



The genera *Isorineloricaria* and *Aphanotorulus* (Siluriformes: Loricariidae) with description of a new species

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Abstract

We review the complex history of those species included in the *Hypostomus emarginatus* species complex and recognize them in *Isorineloricaria* and *Aphanotorulus*. *Isorineloricaria* consists of four valid species: *I. acuarius* n. sp., *I. spinosissima*, *I. tenuicauda*, and *I. villarsi*. *Aphanotorulus* consists of six valid species: *A. ammophilus*, *A. emarginatus*, *A. gomesi*, *A. horridus*, *A. phrixosoma*, and *A. unicolor*. *Plecostomus annae* and *Hypostoma squalinum* are placed in the synonymy of *A. emarginatus*; *Plecostomus biseriatus*, *P. scopularius*, and *P. virescens* are placed in the synonymy of *A. horridus*; *Plecostomus winzi* is placed in the synonymy of *I. tenuicauda*, and one new species, *I. acuarius* is described from the Apure River basin of Venezuela. *Aphanotoroulus* can be distinguished from *Isorineloricaria* by having caudal peduncles that do not become greatly lengthed with size and that are oval in cross section (vs. caudal peduncle proportions that get proportionately longer with size and that become round in cross-section), and by having small dark spots (less than half plate diameter) on a light tan background (vs. spots almost as large as lateral plates on a nearly white background).

Key words: Amazonas, Andean, Brazilian Shield, Guiana Shield, *Hypostomus*, *Squaliforma*, taxonomy

Introduction

With over 800 valid species, the family Loricariidae (suckermouth armored catfishes) is the largest catfish family in the world with members found in freshwater and brackish water habitats in South America (to northern Argentina), Panama, and Costa Rica (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), as four genera (Weber 2003), or as six (Isbrücker 2001). Three of Isbrücker's genera (*Aphanotorulus*, *Isorineloricaria*, *Squaliforma*) were recognized as the *H. emarginatus* species group by Armbruster (2004), but most subsequent studies have recognized each of the genera as valid. We have undertaken a review of the species of Armbruster's *H. emarginatus* group, and in light of recent molecular analyses, recognize the species in two genera, *Aphanotorulus* and *Isorineloricaria* as in Lujan *et al.* (2015).

Isorineloricaria was described by Isbrücker (1980) for *Plecostomus festae* Boulenger, 1898 and *P. spinosissimus* Steindachner 1880, two species considered synonymous by Eigenmann (1922), Weber (2003), and Armbruster (2004). Isbrücker defined the species based on the presence of a very long caudal peduncle that is round in cross section, and elongate odontodes on the bodies of breeding males and slightly longer odontodes even in females. Armbruster (2004) recognized the elongate odontodes as a synapomorphy for his *H. emarginatus* group.

Aphanotorulus was described by Isbrücker and Nijssen (1993) for a species they described as *A. frankei*, from the Amazon River basin, and which has numerous small buccal papillae. Armbruster and Page (1996) and Armbruster (1998) further revised *Aphanotrulus* describing a species from the Orinoco (*A. ammophilus*) and recognizing that the Amazonian species was described six times with the senior synonym being *A. unicolor* Steindachner 1908.

Squaliforma was described by Isbrücker and Michels (Isbrücker 2001), and it includes the remaining species of Armbruster's *Hypostomus emarginatus* group. No diagnosis was provided for the genus. It was recognized as a synonym of *Hypostomus* by Armbruster (2004), but valid by Weber (2003) and Ferraris (2007).

Taxonomic history of species. *Hypostomus emarginatus* was the first described species within the *H. emarginatus* species group, 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 in the generic identification of the species and subsequent authors used *Plecostomus* Gronovius 1754.

Before the invalidation of Gronovius' (1754) works, 17 species currently in *Isorineloricaria* and *Aphanotorulus* 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 (1874), and several syntypes were designated; yet the exact locality is unclear. It was originally noted as Caracas (Venezuela), followed by a question mark. We disagree with 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. Steindachner (1878, 1880, 1881, 1908) described *P. tenuicauda*, *P. spinosissimus*, *P. annae*, and *P. unicolor*, respectively. Fowler (1913, 1940a, 1940b, 1941, 1942, 1945) described *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 remaining 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 (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 hypothesized 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* species group in *Hypostomus* made this genus polyphyletic, but did not mention elevating the group to a separate genus.

Armbruster (2004, 2008) provided the most complete morphological phylogeny for loricariids to date, but focused on the Hypostominae. Armbruster's analysis confirmed Armbruster and Page's (1996) findings, and he diagnosed 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*.

Lujan *et al.* (2015) provide the largest phylogenetic treatment of loricariids to date (181 species in 91 genera). *Hypostomus* is found to be polyphyletic, with *Isorineloricaria* and *Aphanotorulus* more closely related to *Panaqolus*, *Peckoltia*, *Hypancistrus*, and *Scobinancistrus* (among others) than to *Hypostomus*. Lujan *et al.* recognize species of *Squaliforma* in *Aphanotorulus*.

In this paper, we recognize the trans-Andean species of *Squaliforma* in *Isorineloricaria*, describe one cis-Andean species of *Isorineloricaria*, recognize the remainder of *Squaliforma* in *Aphanotorulus*, and redescribe all species. *Plecostomus annae* and *Hypostoma squalinum* are placed in the synonymy of *A. emarginatus*, *Plecostomus biseriatus*, *P. scopularius*, and *P. virescens* are placed in the synonymy of *A. horridus*, and *Plecostomus winzi* is placed in the synonymy of *I. tenuicauda*.

Material 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 Sabaj Pérez (2014).

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.

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 remaining principal components were plotted against standard length to show that they represent relative size differences (shape). Specimens of *Aphanotorulus ammophilus* and *A. 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.

Results and discussion

Classically, *Isorineloricaria* was diagnosed based mainly by the elongation of the caudle peduncle (Isbrücker 1980); *Aphanotorulus* was diagnosed based on the presence of multiple buccal papillae (Armbruster 1998); and *Squaliforma* was not formally diagnosed using morphological characteristics (Isbrücker and Michels; in Isbrücker *et al.* 2001). Armbruster (2004; 2008) found the genera to form a monophyletic group, and the relationship between *Aphanotorulus* and *Squaliforma* was particularly strong (see also Armbruster and Page, 1998). The molecular phylogeny of Lujan *et al.* (2015) suggested separation of the taxa into two genera (*Aphanotorulus* and

Isorineloricaria), and that taxonomy is followed here. Given the complexity of the taxonomic changes, each species that has been assigned to *Aphanotorulus*, *Isorineloricaria*, and *Squaliforma* are summarized in Table 1 with their taxonomic position noted in two previous and disparate studies (Isbrücker 2001 and Armbruster 2004) and are reviewed below.

TABLE 1. The species that have been assigned to *Aphanotoulus*, *Isorineloricaria*, and *Squaliforma* and how they have been treated taxonomically particularly in Isbrücker (2001), Armbruster (2004), and this study.

Species	Isbrücker, 2001	Armbruster, 2004	Now
<i>Isorineloricaria acuarius</i> n. sp.			<i>I. acuarius</i>
<i>Aphanotorulus ammophilus</i> Armbruster & Page, 1996	<i>A. ammophilus</i>	<i>H. ammophilus</i>	<i>A. ammophilus</i>
<i>Plecostomus annae</i> Steindachner, 1881	<i>S. annae</i>	<i>H. annae</i>	<i>A. emarginatus</i>
<i>Plecostomus biseriatus</i> Cope, 1872	<i>S. biseriata</i>	<i>H. biseriatus</i>	<i>A. horridus</i>
<i>Plecostomus chaparae</i> Fowler, 1940	<i>A. popoi</i>	<i>H. unicolor</i>	<i>A. unicolor</i>
<i>Hypostomus emarginatus</i> Valenciennes, 1840	<i>S. emarginata</i>	<i>H. emarginatus</i>	<i>A. emarginatus</i>
<i>Plecostomus festae</i> Boulenger, 1898	<i>I. festae</i>	<i>H. festae</i>	<i>I. spinosissima</i>
<i>Aphanotorulus frankei</i> Isbrücker & Nijssen, 1983	<i>A. frankei</i>	<i>H. unicolor</i>	<i>A. unicolor</i>
<i>Plecostomus gomesi</i> Fowler, 1942	<i>S. gomesi</i>	<i>H. gomesi</i>	<i>A. gomesi</i>
<i>Hypostomus horridus</i> Kner, 1854	<i>S. horrida</i>	<i>H. horridus</i>	<i>A. horridus</i>
<i>Plecostomus iheringi</i> Fowler, 1941	<i>S. gomesi</i>	<i>H. gomesi</i>	<i>A. gomesi</i>
<i>Plecostomus madeirae</i> Fowler, 1913	<i>A. madeirae</i>	<i>H. unicolor</i>	<i>A. unicolor</i>
<i>Plecostomus micropunctatus</i> La Monte, 1935	<i>A. micropunctatus</i>	<i>H. unicolor</i>	<i>A. unicolor</i>
<i>Plecostomus phrixosoma</i> Fowler, 1940	<i>S. phrixosoma</i>	<i>H. phrixosoma</i>	<i>A. phrixosoma</i>
<i>Plecostomus popoi</i> Pearson, 1924	<i>A. popoi</i>	<i>H. unicolor</i>	<i>A. unicolor</i>
<i>Plecostomus scopularius</i> Cope, 1871	<i>S. scopularia</i>	<i>H. scopularius</i>	<i>A. horridus</i>
<i>Plecostomus spinosissimus</i> Steindachner, 1880	<i>I. spinosissima</i>	<i>H. spinosissimus</i>	<i>I. spinosissima</i>
<i>Hypostoma squalinum</i> Jardine, 1841	<i>S. squalina</i>	<i>H. squalinus</i>	<i>A. emarginatus</i>
<i>Plecostomus tenuicauda</i> Steindachner, 1878	<i>S. tenuicauda</i>	<i>H. tenuicauda</i>	<i>I. tenuicauda</i>
<i>Hypostomus tenuis</i> Boeseman 1968	<i>S. tenuis</i>	<i>H. tenuis</i>	<i>H. tenuis</i>
<i>Plecostomus unicolor</i> Steindachner, 1908	<i>A. unicolor</i>	<i>H. unicolor</i>	<i>A. unicolor</i>
<i>Hypostomus verres</i> Valenciennes, 1840	<i>S. verres</i>	<i>H. verres</i>	<i>H. watwata</i>
<i>Plecostomus villarsi</i> Lütken, 1874a	<i>S. villarsi</i>	<i>H. villarsi</i>	<i>I. villarsi</i>
<i>Plecostomus virescens</i> Cope, 1874	<i>S. virescens</i>	<i>H. virescens</i>	<i>A. horridus</i>
<i>Hypostomus watwata</i> Hancock, 1828	<i>S. watwata</i>	<i>H. watwata</i>	<i>H. watwata</i>
<i>Plecostomus winzi</i> Fowler, 1945	<i>H. winzi</i>	<i>H. winzi</i>	<i>I. tenuicauda</i>

Several problems exist with the recognition of these three genera. The first is that we have observed, at least in *Plecostomus villarsi* Lütken (considered in *Squaliforma*), a similar elongation of the caudal peduncle and in *P. tenuicauda* Steindachner (considered *Squaliforma*) and *P. villarsi* the considerable lengthening of the body with ontogeny considered diagnostic for *Isorineloricaria* (Isbrücker 1980). These characteristics are also present in the species described herein as *I. acuarius* **n. sp.**, and we feel that *Isorineloricaria* should be expanded to include all Trans-Andean members of Armbruster's *H. emarginatus* group and the new species from the Orinoco.

With the remainder of the species, *Plecostomus phrixosoma* Fowler provides another problem. The species is known only from the type, and it has similarities both to species of *Squaliforma* and species of *Aphanotorulus*. It has hypertrophied odontodes from behind the head to and including the caudal fin as is seen in *Isorineloricaria* and *Squaliforma* (vs. hypertrophied odontodes beginning below the dorsal fin in *Aphanotorulus*), it has bicuspid teeth (vs. unicuspid in nuptial *Aphanotorulus*), but it is the smallest member of the *H. emarginatus* group to possess hypertrophied odontodes other than the two species of *Aphanotorulus*. Armbruster and Page (1996) suggested that

P. phrixosoma was the sister to *Aphanotorulus*, but this has not been examined phylogenetically because only the type is known. In all likelihood, the remainder of species of *Squaliforma* grade into *Aphanotorulus*. Given the molecular phylogeny of Lujan *et al.* (2015), we recognize all previously described cis-Andean species of *Squaliforma* in *Aphanotorulus*.

