downstream of bridge, Meta, J.E.Bohlke et al., 15 March 1973; AUM 35432 (1), Rìo Manacìas, Sandbar on right (E) bank 31 airkm SSW Puerto Gaitan, Meta, J.S. Ramsey, R. J. Scully, M.C. Blanco, et al., 10 October 1978. Guyana: ANSP 175912 (1), Essequibo River: 180 yd. upstream from Essequibo campsite (Maipuri), Siparuni VIII-2, D. Allicock, 27 January 1997; ANSP 175913 (1), Essequibo River: sandbar ca.800 m downstream from Essequibo campsite (Maipuri), Siparuni VIII-2, W.G.Saul, G.G.Watkins, N.R.Liley, C.Watson, 29 January 1997; AUM 35514 (1), Rupununi River 3.7 km SSE Massara, col. by J.W.

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col. by N.K. Lujan, L.S. deSouza, D.C. Werneke, and M.H. Sabaj, 14 April 2004; AUM 39844 (1), Rio Ventuari, beach below Raudales Tencua, 56 km ESE of San Juan de Manapiare, Amazonas, col. by N.K. Lujan, O. Leon, and R. Pajua; AUM 40579 (1), Rio Orinoco, at Macuruco landing, 75 km E. of San Fernando de Atabapo, Amazonas, col. by M.H. Sabaj, L.S. deSouza, D.C. Werneke, and N.K. Lujan, 4 April 2004; AUM 40751 (1), Rìo Ventuari, beach across the river from Picua Village, 34 km ENE of Macuruco, 104 km E of San Fernando de Atabapo, Amazonas, col. by M.H. Sabaj, N.K. Lujan, D.C. Werneke, L.S. deSouza, and O. Leon, 5 April 2004; AUM 41558 (2), Rio Manapiare, at Laja Pelada landing, 27 km SSW of San Juan de Manapiare, Amazonas, col. by O. Leon, D.C. Werneke, and N.K. Lujan, 18 April 2004; AUM 42092 (2), Rìo Orinoco, beach, 16.1 km W of La Esmeralda, Amazonas, col. by N.K. Lujan, M. Arce, E.L. Richmond , M.B. Grant, J. Valadez, D. Brooks, and T.E. Wesley, 25 March 2005; AUM 42122 (2), Rìo Orinoco, 33.9 km W of La Esmeralda, Punto Piaroa, Amazonas, col. by N.K. Lujan, M. Arce, T.E. Wesley, M.B. G., E.L. R., J. B., D. B., 29 March 2005; AUM 42128 (1), Rìo Casiquiare, bedrock in stream, 73 km NE of San Carlos de Rìo Negro, Amazonas, col. by N.K. Lujan, D.C. Werneke, M.H. Sabaj, M. Arce, R. Betancur, and T.E. Wesley, 9 March 2005; AUM 42165 (3), Rìo Orinoco, bedrock outcrop, 52.9 km SE of San Antonio, 102 km W of La Esmeralda, Amazonas, col. by N.K. Lujan, D.C. Werneke, M.H. Sabaj, O. Leon, M. Arce, R. Betancur, and T.E. Wesley, 4 March 2005; AUM 42182 (6), Rìo Siapa, Raudales Gallineta, 142 km E of San Carlos de Rìo Negro, Amazonas, col. by N.K. Lujan, D.C. Werneke, M.H. Sabaj, O. Leon, M. Arce, and T.E. Wesley, 17 March 2005; AUM 42196 (1), Rìo Casiquiare, bedrock outcrop, 59.5 km SW of La Esmeralda, Amazonas, col. by N.K. Lujan, D.C. Werneke, M.H. Sabaj, M. Arce, R. Betancur, T.E. Wesley, and O. Santa

Ella, 8 March 2005; AUM 42199 (1), Rìo Casiquiare, 153 km NE of San Carlos de Rìo Negro, Amazonas, col. by N.K. Lujan, O. Leon, M. Arce, E.L. Richmond, M.B. Grant, J. Valadez, D. Brooks, and T.E. Wesley, 24 March 2005; AUM 42208 (1), Rìo Ventuari, near ornamental fish market in the river, Amazonas, col. by N.K. Lujan, M. Arce, E.L. R., M.B. G., and T.E. Wesley, 3 March 2005; AUM 42222 (3), Rìo Orinoco, near Puerto Ayacuho on a beach called Playa Bagre, Amazonas, col. by N.K. Lujan, M. Arce, and T.E. Wesley, 13 March 2005; AUM 42994 (2), Rìo Orinoco, at Puerto Venado, 4.3 km S of Samariapo, 56.4 km SSW of Puerto Ayacucho, Amazonas, col. by N.K. Lujan, D.C. Werneke, M.H. Sabaj, M. Arce, R. Betancur, and T.E. Wesley, 26 February 2005; AUM 43345 (3), Rìo Casiquiare, at mouth of Caño Caripo, 37 km WSW of La Esmeralda, Amazonas, col. by N.K. Lujan, D.C. Werneke, M.H. Sabaj, O. Leon, M. Arce, R. Betancur, and T.E. Wesley, 5 March 2005; AUM 44971 (15), Essequibo River, at Kwaimatta, beach in main channel and mouth of side channel, Reg. 9, col. by L.S. deSouza, N.K. Lujan, D.C. Taphorn, J.A. Hartsell, E. Liverpool, and S. Lord, 1 December 2005; INHS 29085 (1); INHS 34779 (1); MCNG 20045 (1); MCNG 21575 (1); MCNG 23800 (1); MCNG 28843 (1); MCNG 30360 (1); USNM 265664 (2), Rio Orinoco, Cove, Islote De Fajardo, 182 Naut. mi. Upstream From Sea Buoy, Bolivar, 8.367, -62.700, col. by J. Baskin, D. Taphorn, 15 February 1978; USNM 269964 (2), Small Cano Connecting With Rio Orinoco Immediately South of El Burro, Bolivar, 6.183 -67.417, co. by R.P. Vari, O. Castillo, C.J. Ferraris, 9 December 1984.

Isorineloricaria horridus: Bolvia: AMNH 77469 (2), Rio Mamore; 8 kilometers north of Exaltacion, Depto Beni, Col. by S. Anderson, 29 September 1965; INHS 36997 (1), ; USNM 305509 (2), Rio Curiraba @ 10 km NE El Porvenir Biol. Sta., @ 40 Air km E San

Borja, Dept. Beni, Ballivia Prov., -14.917, -66.283, col. by W.C. Starnes, T.A. Monroe, J. Sarmiento, et al., 31 August 1987. Brazil: AMNH 12604 (1), Vicinity of mouth of Rio Macaua (tributary Rio Iaco), near Sena Madureira, 09º20'S, ca. 68º45'W, col. by B.A. Krukoff, 1934; ANSP 8081 (1), (Holotype: *Plecostomus scopularus*, Cope 1871), Amazon River, above the mouth of the Rio Negro, R. Perkins; MCZ 33518 (2), Rio Jurua [vicinity of mouth of Rio Embira, trib. of Rio Tarauaca, in turn a trib. of Rio Jurua], Amazonas, col. by B.A. Krukoff, 1934; MCZ 33524 (2), Rio Purus [vicinity of mouth of Rio Macaua, trib. of Rio Iaco, in turn a tri. of Rio Purus], Acre, col. by B.A. Krukoff, 1933; MCZ 7794 (1), ; MCZ 7799 (2), Tabatinga [Rio Solimoes at Tabatinga (aka Sapurara) and environs], Amazonas, THAYER 133, col. by D. Bourget, 1865; MCZ 7802 (2), Lago Cudajas [Lago Badajos], Amazonas, THAYER 025, col. by S.V.R. Thayer, D. Bourget, 1865; MCZ 7803 (2), Lago Manacapuru; Manacapuru [Lago Grande de Manacapuru], Amazonas, THAYER 060, col. by W. James, 1865; MCZ 7879 (3), Obidos; Obydos [Rio Amazonas at Obidos], Pará, THAYER 076, col. by L. Agassiz and party, 26 August 1865; MZUSP 23260 (1), Rio Solimões, Amazonas, 4º5'S 63º9'W, Expedição Permanente à Amazônia, 28 September 1968; MZUSP 28368 (2), Rio Machado, próximo à foz, Rondônia, 8º4ºS 62º54'W, Expedição Permanente à Amazônia, 21 November 1975; MZUSP 49682 (1), Rio Acre, Seringal Bom Destino (1 hora acima de Porto Acre), Acre, 9º36'S, 67º32'W, 19 October 1994; MZUSP 49839 (1), Rio Acre, seringal Perseverança, Rio Purus drainage, Acre, ; MZUSP 50374 (1), Rio Juruá, Colocacão São João, Acre, 9º9'S, 72º41'W, 8 July 1993; MZUSP 50377 (1), Rio Tejo, Ponto 13, Foz Bajé, Acre, 8º56'S 72º34'W, 8 March 1994; MZUSP 50489 (1), Foz do São João, Rio Juruá, Acre, 9º9'S, 72º41'W, 18 July 1994; MZUSP 50491(1), Foz do Breu, Rio Juruá, Acre, 9º25'S 72º43'W, 21 July 1994; MZUSP

