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**The species of the *Hypostomus cochliodon* group
(Siluriformes: Loricariidae)**

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Abstract

The *Hypostomus cochliodon* group consists of eight species that were formerly recognized as *Cochliodon* Kner: *H. cochliodon* Kner, *H. hondae* (Regan), *H. levis* (Pearson), *H. oculatus* (Fowler), *H. plecostomoides* (Eigenmann), *H. pospisili* (Schultz; a synonym of *H. hondae*), *H. pyrineusi* (Miranda-Ribeiro), and *H. taphorni* (Lilyestrom) and four additional species described herein: *H.*

ericius, *H. hemicochliodon*, *H. pagei*, and *H. sculpodon*. The species occur in four phenetic groups: the intermediate group of *H. hemicochliodon* and *H. sculpodon* that appear to be transitional species between other *Hypostomus* and the *H. cochliodon* group in terms of diet and tooth shape, a monotypic group containing *H. cochliodon*, a group characterized by an odontodeless opercle that contains *H. ericius*, *H. levis*, *H. oculatus*, *H. pyrineusi*, and *H. taphorni*, and an undifferentiated northern group that contains *H. hondae*, *H. pagei*, and *H. plecostomoides*.

Key words: *Cochliodon*, Hypostominae, phylogeny, South America, suckermouth armored catfish, wood-eating

Introduction

With 650 species currently considered valid (Eschmeyer 2003), the Loricariidae is the most speciose family of catfishes in the world. Loricariids are typically algivorous or detritivorous, but the *Hypostomus cochliodon* group (formerly the genus *Cochliodon* Kner) and *Panaque* Eigenmann are unique among fishes in that they consume wood (Schaefer & Stewart 1993; Nelson *et al.* 1999). The *H. cochliodon* group and *Panaque* share the derived presence of large, spoon-shaped teeth; however, they are unrelated and are placed in two different tribes, the Hypostomini and the Ancistrini, respectively (Armbruster 1997; in press).

The original description of *Cochliodon* was by Heckel (in Kner 1853), but the genus was described in the synonymy of *Hypostomus* Lacépède. Eigenmann (1922) described *Cheiridodus* and separated the genus from *Cochliodon* based on the presence of a small medial tooth cusp (vs. medial cusp absent). Most loricariids have bicuspid teeth (Muller & Weber 1992), and the presence of a mesial cusp represents a plesiomorphic characteristic within the Loricariidae. *Cochliodon* do actually have a small mesial cusp, but this cusp is occasionally fused into the lateral cusp and visible as a darker, thicker ridge on the tooth (pers. obs.). Isbrücker (1980) recognized *Cheiridodus* as a synonym of *Cochliodon*, but did so without comment. Armbruster (1997; in press) provided a phylogeny for the species of the Hypostominae based on morphology and determined that *Cochliodon* is derived from *Hypostomus*. In addition, Montoya-Burgos *et al.* (1998) found *Cochliodon* to be related to *Hypostomus* based on sequences of the 12s and 16s rRNA genes, Montoya-Burgos *et al.* (2002) found *Cochliodon* to be nested within *Hypostomus* based on sequence data from the mitochondrial D-loop, and Zawadzki (pers comm.) has found *Cochliodon* to be derived from *Hypostomus* based on allozymes. Armbruster (1997, in press) recognized *Cochliodon* as a synonym of *Hypostomus* and refers to the species formerly in *Cochliodon* as the *H. cochliodon* group. Weber and Montoya-Burgos (2002) and Montoya-Burgos *et al.* (2002) also placed *Cochliodon* in the synonymy of *Hypostomus*.

The *Hypostomus cochliodon* group has received little attention from authors except for original species descriptions. The seven currently accepted species of the *H. cochliodon* group are distributed in the Orinoco, Amazon, Essequibo, Magdalena, Paraguay, and

Atrato river basins and in the Lake Maracaibo basin (Lilyestrom 1984; Armbruster & Page 1997). There has only been one modern attempt to examine the species of the *H. cochliodon* group. Lilyestrom (1984) provides descriptions of the species of the *H. cochliodon* group in Venezuela, a key to all of the species of the *H. cochliodon* group, and places *Cochliodon possisili* Schultz into the synonymy of *H. hondae*. The characteristics used in Lilyestrom's key are mostly proportions and tooth counts and do not adequately separate the species of the *H. cochliodon* group (pers. obs.). Armbruster and Page (1997) redescribe *Rhinelepis levis* Pearson, and place the species in *Cochliodon*. *Hypostomus levis* is unique among the *H. cochliodon* group in the absence of an adipose fin. Weber and Montoya-Burgos (2002) describe *H. fonchii* and suggest that it is related to the *H. cochliodon* group; however, they present no credible evidence for this assertion and *H. fonchii* is not considered to be part of the *H. cochliodon* group in this study.

Placing *Cochliodon* into the synonymy of *Hypostomus* is further supported by two species described herein. *Hypostomus hemicochlodon* and *H. sculpodon* predominantly eat wood, but do not have spoon-shaped teeth. These species have teeth that appear to be intermediate between other *Hypostomus* and other species of the *H. cochliodon* group (Fig. 1) and also appear to eat less wood than the other species of the *H. cochliodon* group (pers. obs. based on gut contents). Although many other *Hypostomus* will occasionally consume small amounts of wood, wood only amounts to a very small fraction of the diet (pers. obs.). In this manuscript all species of the *H. cochliodon* group are redescribed, four new species of the *H. cochliodon* group are described, and distribution maps, a key, and a phylogeny for the species of the *H. cochliodon* group is provided.

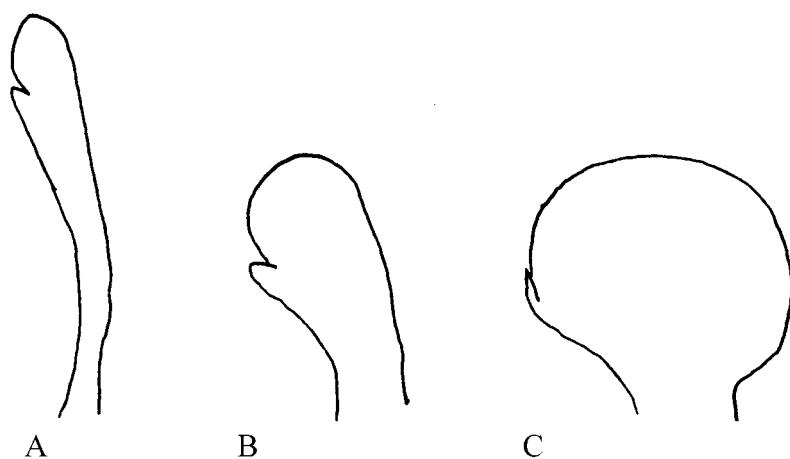


FIGURE 1. Transition of teeth between normal *Hypostomus* and the *H. cochliodon* group . A. *Hypostomus* sp. INHS 28903, 120.7 mm SL, B. *Hypostomus hemicochlodon*, 114.7 mm SL, C. *H. plecostomoides*, 116.3 mm SL. Dentary teeth, ventral view. All teeth X50.