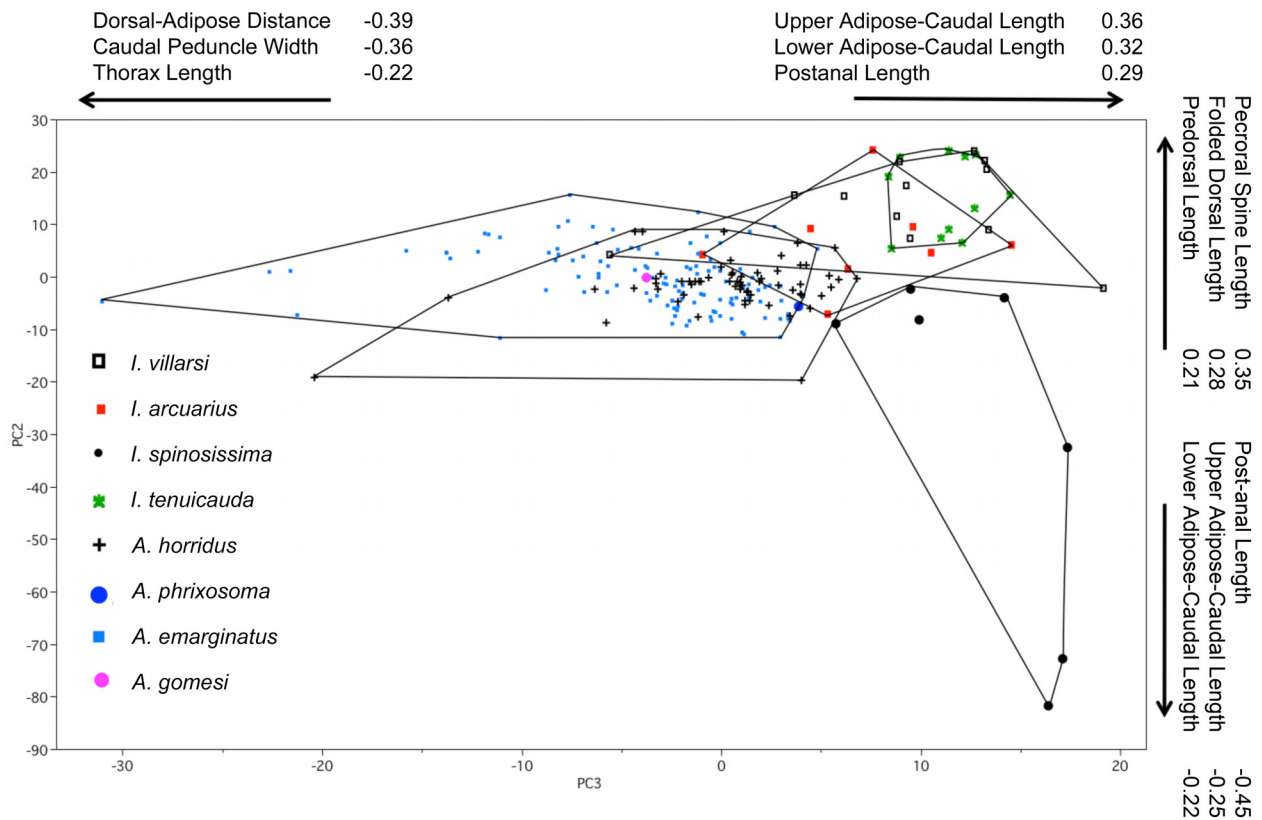


FIGURE 1. Results of the PCA of the all species of *Aphanotorulus* and *Isorineloricaria* except *A. ammophilus* and *A. unicolor*.

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 (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.

Morphometrics. The PCA (Fig. 1) 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 affected by measurements associated with their long, narrow caudal peduncles. The remainder of *Isorineloricaria* occupy high values of PC3 while *Aphanotorulus* occupy low values, although the two genera overlap some. The rest of the species form two overlapping groups separating largely along PC3. Within each group, there was a large amount of overlap. *Isorineloricaria arcuarius* has the smallest range on the graph, and was nested within the distribution of *I. villarsi*, with which we assume it to share a sister relationship.

There were few discrete morphometric differences among species. *Aphanotorulus emarginatus* and *A. horridus* are very similar morphologically, but almost do not overlap in Snout-Nares Width vs. Interorbital Width (Fig. 2). *Isorineloricaria spinosissima* differs from all other species in *Isorineloricaria* or *Aphanotorulus* by Caudal Peduncle Depth vs. Head Length (Fig. 3).

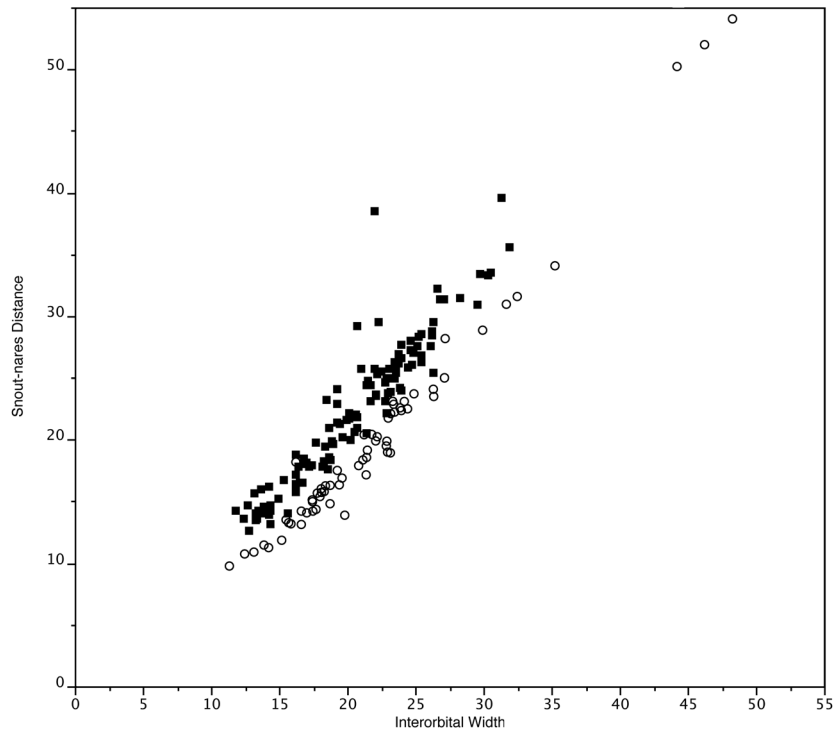


FIGURE 2. Bivariate plot of Snout-nares Width by Interorbital Width. Red crosses - *Aphanotorulus horridus*, blue squares - *A. emarginatus*.

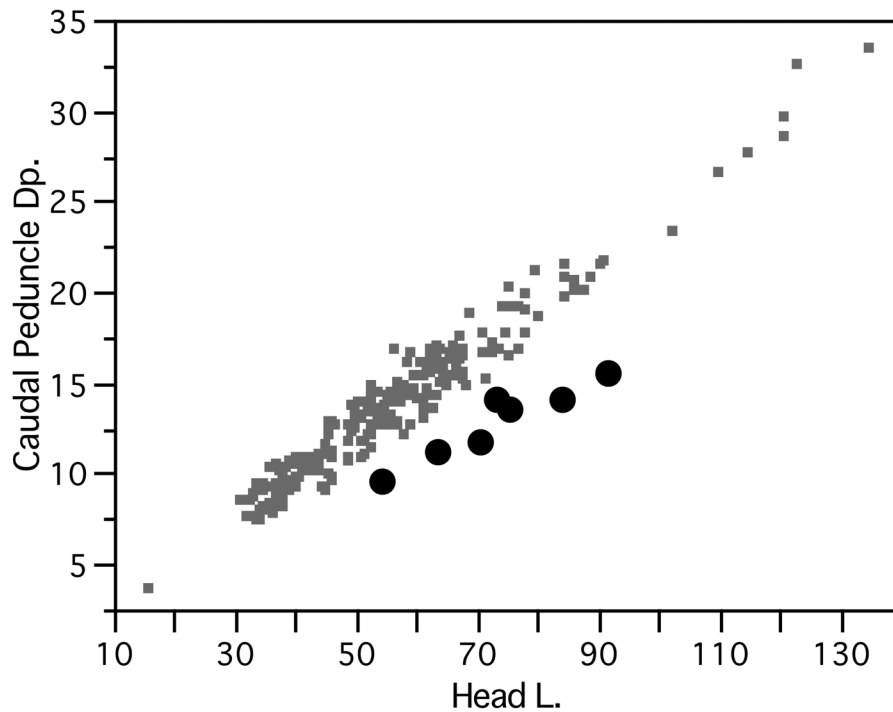


FIGURE 3. Bivariate plot of Caudal Peduncle Depth By Head Length. Black circles represent- *I. spinosissima*, red squares - all other *Aphanotorulus* and *Isorineloricaria* (except *A. ammophilus* and *A. unicolor*).

Biogeography. A discussion of biogeography within this group is limited without an inclusive phylogenetic hypothesis; however, there are patterns that occur amongst the distributions of the members of *Aphanorulus* and *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 likely led to a vicariant event that isolated the Pacific Slope drainages from the rest of the western basins on the continent, and the ancestors of *I. spinosissima*. The proto-Amazon has been suggested to have flowed west into the Pacific Ocean up until ~15mya (Hoorn *et al.* 1995) or 9.0mya (Campbell *et al.* 2006). The area where the Amazon entered the Pacific is known as the Marañon Portal or Guayaquil Gap (Lundberg 1998). The isolation of *Isorineloricaria* in mainly trans-Andean streams may have coincided with the closure of the Marañon Portal, and *I. spinosissima* is found in the Guayas River, which enters into the Pacific at the Gulf of Guyauquil. Although there is geological evidence for this portal (Hoorn *et al.* 1995; Lundberg 1998; Campbell *et al.* 2006) and there is good information on its presence with botanical data (Taylor 1991; Antonelli *et al.* 2009), there has been no evidence of the influence of such a connection on studies of freshwater organisms (Nuttall 1990; Lovejoy 1996).

During the middle to late Miocene, the vicariant events that divided the Magdalena and Maracaibo basins from the Amazonas and Orinoco rivers (Hoorn *et al.* 1995) were likely 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 (Hoorn *et al.* 1995; 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 *I. acuarius* in the Apure. This pattern of isolation would suggest the following relationships: (*I. spinosissima* + (*I. tenuicauda* + (*I. villarsi* + *I. acuarius*))).

Aphanotorulus may have had an origin in the Guiana and/or Brazilian Shields. *Aphanotorulus 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 *Aphanotorulus* prior to the uplift of the Andes. The rise of the Andes provided a broad piedmont where the smaller species (*A. ammophilus*, *A. phrixosoma*, and *A. unicolor*) likely evolved. It should be noted that the approximate dividing point of the ranges of *A. horridus* and *A. emarginatus* is the Purus arch, though no conclusions of its importance can be made here, and the influence of such arches as proposed by Lundberg (1998) may not be consequential (Campbell *et al.* 2006).

The distribution of *Aphanotorulus ammophilus* and *A. unicolor* are unique and represent more recent vicariant events (Armbruster and Page 1996). These sister taxa have a distribution that is suggestive of the drainage patterns of the Late Miocene (10.8–8mya; Hoorn *et al.* 1995) 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 ancestor to *A. ammophilus* and *A. unicolor* probably had a broad distribution in the cis-Andean piedmont, and was separated into two populations with the emergence of the modern Amazon and Orinoco Rivers 8–2.5mys (Hoorn *et al.* 1995; Campbell *et al.* 2006).

Taxonomy

Aphanotorulus Isbrücker and Nijssen 1983

Aphanotorulus Isbrücker & Nijssen, 1983: 105. Type species: *Aphanotorulus frankei* Isbrücker & Nijssen, 1983. Type by original designation.

Squaliforma Isbrücker & Michels, in Isbrücker *et al.*, 2001: 22. Type species: *Hypostomus horridus* Kner, 1854. Type by original designation.

Diagnosis. *Aphanotorulus* can be separated from *Hypostomus* by having hypertrophied odontodes on the heads and lateral plates of nuptial males (vs. hypertrophied odontodes absent) and from all sympatric *Hypostomus* by having a light tan background (vs. dark tan to brown), from *Isorineloricaria* by having caudal peduncles that do not become greatly lengthed with size and that are oval in cross section (vs. caudal peduncle proportions that get proportionately longer with size and that become round in cross-section), and by having small dark spots (less than half plate diameter) on a light tan background (vs. spots almost as large as lateral plates on a nearly white background). *Aphanotorulus* can be further separated from the taxa recognized in Armbruster's Corymbophanini by

having an adipose fin (vs. adipose fin replaced by postdorsal ridge of 13–17 azygous plates); from the Corymbophanini and Rhinelepineae by having the iris operculum (vs. iris operculum absent); from the Rhinelepineae 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 Pterygoplichthyini 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 supra-preopercle and opercle, rarely two (vs. two to three); from the Ancistrini (except *Spectracanthicus murinus* and some *Pseudancistrus*) and the Pterygoplichthyini 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 having three plates between the head and dorsal fin (including the nuchal plate, vs. four or more).