50494 (1), Foz do Tejo, Rio Juruá, Acre, 8º58'S 72º42'W, 15 July 1994; MZUSP 57622 (1), Rio Madeira, Amazonas, 3º49'54"S 59º3'58"W, col. by Zanata et al., 7 August 1996; MZUSP 60372 (1), Rio Aripuanã, Porto de Balsa (rio acima), estrada que liga o distrito de Colniza a Panelas, km 18, Aripuanã, Mato Grosso, 9º34'45"S 59º25'19"W, col. by F. Machado, C.H. Melo, C.M.C. Leite & M.F. Catarino; USNM 041540 (1), Manacapouru; USNM 308227 (2), Ressaca Da Ilha De Marchantaria, Amazonas, col. by P. Bayley, 2 March 1977. Colombia: FMNH 96065 (5), Amazon River 1 mi. upstream from Leticia, Amazonas, col. by Thomerson et al., 11 November 1973. Ecuador: USNM 177235 (1), Rio Cotapino, Trib. of the Suno, -0.708, -77.342, col. by J. Olalla, October 1950. Peru: ANSP 21280-83 (4), (Syntypes: *Plecostomus virescens* Cope 1874), Upper Amazon, col. by Prof. James Orton; AUM 42001 (1), Rìo Tahuamanu, road crossing in vicinity of San Lorenzo, Madre de Dios, col. by M.H. Sabaj, L. Souza, M. Arce, L. deSouza, and N.J. Salcedo, 1 August 2004; AUM 45568 (1), Rìo Nieva, 7.4 km SSW Juan Velasco (Sta Maria de Nieva), Condorcanqui, Amazonas, col. by N.K. Lujan, D.C. Werneke, D.C. Taphorn, D.P. German, and D. Osorio, 5 August 2006; AUM 45585 (1), Rìo Marañon, pongo above Borja, 35.5 km NE Juan Velasco (Sta Maria de Nieva), Condorcanqui, Amazonas, col. by N.K. Lujan, D.C. Werneke, D.C. Taphorn, A.S. Flecker, K.A. Capps, D.P. German, and D. Osorio, 6 August 2006; FMNH 70157 (1), Madre de Dios: Rio Inambari, col. by E.R. Blake, 6 October 1958; INHS 36566 (1), ; INHS 36796 (1); INHS 55406 (1); MUSM 12628 (1); MUSM 19897 (1); MUSM 26699 (1); MUSM 9976 (1); MZUSP 26754 (1), Rio Aguaytia, Nuevo Requena, Pucallpa, col. by H. Ortega, 23 October 1973; MZUSP 26788 (1), Rio Neshuya, estrada Pucallpa-Huanuco, Pucallpa, Ucayali, col. by H. Ortega, 24 July 1978; MZUSP 26789 (2), Yarinacocha, Pucallpa, Cel. Portillo, Ucayali, col. by H. Ortega, 10 August 1973; UF

126268 (1), Cano Puinahua, opposite mouth of Rio Pacaya. Habitat - Beaches & Muddy bottom, Loreto, col. by J.S. Albert et al., 23 September 2002; USNM 086834 (2), Yurimaguas, Rio Paranapura, col. by W.R. Allen, November 1920; USNM 123268 (1), Rio Morona, col. by W.R. Allen, October 1920; USNM 124911 (2), Shansho Cano, col. by W.G. Scherer, 18 October 1935; USNM 167886 (1), Yurimaguas, Rio Huallaga, col. by W.R. Allen, November 1920; USNM 167887 (2), Iquitos, Loreto Region, col. by W.R. Allen, September 1920; USNM 167888 (1), Yurimaguas, Rio Paranapura, col. by W.R. Allen, November 1920; USNM 263916 (3), Madre De Dios; Rio Tambopata, Opposite Boat Landing For Explorer'S Inn., Madre de Dios Region, -12.833 S, -69.300 W, col. by H. Ortega, R.P. Vari, 21 August 1983; USNM 263919 (1), Shore of Isla About 15 km Downriver of Junction of Rio Tambopata and Rio Madre De Dios., Madre de Dios Region, -12.500 S, -69.147 W, col. by R.P. Vari, H. Ortega, S.L. Jewett, 25 August 1983; USNM 350530 (1), Department Madre De Dios: Parque Nacional Manu, Pakitza and Vicinity, Madre de Dios Region, col. by H. Ortega, October 1987. Unknown: ANSP 8279 (1), Amazon River, col. by R.C. Perkins.

Isorineloricaria spinosissima: Ecuador: AUM 4251 (1); Los Rios, Rio Vinces, at Vinces, col. by T. Roberts, R. Gilbert, and F. Silva M., 5 November 1971. FMNH 58546 (3); Rio Duales, Colimes, A.W. Henn, 1913. FMHN 59369 (1); Guayaquil, A.W. Henn, 1913. MCZ 48773 (2); Fish market at Quevedo, 0˚59’S 79˚27’W, T.R. Roberts and party, 11 April 1971. MCZ 51699 (2); Rio Vinces at Vinces, Roberts, Gilbert, and Silva, 11 May 1971. MSUM 2505.4.A (2).

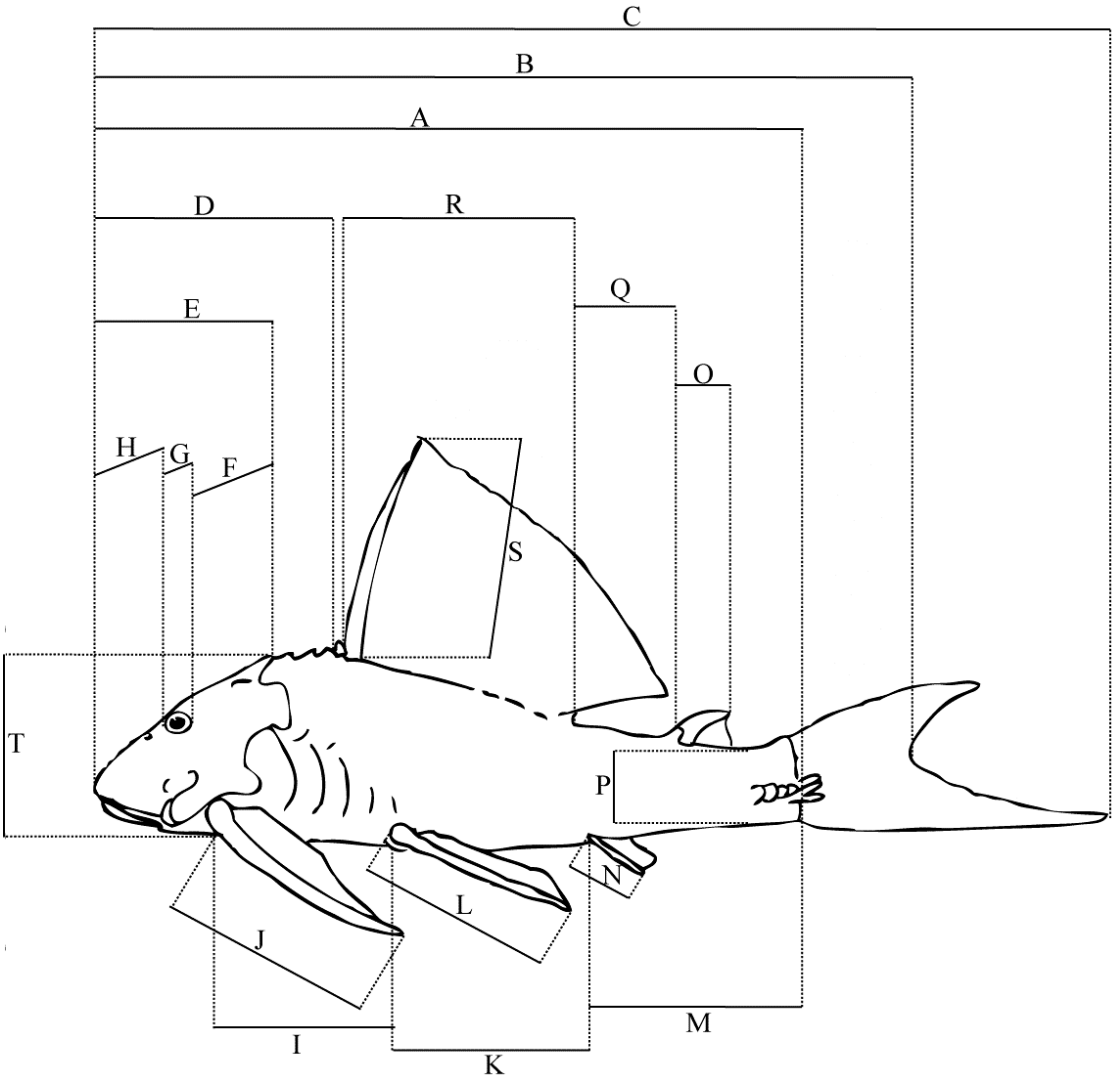
Isorineloricaria tenuicauda: Syntypes: NMW 44265 (1); NMW 44266 (3). Nontype material: Colombia: ANSP 71263 (*Plecostomus winzi* holotype) (1); Honda, Rio Magdalena Basin, C. Miles, November 1940. CU 47928 (1), Lake San Sylvestre by city of Barranca-Bermeja, Santander, col. by F. Archer, J.D. Archer, 20 August 1964; FMNH 55169 (3); Soplaviento, Eigenmann. FMNH 76408 (1); Honda, Eigenmann. FMNH 76424 (1); Calamar Cienega, Eigenmann. FMNH 96234 (1); Puerto del Rio, Magdalena River, Cienega on Central Magdalena, M. Gonzales, 1913.

Isorineloricaria villarsi: Venezuela: AUM 22584 (1); Zula, Lago Maracaibo, Southern part of lake, Santa Barbara fish market, 20 December 1999. FMNH 6338 (4); Encontrados, N. Dearborn, February 1908. MCNG 33523 (2); USNM 121019 (1); Rio Apon about 35km. south of Rosario in Maracaibo basin, col. by L. Schultz, 26 February 1942. USNM 12120 (3); Rio Socuy 3km above mouth, Maracaibo Basin, col. by L. Shultz, 24 February 1942. USNM 121021 (1); Rio Negro, 75km west of Rosario, col. by L. Shultz, 2 March 1942. USNM 121022 (1); Cienaga del Guanavana about 10km. north of Sinamaica, col. by L. Shultz, 11 March 1942. USNM 121031 (2); Lago Maracaibo, near mouth of Rio Concha, col. by L. Schultz, 2 May 1942.

Figures

Fig. 1: Range of Loricariidae (from Armbruster 2004).

Fig. 2: Diagram of selected measurements, adapted from Boeseman (1968) and Armbruster and Page (1996).



A.	Sandard Length	K.	Abdominal length
B.	Axial length	L.	Pelvic spine length
C.	Total length	M.	Post-anal length
D.	Predorsal length	N.	Anal fin length
E.	Head length	O.	Adipose spine length
F.	Head- eye length	P.	Caudal depth
G.	Orbit diameter	Q.	Interdorsal length
H.	Snout length	R.	Base of dorsal fin length
I.	Thoracic length	S.	Dorsal spine length
J.	Pectoral spine length	T.	Head depth

Fig. 3: Selected head measurements, adapted from Boeseman (1968) and Armbruster and Page (1996).