Methods

Measurements were made with digital calipers to the nearest 0.1 mm. Measurements and counts of bilaterally symmetrical features were made on the left side of the body when possible; or on the right side if that was not possible. Counts and measurements are based on Boeseman (1968) as modified in Armbruster and Page (1996) and Armbruster and Provenzano (2000). Morphometric features are presented in Tables 1-6. Measurements involving the adipose fin were excluded for *Hypostomus levis* and caudal peduncle depth in *H. levis* is the minimal depth of the caudal peduncle. Dentary angle was measured by holding a specimen under a stereomicroscope with the mouth parallel with the objective of the scope. The relative angle of the dentaries was estimated by marking the tips of the dentaries on a piece of paper using a camera lucida and scanning the dots into a computer. The dots of each jaw ramus were connected by a line through their centers in Claris Draw ver. 5.0 for the Macintosh. Angle between the dentaries was estimated by selecting each line, using the get info function of Claris Draw which provides the relative angle of each line, and then subtracting the lesser from the greater of the two angles. Names of lateral plate rows follow Chockley and Armbruster (2002).

For ease of analysis, the species of the *Hypostomus cochliodon* group were divided into four phenetic groups based on overall similarity, the presence of derived features, and/or geography. These groups are an intermediate group with *H. hemicochliodon* and *H. sculpodon*, *H. cochliodon* as a monotypic group, an odontodeless opercle group with *H. ericius*, *H. levis*, *H. oculatus*, *H. pyrineusi*, and *H. taphorni*, and an undifferentiated northern group with *H. hondae*, *H. pagei*, and *H. plecostomoides*. “Wood specializing members of the *H. cochliodon* group” excludes *H. hemicochliodon* and *H. sculpodon*. All measurements were natural log-transformed and a principal components analysis (PCA) was performed using a covariance matrix in SYSTAT (ver. 5.0, Systat Inc. 1992) on each of the phenetic groups. Normal odontodes on the bodies of loricariids are pointed and conical; however, the odontodeless opercle group and *H. cochliodon* have odontodes on the body plates of nuptial males that are slightly longer and considerably wider than normal loricariid odontodes (Fig. 2B). The modified odontodes are roughly triangular in shape and are referred to as “nuptial body odontodes” below.

In the phylogenetic analysis, the outgroup consisted of specimens of *Hypostomus plecostomus* which was found to be closely related to the *H. cochliodon* group (Armbruster 1997, in press). All other species of *Hypostomus* examined had the same character states in this analysis as *H. plecostomus*, so no other outgroup was necessary. The ingroup consisted of all members of the *H. cochliodon* group, but internal osteological characteristics are missing for *H. ericius* and *H. sculpodon* because no skeletons are available. An exhaustive search was performed in PAUP*, version 4.0b10, (Swofford 2002).

Comparative specimens of other loricariids examined are listed in Armbruster (1998). Institution abbreviations are as in Leviton *et al.* (1985). In locality information, “dr.” is drainage and “cs” refers to specimens that are cleared and stained.

TABLE 1. Morphometrics of *Hypostomus cochliodon* and *H. ericius*.

	<i>H. cochliodon</i>		<i>H. ericius</i>	
	Mean ± SD	Range	Mean ± SD	Range
SL (mm)	120.4 ± 35.8	66.1 - 211.4	112.5 ± 38.0	80.1 - 186.8
% SL				
Predorsal length	40.6 ± 1.7	37.0 - 44.7	41.9 ± 2.0	39.6 - 45.1
Head length (HL)	33.2 ± 1.7	29.9 - 37.6	35.2 ± 2.1	32.0 - 38.7
Snout-pectoral length	24.7 ± 1.1	22.4 - 27.2	24.9 ± 1.0	23.3 - 25.9
Thorax length	22.5 ± 1.3	19.6 - 24.9	22.9 ± 1.9	20.5 - 26.0
Pectoral spine length	31.1 ± 1.5	26.8 - 35.1	34.1 ± 1.1	32.8 - 36.3
Abdomen length	22.2 ± 0.9	20.4 - 24.0	22.8 ± 1.5	21.2 - 25.7
Pelvic spine length	27.1 ± 1.3	24.2 - 31.0	27.5 ± 1.1	25.7 - 29.3
Postanal length	33.1 ± 1.1	30.4 - 35.2	31.7 ± 2.1	27.2 - 33.3
Anal fin length	13.7 ± 0.8	12.1 - 15.4	14.3 ± 1.2	13.4 - 17.0
Caudal depth	10.5 ± 1.1	9.3 - 17.0	10.4 ± 0.4	9.7 - 11.0
Adipose spine length	6.6 ± 0.8	5.3 - 8.3	6.6 ± 0.6	5.7 - 7.6
Adipose-caudal length	16.7 ± 1.1	14.4 - 18.6	16.0 ± 1.2	14.5 - 17.9
Interdorsal length	19.0 ± 1.2	16.6 - 22.5	17.2 ± 1.6	15.4 - 19.7
Base of dorsal length	25.3 ± 1.3	22.7 - 28.4	28.9 ± 1.6	26.5 - 31.4
Dorsal spine length	32.4 ± 2.9	21.4 - 37.2	36.5 ± 4.1	31.1 - 41.8
Head depth	22.7 ± 1.0	20.6 - 25.9	24.7 ± 1.0	23.1 - 25.7
Dorsal-pectoral length	28.1 ± 1.2	25.6 - 31.0	29.9 ± 1.5	27.4 - 32.0
Dorsal-pelvic length	25.2 ± 2.4	17.0 - 37.0	27.6 ± 1.9	24.7 - 31.1
Pelvic-dorsal length	26.4 ± 1.4	22.6 - 30.5	28.9 ± 2.5	23.9 - 31.1
Dorsal-anal length	15.7 ± 0.9	13.9 - 20.4	16.4 ± 1.1	15.4 - 18.2
Adipose-anal length	20.3 ± 1.2	14.3 - 22.1	20.2 ± 0.8	19.1 - 20.9
Anal fin width	16.8 ± 1.3	13.9 - 20.0	17.1 ± 1.5	15.5 - 19.2
Cleithral width	29.4 ± 1.2	26.6 - 31.2	29.7 ± 1.8	27.2 - 32.1
%HL				
Head-eye length	39.3 ± 1.4	36.4 - 42.8	41.8 ± 1.6	39.8 - 44.9
Orbit length	18.4 ± 1.9	15.1 - 22.1	18.7 ± 1.9	15.4 - 21.6
Snout length	64.3 ± 1.8	60.4 - 67.6	65.5 ± 2.0	63.2 - 69.4
Eye-nare length	16.8 ± 1.4	12.2 - 19.3	18.2 ± 0.8	17.0 - 19.3
Snout-nare length	40.8 ± 1.5	36.8 - 43.7	41.6 ± 1.5	39.3 - 44.0
Internares width	15.8 ± 1.3	12.5 - 19.1	15.4 ± 1.1	13.8 - 17.3
Interorbital width	48.0 ± 2.6	40.9 - 54.6	53.4 ± 2.4	50.5 - 56.6
Eye height	29.1 ± 2.9	21.6 - 34.4	28.9 ± 3.0	24.7 - 32.6
Head width	85.7 ± 4.0	78.1 - 94.5	82.3 ± 2.8	77.7 - 86.8
Mouth width	43.6 ± 2.7	37.1 - 50.5	40.9 ± 1.7	38.5 - 42.6
Mouth length (ML)	47.1 ± 2.5	40.2 - 52.0	47.1 ± 2.2	44.1 - 49.6
Dentary length	14.3 ± 1.3	11.3 - 17.0	13.8 ± 1.0	12.7 - 15.5
%ML				
Mouth width	92.7 ± 6.2	76.2 - 105.9	86.8 ± 2.0	84.2 - 90.1