Key to the species of *Aphanotorulus*

- 1a. Multiple buccal papillae. Teeth unicuspid in nuptial males 2
- 1b. Single, large buccal papilla. Teeth bicuspid in all individuals 3
- 2a. Ridges formed by the compound pterotics on the head present and depressed pectoral fin that reaches well past insertion point of last pelvic-fin ray. In specimens larger than 75mm SL, orbit diameter to snout length ratio 18.5–27.9%, caudal depth to pectoral spine length ratio 19.8–25.5%, and pectoral spine length to thorax length ratio 117.0–136.3% *A. ammophilus*
- 2b. Ridges formed by the compound pterotics on the head absent and depressed pectoral fin that extends maximally to insertion point of last pelvic-fin ray. In specimens larger than 75mm SL, orbit diameter to snout length ratio 28.0–42.2%, caudal depth to pectoral spine length ratio 25.6–35.1%, and pectoral spine length to thorax length ratio 99.3–116.9% *A. unicolor*
- 3a. Hypertrophied odontodes covering all lateral and ventral surfaces except the head in breeding males. *A. phrixosoma*
- 3b. Hypertrophied odontodes present on covering lateral and dorsal surfaces in breeding males, but very reduced in size. Elongate hypertrophied odontodes present mostly on pectoral, pelvic, and caudal fins spines. 4
- 4a. Found in the Jaguaribe River, Ceará state, Brazil *A. gomesi*
- 4b. Found in other waters of South America 5
- 5a. Circular spots on the dorsal and paired fins remain unfused across the length of the fin. Snout-nares distance to interorbital width ratio generally 98–175.4% (separates 92% of specimens examined) *A. emarginatus*
- 5b. Spots fuse into bands across the dorsal and paired fins in adults. Snout-nares distance to interorbital width ratio generally 70.5–97.8% (separates 92% of specimens examined) *A. horridus*

Aphanotorulus ammophilus (Armbruster and Page 1996)

(Fig. 4)

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 – 9°31'51"N, 68°39'39"W. Holotype: INHS 32035, 86.0 mm SL.

Material examined. See Armbruster and Page (1996) and Armbruster (1998).

Diagnosis. *Aphanotorulus ammophilus* differs from all congeners, except *A. unicolor*, by its numerous buccal papillae (Fig. 5). *Aphanotorulus ammophilus* differs from *A. unicolor* by the presence of ridges on the compound pterotics on the head (vs. ridges absent in *A. unicolor*); in having a pectoral fin that, when depressed, reaches well past insertion of last pelvic-fin ray (vs. pectoral fin extending at most to insertion of last pelvic-fin ray in *A. unicolor*). See diagnosis of *A. unicolor* below for further diagnostic features for specimens greater than 75mm SL.

Description. Morphometric data given in Table 2. 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.

TABLE 2. Selected morphometrics of *Aphanotorulus ammophilus* and *A. unicolor*.

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

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 anal fin. Adipose-fin membrane extending to end of fourth adipose base plate (two plates separate 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).



FIGURE 4. Dorsal, lateral, and ventral views of *Aphanotorulus ammophilus*, AUM 22659. Scale = 1 cm.

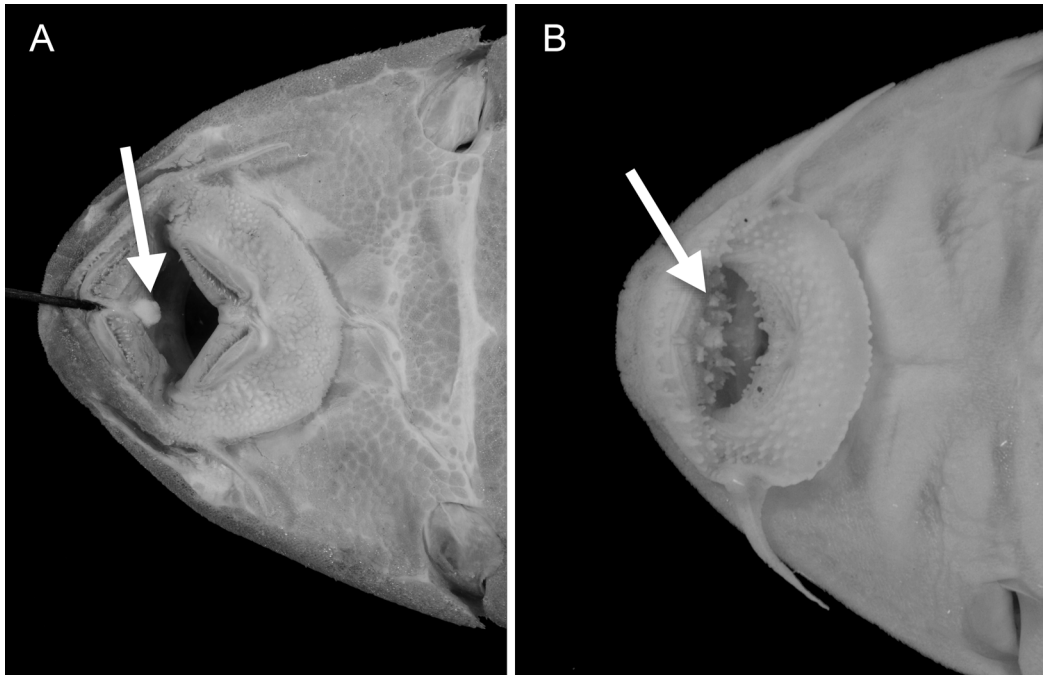


FIGURE 5. A. Ventral view of mouth of *Aphanotorulus gomesi*, ANSP 69409, illustrating the large central buccal papilla characteristic of most members of *Aphanotorulus* and *Isorineloricaria*. Photograph by M. Sabaj-Pérez and K. Luckenbill. B. Ventral view of mouth of *A. ammophilus*, AUM 22659, illustrating multiple buccal papillae found in *A. ammophilus* and *A. unicolor*.

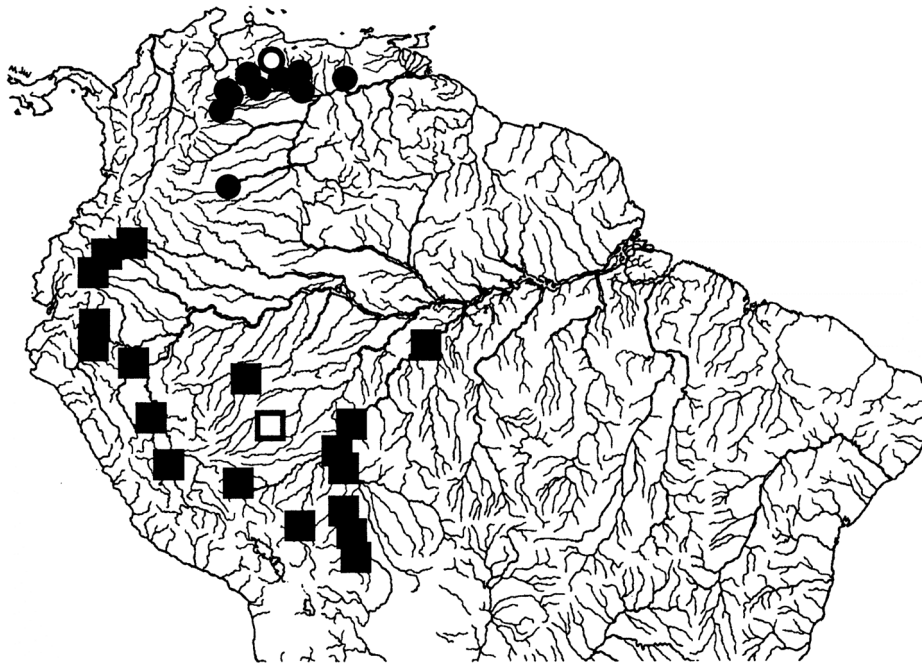


FIGURE 6. Distribution of *Aphanotorulus ammophilus* and *A. unicolor*. Circles represent *A. ammophilus*, squares represent *A. unicolor*. Open shapes represent type localities. From Armbruster (1998).

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 almost white background. Ventral surface almost 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 others. Spots on caudal fin align to 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.

Distribution. Río Orinoco drainage in Venezuela, mainly from the Río Apure system (Fig. 6).

Aphanotorulus emarginatus (Valenciennes 1840)

(Fig. 7)

Hypostomus emarginatus Valenciennes, in Cuvier & Valenciennes, 1840: 500 (369 in Strasbourg deluxe edition). Type locality: Probablement originaire du Brésil. Holotype: MNHN a-9447 (dry). *Plecostomus annae* Steindachner, 1881: 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 Rios Branco, Negro, and Essequibo. No types known.

Material examined. Brazil: ANSP 187270 (3) (ex MZUSP 88601), Rio Culuene (Xingu basin), Canarana/Gaucha do Norte, Gaucha do Norte, Mato Grosso, 13°30'53"S 53°5'34"W, O.Oyakawa, J.L. Birindelli, C. Moreira et al, 19 October 2004; MCZ 7805 (1) Pará [*Belem and environs*], Brazil, col. by L. Agassiz and D. Bourget; MCZ 7807 (2), Ilha de Marajo, Furo Tajapurú at Tajapurú, Pará, Brazil, 20–21 August 1865, col. by L. Agassiz; MCZ 7824 (1), Santarem, Pará, Brazil, August 1865, col. by D. Bourget; MCZ 7840 (2), Rio Ica; Rio Putomajo [Rio Ica (tributary of Rio Solimoes) near the Brazilian-Colombian border], Amazonas, Brazil, September 1865, col. by W. James and S. Talisman; MCZ 7860 (1), Obidos; Obydos [Rio Amazonas at Obidos], Pará, Brazil, December 1865, col. by W. James and W. Hunnewell; MCZ 7992 (1), GURUPA [Rio Amazonas delta at Gurupa], Pará, Brazil, 22 August 1865, col. by L. Agassiz *et al.*; MNRJ 12710 (1), rio Passa Três, afluyente esquerdo rio Maranhão, alto Tocantins, Uruaçu, Goiás, 14°30'S, 49°9'W, G.W. Nunan, D.F. Moraes Jr., 26 October 1996; MNRJ 12781 (1), Rio Bagagem, à montante da foz do córrego Barriguda, afluyente direito Rio Maranhão, alto Tocantins, Niquelândia, Goiás, 14°5'S 48°14'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, 13°34'5"S 48°6'4"W, col. by D.F. Moraes Jr., 13 January 1988; MNRJ 12944 (1), Afluyente do córrego Lageado (afluyente margem esquerda Rio Tocantins) na estrada para Porto Rubião, Minaçu, Goiás, 13°38'85"S 48°19'12"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. Halboth, 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), Riacho (drenagem do Juruena) na estrada MT-208, 1 km a oeste da balsa Ariel, Fazenda São Nicolau, município de Cotriguaçu. 9°52'42"S 58°14'40"W, col. by P.A. Buckup, L.F.S. Ingenito, I.L. Assumpção, F.B. Freitas, 6 May 2006; MNRJ 31177 thru 31196, Rio Tocantins, a jusante da UHE Serra da Mesa, poções formados durante o enchimento do reservatório, Município de Minaçu/Colinas do Sul, 13°49'S, 47°17'W, col. by D.F. Moraes, D.A. Halboth, O.T. Oyakawa, *et al.*, 28 October–4 November 1996; MZUSP 24064 (1), Rio Tocantins, entre Mocajuba e Baião, Baião, Pará, 2°40'S 49°42'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, 3°46'S 49°41'W, col. by Expedição Permanente à Amazônia, 11 September 1970; MZUSP 27637 (1), Rio Negro, Pedra do Gavião, Moura, Amazonas, 1°28'S 61°38'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, 3°25'N 60°20'W, col. by M. Goulding, 13 January 1984; MZUSP 40478 (1), Rio Paranã (cachoeira), fazenda Olho d'Água, Flores de Goiás, Goiás, 14°26'S 47°3'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, 13°40'S 50°48'W; MZUSP 52342 (1), Rio Araguaia, Araguaiana, Rio Tocantins, Mato Grosso, 15°43'S 51°51'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) Rio 7 de Setembro, afl. rio Xingu, ca. 20 km W Canarana pela estr. MT-020 (Canaran-Garapu), Brasil, Mato Grosso, Canarana, 13°30'19.0"S, 52°24'57.0"W, col. by Moreira, Landim, Nolasco and Datovo, 17 October 2004; MZUSP 87081 (3), Rio Batovi (Tamitatoala) afl. Xingu Salto da Alegria, faz. Dois Netos (prop. André Parente), Mato Grosso, Gaúcha do Norte, 13°14'46.0"S, 54°1'30.0"W, col. by Equipe AXE, 21 October 2004; MZUSP 87082 (4), Rio Batovi (Tamitatoala)