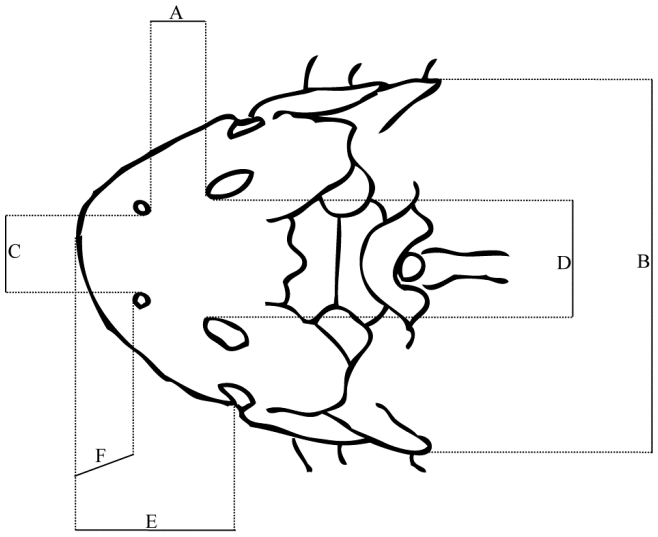
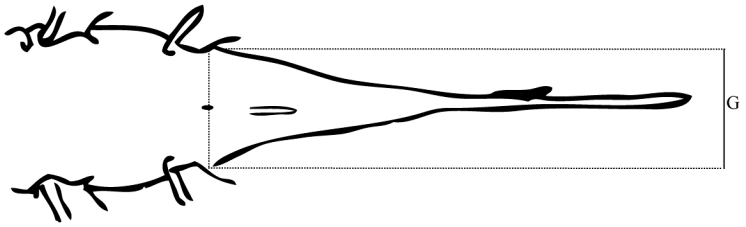


Fig. 4: Illustration of caudal fin width measurement, adapted from Boeseman (1968) and Armbruster and Page (1996).



A. Eye- nare length
B. Cleithral width
C. Internares width
D. Interorbital width
E. Snout– opercle distance
F. Snout– nares length
G. Caudal peduncle width

Fig. 5: Results of the PCA of the species of *Isorineloricaria*.

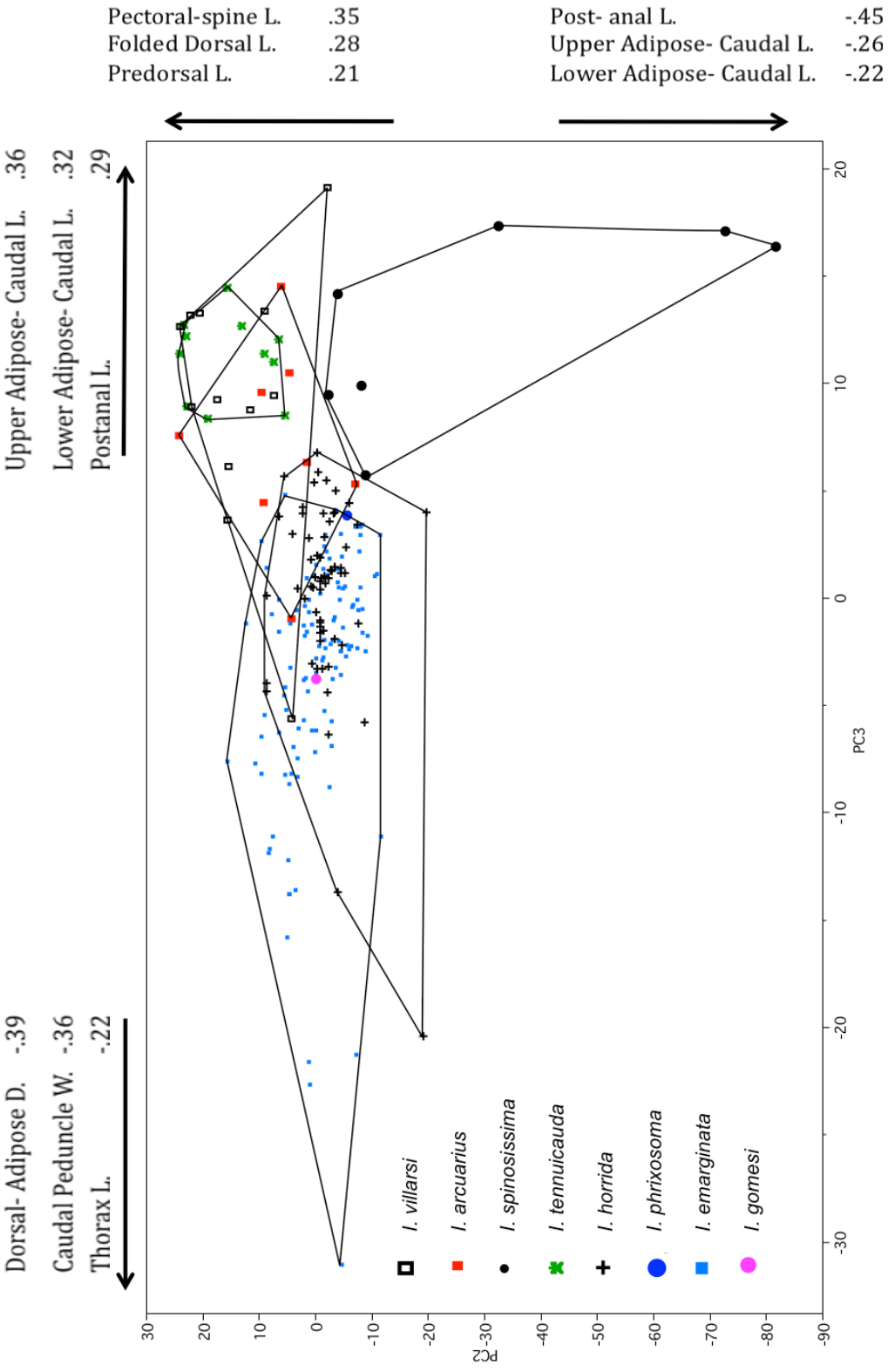


Fig. 6: Bivariate Fit of Snout-nares Wd. By Interorbital Wd. Red crosses- *Isorineloricaria horrida*, Blue squares- *I. emarginata*.

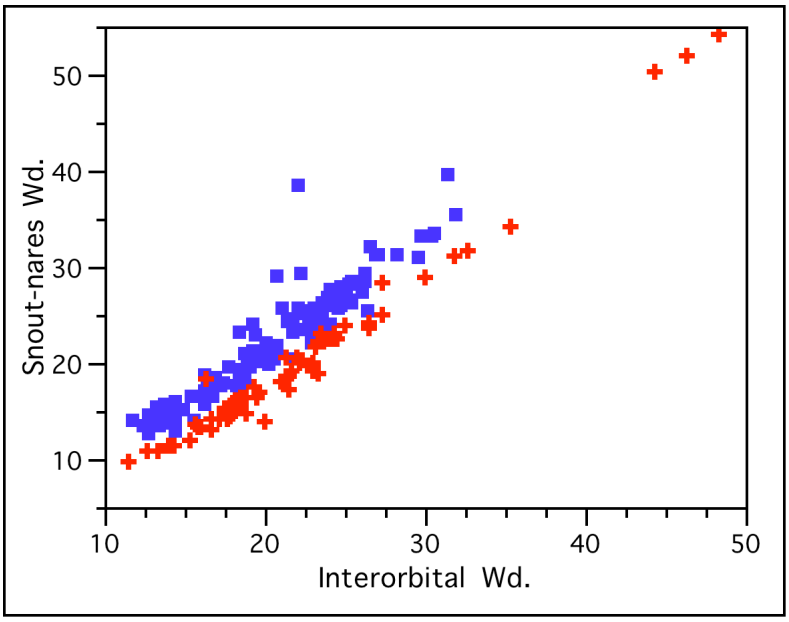


Fig. 7: Bivariate Fit of Caudal Peduncle Dp. By Head L., black circles represent *I. spinosissima*, red squares represent all other *Isorineloricaria* (except *I. ammophila* and *I. unicolor*).

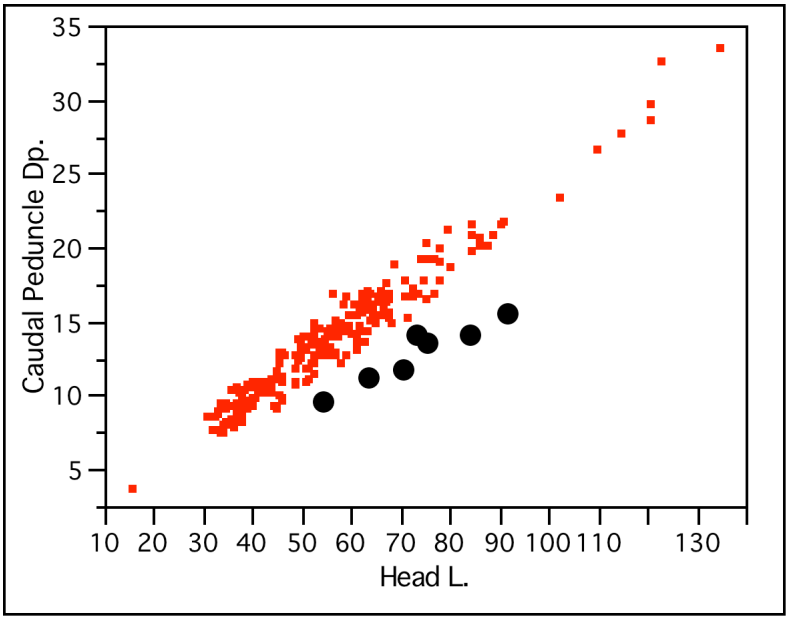


Fig. 8: A. Ventral view of mouth of *Isorineloricaria gomesi*, ANSP 69409, illustrating the large central buccal papilla characteristic of most memebers of *Isorineloricaria*. Photograph by M. Sabaj-Perez and K. Luckenbill. B. Ventral view of mouth of *I. ammophila*, AUM 22659, illustrating multiple buccal pappilae found in *I. ammophila* and *I. unicolor*.