TABLE 2. Morphometrics of *Hypostomus hemicochliodon* and *H. hondae*.

	<i>H. hemicochliodon</i>		<i>H. hondae</i>	
	Mean ± SD	Range	Mean ± SD	Range
SL (mm)	121.4 ± 40.5	78.6 - 208.7	120.8 ± 50.6	57.4 - 237.9
% SL				
Predorsal length	37.5 ± 1.5	34.5 - 41.2	39.7 ± 1.6	35.9 - 42.5
Head length (HL)	31.9 ± 2.1	26.8 - 36.1	32.8 ± 2.1	28.7 - 37.3
Snout-pectoral length	23.7 ± 1.0	21.7 - 25.7	24.7 ± 1.1	22.2 - 26.8
Thorax length	22.2 ± 1.2	19.4 - 25.1	21.8 ± 1.6	17.1 - 25.4
Pectoral spine length	31.3 ± 1.5	26.8 - 34.5	32.2 ± 1.5	30.2 - 35.8
Abdomen length	21.1 ± 0.9	19.6 - 23.2	22.3 ± 0.8	20.4 - 24.0
Pelvic spine length	25.4 ± 1.2	23.0 - 28.8	28.7 ± 1.8	25.4 - 33.6
Postanal length	33.5 ± 1.3	30.6 - 36.5	32.0 ± 1.4	28.2 - 34.5
Anal fin length	12.9 ± 1.0	11.0 - 15.7	15.5 ± 1.1	13.7 - 17.9
Caudal depth	9.1 ± 0.5	8.2 - 10.4	9.4 ± 0.5	8.2 - 10.4
Adipose spine length	6.3 ± 0.7	5.4 - 7.8	6.6 ± 0.6	5.6 - 7.8
Adipose-caudal length	15.8 ± 1.2	13.2 - 18	15.3 ± 1.4	12.1 - 18.4
Interdorsal length	20.3 ± 1.5	17.5 - 24.3	18.9 ± 1.3	16.9 - 22.3
Base of dorsal length	27.9 ± 1.0	26.2 - 29.7	27.5 ± 1.1	24.3 - 29.4
Dorsal spine length	34.8 ± 3.9	27.0 - 42	37.3 ± 2.6	33.4 - 42.4
Head depth	21.4 ± 1.3	18.2 - 24	21.7 ± 1.1	19.6 - 24.1
Dorsal-pectoral length	25.9 ± 1.2	23.2 - 28.2	27.3 ± 1.3	24.1 - 29.6
Dorsal-pelvic length	24.6 ± 1.2	21.1 - 26.6	25.2 ± 1.7	22.4 - 28.4
Pelvic-dorsal length	26.1 ± 1.3	23.6 - 28.8	27.1 ± 1.3	25.1 - 29.5
Dorsal-anal length	14.2 ± 0.8	12.9 - 16.2	14.6 ± 0.9	12.4 - 16.1
Adipose-anal length	21.8 ± 0.9	19.3 - 23.3	20.7 ± 1.1	18.0 - 22.6
Anal fin width	15.9 ± 1.3	13.4 - 19.4	16.0 ± 3.7	10.8 - 31.5
Cleithral width	25.2 ± 0.9	23.7 - 28.1	27.4 ± 1.0	24.9 - 29.6
% HL				
Head-eye length	41.3 ± 1.8	37.4 - 45.0	40.8 ± 1.6	37.6 - 43.1
Orbit length	19.5 ± 1.8	16.4 - 23.6	17.2 ± 1.9	13.5 - 20.6
Snout length	62.3 ± 2.0	58.4 - 65.9	63.3 ± 2.5	57.2 - 68.3
Eye-nare length	16.1 ± 1.0	14.0 - 18.5	15.6 ± 1.7	11.5 - 19.2
Snout-nare length	39.6 ± 1.4	37.3 - 42.5	41.2 ± 2.2	37.6 - 46.8
Internares width	15.8 ± 1.2	13.1 - 18.3	15.5 ± 1.2	12.3 - 18.0
Interorbital width	49.9 ± 2.7	44.1 - 55.6	49.3 ± 2.5	45.0 - 55.7
Eye height	25.1 ± 2.7	20.2 - 31.2	26.5 ± 2.9	21.9 - 32.6
Head width	76.8 ± 4.2	68.1 - 86.8	82.6 ± 4.8	73.3 - 93.4
Mouth width	40.4 ± 2.1	35.0 - 44.2	42.8 ± 3.1	37.9 - 50.5
Mouth length (ML)	46.9 ± 2.3	42.1 - 51.7	46.6 ± 2.8	41.4 - 52.1
Dentary length	12.4 ± 0.9	10.5 - 14.5	14.6 ± 1.3	12.2 - 17.5
% ML				
Mouth width	86.4 ± 5.3	73.0 - 102.9	92.1 ± 6.5	80.2 - 113.5

TABLE 3. Morphometrics of *Hypostomus levis* and *H. ocaleus*.