afl. Xingu Salto da Alegria, faz. Dois Netos (prop. André Parente), Mato Grosso, Gaúcha do Norte, 13°14'46.0"S, 54°1'30.0"W, col. by Equipe AXE, 21 October 2004; MZUSP 89734 (1), Rio Culuene, trecho entre cachoeira até ribeirão Corgão, Mato Grosso, Paranatinga, 13°49'0.0"S, 53°15'0.0"W, col. by A. Akama & J.L. Birindelli, 15 January 2006; MZUSP 92720 (1), Rio Tapajós, na corredeira do Pajaú e arredores, Pará, Pimental, 4°35'4.0"S, 56°15'32.0"W, col. by L.M. Sousa and J.L. Birindelli, 11 November 2006; MZUSP 94085 (1), Rio Culuene, fazenda do Sr. Zezé (c. 2 km acima da ponte), Mato Grosso, Gaúcha do Norte, 13°30'53.0"S, 53°5'40.0"W, col. by F.C.T. Lima, F.A. Machado, C.A. Figueiredo and J.L. Birindelli, 21–26 May 2007; MZUSP 94415 (1), Lago da Miriam, margem direita do rio Culuene (23–24.v.2007), Mato Grosso, Canarana, 13° 25' 48.0" S, 53° 2' 24.0" W, col. by F.C.T. Lima, F.A. Machado, C.A. Figueiredo and J.L. Birindelli, 23 May 2007; MZUSP 95627 (5), Rio Teles Pires próximo da balsa da rodovia MT-416, Mato Grosso, Paranaíta, 9° 27' 7.0" S, 56° 30' 46.0" W, col. by L.M. Sousa and A.L. Netto-Ferreira, 2007; MZUSP 96132 (1), corredeiras no rio Teles Pires, abaixo das "Sete Quedas", Pará, Jacareacanga, 9°19'34.0"S, 56°46'52.0"W, col. by L.M. Sousa and A.L. Netto-Ferreira, 2007; MZUSP 96598 (1), Rio Peixoto de Azevedo, afl. Rio Teles Pires, próximo a cidade de Peixoto de Azevedo, Mato Grosso, Peixoto de Azevedo, 10°13'14.0"S, 54°58'2.0"W, col. by J.L. Birindelli, L.M. Sousa, A.L. Netto-Ferreira, M. Sabaj-Perez, N.K. Lujan, 16 October 2007; MZUSP 97217 (2), Rio Curuá, bacia do Iriri, na vila de Castelo dos Sonhos, Pará, Altamira, 8° 19' 7.0" S, 55° 5' 23.0" W, col. by J.L. Birindelli, L.M. Sousa, A.L. Netto-Ferreira, M. Sabaj-Perez, N.K. Lujan, 22 October 2007; 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), Rio Manacias, 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. Armbruster, M.H. Sabaj, D.C. Werneke, C.L. Allison, M.R. Thomas, C.J. Chin, D. Arjoon, S. Mario, S.M. James, 27 October 2002; AUM 35535 (2), Rupununi River 4.6 km NW Massara, col. by J.W. Armbruster, M.H. Sabaj, D.C. Werneke, C.L. Allison, M.R. Thomas, C.J. Chin, D. Arjoon, S.M. James, S. Mario, 26 October 2002; AUM 35551 (3), Rupununi River at Kwatamang, 4 km SE Annai, col. by J.W. Armbruster, M.H. Sabaj, D.C. Werneke, C.L. Allison, M.R. Thomas, C.J. Chin, D. Arjoon, S.M. James, 25 October 2002; AUM 35666 (2), Rupununi River at Karanambo, col. by J.W. Armbruster, M.H. Sabaj, D.C. Werneke, C.L. Allison, M.R. Thomas, C.J. Chin, D. Arjoon; AUM 36611 (1), Rio Macaruma, 134 km SE. of Ciudad Guiana, 5 km SE. of Guasipati, at old bridge just W. of the main road, Bolivar, col. by J.W. Armbruster, D.C. Werneke, T.P. Pera, N.K. Lujan, and O. Leon, 11 June 2003; AUM 38885 (1), Takutu River 3.77 km SSW Lethem, Reg. 9, col. by J.W. Armbruster, M.H. Sabaj, M. Hardman, D. Arjoon, N.K. Lujan, L.S. de Souza, 1 November 2003; AUM 44344 (2), Essequibo River, shoreline and sandbeach downstream of Kurukapari Falls and upstream from Iwokrama, Region 8, col. by L.S. deSouza, N.K. Lujan, D.C. Taphorn, J.A. Hartsell, E. Liverpool, and S. Lord, 23 November 2005; AUM 45033 (1), Pond at Yukupari, Region 9, col. by N.K. Lujan, D.C. Taphorn, and E. Liverpool, 29 November 2005. Venezuela: ANSP 182988 (3), Rio Siapa (Casiquiare Dr.), raudale Gallineta, 142 km E of San Carlos de Rio Negro, M.H. Sabaj, D.C. Werneke, N.K. Lujan, M. Arce, 17 March 2005; AUM 39309 (1), Rio Manapiare, 14.5 km NW of San Juan de Manapiare, Amazonas, col. by N.K. Lujan, M.H. Sabaj, L.S. deSouza, and D.C. Werneke, 12 April 2004; AUM 39507 (1), Rio Ventuari, at Raudales Tencua, 56 km ESE of San Juan de Manapiare, Amazonas, col. by D.C. Werneke, N.K. Lujan, O. Leon, A. Luna, and R. Pajua; AUM 39836 (1), Rio Manapiare, 10 km NW of San Juan de Manapiare, Amazonas, 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), Rio 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), Rio 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), Rio Orinoco, 33.9 km W of La Esmeralda, Punto Piara, 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), Rio Casiquiare, bedrock in stream, 73 km NE of San Carlos de Rio 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), Rio 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), Rio Siapa, Raudales Gallineta, 142 km E of San Carlos de Rio 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), Rio 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), Rio Casiquiare, 153 km NE of San Carlos de Rio 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), Rio 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), Rio Orinoco, near Puerto Ayacucho on a beach called Playa Bagre, Amazonas, col. by N.K. Lujan, M. Arce, and T.E. Wesley, 13 March 2005; AUM 42994 (2), Rio 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), Rio 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), Rio Mavaca, Amazonas, Venezuela, 1991; INHS 34779 (1), Rio Masparro, Barinas, Venezuela, 1995; MCNG 20045 (1) Rio Capanaparo 200m.del Paso de la MAcanilla, en una playa, Dto. Pedro Camejo, 7°04'58"N 67°71'11"W, 5 April 1989; MCNG 21575 (1), Río Caura, río arriba de caño la Prisión, Bolivar, Dto. Sucre, 7°00'00"N 64°66'67"W, col. by D.C.Taphorn, E. Suttón, E. Sanoja, A. Fernandez, 2 February 1989; MCNG 23800 (1), Rio Matacuni, al frente del N°4, Amazonas, Atabapo, col. by Basil Stergios, 25 January 1990; MCNG 28843 (1), Caño entrando a una laguna del Río Mavaca, Amazonas, Dpto. Río Negro, col. by L. Nico, G. Aragua, 29 January 1991; MCNG 30360 (1), Rio Orinoco al frente de Macurucu, Amazonas, col. by A.Barbarino, I.Lopez, R.Berrios, 5 August 1994; 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.

Diagnosis. *Aphanotorulus emarginatus* differs from *A. ammophilus* and *A. unicolor* by the presence of a single, large buccal papilla (vs. multiple buccal papillae); from *A. horridus* 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); and from *A. phrixosoma* by having fewer elongate hypertrophied odontodes covering the dorsal and ventral surfaces of body except the head (vs. many hypertrophied odontodes present—see *A. phrixosoma* description); and from *A. gomesi* only by distribution. *Aphanotorulus emarginatus* further differs from *Isorineloricaria spinosissima*, *I. tenuicauda*, and *I. villarsi* by having flat compound pterotics (vs. rounded ridge present in *I. spinosissima* and *I. tenuicauda* and a sharp ridge present in *I. villarsi*); from *I. villarsi* by lack of sharp ridge on compound pterotics (vs. sharp ridge present); and from *I. acuarius* by having a smaller orbit diameter to interorbital width ratio (32.4–40.5% vs. 40.6–63.7%), which separates 96% of individuals, and by having smaller, more circular spots on the head (vs. larger, oval spots in *I. acuarius*).

Description. Morphometrics given in Table 3. Head moderately compressed. Supraoccipital crest not elevated, 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).

TABLE 3. Selected morphometrics of *Aphanotorulus emarginatus* and *A. horridus*.: Dorsal-fin spine lengths are not included for either species because too many specimens had broken spines, and it was too difficult to determine accurate lengths.

Measurement	<i>Aphanotorulus emarginatus</i>				<i>Aphanotorulus horridus</i>			
	N	Average	SD	Range	N	Average	SD	Range
Standard Length (SL, mm)	153			46.5–357.0	73			44.9–513.0
% SL								
Predorsal Length	153	36.5	2.3	29.8–41.9	73	36.8	2.2	29.6–41.2
Head Length (HL)	153	29.8	2.5	23.3–36.2	73	30.2	2.3	23.5–38.8
Cleithral Width	153	23.8	1.5	20.0–27.2	72	24.8	1.8	19.2–27.6
Dorsal spine Length				–				–
Folded dorsal-fin Length	153	36.0	1.7	30.0–41.5	72	36.5	1.2	31.1–40.9
Dorsal-fin base Length	153	23.5	1.0	20.1–28.3	73	23.6	1.2	19.6–26.0
Dorsal-adipose Length	153	24.6	2.0	19.6–31.4	73	24.2	1.8	20.3–28.5
Thorax Length	153	23.6	1.4	20.0–27.5	73	24.2	1.6	19.2–28.7
Pectoral spine Length	153	25.4	2.1	18.8–31.4	72	25.9	2.3	18.1–30.3
Abdominal Length	153	20.3	1.1	16.5–24.8	73	20.2	1.2	18.0–24.8
Pelvic spine Length	153	20.1	1.8	14.1–25.6	73	20.8	2.4	14.7–26.0
Postanal Length	153	39.9	2.8	32.9–45.9	73	39.8	4.1	20.6–46.8
Caudal peduncle Depth	153	7.2	0.6	5.7–8.9	73	7.8	0.9	5.6–9.1
Caudal peduncle Width	153	16.7	1.3	13.4–21.0	73	16.7	1.5	10.0–19.2
Adipose-fin spine Length	151	6.7	1.0	4.2–9.8	72	6.8	1.0	4.6–11.0
Anal-fin Length	153	12.0	1.6	6.8–17.5	72	13.2	1.7	10.4–17.9
Anal-fin base Length	152	4.0	0.5	2.3–5.3	72	4.1	0.6	1.9–5.8
Adipose-upper caudal Length	152	20.4	1.2	17.0–23.5	73	21.2	1.6	16.6–24.7
Adipose-lower caudal Length	153	24.8	1.3	20.4–28.2	72	25.7	1.3	22.7–28.9
%HL								
Head Depth	153	57.3	3.4	48.7–73.5	73	59.0	3.5	50.5–66.0
Snout Length	153	60.4	2.4	55.7–73.5	73	59.1	3.8	42.0–71.3
Orbit Diameter	153	19.4	3.0	14.4–36.5	73	17.9	2.4	11.7–24.2
Interorbital Width	153	38.5	2.0	34.1–44.3	73	43.5	3.9	30.0–49.5
Snout opercle Distance	153	71.2	2.5	66.7–86.3	73	70.5	3.2	53.0–77.3
Head Width	153	80.3	3.4	72.0–97.3	73	82.6	3.4	67.4–90.4
Head eye Length	153	36.5	2.6	32.5–61.1	73	39.4	1.6	32.8–43.9
Eye nare Length	153	11.4	1.4	6.9–15.1	73	11.9	1.2	9.0–14.3
Internares Width	153	17.4	1.6	12.3–22.5	73	18.0	1.9	11.5–22.2
Snout nares Length	153	41.3	3.1	36.7–68.2	73	38.6	4.5	14.1–44.1
Snout pectoral Length	153	74.1	3.0	68.9–92.0	73	73.0	3.4	54.7–80.1
Pectoral orbit Distance	153	27.1	3.5	19.1–37.0	73	27.2	2.8	20.3–34.2
Mouth Width	153	41.8	3.8	34.8–54.3	73	40.7	3.1	34.8–49.4
Mouth Length	153	43.4	3.7	33.3–59.7	73	41.9	3.5	30.4–47.8
Dentary Length	153	13.1	1.9	7.4–19.9	73	12.5	1.2	8.8–15.0

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 present on caudal fin, with largest odontodes on spines and rays and also covering posteromedial edge of most plates on lateral

surface of body; most relatively short (less than 2–3mm). 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 (less than or equal to pupil width) 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.

Distribution. (Fig. 8) A wide-ranging species, *A. emarginatus*'s range includes the upper Orinoco River (except the Rio Apure); the Essequibo River and its tributaries; the lower Amazon River including the Rio Negro, the Rio Tapajós, and the Rio Xingu.



FIGURE 7. Dorsal, lateral, and ventral views of *Aphanotorulus emarginatus*, MZUSP 97217, 227.0 mm SL.