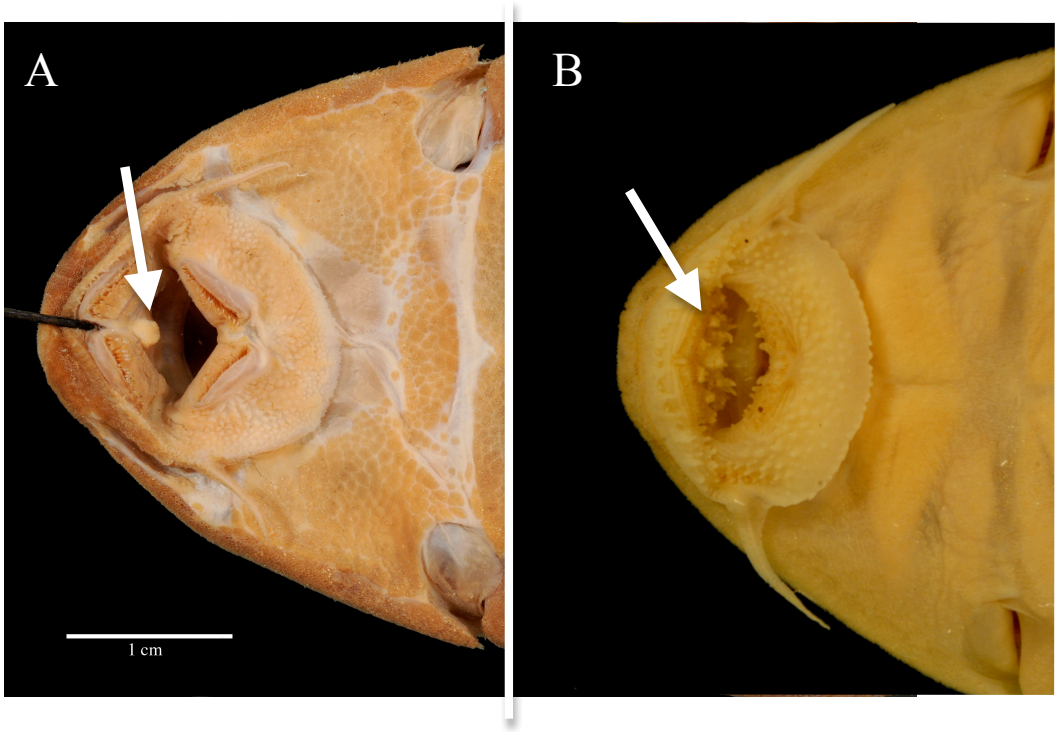


Fig. 9: Dorsal, lateral, and ventral views of *Isorineloricaria ammophila*, AUM 22659.

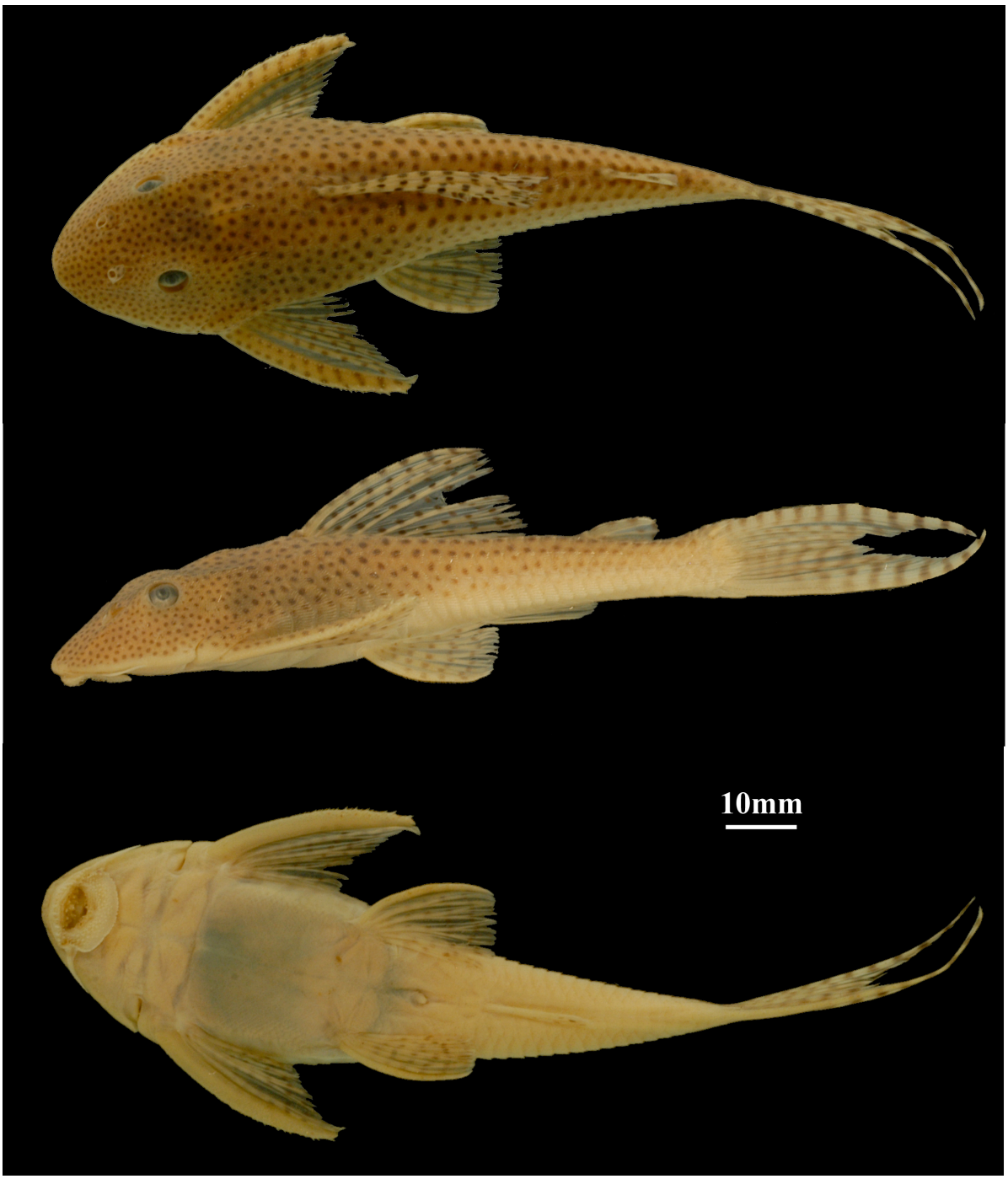


Fig. 10: Dorsal and ventral views of *Isorineloricaria* n. sp. ‘Apure’, INHS 35685 (holotype), 269.11mm SL.

Fig. 11: Lateral view of *Isorineloricaria* n. sp. ‘Apure’, INHS 35685 (holotype), 269.11mm SL.

Fig. 12: Dorsal, lateral, and ventral views of *Isorineloricaria emarginata*, MZUSP 97217, 227mm SL.

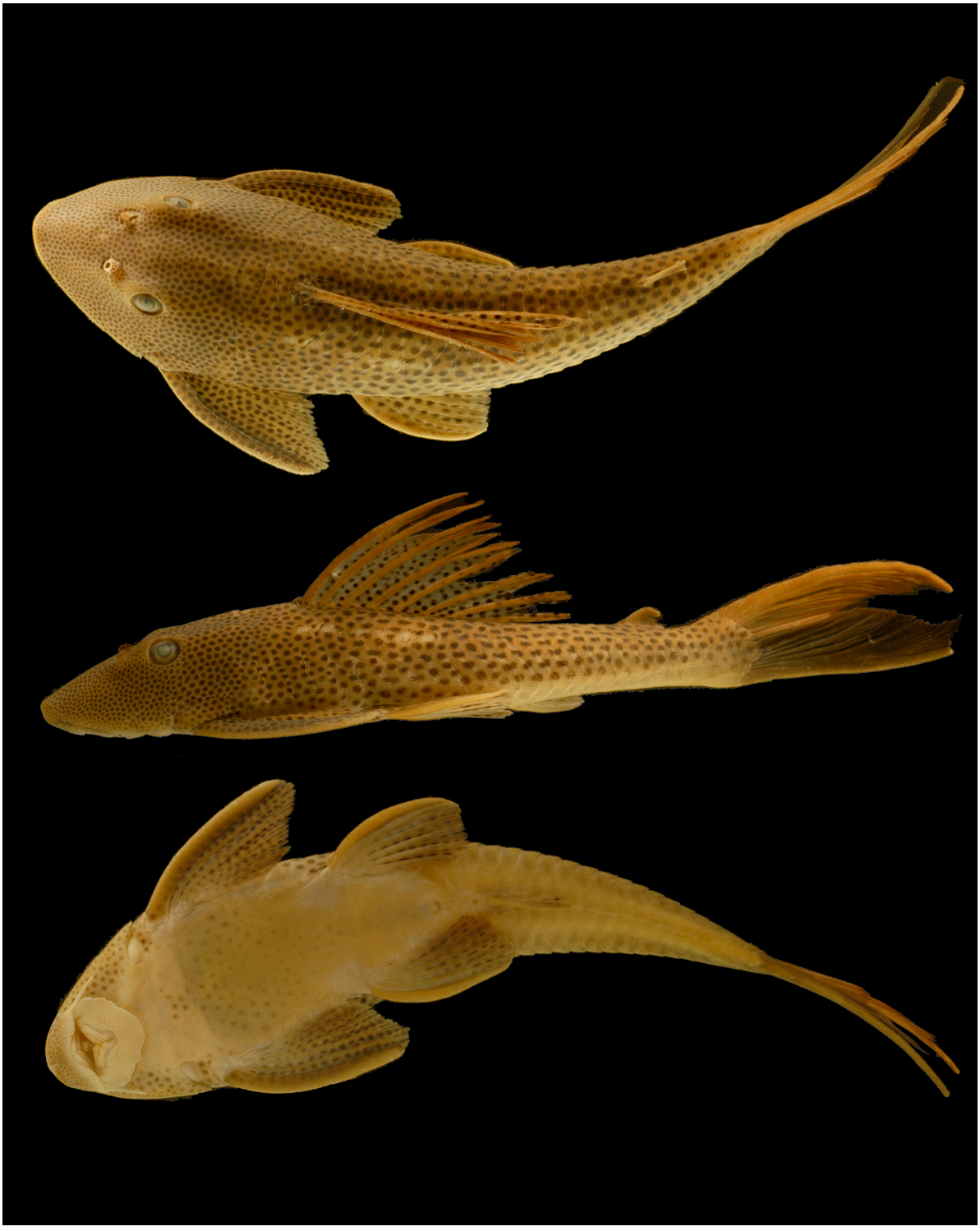


Fig. 13: Dorsal, lateral, and ventral views of *Isorineloricaria gomesi*, ANSP 69409 (holotype), 141.3mm SL. Photograph by Kyle Luckenbill.