	<i>H. levis</i>		<i>H. ocaleus</i>	
	Mean ± SD	Range	Mean ± SD	Range
SL (mm)	107.4 ± 38.9	57.6 - 152.9	137.8 ± 44.2	62.5 - 216.9
% SL				
Predorsal length	37.6 ± 1.6	35.7 - 40.0	39.4 ± 1.5	35.2 - 43.3
Head length (HL)	31.6 ± 1.7	30.3 - 34.6	32.2 ± 1.5	28.7 - 35.5
Snout-pectoral length	23.4 ± 0.9	22.0 - 24.4	23.5 ± 0.7	22.0 - 25.0
Thorax length	22.2 ± 1.5	20.0 - 24.4	24.0 ± 1.6	21.4 - 26.6
Pectoral spine length	29.2 ± 1.0	27.1 - 29.9	31.0 ± 2.6	25.2 - 35.7
Abdomen length	20.5 ± 0.7	19.7 - 21.4	21.5 ± 1.2	19.3 - 23.5
Pelvic spine length	25.1 ± 0.9	23.7 - 26.1	26.7 ± 1.5	24.3 - 30.4
Postanal length	34.9 ± 0.8	34.2 - 36.4	33.2 ± 1.6	29.9 - 36.5
Anal fin length	13.3 ± 1.2	12.0 - 14.8	12.6 ± 0.8	10.8 - 13.9
Caudal depth	9.0 ± 0.4	8.5 - 9.5	10.0 ± 0.8	8.6 - 11.2
Adipose spine length	NA		6.1 ± 0.8	4.6 - 7.2
Adipose-caudal length	NA		18.6 ± 2.0	13.0 - 21.8
Interdorsal length	NA		17.0 ± 1.3	14.0 - 19.6
Base of dorsal length	23.6 ± 1.5	21.8 - 24.9	27.3 ± 2.0	22.6 - 31.6
Dorsal spine length	31.6 ± 1.6	29.5 - 33.4	34.7 ± 3.2	27.0 - 41.1
Head depth	19.9 ± 0.5	19.2 - 20.5	22.1 ± 1.1	19.5 - 24.1
Dorsal-pectoral length	25.3 ± 0.9	24.0 - 26.5	27.8 ± 1.1	25.7 - 30.1
Dorsal-pelvic length	21.4 ± 1.5	19.1 - 23.3	26.0 ± 1.8	22.0 - 29.4
Pelvic-dorsal length	24.4 ± 1.0	23.1 - 25.5	27.1 ± 1.4	23.8 - 29.7
Dorsal-anal length	13.4 ± 0.8	12.4 - 14.6	15.1 ± 1.1	12.4 - 17.2
Adipose-anal length	NA		19.5 ± 1.0	17.8 - 21.5
Anal fin width	14.5 ± 1.3	12.8 - 15.9	15.8 ± 1.1	14.1 - 18.0
Cleithral width	26.5 ± 0.5	25.7 - 27.0	28.4 ± 1.2	26.2 - 30.3
% HL				
Head-eye length	39.7 ± 1.4	37.5 - 41.0	38.5 ± 3.4	24.4 - 41.3
Orbit length	16.7 ± 1.9	14.4 - 19.7	17.2 ± 1.6	13.1 - 19.9
Snout length	63.6 ± 2.0	59.8 - 65.3	64.2 ± 2.0	58.9 - 67.9
Eye-nare length	14.7 ± 1.3	13.5 - 17.0	16.0 ± 1.2	13.9 - 19.2
Snout-nare length	41.1 ± 1.5	39.1 - 42.3	41.4 ± 1.5	37.7 - 44.6
Internares width	15.3 ± 1.1	13.8 - 16.7	15.7 ± 1.2	13.1 - 18.3
Interorbital width	46.2 ± 2.4	43.9 - 50.8	46.6 ± 1.9	42.4 - 50.2
Eye height	28.5 ± 4.1	22.4 - 32.8	29.7 ± 2.9	23.3 - 34.1
Head width	84.4 ± 4.5	78.1 - 89.8	86.1 ± 4.3	78.4 - 93.5
Mouth width	43.4 ± 2.7	40.0 - 46.5	42.1 ± 2.6	37.6 - 47.3
Mouth length (ML)	48.8 ± 3.3	43.6 - 52.0	45.9 ± 3.0	39.6 - 50.9
Dentary length	14.9 ± 1.1	12.6 - 15.8	14.0 ± 1.2	11.5 - 16.7
% ML				
Mouth width	89.1 ± 3.4	84.2 - 92.1	92.2 ± 7.7	78.5 - 115.7

TABLE 4. Morphometrics of *Hypostomus pagei* and *H. plecostomoides*.