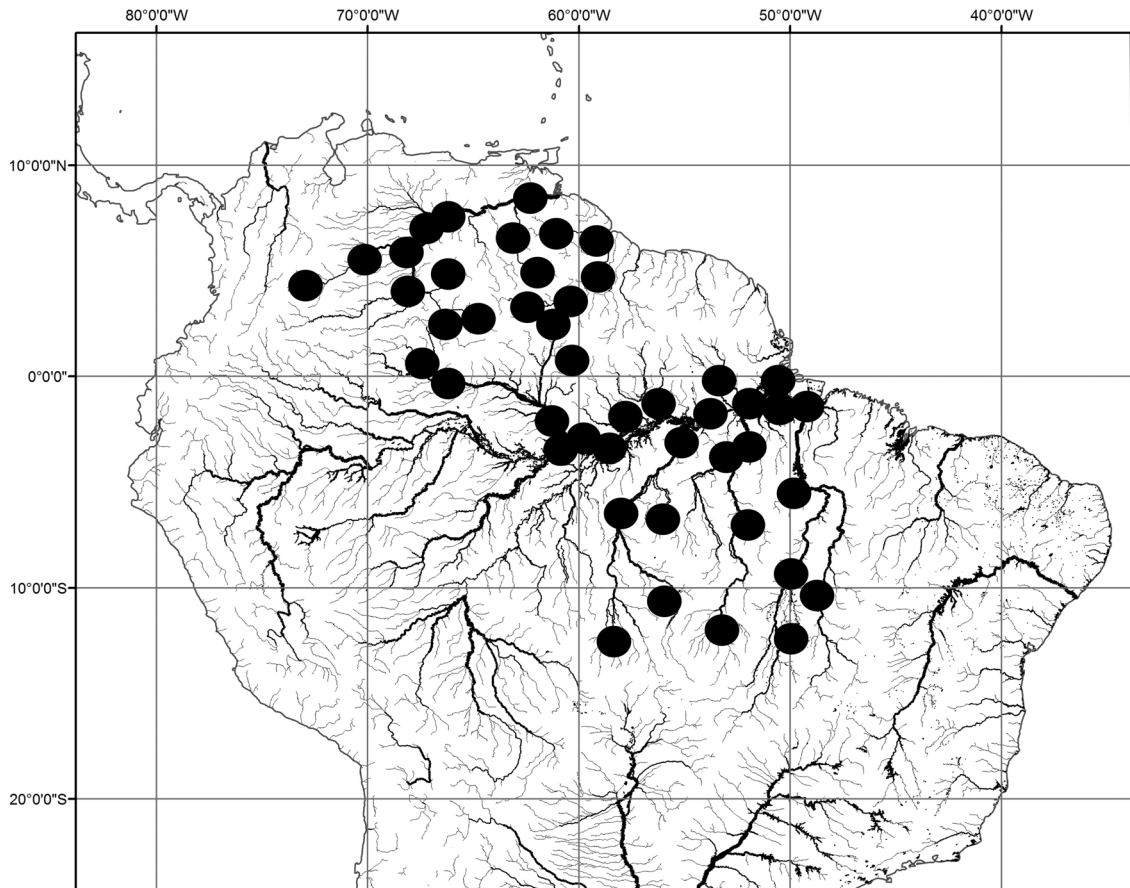


FIGURE 8. Distribution of *Aphanotorulus emarginatus*. Type locality is unknown.

***Aphanotorulus gomesi* (Fowler 1941)**

(Fig. 9)

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.

Material examined. Holotype: ANSP 69409, Ceará [Brazil].

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

Description. Morphometrics given in Table 4. Head moderately compressed. Supraoccipital crest not elevated, 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.

Distribution. *Aphanotorulus gomesi* is only known from its type locality. No other specimens are known (Fig. 10).

TABLE 4. Selected morphometrics of *Aphanotorulus gomesi* and *A. phrixosoma*.: Dorsal-fin spines were broken.

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

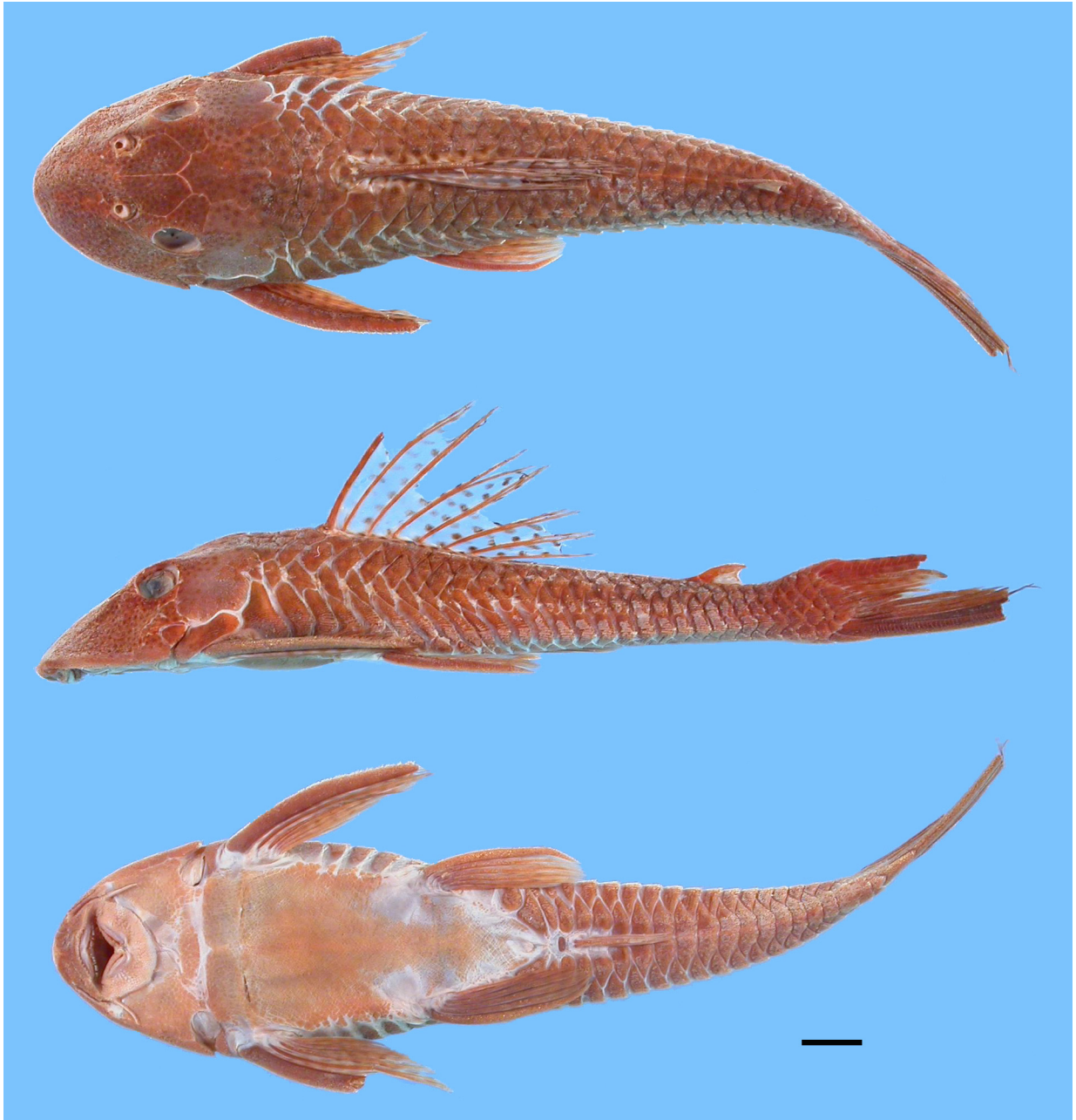


FIGURE 9. Dorsal, lateral, and ventral views of *Aphanotorulus gomesi*, ANSP 69409 (holotype), 141.3mm SL Photograph by Kyle Luckenbill. Scale = 1 cm.

***Aphanotorulus horridus* (Kner 1854)**
(Fig. 11)

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, 1872: 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, 1871: 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, 1874: 137. Type locality: not explicitly given [Upper Amazon]. Syntypes: ANSP 21280 (4).

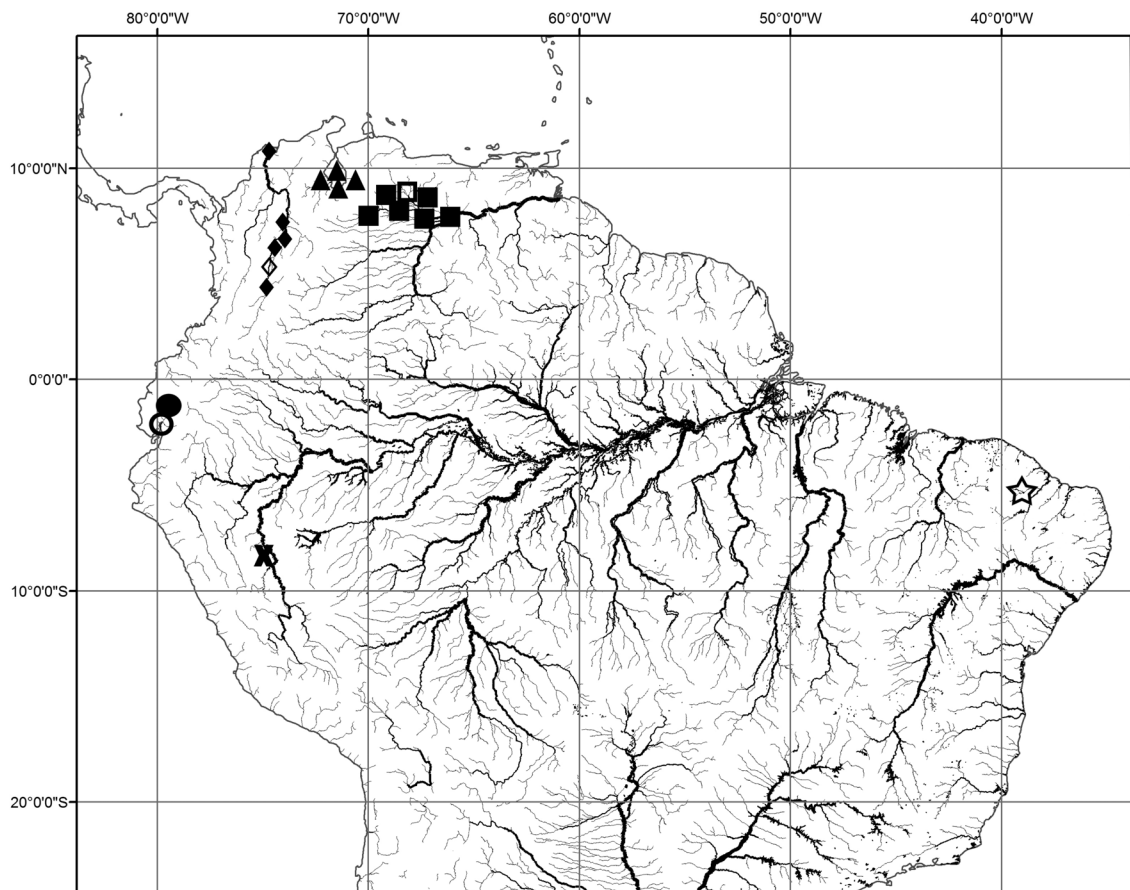


FIGURE 10. Distribution of *Aphanotorulus gomesi* (star), *A. phrixosoma* (X), *Isoneloricaria acuarius* (squares), *I. spinosissima* (circles), *I. tenuicauda* (diamonds), and *I. villarsi* (triangles). Type localities represented by open symbols when there is more than one known locality.