Fig. 14: Dorsal, lateral, and ventral views of *Isorineloricaria horrida*, AUM 42001.

Fig. 15 A-C: Ventral (A), dorsal (B), and lateral (C) views of *Isorineloricaria phrixosoma*, ANSP 68650, 109.5mm SL. Photographs taken by K. Luckenbill.

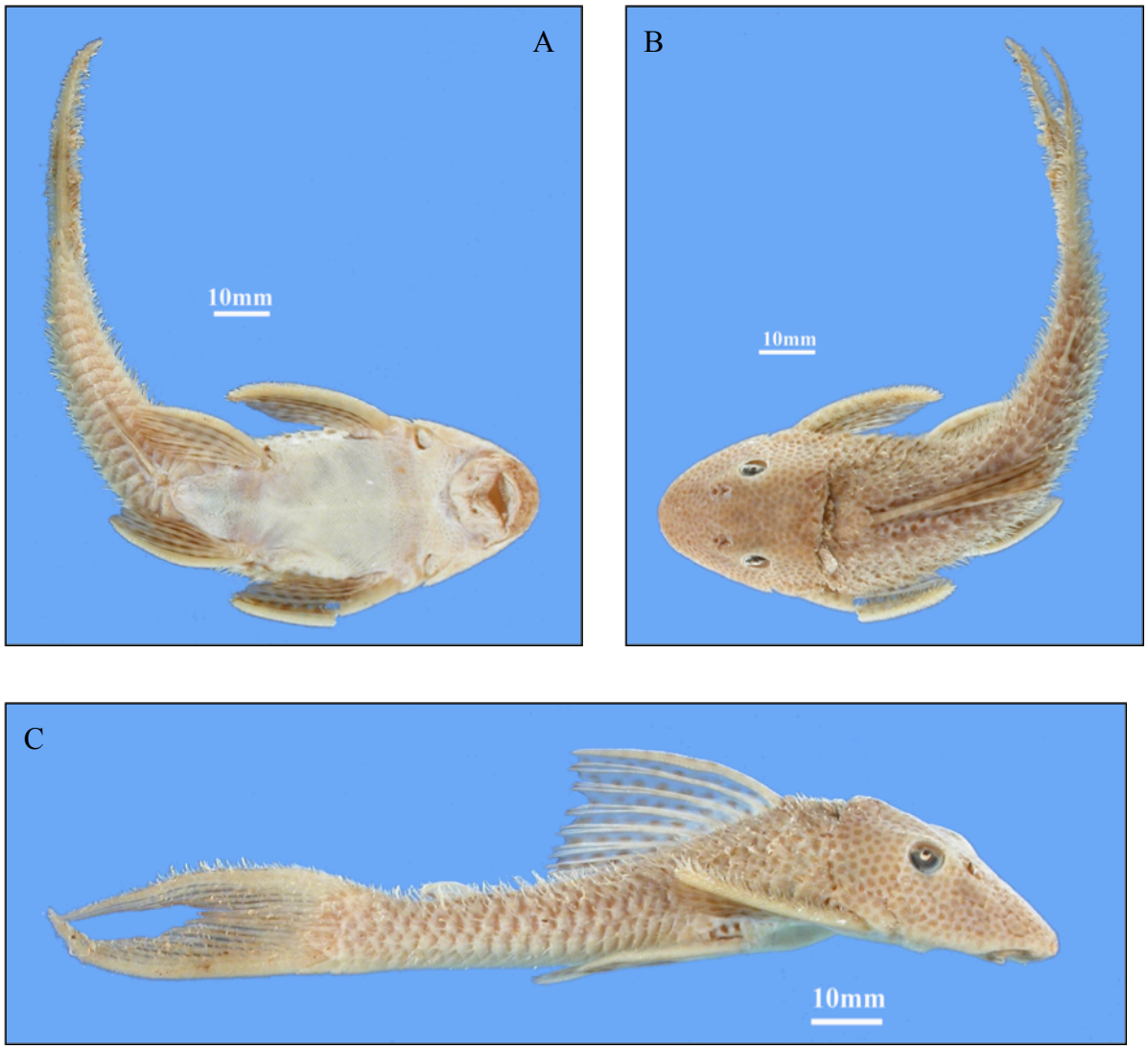


Fig. 16: Dorsal, lateral, and ventral views of *Isorineloricaria spinosissima*, BMNH 1898.11.4.32 (syntype of *Plecostomus festae*), 357.6 mm SL. Photographs by C. Zawadzki.

Fig. 17: Lateral, dorsal, and ventral views of *Isorineloricaria tenuicauda*, MSNG 8856 (syntype). Photographs by M. Allen.

Fig. 18: Lateral, dorsal, and ventral view of *Isorineloricaria unicolor*, ZMA 116640 (*Aphanotorulus frankei* holotype), 105.4mm SL. Photographs by K.S. Cummings.

Fig. 19: Dorsal, lateral, and ventral views of *Isorineloricaria villarsi*, USNM 121031, 301.5mm SL.

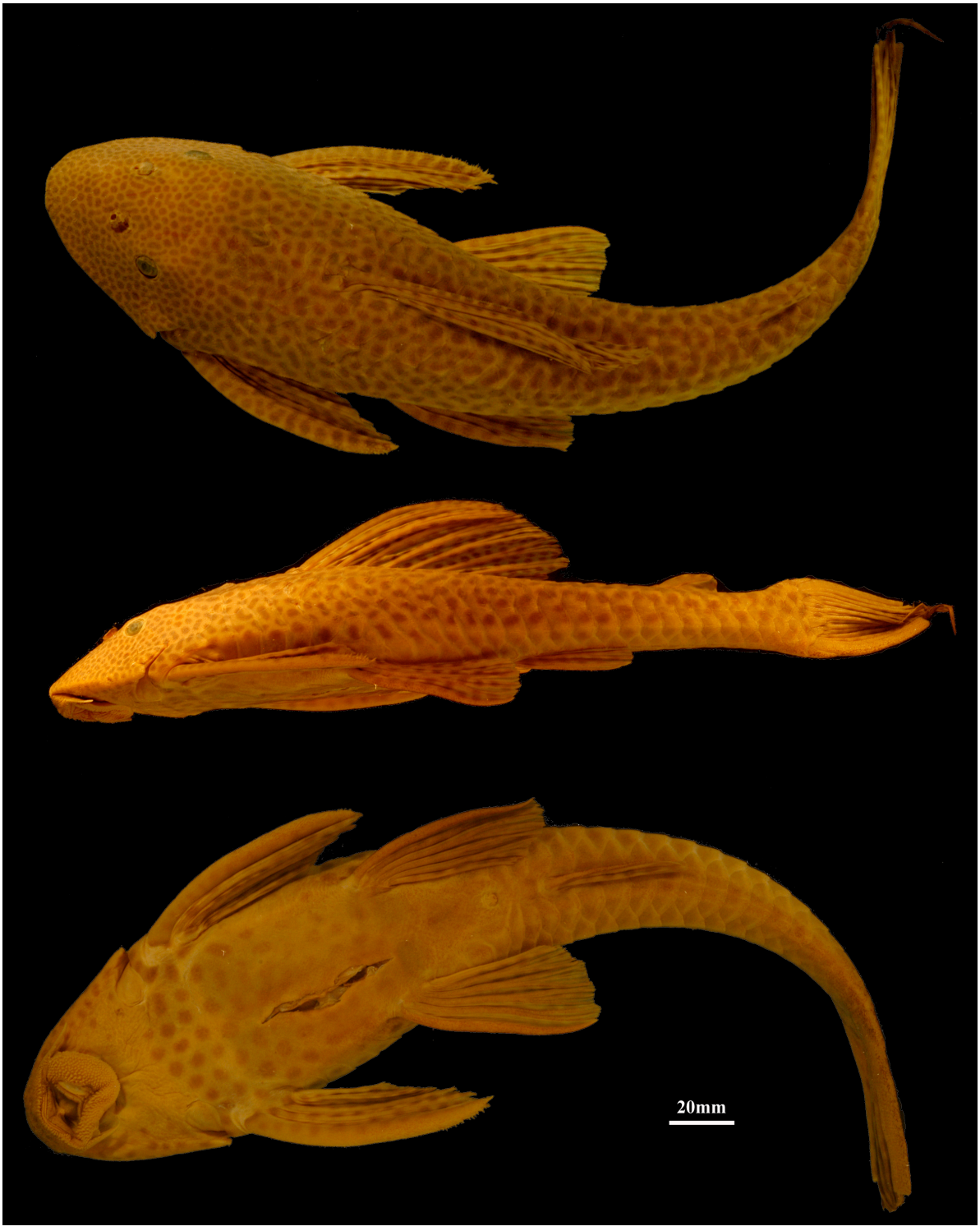


Fig. 20: Range map of *Isorineloricaria ammophila* and *I. unicolor*. Circles represent *I. ammophila*, squares represent *I. unicolor*. Open shapes represent type localities. From Armbruster (2008).