	<i>H. pagei</i>		<i>H. plecostomoides</i>	
	Mean ± SD	Range	Mean ± SD	Range
SL (mm)	106.1 ± 41.8	64.8 - 187.7	144.6 ± 45.3	69.4 - 248.5
% SL				
Predorsal length	39.2 ± 1.8	35.5 - 42.4	38.6 ± 1.6	34.2 - 42.5
Head length (HL)	32.1 ± 2.1	28.3 - 35.2	31.8 ± 1.9	27.1 - 35.9
Snout-pectoral length	24.2 ± 1.1	22.3 - 26.3	24.5 ± 1.2	22.0 - 27.4
Thorax length	21.2 ± 1.0	20.0 - 22.8	20.6 ± 1.3	15.8 - 23.2
Pectoral spine length	28.7 ± 1.7	26.2 - 32.7	32.6 ± 1.9	28.5 - 36.8
Abdomen length	21.2 ± 1.1	18.2 - 22.6	22.1 ± 0.9	19.2 - 24.7
Pelvic spine length	26.5 ± 2.1	22.0 - 28.9	26.6 ± 1.7	21.3 - 29.9
Postanal length	33.9 ± 1.2	31.6 - 35.8	33.3 ± 1.3	30.2 - 36.8
Anal fin length	13.8 ± 0.8	11.9 - 15.0	14.1 ± 1.5	11.1 - 19.1
Caudal depth	8.9 ± 0.5	7.9 - 10.2	9.2 ± 0.4	8.1 - 10.5
Adipose spine length	5.2 ± 0.4	4.6 - 6.2	5.6 ± 0.6	4.0 - 7.7
Adipose-caudal length	17.2 ± 1.2	15.2 - 19.1	17.2 ± 1.3	14.2 - 20.4
Interdorsal length	20.6 ± 1.4	18.2 - 23.0	19.2 ± 1.4	16.3 - 23.1
Base of dorsal length	23.1 ± 1.1	21.6 - 24.6	26.3 ± 1.6	17.2 - 29.3
Dorsal spine length	31.9 ± 3.3	23.7 - 35.8	34.3 ± 3.0	25.6 - 43.0
Head depth	20.7 ± 1.5	18.2 - 24.4	21.9 ± 1.2	19.6 - 24.5
Dorsal-pectoral length	26.2 ± 1.6	22.7 - 29.9	26.6 ± 1.5	22.8 - 29.6
Dorsal-pelvic length	23.4 ± 1.7	20.6 - 27.5	24.9 ± 1.9	14.6 - 28.4
Pelvic-dorsal length	25.5 ± 1.9	22.1 - 28.9	26.2 ± 1.4	20.7 - 29.3
Dorsal-anal length	14.4 ± 0.8	12.7 - 16.1	14.4 ± 0.9	12.7 - 20.2
Adipose-anal length	20.5 ± 1.4	17.7 - 22.4	20.0 ± 1.2	14.1 - 22.9
Anal fin width	15.1 ± 1.2	12.9 - 17.3	15.7 ± 1.2	13.1 - 19.4
Cleithral width	26.0 ± 1.6	24.0 - 29.7	26.8 ± 1.3	23.8 - 29.4
% HL				
Head-eye length	39.4 ± 2.4	35.4 - 44.2	41.7 ± 1.8	37.8 - 45.8
Orbit length	16.5 ± 1.6	13.9 - 18.3	16.8 ± 1.7	13.7 - 21.1
Snout length	65.3 ± 3.1	60.0 - 72.7	66.7 ± 2.3	60.5 - 76.5
Eye-nare length	15.8 ± 1.3	14.2 - 18.4	18.5 ± 1.0	15.9 - 22.0
Snout-nare length	42.0 ± 2.0	38.4 - 46.5	42.9 ± 4.2	38.8 - 78.9
Internares width	16.2 ± 1.0	14.4 - 18.0	17.8 ± 1.1	15.3 - 20.3
Interorbital width	47.5 ± 2.6	42.1 - 52.5	54.4 ± 2.8	46.0 - 62.3
Eye height	26.5 ± 3.1	21.4 - 31.6	28.0 ± 2.3	22.4 - 33.9
Head width	78.5 ± 5.1	68.9 - 85.4	81.4 ± 4.5	58.0 - 91.0
Mouth width	42.1 ± 2.8	37.6 - 48.9	41.5 ± 2.9	31.2 - 47.2
Mouth length (ML)	47.5 ± 2.4	42.8 - 51.8	47.7 ± 2.3	41.7 - 55.7
Dentary length	14.3 ± 0.9	12.0 - 15.3	13.4 ± 1.2	10.0 - 16.1
% ML				
Mouth width	88.5 ± 5.5	77.9 - 98.6	86.9 ± 5.4	67.8 - 100.9

TABLE 5. Morphometrics of *Hypostomus pyrineusi* and *H. sculpodon*.

	<i>H. pyrineusi</i>		<i>H. sculpodon</i>	
	Mean ± SD	Range	Mean ± SD	Range
SL (mm)	140.8 ± 46.0	52.5 - 228.0	162.9 ± 72.7	85.8 - 239.7
% SL				
Predorsal length	38.9 ± 1.7	35.4 - 43.4	36.9 ± 2.2	34.1 - 39.3
Head length (HL)	31.9 ± 2.0	28.1 - 37.0	32.0 ± 3.0	28.7 - 35.6
Snout-pectoral length	23.8 ± 1.1	21.4 - 27.3	24.3 ± 1.1	23.1 - 25.6
Thorax length	23.2 ± 1.6	19.1 - 28.2	20.6 ± 0.7	19.8 - 21.5
Pectoral spine length	31.3 ± 1.5	27.8 - 34.9	31.7 ± 1.5	30.2 - 33.9
Abdomen length	22.0 ± 0.9	19.7 - 24.9	21.6 ± 0.8	20.5 - 22.3
Pelvic spine length	26.4 ± 1.5	22.6 - 29.9	25.5 ± 1.2	24.6 - 27.2
Postanal length	33.0 ± 1.4	29.3 - 37.4	31.9 ± 2.0	29.6 - 35.1
Anal fin length	13.7 ± 1.0	11.0 - 15.9	15.6 ± 1.3	14.4 - 17.1
Caudal depth	10.3 ± 1.3	9.0 - 18.6	8.4 ± 0.4	8.0 - 9.0
Adipose spine length	6.2 ± 0.7	4.0 - 7.2	6.7 ± 0.4	6.2 - 7.1
Adipose-caudal length	17.4 ± 1.7	12.8 - 21.3	14.9 ± 1.0	13.5 - 16.0
Interdorsal length	17.6 ± 1.5	15.2 - 22.5	21.5 ± 1.0	20.0 - 22.8
Base of dorsal length	27.1 ± 1.6	23.1 - 31.6	28.9 ± 1.1	27.8 - 30.7
Dorsal spine length	32.8 ± 3.4	21.6 - 40.2	34.1 ± 2.3	31.8 - 36.5
Head depth	22.2 ± 1.3	16.0 - 24.9	21.2 ± 1.0	20.0 - 22.4
Dorsal-pectoral length	27.6 ± 1.2	24.7 - 31.5	24.9 ± 1.0	23.7 - 26.2
Dorsal-pelvic length	25.2 ± 1.6	20.2 - 29.9	24.4 ± 1.0	22.9 - 25.6
Pelvic-dorsal length	26.8 ± 1.6	20.6 - 30.1	25.7 ± 0.8	24.9 - 26.7
Dorsal-anal length	15.5 ± 1.1	13.2 - 22.3	12.3 ± 0.8	11.2 - 13.4
Adipose-anal length	20.3 ± 1.3	16.8 - 25.0	22.2 ± 0.5	21.5 - 22.7
Anal fin width	16.5 ± 1.2	13.1 - 19.3	14.5 ± 1.0	13.5 - 16.0
Cleithral width	28.4 ± 1.2	25.7 - 31.7	23.9 ± 1.0	23.0 - 25.6
%HL				
Head-eye length	41.5 ± 1.5	37.9 - 44.6	39.6 ± 0.5	38.9 - 40.3
Orbit length	17.0 ± 2.0	13.5 - 24.0	19.1 ± 1.7	17.5 - 21.0
Snout length	65.0 ± 3.2	42.8 - 69.3	58.8 ± 3.5	54.4 - 62.5
Eye-nare length	17.5 ± 1.4	13.3 - 19.7	14.6 ± 1.7	12.4 - 15.9
Snout-nare length	41.3 ± 3.1	17.2 - 45.4	38.4 ± 2.5	35.7 - 42.0
Internares width	16.5 ± 1.4	11.9 - 19.7	16.1 ± 1.4	14.1 - 18.1
Interorbital width	51.4 ± 3.1	42.4 - 57.1	41.5 ± 2.7	38.5 - 45.4
Eye height	30.1 ± 2.7	21.1 - 34.3	27.9 ± 2.1	25.5 - 30.1
Head width	84.9 ± 6.6	42.5 - 95.8	78.1 ± 4.9	72.0 - 82.2
Mouth width	42.4 ± 3.4	35.4 - 53.1	40.1 ± 2.0	37.1 - 41.9
Mouth length (ML)	47.5 ± 2.1	42.9 - 52.3	47.8 ± 1.4	46.1 - 49.7
Dentary length	14.2 ± 1.0	10.8 - 16.6	11.5 ± 1.1	10.3 - 12.6
%ML				
Mouth width	89.2 ± 6.6	73.6 - 118.9	84.1 ± 6.5	74.7 - 89.0