Material examined. Bolivia: AMNH 77469 (2), Rio Mamore; 8 kilometers north of Exaltacion, Depto Beni, Col. by S. Anderson, 29 September 1965; INHS 36997 (1), Rio Maniqui at San Borja, Beni, Bolivia; 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 Macaúa (tributary Rio Iaco), near Sena Madureira, 09°20'S, ca. 68°45'W, col. by B.A. Krukoff, 1934; ANSP 8081 (1), (Holotype: *Plecostomus scopularius*, Cope 1871), Amazon River, above the mouth of the Rio Negro, R. Perkins; MCZ 33518 (2), Rio Juruá [vicinity of mouth of Rio Embira, trib. of Rio Tarauaca, in turn a trib. of Rio Juruá], Amazonas, col. by B.A. Krukoff, 1934; MCZ 33524 (2), Rio Purus [vicinity of mouth of Rio Macaúa, 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 Solimões 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 Length Agassiz and party, 26 August 1865; MZUSP 23260 (1), Rio Solimões, Amazonas, 4°5'S 63°9'W, Expedição Permanente à Amazônia, 28 September 1968; MZUSP 28368 (2), Rio Machado, próximo à foz, Rondônia, 8°4'S 62°54'W, Expedição Permanente à Amazônia, 21 November 1975; MZUSP 49682 (1), Rio Acre, Seringal Bom Destino (1 hora acima de Porto Acre), Acre, 9°36'S, 67°32'W, 19 October 1994; MZUSP 49839 (1), Rio Acre, seringal Perseverança, Rio Purus drainage, Acre, ; MZUSP 50374 (1), Rio Juruá, Colocação São João, Acre, 9°9'S, 72°41'W, 8 July 1993; MZUSP 50377 (1), Rio Tejo, Ponto 13, Foz Bajé, Acre, 8°56'S 72°34'W, 8 March 1994; MZUSP 50489 (1), Foz do São João, Rio Juruá, Acre, 9°9'S, 72°41'W, 18 July 1994; MZUSP 50491(1), Foz do Breu, Rio Juruá, Acre, 9°25'S 72°43'W, 21 July 1994; MZUSP 50494 (1), Foz do Tejo, Rio Juruá, Acre, 8°58'S 72°42'W, 15 July 1994; MZUSP 57622 (1), Rio Madeira, Amazonas, 3°49'54"S

59°3'58"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, 9°34'45"S 59°25'19"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), Rio Tahuamanu, road crossing in vicinity of San Lorenzo, Madre de Dios, col. by M.H. Sabaj, Length Souza, M. Arce, Length deSouza, and N.J. Salcedo, 1 August 2004; AUM 45568 (1), Rio 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), Rio 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), Rio Napo at Mazan, Dept. Loreto, Peru; INHS 36796 (1), Iquitos, at fish market, Dept. Loreto, Peru; INHS 55406 (1), Rio Amazonas at beach along E bank of E channel opposite Iquitos, Dept. Loreto, Peru; MUSM 12628 (1), Tambopata, Rio Madre de Dios, El Bacon, Madre de Dio, Peru, 20 August 1997; MUSM 19897 (1), Tambopata, Rio Los Amigos, Madre de Dios, Peru, 17 August 2001; MUSM 26699 (1), Alto Amazonas, Trompeteros, Rio Corrientes, Loreto, Peru, 20 October 2005; MUSM 9976 (1), Tambopata, lago Valencia, Madre de Dios, Peru, 24 October 1995; 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.

Diagnosis. *Aphanotorulus horridus* can be diagnosed from *A. ammophilus* and *A. unicolor* by a single, large buccal papillae (vs. multiple buccal papillae); from *A. emarginatus* by having a smaller snout-nares distance to interorbital width ratio (70.5– 97.8% vs. 98.0– 175.4%), which separates 92% of individuals (Fig. 2); from *A. phrixosoma* by having fewer elongate hypertrophied covering the dorsal and ventral surfaces of body except the head (vs. many hypertrophied odontodes present—see *A. phrixosoma* description); and from *A. gomesi* only by range. *Aphanotorulus horridus* can be further diagnosed 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. spinosissima* by having a larger caudal fin depth to head length ratio (see diagnosis of *I. spinosissima*); from *I. acuarius* by having a supraoccipital crest with posterior edge gently sloping into nape (vs. *I. acuarius* with posterior edge perpendicular to head).

Description. Morphometric data given in Table 3. Head moderately deep with elevated supraoccipital crest; supraoccipital 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).



FIGURE 11. Dorsal, lateral, and ventral views of *Aphanotorulus horridus*, AUM 42001. Scale = 1 cm.

Sexual Dimorphism. Breeding males with short hypertrophied odontodes on ventral surfaces of body except 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.

Distribution. *Aphanotorulus horridus* is found in the upper Amazon River, including the mainstem, Rio Napo, Rio Marañon, Rio Ucayali, Rio Juruá, Rio Purus, and Rio Madera (Fig. 12).

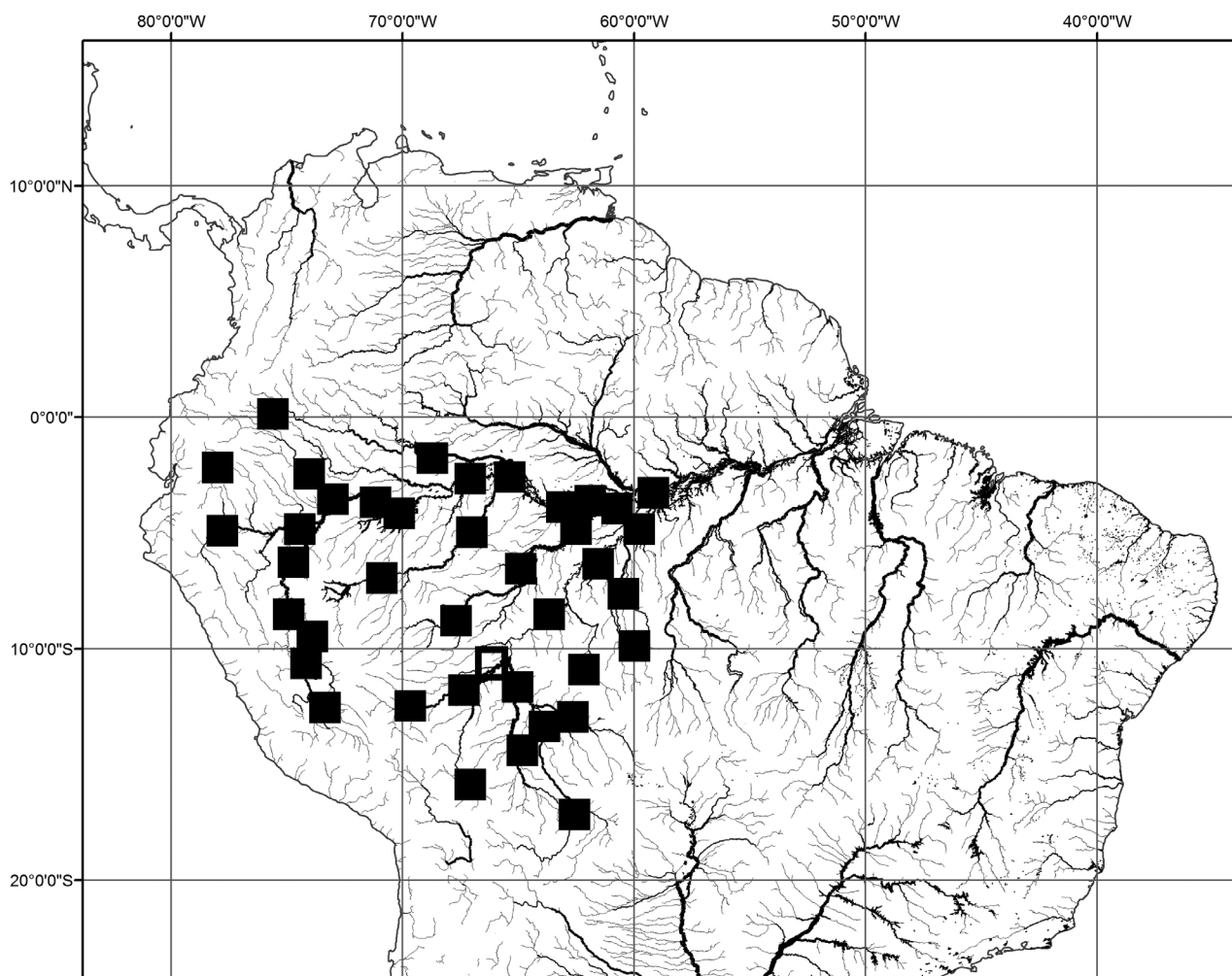


FIGURE 12. Range map of *Aphanotorulus horridus*. Type locality indicated by open square.

***Aphanotorulus phrixosoma* (Fowler 1940)**

(Fig. 13)

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

Material examined. Holotype: ANSP 68650, Ucayali River basin, Contamana, Peru.

Diagnosis. *Aphanotorulus phrixosoma* differs from *A. ammophilus* and *A. unicolor* by a single, large buccal papillae (vs. multiple buccal papillae in *A. ammophilus* and *A. unicolor*); from all other *Aphanotorulus* and *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* and *Aphanotorulus*). This species is known only from its holotype, which is a breeding male.

Description. Morphometric data given in Table 4. Head moderately deep. Interorbital surface flat; nape of unknown shape due to damage.

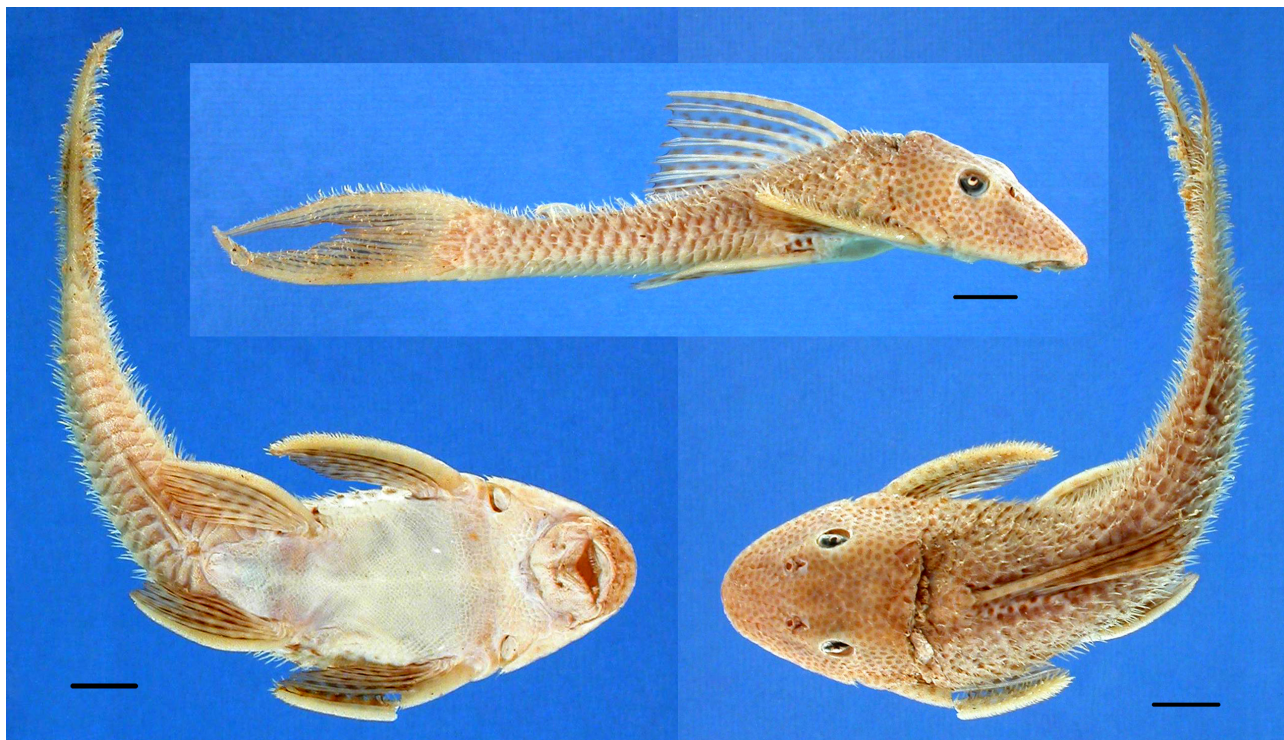


FIGURE 13. Ventral, dorsal, and lateral views of *Aphanotorulus phrixosoma*, ANSP 68650, 109.5mm SL Photographs by K. Luckenbill. Scale = 1 cm.

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 hypertrophied 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.

Distribution. Rio Ucayali, near Contamana, Peru. Known only from type locality (Fig. 10).

Comments. We hypothesize that this species is a hybrid. This specimen was collected in an area where both *A. horridus* and *A. unicolor* are sympatric. It should be noted that the specimen does not share the multiple buccal papillae or the unicuspid teeth of nuptial *A. unicolor*, yet it is the smallest breeding male (with hypertrophied odontodes) collected of any species of *Aphanotorulus* or *Isorineloricaria*, other than *A. ammophilus* and *A. unicolor*. Given these combinations of characters and the high sampling effort in the drainages around the type locality resulting in no more specimens of the species, hybridization is a credible possibility.

***Aphanotorulus unicolor* (Steindachner 1908)**

(Fig. 14)

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

Plecostomus madeirae Fowler, 1913: 571, fig. 23. Type locality: Madeira River, about 200 miles east of W. long. 63°54'W, Brazil. Holotype: ANSP 39312.



FIGURE 14. Lateral, dorsal, and ventral view of *Aphanotorulus unicolor*, ZMA 116640 (*Aphanotorulus frankei* holotype), 105.4 mm SL Photographs by K.S. Cummings. Scale = 1 cm.

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 (70°15'W, 7°30'S). Holotype: AMNH 12598.

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

Aphanotorulus frankei Isbrücker & Nijssen, 1983: 108, figs. 1–2. Type locality: [...] du Pérou, Dept. Ucayali, Prov. Coronel Portillo, système du Río Aguaytia. Rio Neshua (environ 08°36'S, 74°50'W), 60 km S.O. de Pucallpa, le long de la route de Tingo Maria. Holotype: ZMA 116.640.