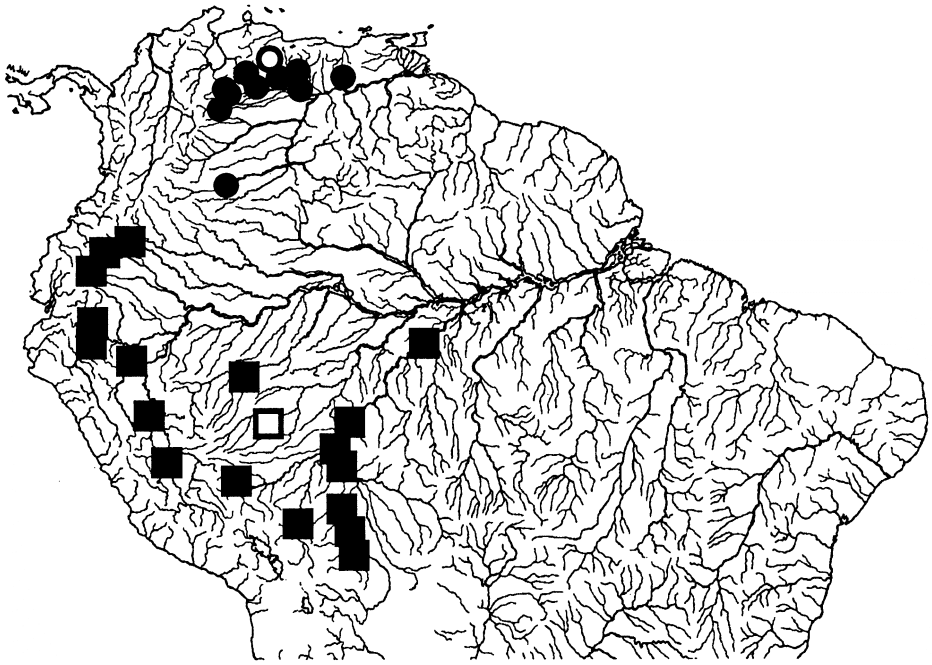


Fig. 21: Range map of *Isorineloricaria* n. sp. ‘Apure’, *I. gomesi*, *I. phrixosoma*, *I. spinosissima*, *I. tenuicauda*, and *I. villarsi*. Squares represent *Isorineloricaria* n. sp. ‘Apure’, stars represent *I. gomesi*, X represents *I. phrixosoma*, circles represent *I. squaliforma*, diamonds represent *I. tenuicauda*, and triangles represent *I. villarsi*. Open shapes represent type localities.

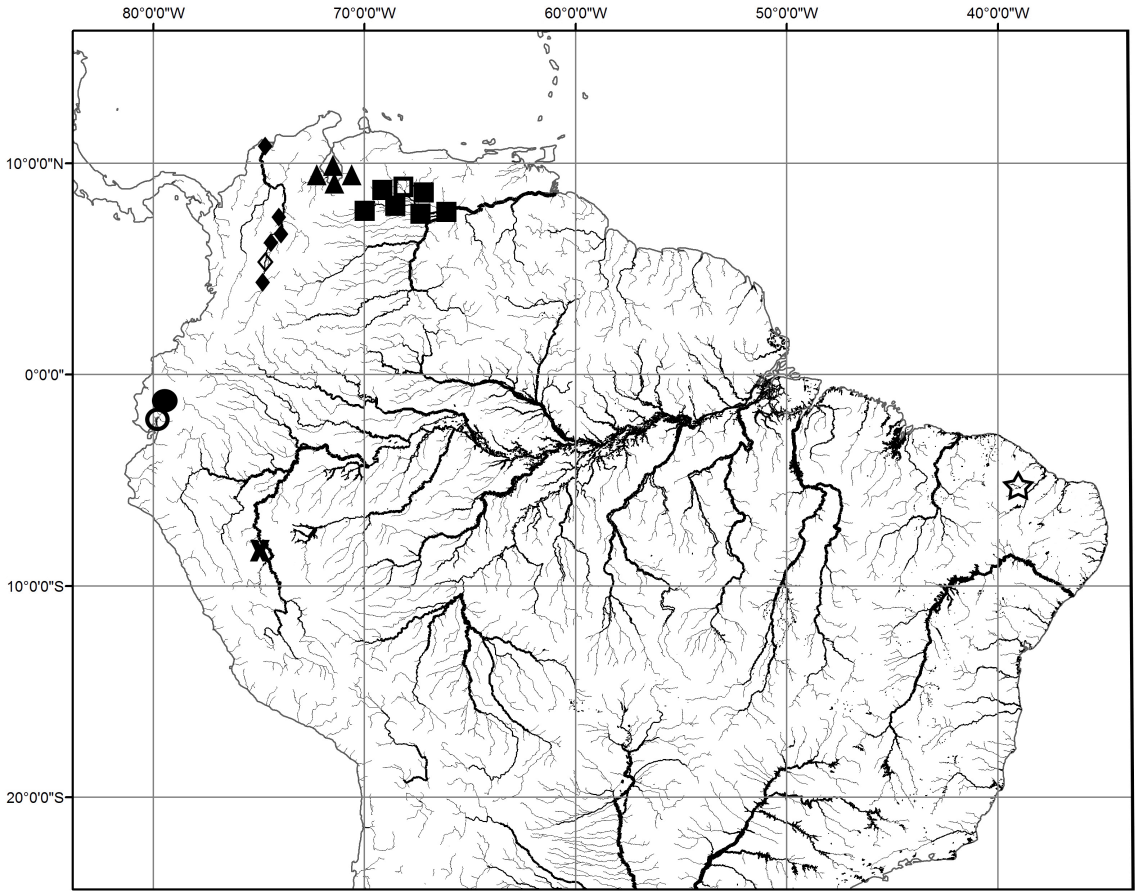


Fig. 22: Range map of *Isorineloricaria emarginata*.

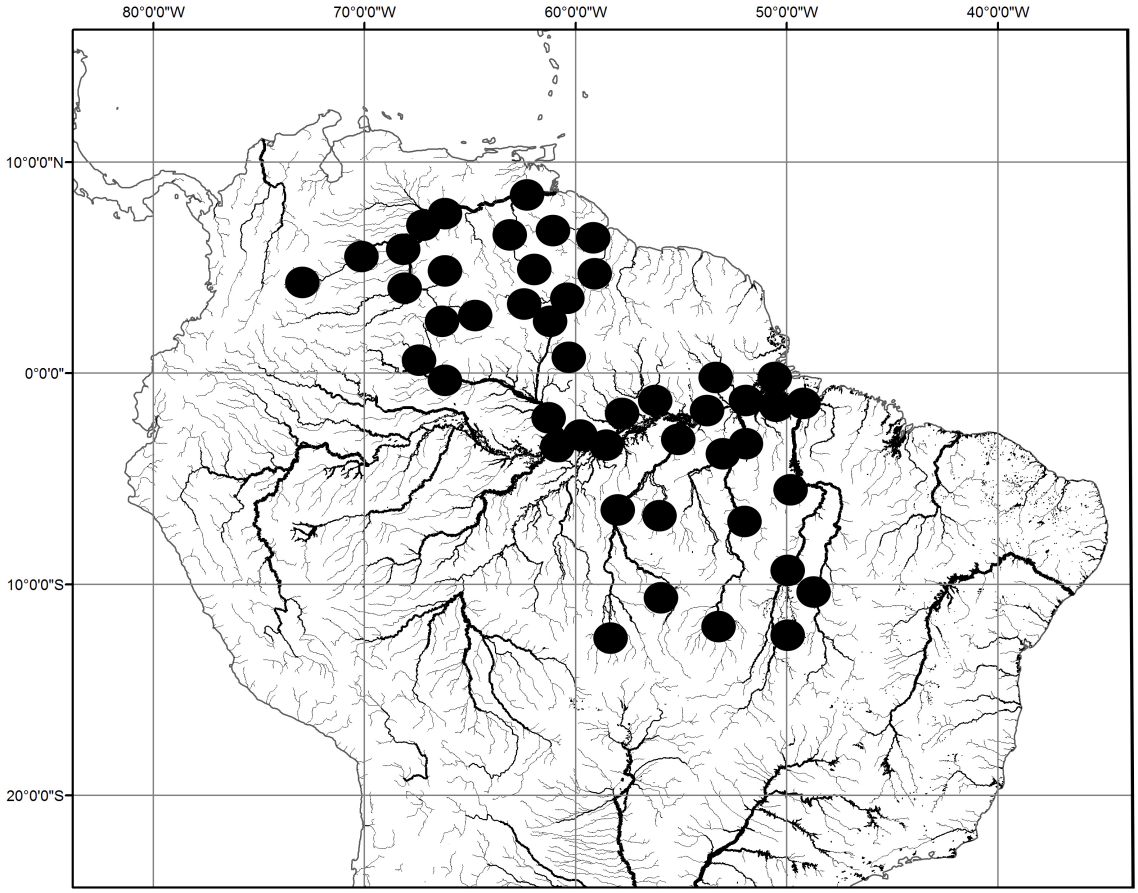


Fig. 23: Range map of *Isorineloricaria horrida*. Type locality indicated by open square.