TABLE 6. Morphometrics of *Hypostomus taphorni*.

	<i>H. taphorni</i>	
	Mean ± SD	Range
SL (mm)	134.6 ± 41.8	60.1 - 228.0
% SL		
Predorsal length	39.1 ± 1.9	36.5 - 47.2
Head length (HL)	32.9 ± 2.2	29.2 - 39.4
Snout-pectoral length	24.1 ± 1.2	22.4 - 28.6
Thorax length	22.9 ± 1.4	20.4 - 27.6
Pectoral spine length	32.6 ± 1.9	29.4 - 40.0
Abdomen length	21.8 ± 1.2	20.5 - 27.1
Pelvic spine length	25.0 ± 1.4	22.0 - 29.6
Postanal length	33.1 ± 1.1	31.3 - 36.8
Anal fin length	12.3 ± 1.2	10.3 - 15.8
Caudal depth	9.3 ± 0.5	8.6 - 11.3
Adipose spine length	5.4 ± 0.5	4.4 - 6.9
Adipose-caudal length	16.0 ± 1.2	13.3 - 18.9
Interdorsal length	20.3 ± 1.3	18.0 - 23.6
Base of dorsal length	27.2 ± 1.8	24.3 - 34.8
Dorsal spine length	30.4 ± 1.4	27.3 - 32.2
Head depth	22.7 ± 1.4	20.2 - 28.1
Dorsal-pectoral length	27.5 ± 1.4	25.8 - 32.8
Dorsal-pelvic length	26.1 ± 1.6	23.7 - 31.1
Pelvic-dorsal length	26.1 ± 1.5	24.0 - 32.2
Dorsal-anal length	14.4 ± 1.1	12.3 - 18.2
Adipose-anal length	20.8 ± 1.2	18.8 - 25.1
Anal fin width	15.6 ± 1.2	13.3 - 19.5
Cleithral width	27.7 ± 1.8	25.0 - 34.5
% HL		
Head-eye length	39.2 ± 1.5	35.8 - 42.3
Orbit length	18.1 ± 1.6	15.6 - 23.9
Snout length	64.0 ± 2.3	56.4 - 67.1
Eye-nare length	17.8 ± 1.6	14.5 - 23.3
Snout-nare length	40.5 ± 1.5	36.5 - 42.9
Internares width	15.6 ± 0.8	13.3 - 17.5
Interorbital width	46.9 ± 3.0	32.8 - 50.4
Eye height	29.6 ± 3.3	19.9 - 34.4
Head width	80.6 ± 4.4	69.7 - 86.8
Mouth width	39.2 ± 1.8	34.4 - 43.5
Mouth length (ML)	45.2 ± 1.6	41.4 - 47.9
Dentary length	12.7 ± 0.7	11.0 - 13.6
% ML		
Mouth width	86.8 ± 3.7	75.1 - 94.6