Material examined. See Armbruster and Page (1996) and Armbruster (1998).

Diagnosis. *Aphanotorulus unicolor* differs from all other members of *Isorineloricaria*, except *A. ammophilus*, by its numerous buccal papillae (vs. single, large papilla). *Aphanotorulus unicolor* is diagnosable from *A. ammophilus* by the absence of a ridge on the compound pterotic (vs. ridge present in *A. ammophilus*). The urohyal is also uniquely modified in *A. unicolor*. The urohyal in *A. 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, *A. 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 *A. ammophilus* (Armbruster 1998).

Description. Morphometric data given in Table 2. 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 in size, less than half the width of the pupil. 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.

Distribution. A wide-ranging species, with populations known from upper Amazon tributaries of Bolivia, Brazil, Colombia, Ecuador, and Peru (Fig. 6).

***Isorineloricaria* Isbrücker 1980**

Isorineloricaria Isbrücker, 1980: 15. Type species: *Plecostomus spinosissimus* Steindachner, 1880. Type by original designation.

Diagnosis. *Isorineloricaria* can be separated from *Hypostomus* by having hypertrophied odontodes on the heads and lateral plates of nuptial males (vs. hypertrophied odontodes absent), from *Aphanotorulus* and *Hypostomus* by having caudal peduncles that greatly lengthened with size and that are round in cross section (vs. caudal peduncle proportions remaining the same through life and caudal peduncle oval in cross section), and by having large dark spots (spots almost as large as lateral plates) on a nearly white background (vs. small spots, several per plate, and light tan background). *Isorineloricaria* can be further separated from the taxa recognized in Armbruster's Corymbophanini by having an adipose fin (vs. adipose fin replaced by postdorsal ridge of 13–17 azygous plates); from the Corymbophanini and Rhinelepininae by having the iris operculum (vs. iris operculum absent); from the Rhinelepininae 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 Pterygoplichthyini 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 supra-preopercle and opercle, rarely two (vs. two to three); from the Ancistrini (except *Spectracanthicus murinus* and some *Pseudancistrus*) and the Pterygoplichthyini 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 having three plates between the head and dorsal fin (including the nuchal plate, vs. four or more).

Key to the species of *Isorineloricaria*

- 1a. Caudal fin depth to head length ratio 16.5–19.1% *I. spinosissima*
- 1b. Caudal fin depth to head length ratio 20.6–30.1% 2
- 2a. Sharp ridges on compound pterotics *I. villarsi*
- 2b. Rounded ridges on compound pterotics 3
- 3a. Caudal peduncle width to pectoral spine length ratio 31.5–56.2% (separates 95% of individuals examined) *I. tenuicauda*
- 3b. Caudal peduncle width to pectoral spine length ratio 59.6–65.2% (separates 95% of individuals examined) *I. acuarius*

Isorineloricaria acuarius new species

(Fig. 15)

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.*; ANSP 166888, 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, 07°40'00"N 070°28'00"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 (1), Rio Tucupido at Santuario de la Coromoto, Portuguesa, Venezuela, 08°54'46"N, 69°46'16"W, col. by L. M. Page *et al.*, 31 December 1994; INHS 35685 (1), Rio Portuguesa, 3 km northeast of El Barriero, Portuguesa Venezuela, 09°03'08"N, 069°29'18"W, col. by J.W. Armbruster, P.A. Ceas, M.H. Sabaj, C.A. Laird, S.M. Phelps, M.L. Manrique, F.T. Burbrink, 1 January 1995; MCNG 34719 (3), Río Arauca, playa al oeste del hato Doña Barbara, 7°25'00"N 69°25'00"W, col. by D. Jepsen, D. Rodríguez, 4 July 1997; UF 80345, Rio Guanare on Las Garcitas, near Laguna Chiriguare, 8°33'20"N 68°40'0"W, col. by D.C.. Taphorn, C.R. Gilbert, L. Nico, 3 April 1984; UF 80390 (3), Rio Apure in Apurito, near chalana site., Apure, 7°56'0"N 68°28'50"W, col. by 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 acuarius* can be diagnosed from from *I. spinosissima* by having a larger caudal fin depth to head length ratio (see diagnosis of *I. spinosissima*); 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; and from *I. spinosissima* and *I. villarsi* by having a flattened compound pterotic (vs. sharp ridges present in *I. villarsi*). *Isorineloricaria acuarius* can be further diagnosed from *Aphanotorulus ammophilus* and *A. unicolor* by having a single, large buccal papillae (vs. multiple buccal papillae present in *A. ammophilus* and *A. unicolor*); from *A. emarginatus* 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 *A. horridus* by having a supraoccipital crest with posterior edge perpendicular to head (vs. *A. horridus* with posterior edge gently sloping into nape)

Description. Morphometric data given in Table 5. Head deep with elevated supraoccipital crest; crest ending abruptly with posterior edge perpendicular to head. Rounded ridge forming on outer edge of each nare, rising dorsally over orbit, abruptly ending postorbitally. Large flap covering posterior opening of nare. Interorbital surface flat. Nape flat.



FIGURE 15. Lateral, dorsal, and ventral views of *Isorineloricaria acuarius*, INHS 35685 (holotype), 269.1 mm SL. Scale = 1 cm.

TABLE 5. Selected morphometrics of *Isorineloricaria acuarius* and *I. spinosissima*.

Measurement	<i>Isorineloricaria acuarius</i>				<i>Isorineloricaria spinosissima</i>			
	N	Average	SD	Range	N	Average	SD	Range
Standard Length (SL, mm)	23			53.2–208.4	11			39.4–416.0
% SL								
Predorsal Length	23	39.1	3.2	33.4–33.5	11	33.5	4.4	25.1–38.3
Head Length (HL)	23	32.9	3.9	20.9–27.9	11	27.9	4.4	19.9–33.7
Cleithral Width	22	26.1	1.4	23.2–22.3	11	22.3	3.3	16.3–25.6
Dorsal spine Length	21	29.4	4.6	18.4–27.3	11	27.3	3.8	19.9–31.3
Folded dorsal-fin Length	23	36.8	2.0	32.8–33.9	11	33.9	2.9	28.5–37.6
Dorsal-fin base Length	23	24.1	1.0	21.7–22.6	11	22.6	1.8	20.3–27.0
Dorsal- adipose Length	23	21.5	1.9	19.0–22.1	11	22.1	2.9	16.6–26.3
Thorax Length	23	23.0	1.5	20.4–21.4	11	21.4	1.8	18.4–23.6
Pectoral spine Length	23	28.6	2.0	24.6–22.2	11	22.2	4.6	15.1–28.5
Abdominal Length	23	19.1	1.0	16.9–18.3	11	18.3	1.2	16.7–20.4
Pelvic spine Length	23	22.7	2.1	17.4–20.2	11	20.2	2.6	14.9–23.8
Postanal Length	23	38.9	2.8	35.3–42.7	11	42.7	4.0	37.0–51.0
Caudal peduncle Depth	23	8.1	0.6	6.7–5.2	11	5.2	1.1	3.7–6.6
Caudal peduncle Width	23	15.7	1.4	12.1–11.5	11	11.5	1.7	8.3–13.5
Adipose-fin spine Length	23	7.8	1.2	5.5–6.9	11	6.9	1.6	4.3–9.8
Anal-fin Length	23	13.2	2.2	9.6–13.7	11	13.7	1.2	11.8–15.4
Anal-fin base Length	23	4.0	0.5	2.6–4.1	11	4.1	1.0	2.2–5.9
Adipose- upper caudal Length	23	20.9	1.2	18.5–26.0	11	26.0	2.3	22.8–29.5
Adipose- lower caudal Length	23	26.7	1.4	22.7–28.7	11	28.7	2.3	26.1–33.4
%HL								
Head Depth	23	59.0	9.1	52.9–55.3	11	55.3	2.8	49.4–57.9
Snout Length	23	61.1	8.6	55.2–59.6	11	59.6	3.6	52.9–64.7
Orbit Diameter	23	20.9	5.6	14.0–18.5	11	18.5	3.9	14.7–27.4
Interorbital Width	23	44.7	7.2	39.2–37.7	11	37.7	1.6	33.5–39.5
Snout opercle Distance	23	72.7	10.9	67.7–71.9	11	71.9	4.7	67.1–83.9
Head Width	23	81.3	11.2	72.7–80.2	11	80.2	3.7	76.2–86.3
Head eye Length	23	38.5	6.8	32.9–34.9	11	34.9	3.7	28.7–42.7
Eye nare Length	23	13.1	2.2	9.6–11.9	11	11.9	1.9	9.0–14.5
Internares Width	23	17.4	3.5	13.5–15.2	11	15.2	1.2	13.4–18.1
Snout nares Length	23	40.1	6.3	33.7–39.9	11	39.9	2.7	35.0–44.3
Snout pectoral Length	23	75.1	11.6	68.6–76.5	11	76.5	4.0	72.3–83.9
Pectoral orbit Distance	23	25.5	5.0	20.1–27.9	11	27.9	4.0	22.7–36.7
Mouth Width	23	42.7	6.1	37.5–41.4	11	41.4	3.0	37.5–45.6
Mouth Length	23	45.7	7.4	40.2–44.2	11	44.2	4.4	37.4–51.9
Dentary Length	23	14.4	2.9	11.1–12.8	11	12.8	1.3	11.0–15.7

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 larger than orbit diameter. 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 *A. ammophilus* (Armbruster and Page, 1996).

Distribution. This species has so far only been found in the Apure River 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 (Fig. 10).

Comments. The one specimen of *Isorineloricaria acuarius* collected in the Orinoco River was also collected with a specimen of *Aphanotorulus emarginatus*. 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 acuarius* appears to be restricted to white waters and *A. emarginatus* to clear and blackwater rivers, or rivers intermediate between black- and whitewater.

Etymology. The name *acuarius* is latin for needle maker. This is in reference to the numerous hypertrophied odontodes found on breeding males, which can make study of these fishes difficult. Treated as a noun in apposition.

***Isorineloricaria spinosissima* (Steindachner 1880)**

(Fig. 16)

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

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

Material examined. 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 5205.4.A (2), Napo-Pastanza Province, Ecuador, col. By C.M. Fugler, 1 September 1964.

Diagnosis. *Isorineloricaria spinosissima* can be diagnosed from *Aphanotorulus* and all other *Isorineloricaria* by having a smaller caudal fin depth to head length ratio (16.5–19.1% vs. 20.6–30.1%). *Isorineloricaria spinosissima* can be further diagnosed from *A. ammophilus* and *A. unicolor* by the presence of a single, large buccal papillae (vs. multiple buccal papillae present in *A. ammophilus* and *A. unicolor*; and from *A. emarginatus* and *A. horridus* by having rounded ridges on the compound pterotics (vs flat compound).

Description. Morphometric data given in Table 5. Head moderately deep; elevated 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.



FIGURE 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.

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

Distribution. Endemic to the Guayas River basin, Ecuador (Fig. 10).

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 (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: Magdalenaen-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 (1879: 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).

Material examined. Syntypes: NMW 44265 (1), Magdalena stream; NMW 44266 (3), Magdalena stream. 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.

Diagnosis. *Isorineloricaria tenuicauda* can be diagnosed from from *I. acuarius* by having a smaller caudal peduncle width to pectoral spine length ratio (31.5–56.2% vs. 59.6–65.2%), which separates 95% of individuals; from *I. spinosissima* by having a larger caudal fin depth to head length ratio (see diagnosis of *I. spinosissima*); and from *I. villarsi*, by a rounded ridge present on the compound pterotics (vs. sharp ridge). *Isorineloricaria tenuicauda* can be further diagnosed from *A. ammophilus* and *A. unicolor* by a single, large buccal papillae (vs. multiple buccal papillae); and from *A. emarginatus* and *A. horridus* by having rounded ridges on the compound pterotics (vs flat compound pterotics).

Description. Morphometric data given in Table 6. Head moderately deep with elevated 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.

TABLE 6. Selected morphometrics of *Isorineloricaria tenuicauda* and *I. villarsi*.

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

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

Distribution. *Isorineloricaria tenuicauda* is restricted to the Río Magdalena basin, Colombia (Fig. 10).



FIGURE 17. Lateral, dorsal, and ventral views of *Isorineloricaria tenuicauda*, MSNG 8856 (syntype). Photographs by M. Allen. Scale = 3 cm.

***Isorineloricaria villarsi* (Lütken 1874)**

(Fig. 18)

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



FIGURE 18. Lateral, dorsal, and ventral views of *Isorineloricaria villarsi*, USNM 121031, 301.5 mm SL. Scale = 1 cm.

Material examined. 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. Shultz, 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.

Diagnosis. *Isorineloricaria villarsi* can be diagnosed from all other members of *Isorineloricaria* by having distinct raised ridges on the compound pterotics (vs. rounded ridges). *Isorineloricaria villarsi* can be further separated from *Aphanotorulus ammophilus* and *A. unicolor* by a single, large buccal papillae (vs. multiple buccal papillae) and from *A. emarginatus* and *A. horridus* by distinct raised ridges on the compound pterotics (vs. compound pterotics flat).