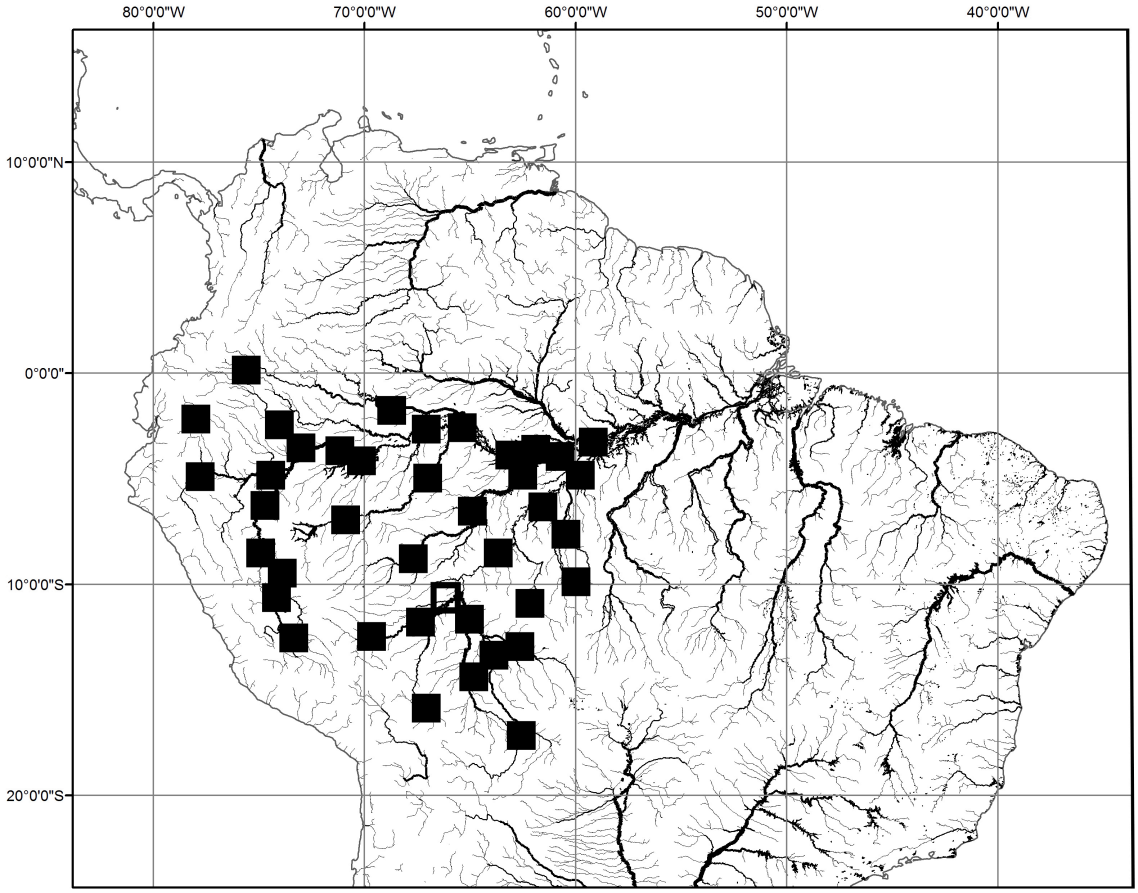


Table 1: Selected morphometrics of *Isorineloricaria* n. sp. 'Apure' and *I. emarginata*.

	Isorineloricaria n. sp. 'Apure'						*Isorineloricaria emarginata*					
Measurement (mm)	N	Average	SD	Range			N	Average	SD	Range		
Standard Length (SL)	23	118.4	81.9	53.2	-	301.0	153	163.4	67.5	46.5	-	357.0
% SL												
Predorsal L.	23	39.1	3.2	33.4	-	44.7	153	36.5	2.3	29.8	-	41.9
Head L. (HL)	23	32.9	3.9	20.9	-	36.7	153	29.8	2.5	23.3	-	36.2
Cleithral W.	22	26.1	1.4	23.2	-	28.3	153	23.8	1.5	20.0	-	27.2
Dorsal spine L.	21	29.4	4.6	18.4	-	34.8	153				-	
Folded dorsal-fin L.	23	36.8	2.0	32.8	-	40.0	153	36.0	1.7	30.0	-	41.5
Dorsal-fin base L.	23	24.1	1.0	21.7	-	26.0	153	23.5	1.0	20.1	-	28.3
Dorsal- adipose L.	23	21.5	1.9	19.0	-	26.0	153	24.6	2.0	19.6	-	31.4
Thorax L.	23	23.0	1.5	20.4	-	26.2	153	23.6	1.4	20.0	-	27.5
Pectoral spine L.	23	28.6	2.0	24.6	-	32.6	153	25.4	2.1	18.8	-	31.4
Abdominal L.	23	19.1	1.0	16.9	-	20.5	153	20.3	1.1	16.5	-	24.8
Pelvic spine L.	23	22.7	2.1	17.4	-	25.8	153	20.1	1.8	14.1	-	25.6
Postanal L.	23	38.9	2.8	35.3	-	46.5	153	39.9	2.8	32.9	-	45.9
Caudal peduncle Dp.	23	8.1	0.6	6.7	-	9.0	153	7.2	0.6	5.7	-	8.9
Caudal peduncle W.	23	15.7	1.4	12.1	-	18.7	153	16.7	1.3	13.4	-	21.0
Adipose-fin spine L.	23	7.8	1.2	5.5	-	10.0	151	6.7	1.0	4.2	-	9.8
Anal-fin L.	23	13.2	2.2	9.6	-	17.7	153	12.0	1.6	6.8	-	17.5
Anal-fin base L.	23	4.0	0.5	2.6	-	4.8	152	4.0	0.5	2.3	-	5.3
Adipose- upper caudal L.	23	20.9	1.2	18.5	-	22.8	152	20.4	1.2	17.0	-	23.5
Adipose- lower caudal L.	23	26.7	1.4	22.7	-	29.0	153	24.8	1.3	20.4	-	28.2
%HL												
Head Dp.	23	59.0	9.1	52.9	-	99.3	153	57.3	3.4	48.7	-	73.5
Snout L.	23	61.1	8.6	55.2	-	98.5	153	60.4	2.4	55.7	-	73.5
Orbit Diameter	23	20.9	5.6	14.0	-	41.1	153	19.4	3.0	14.4	-	36.5
Interorbital W.	23	44.7	7.2	39.2	-	76.6	153	38.5	2.0	34.1	-	44.3
Snout opercle D.	23	72.7	10.9	67.7	-	121.9	153	71.2	2.5	66.7	-	86.3
Head W.	23	81.3	11.2	72.7	-	131.0	153	80.3	3.4	72.0	-	97.3
Head eye L.	23	38.5	6.8	32.9	-	69.0	153	36.5	2.6	32.5	-	61.1
Eye nare L.	23	13.1	2.2	9.6	-	20.0	153	11.4	1.4	6.9	-	15.1
Internares W.	23	17.4	3.5	13.5	-	31.4	153	17.4	1.6	12.3	-	22.5
Snout nares L.	23	40.1	6.3	33.7	-	66.4	153	41.3	3.1	36.7	-	68.2
Snout pectoral L.	23	75.1	11.6	68.6	-	127.9	153	74.1	3.0	68.9	-	92.0
Pectoral orbit D.	23	25.5	5.0	20.1	-	42.6	153	27.1	3.5	19.1	-	37.0
Mouth W.	23	42.7	6.1	37.5	-	68.0	153	41.8	3.8	34.8	-	54.3
Mouth L.	23	45.7	7.4	40.2	-	77.7	153	43.4	3.7	33.3	-	59.7
Dentary L.	23	14.4	2.9	11.1	-	24.9	153	13.1	1.9	7.4	-	19.9

Table 2: Selected morphometrics of *Isorineloricaria horrida* and *I. spinnosissima*.

	Isorineloricaria horrida						*Isorineloricaria spinosissima*					
Measurement (mm)	N	Average	SD	Range			N	Average	SD	Range		
Standard Length (SL)	73	162.9	85.1	44.9	-	513.0	11	208.4	138.7	39.4	-	416.0
% SL												
Predorsal L.	73	36.8	2.2	29.6	-	41.2	11	33.5	4.4	25.1	-	38.3
Head L. (HL)	73	30.2	2.3	23.5	-	38.8	11	27.9	4.4	19.9	-	33.7
Cleithral W.	72	24.8	1.8	19.2	-	27.6	11	22.3	3.3	16.3	-	25.6
Dorsal spine L.	73				-		11	27.3	3.8	19.9	-	31.3
Folded dorsal-fin L.	72	36.5	1.2	31.1	-	40.9	11	33.9	2.9	28.5	-	37.6
Dorsal-fin base L.	73	23.6	1.2	19.6	-	26.0	11	22.6	1.8	20.3	-	27.0
Dorsal- adipose L.	73	24.2	1.8	20.3	-	28.5	11	22.1	2.9	16.6	-	26.3
Thorax L.	73	24.2	1.6	19.2	-	28.7	11	21.4	1.8	18.4	-	23.6
Pectoral spine L.	72	25.9	2.3	18.1	-	30.3	11	22.2	4.6	15.1	-	28.5
Abdominal L.	73	20.2	1.2	18.0	-	24.8	11	18.3	1.2	16.7	-	20.4
Pelvic spine L.	73	20.8	2.4	14.7	-	26.0	11	20.2	2.6	14.9	-	23.8
Postanal L.	73	39.8	4.1	20.6	-	46.8	11	42.7	4.0	37.0	-	51.0
Caudal peduncle Dp.	73	7.8	0.9	5.6	-	9.1	11	5.2	1.1	3.7	-	6.6
Caudal peduncle W.	73	16.7	1.5	10.0	-	19.2	11	11.5	1.7	8.3	-	13.5
Adipose-fin spine L.	72	6.8	1.0	4.6	-	11.0	11	6.9	1.6	4.3	-	9.8
Anal-fin L.	72	13.2	1.7	10.4	-	17.9	11	13.7	1.2	11.8	-	15.4
Anal-fin base L.	72	4.1	0.6	1.9	-	5.8	11	4.1	1.0	2.2	-	5.9
Adipose- upper caudal L.	73	21.2	1.6	16.6	-	24.7	11	26.0	2.3	22.8	-	29.5
Adipose- lower caudal L.	72	25.7	1.3	22.7	-	28.9	11	28.7	2.3	26.1	-	33.4
%HL												
Head Dp.	73	59.0	3.5	50.5	-	66.0	11	55.3	2.8	49.4	-	57.9
Snout L.	73	59.1	3.8	42.0	-	71.3	11	59.6	3.6	52.9	-	64.7
Orbit Diameter	73	17.9	2.4	11.7	-	24.2	11	18.5	3.9	14.7	-	27.4
Interorbital W.	73	43.5	3.9	30.0	-	49.5	11	37.7	1.6	33.5	-	39.5
Snout opercle D.	73	70.5	3.2	53.0	-	77.3	11	71.9	4.7	67.1	-	83.9
Head W.	73	82.6	3.4	67.4	-	90.4	11	80.2	3.7	76.2	-	86.3
Head eye L.	73	39.4	1.6	32.8	-	43.9	11	34.9	3.7	28.7	-	42.7
Eye nare L.	73	11.9	1.2	9.0	-	14.3	11	11.9	1.9	9.0	-	14.5
Internares W.	73	18.0	1.9	11.5	-	22.2	11	15.2	1.2	13.4	-	18.1
Snout nares L.	73	38.6	4.5	14.1	-	44.1	11	39.9	2.7	35.0	-	44.3
Snout pectoral L.	73	73.0	3.4	54.7	-	80.1	11	76.5	4.0	72.3	-	83.9
Pectoral orbit D.	73	27.2	2.8	20.3	-	34.2	11	27.9	4.0	22.7	-	36.7
Mouth W.	73	40.7	3.1	34.8	-	49.4	11	41.4	3.0	37.5	-	45.6
Mouth L.	73	41.9	3.5	30.4	-	47.8	11	44.2	4.4	37.4	-	51.9
Dentary L.	73	12.5	1.2	8.8	-	15.0	11	12.8	1.3	11.0	-	15.7

Table 3: Selected morphometrics of *Isorineloricaria tenuicauda* and *I. villarsi*.