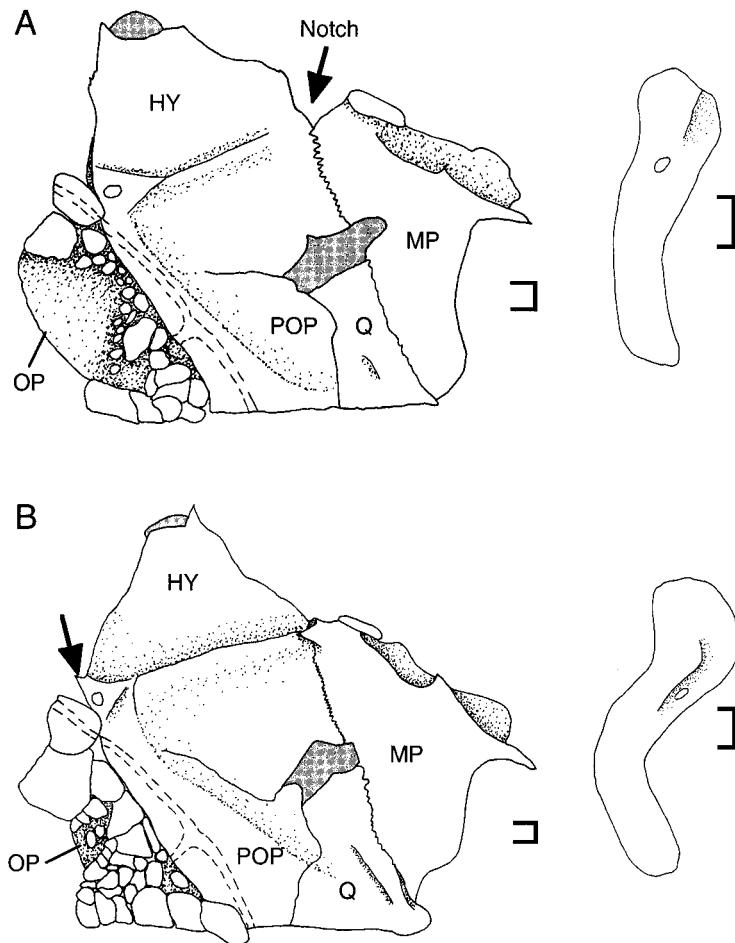


FIGURE 2. Opercles and modified odontodes of A. *Hypostomus plecostomoides*, INHS 30000 and B. *H. ericus*, MUSM 17441. Anterior arrows indicate opercle in A and the area where the opercle is located in B. Posterior arrow in B indicates region of modified odontodes. Anterior is to the left.

Hypostomus cochliodon Group

Diagnosis: The *Hypostomus cochliodon* group is diagnosed by the following characteristics, none of which is unique among loricariids: dentary angle averaging less than 80° and the preoperculo-hyomandibular ridge deflected posterior to the main body of the hyomandibula (Armbruster, in press). Wood-specializing members of the *H. cochliodon* group are additionally diagnosed by the following characteristics, none of which are unique among loricariids: the presence of large spoon-shaped teeth (Fig. 1C), the hyomandibula and metapterygoid sutured to their dorsal margins vs. not sutured dorsally with a notch between the two bones (Fig. 3B), the presence of a highly curved maxilla (Fig. 3B), and loss of the buccal papilla (Fig. 4B).

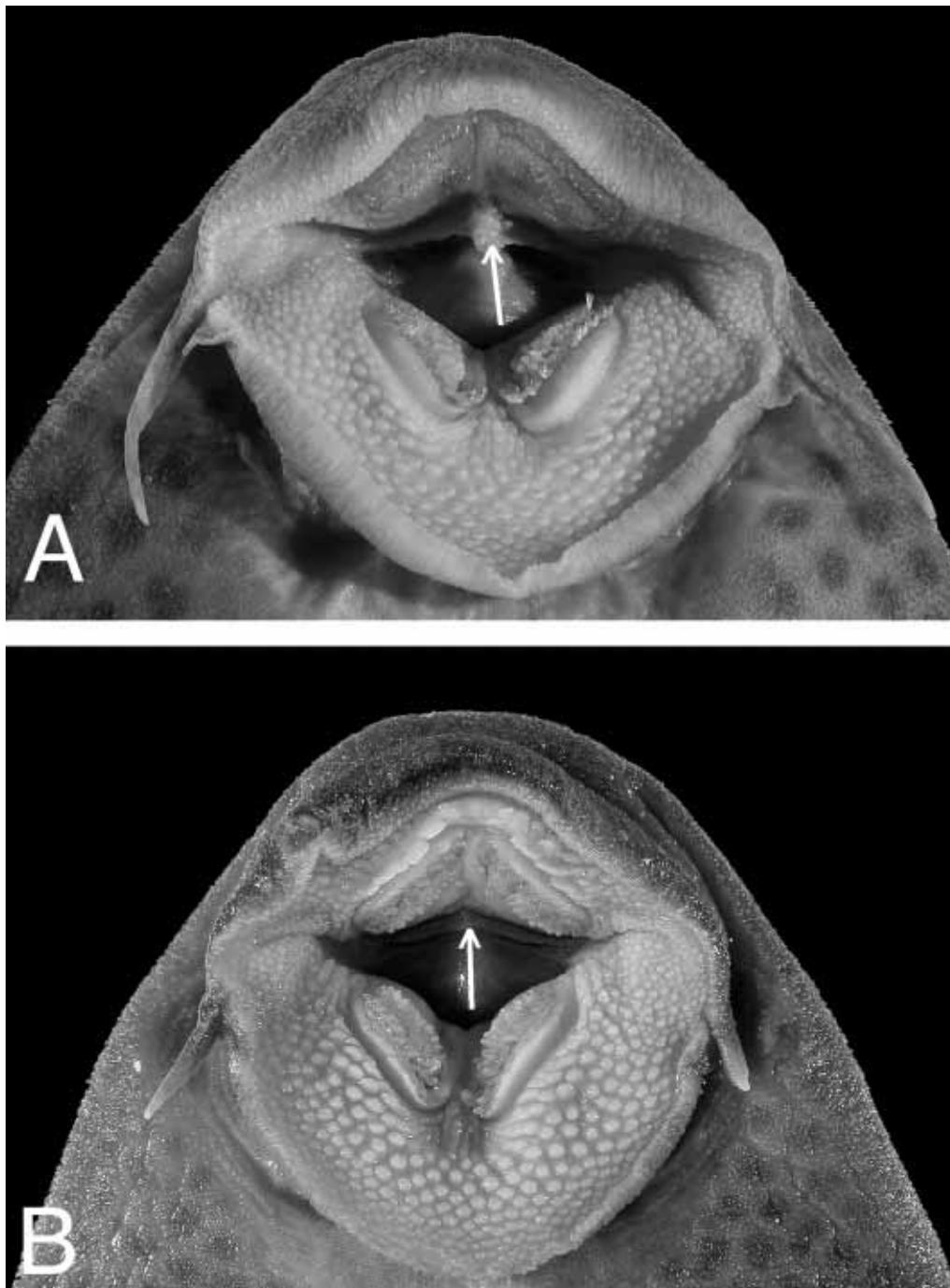


FIGURE 3. Lateral view of suspensorium (left) and maxilla (right) of A. *Hypostomus plecostomus*, ZMA 105.306 and B. *Hypostomus taphorni*, ANSP 168195. Arrow in A indicates notch between hyomandibula and metapterygoid (absent in B). Arrow in B indicates the area of the preoperculo-hyomandibular ridge that is deflected posteriorly (absent in A). Shaded area is cartilage. Scale = 1 mm.