Description. Morphometric data given in Table 6. 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. Pectoral-fin spine reaches past point of insertion on pelvic fin. Pelvic-fin spine reaches anal-fin insertion. 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 same manner, though not as large as on caudal-fin spines. Hypertrophied 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 it is depressed in juveniles.

Ecology. Unknown.

Distribution. *Isorineloricaria villarsi* is restricted to the Maracaibo basin in northwestern Venezuela and extreme eastern Colombia (Fig. 10).

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

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References

- Antonelli, A., Nylander, J.A.A., Persson, C. & Sanmartín, I. (2009) Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences*, 106, 9749–9754.
<http://dx.doi.org/10.1073/pnas.0811421106>
- Armbruster, J.W. (1998) Review of the loricariid catfish genus *Aphanotorulus* and redescription of *A. unicolor* (Teleostei: Siluriformes). *Ichthyological Exploration of Freshwaters*, 8, 253–262.
- Armbruster, J.W. (2004) Phylogenetic relationships of the suckermouth armoured catfishes (Loricariidae) with emphasis on the Hypostominae and the Ancistrinae. *Zoological Journal of the Linnean Society*, 141, 1–80.
<http://dx.doi.org/10.1111/j.1096-3642.2004.00109.x>
- Armbruster, J.W. (2005) The loricariid catfish genus *Lasiancistrus* (Siluriformes) with descriptions of two new species. *Neotropical Ichthyology*, 3, 549–569.
<http://dx.doi.org/10.1590/S1679-62252005000400013>
- Armbruster, J.W. (2008) The genus *Peckoltia* with the description of two new species and a reanalysis of the phylogeny of the genera of the Hypostominae (Siluriformes: Loricariidae). *Zootaxa*, 1822, 1–76.
- Armbruster, J.W. & Page, L.M. (1996) Redescription of *Aphanotorulus* (Teleostei: Loricariidae) with description of one new species, *A. ammophilus*, from the Río Orinoco Basin. *Copeia*, 1996, 379–389.
<http://dx.doi.org/10.2307/1446854>
- Boeseman, M. (1968) The genus *Hypostomus* Lacépède, 1803, and its Surinam representatives (Siluriformes, Loricariidae). *Zoologische Verhandelingen*, 99, 1–89. [Leiden]
- Boulenger, G.A. (1898) Viaggio del Dr. Enrico Festa nell' Equateur e regioni vicine. Poissons de l'Équateur.— Part I. *Bollettino dei Musei di Zoologia ed Anatomia Comparata della Università di Torino*, 13, 1–13.
- Campbell, K.E. Jr., Frailey C.D. & Romero-Pittman, L. (2006) The Pan-Amazonian Ucayali Peneplain, late Neogene sedimentation in Amazonia, and the birth of the modern Amazon River system. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 239, 166–219.
<http://dx.doi.org/10.1016/j.palaeo.2006.01.020>
- Cope, E.D. (1871) Fishes from the Amazon above the mouth of the Rio Negro. *Proceedings of the Academy of Natural Sciences*, 23, 55. [Philadelphia]
- Cope, E.D. (1872) On the fishes of the Ambyiacu River. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 23 (for 1871), 250–294, pls. 3–16.
- Cope, E.D. (1874) On some Batrachia and Nematognathi brought from the upper Amazon by Prof. Orton. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 26, 120–137.
- Cuvier, G. & Valenciennes, A. (1840) *Histoire naturelle des poissons. Tome quinzième. Suite du livre dix-septième. Siluroïdes*. Ch. Pitois & V^e Levrault, Paris & Strasbourg, xxxi + 540 pp., pls. 421–455.
- Eigenmann, C.H. (1922b) The fishes of western South America, Part I.— The fresh-water fishes of northwestern South America, including Colombia, Panama, and the Pacific slopes of Ecuador and Peru, together with an appendix upon the fishes of the Rio Meta in Colombia. *Memoirs of the Carnegie Museum*, 9, 1–346, pls. 1–38.
- Ferraris, C.J. (2007) Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types. *Zootaxa*, 1418, 1–628.
- Fowler, H.W. (1913) Fishes from the Madeira River, Brazil. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 65, 517–579.

- Fowler, H.W. (1940a) A collection of fishes obtained by Mr. William C. Morrow in the Ucayali River Basin, Peru. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 91 (for 1939), 219–289.
- Fowler, H.W. (1940b) Zoological results of the second Bolivian expedition for the Academy of Natural Sciences of Philadelphia, 1936–1937. Part I. The fishes. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 92, 43103.
- Fowler, H.W. (1941) Los peces del Perú. Catálogo sistemático de los peces que habitan en aguas peruanas (Continuación). *Boletín del Museo de Historia Natural "Javier Prado"*, 5, 466–487.
- Fowler, H.W. (1942) A new cat-fish from Brazil (*Plecostomus gomesi*, new species). *The Fish Culturist*, 21, unpaginated.
- Fowler, H.W. (1945) Descriptions of two new fresh-water fishes from Colombia. *Notulae Naturae* (Philadelphia), 158, 1–11.
- Gronovius, L.T. (1754) *Museum Ichthyologicum, Sistens Piscium Indigenorum & Nonnullorum Exoticorum, quorum Maximum pars in Museo Laurenti Theodori Gronovii, J. U. D. Adservantur; Descriptiones, Ordine Systematico; Accedunt Nonnullorum Exoticorum Piscium Icones, Aeri Incisae*. Theodorum Haak, Lugduni-Batavorum, 70 pp. 4 pls.
- Hoorn, C., Guerrero, J., Sarmiento, G.A. & Lorente, M.A (1995) Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology*, 23, 237–240.
[http://dx.doi.org/10.1130/0091-7613\(1995\)023%3C0237:ATAACF%3E2.3.CO;2](http://dx.doi.org/10.1130/0091-7613(1995)023%3C0237:ATAACF%3E2.3.CO;2)
- Isbrücker, I.J.H. (1980) Classification and catalogue of the mailed Loricariidae (Pisces, Siluriformes). *Versl. Tech. Gegevens*, 22, 1–181.
- Isbrücker, I.J.H. (2001) Nomenklator der Gattungen und Arten der Harnischwelse, Familie Loricariidae Rafinesque, 1815 (Teleostei, Ostariophysi). In: Stawikowski, R. (Ed.), *Harnischwelse 2. Die Aquarien- und Terrarien-Zeitschrift*, Eugen Ulmer, Stuttgart, pp. 25–32.
- Isbrücker, I.J.H. & Nijssen, H. (1983) *Aphanotorulus frankei*, une espèce et un genre nouveaux de poissons-chats cuirassés du Bassin du Rio Ucayali au Pérou (Pisces, Siluriformes, Loricariidae). *Revue française d'Aquariologie Herpetologie*, 9 (for 1982), 105–110.
- Isbrücker, I.J.H., Seidel, I., Michels, J.P., Schraml, E. & Werner, A. (2001) Diagnose vierzehn neuer Gattungen der Familie Loricariidae Rafinesque, 1815 (Teleostei, Ostariophysi). In: Stawikowski, R. (Ed.), *Harnischwelse 2. Die Aquarien- und Terrarien-Zeitschrift, Sonderheft*, Eugen Ulmer, Stuttgart, pp. 17–24.
- Kner, R. (1854) Die Hypostomiden. Zweite Hauptgruppe der Familie der Panzerfische. (Loricata vel Goniodontes). *Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften in Wien*, 7, 251–286, pls. 1–5.
- La Monte, F. (1935) Fishes from Rio Jurua and Rio Purus, Brazilian Amazonas. *American Museum Novitates*, 784, 1–8.
- Lujan, N.K., Armbruster, J.W., Lovejoy, N. & López-Fernández, H. (2015) Multilocus molecular phylogeny of the suckermouth armored catfishes (Siluriformes: Loricariidae) with a focus on subfamily Hypostominae. *Molecular Phylogenetics and Evolution*, 82, 269–288.
<http://dx.doi.org/10.1016/j.ympev.2014.08.020>
- Lundberg, J.G., Marshall, L.G., Guerrero, J., Horton, B., Claudia, M., Malabarba, S.L. & Wesselingh, F. (1998) The stage for neotropical fish diversification: a history of tropical South American rivers. In: Malabarba, L.R., Reis, R.E., Vari, R.P., Lucena, Z.M. & Lucena, C.A.S. (Eds.), *Phylogeny and Classification of Neotropical Fishes*. Edipucrs, Porto Alegre, Brazil, pp. 13–48.
- Lovejoy, N.R. (1996) Systematics of myliobatoid elasmobranchs: with emphasis on the phylogeny and historical biogeography of neotropical freshwater stingrays (Potamotrygonidae: Rajiformes). *Zoological Journal of the Linnean Society*, 117, 207–257.
<http://dx.doi.org/10.1111/j.1096-3642.1996.tb02189.x>
- Lütken, C.F. (1874) Ichthyographische Bidrag. II. Nye eller mindre vel kjendte Malleformer fra forskjellige Verdensdele. *Videnskabelige Meddelelser fra den Naturhistorisk Forening i Kjøbenhavn*, for 1874, 190–220.
- Montoya-Burgos, J.I. (2003) Historical biogeography of the catfish genus *Hypostomus* (Siluriformes: Loricariidae), with implications on the diversification of Neotropical ichthyofauna. *Molecular Ecology*, 2003, 1855–1867.
<http://dx.doi.org/10.1046/j.1365-294X.2003.01857.x>
- Montoya-Burgos, J.I., Weber, C. & Le Bail, P.-Y. (2002) Phylogenetic relationships within *Hypostomus* (Siluriformes: Loricariidae) and related genera based on mitochondrial D-loop sequences. *Revue Suisse de Zoologie*, 2, 369–382.
<http://dx.doi.org/10.5962/bhl.part.79596>
- Nelson, J.S. (2006) *Fishes of the World. 4th Edition*. John Wiley and Sons, New York, 601 pp.
- Nuttall, C.P. (1990) A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America. *Bulletin of the British Museum of Natural History (Geology)*, 45, 165–371.
- Pearson, N.E. (1924) The fishes of the eastern slope of the Andes. I. The fishes of the Rio Beni basin, Bolivia, collected by the Mulford expedition. *Indiana University Studies*, 11, 1–83, pls. 1–12.
- Sabaj Perez, M.H. (2014) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 5.0 (22 September 2014). American Society of Ichthyologists and Herpetologists, Washington, DC. Electronically accessible. Available from: <http://www.asih.org/> (accessed 8 December 2015)
- Schaefer, S.A. (1997) The neotropical cascudinhos: Systematics and biogeography of the *Otocinclus* catfishes (Siluriformes: Loricariidae). *Proceedings of the Academy of Natural Sciences, Philadelphia*, 148, 1–120.
- Schomburgk, R.H. (1841) The Natural History of Fishes of Guiana. Part I. In: Jardine, W. (Ed.), *The Naturalists' Library. Vol. 3*. W.H. Lizars, Edinburgh, 263 pp., 30 pls.

- Steindachner, F. (1878) Zur Fischfauna des Magdalenaen-Stromes. *Anzeiger der Mathematisch- Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften in Wien*, 15, 88–91.
- Steindachner, F. (1879) Zur Fischfauna des Magdalenaen-Stromes. *Denkschriften der Mathematisch- Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften in Wien*, 39, 19–78, pls. 1–15.
- Steindachner, F. (1880) Zur Fisch-fauna des Cauca und der Flüsse bei Guayaquil. *Denkschriften der Mathematisch- Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften in Wien*, 42, 55–104, pls. 1–9.
- Steindachner, F. (1881) Beiträge zur Kenntniss der Flussfische Südamerikas, II. *Denkschriften der Mathematisch- Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften in Wien*, 43, 103–146, pls. 1–7.
- Steindachner, F. (1908) Über zwei neue Siluroiden und zwei *Curimatus*-Arten, sowie über eine Varietät von *Ancistrus vittatus* [sic, *vittatus*] aus dem Amazonasgebiete innerhalb Brasiliens. *Anzeiger der Kaiserlichen Akademie der Wissenschaften, Mathematisch- Naturwissenschaftlichen Classe*, 45, 163–168.
- Taylor, D.W. (1991) Paleobiogeographic relationships of Andean angiosperms of Cretaceous to Pliocene age. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 88, 69–84.
[http://dx.doi.org/10.1016/0031-0182\(91\)90015-J](http://dx.doi.org/10.1016/0031-0182(91)90015-J)
- Taylor, R. & Van Dyke, C.C. (1985) Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9, 107–119
- Weber, C. (2003) Hypostominae. In: Reis, R.E., Kullander, S.O. & Ferraris, C.J. Jr. (Eds.), *Check list of the Freshwater Fishes of South and Central America*, Edipucrs, Porto Alegre, pp. 351–372.