	Isorineloricaria tenuicauda						*Isorineloricaria villarsi*					
Measurement (mm)	N	Average	SD	Range			N	Average	SD	Range		
Standard Length (SL)	12	175.7	72.6	41.5	-	516.9	16	275.4	126.6	85.5	-	516.9
% SL												
Predorsal L.	12	37.8	1.9	34.5	-	40.8	16	35.7	3.2	29.2	-	41.8
Head L. (HL)	12	32.4	2.4	28.6	-	37.8	16	29.4	3.2	24.0	-	36.1
Cleithral W.	12	25.4	1.3	22.6	-	28.0	16	22.9	2.4	19.1	-	26.7
Dorsal spine L.	10	32.1	2.2	28.3	-	35.0	15	27.8	5.6	13.8	-	34.1
Folded dorsal-fin L.	12	40.3	1.5	37.2	-	42.3	16	37.1	2.4	31.2	-	40.1
Dorsal-fin base L.	12	25.9	1.8	21.0	-	28.7	16	23.8	1.7	19.7	-	26.4
Dorsal- adipose L.	12	20.5	1.5	17.6	-	22.7	16	22.0	1.5	18.3	-	24.2
Thorax L.	12	24.3	1.3	22.1	-	26.1	16	22.9	1.6	19.1	-	25.8
Pectoral spine L.	12	30.8	2.6	24.4	-	34.0	16	26.2	2.0	23.4	-	30.7
Abdominal L.	12	20.4	0.8	19.4	-	21.8	16	20.2	1.3	18.0	-	22.7
Pelvic spine L.	12	22.0	1.9	17.7	-	25.2	16	20.2	1.7	16.4	-	23.4
Postanal L.	12	37.0	2.0	31.2	-	38.7	16	40.1	3.3	34.1	-	45.8
Caudal peduncle Dp.	12	8.2	0.7	6.8	-	9.2	16	7.4	1.0	6.3	-	9.1
Caudal peduncle W.	12	14.2	1.6	9.4	-	15.7	16	14.8	1.8	12.5	-	18.3
Adipose-fin spine L.	12	8.2	0.7	7.7	-	9.8	16	7.5	0.6	6.6	-	9.0
Anal-fin L.	12	16.0	1.2	14.0	-	18.0	16	14.6	1.8	10.6	-	16.9
Anal-fin base L.	11	4.4	0.6	3.2	-	5.5	16	4.5	0.5	3.6	-	5.3
Adipose- upper caudal L.	12	23.1	1.1	21.3	-	25.1	16	21.1	1.8	16.9	-	23.3
Adipose- lower caudal L.	12	26.6	1.2	24.7	-	28.5	16	25.0	1.5	21.1	-	26.6
%HL												
Head Dp.	12	58.4	2.3	54.4	-	62.8	16	55.7	2.8	50.6	-	62.0
Snout L.	12	56.6	1.7	52.7	-	59.0	16	57.1	2.5	53.1	-	62.6
Orbit Diameter	12	15.8	2.3	12.7	-	19.1	16	13.7	3.3	10.2	-	22.7
Interorbital W.	12	43.1	1.7	40.2	-	45.8	16	42.6	1.8	38.9	-	45.8
Snout opercle D.	12	71.4	2.2	68.1	-	75.8	16	72.4	2.5	66.6	-	74.7
Head W.	12	81.4	4.1	71.5	-	86.9	16	79.4	2.5	74.6	-	85.6
Head eye L.	12	42.4	1.6	39.6	-	44.5	16	43.1	1.8	38.0	-	45.1
Eye nare L.	12	13.1	1.4	9.9	-	14.5	16	12.8	1.4	10.7	-	16.1
Internares W.	12	15.2	1.3	12.8	-	16.7	16	17.0	1.4	14.8	-	19.3
Snout nares L.	12	35.9	2.1	30.9	-	39.0	15	37.2	2.2	33.0	-	42.8
Snout pectoral L.	12	72.9	1.9	70.9	-	77.4	16	75.0	2.7	67.1	-	78.5
Pectoral orbit D.	12	27.0	2.2	21.4	-	29.1	16	28.6	2.0	24.5	-	31.0
Mouth W.	12	38.3	2.6	34.9	-	42.4	16	38.5	2.6	32.6	-	42.8
Mouth L.	12	43.1	2.7	39.0	-	47.2	16	42.3	2.5	38.6	-	46.8
Dentary L.	12	12.2	1.3	10.1	-	14.1	16	11.9	1.1	10.4	-	14.5

Table 4: Selected morphometrics of *Isorineloricaria ammophila* and *I. unicolor*.

	Isorineloricaria ammophila						*Isorineloricaria unicolor*					
Measurement (mm)	N	Average	SD	Range			N	Average	SD	Range		
Standard Length (SL)	91	81.5	27.9	36.0	-	160.9	323	84.1	17.4	31.1	-	139.0
% SL												
Predorsal L.	91	91.0	1.6	36.1	-	44.0	319	38.3	1.1	35.6	-	43.8
Head L. (HL)	91	33.3	1.9	29.2	-	38.5	323	31.5	1.5	19.0	-	38.2
Cleithral W.	91	26.7	1.0	24.4	-	29.6	317	26.0	1.2	23.2	-	31.6
Dorsal spine L.	72	26.4	1.8	21.6	-	29.5	270	28.4	1.9	22.4	-	34.1
Folded dorsal-fin L.	90	33.8	1.1	30.9	-	36.9	315	33.7	1.4	20.1	-	37.6
Dorsal-fin base L.	91	19.6	1.2	17.2	-	22.8	323	19.3	1.2	15.6	-	23.9
Dorsal- adipose L.	91	20.9	1.6	16.8	-	24.1	322	23.2	1.5	16.9	-	26.5
Thorax L.	91	24.5	1.2	21.3	-	26.8	319	25.5	1.3	21.1	-	32.4
Pectoral spine L.	91	29.8	1.5	26.0	-	33.8	322	28.6	1.4	25.0	-	32.1
Abdominal L.	91	21.7	1.0	19.2	-	24.4	319	23.1	1.0	20.0	-	25.5
Pelvic spine L.	91	19.3	1.0	17.1	-	22.5	318	20.8	1.0	16.4	-	24.2
Postanal L.	91	29.6	1.1	26.2	-	31.8	319	30.3	1.3	26.8	-	35.6
Caudal peduncle Dp.	91	7.0	0.4	5.7	-	8.3	323	8.2	0.6	5.9	-	9.6
Caudal peduncle W.	90	12.9	1.0	9.7	-	16.1	317	14.7	1.4	10.6	-	17.9
Adipose-fin spine L.	90	8.5	0.9	5.7	-	10.6	315	8.3	0.8	6.6	-	10.8
%HL												
Head Dp.	91	46.5	4.0	36.7	-	55.4	317	51.9	8.1	35.0	-	100.6
Snout L.	91	51.1	2.9	43.4	-	56.8	321	51.0	6.6	40.2	-	147.9
Orbit Diameter	91	13.7	1.7	10.2	-	20.7	321	17.4	2.1	12.1	-	32.8
Interorbital W.	91	34.1	2.4	25.7	-	39.5	323	34.6	6.7	28.0	-	139.7
Snout opercle D.	91	69.4	2.3	62.5	-	77.9	321	68.6	3.7	57.9	-	87.3
Head W.	91	78.9	3.9	66.7	-	88.8	321	80.6	6.2	67.6	-	145.0

Table 5: Selected morphometrics of *Isorineloricaria gomesi* and *I. phrixosoma*.

	Isorineloricaria gomesi	*Isorineloricaria phrixosoma*
Measurement (mm)	Holotype	Holotype
Standard Length (SL)	143.6	109.5
% SL		
Predorsal L.	38.3	38.1
Head L. (HL)	31.1	31.6
Cleithral W.	24.2	26.5
Dorsal spine L.		-
Folded dorsal-fin L.	35.5	35.4
Dorsal-fin base L.	20.9	20.8
Dorsal- adipose L.	25.6	24.3
Thorax L.	21.7	24.2
Pectoral spine L.	25.9	28.0
Abdominal L.	19.2	20.4
Pelvic spine L.	19.6	24.3
Postanal L.	35.3	39.9
Caudal peduncle Dp.	6.4	8.5
Caudal peduncle W.	14.7	15.0
Adipose-fin spine L.	6.1	7.7
Anal-fin L.	12.0	13.6
Anal-fin base L.	4.4	4.3
Adipose- upper caudal L.	18.7	22.1
Adipose- lower caudal L.	22.8	27.5
%HL		
Head Dp.	52.4	56.0
Snout L.	58.1	61.0
Orbit Diameter	17.6	17.5
Interorbital W.	40.3	40.5
Snout opercle D.	57.8	72.6
Head W.	78.5	82.7
Head eye L.	37.6	35.8
Eye nare L.	11.2	10.5
Internares W.	16.7	17.4
Snout nares L.	38.2	41.3
Snout pectoral L.	72.3	75.5
Pectoral orbit D.	27.4	27.7
Mouth W.	36.6	43.5
Mouth L.	38.9	45.3
Dentary L.	12.7	16.1