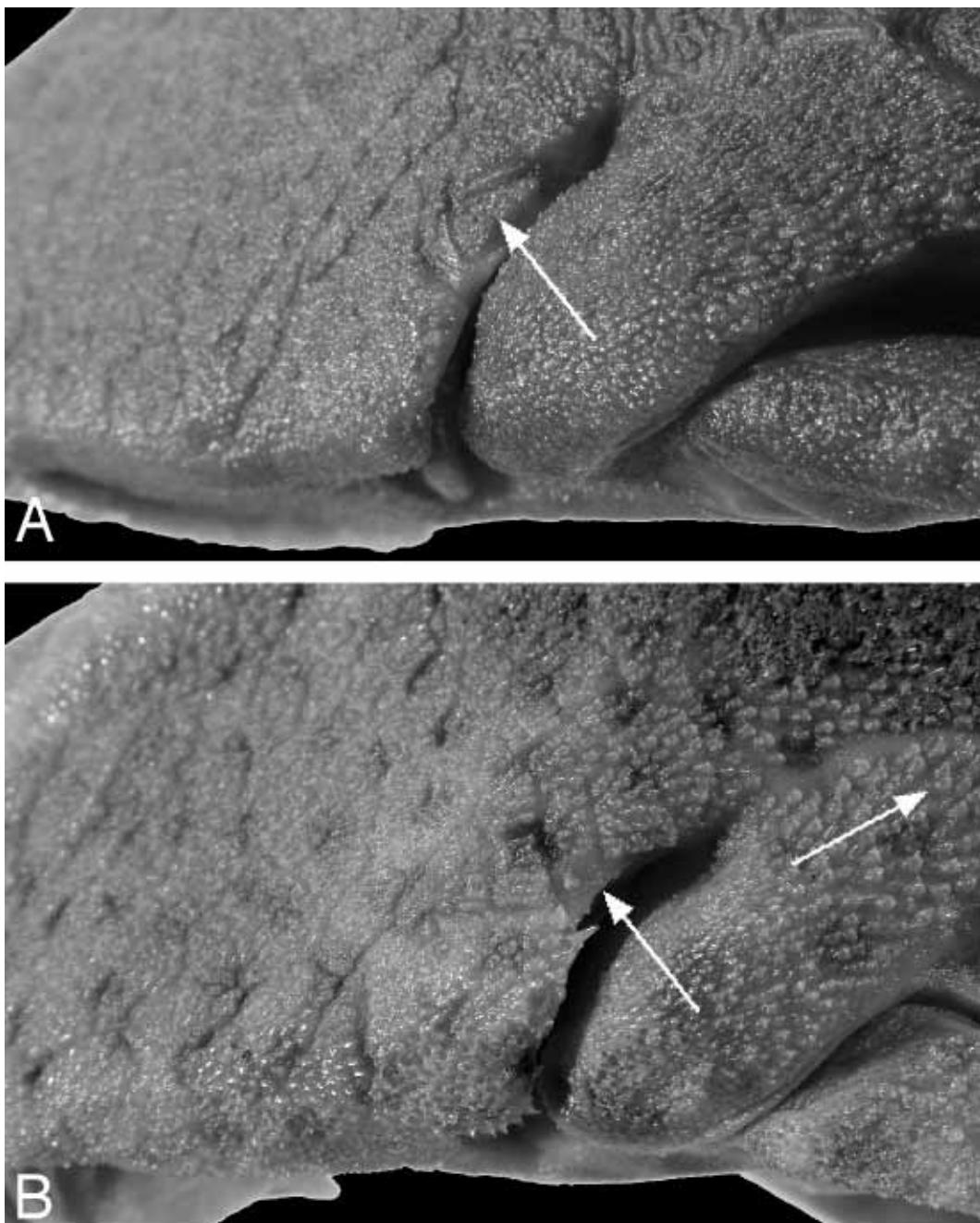


FIGURE 4. Buccal papilla of A. *Hypostomus sculpodon*, MCNG 37042 and B. *H. plecostomoides*, INHS 34682. Arrow indicates papilla in A and area of papilla in B.

The *Hypostomus cochliodon* group can be distinguished from most other loricariids by the combination of highly angled jaws and usually less than 20 teeth per jaw ramus (occa-

sional specimens of *H. cochliodon*, *H. hondae*, and *H. hemicochliodon* have been observed with counts of up to 27 teeth). Among the Hypostominae, the *H. cochliodon* group differs from *Pterygoplichthys* by having seven dorsal-fin rays (vs. nine or more); from *Pogonopoma*, *Pseudorinelepis*, and *Rhinelepis* by having the dorsal flap of the iris present (vs. flap absent; Armbruster 1998) and by having four anal fin rays (vs. five); from *Corymbophanes*, by having 0-2 median, unpaired plates posterior to the dorsal fin (vs. 3 or more); from most of the Ancistrini by not being able to evert the cheek plates any greater than 30° (vs. 75°-90°); from *Spectracanthicus* (Ancistrini) by having the dorsal fin separate from the adipose fin (vs. contacting adipose-fin spine) and by having plates on the abdomen in adults; and from *Pseudancistrus* (Ancistrini) by lacking hypertrophied odontodes on the cheek and snout margin and by having plates on the abdomen in adults.

Hypostomus microstomus Weber shares with the *H. cochliodon* group highly angled jaws and a low number of large teeth (Weber 1987); however, the teeth of *H. microstomus* are not spoon-shaped or tending towards being spoon-shaped. In addition, *H. microstomus* is dark gray to black with light spots versus brown with dark spots as in the *H. cochliodon* group.

Some *Hypostomus* such as *H. plecostomus* are variable in the angle between the dentaries. Some specimens of *H. plecostomus*, for example, have a dentary angle less than 80°. They differ from the *H. cochliodon* group by having greater than 20 teeth per ramus. Species similar to *H. plecostomus* also tend to have the head as wide or wider than tall while species of the *H. cochliodon* group tend to have the head taller than wider.

Description: Fairly large loricariids, reaching 300 mm SL. Color typically dark brown with spots generally developed over most surfaces. Most species observed have a well-developed ability to alter color according to substrate.

Body shape in all except *Hypostomus sculpodon* deep at origin of the dorsal fin (appearing deeper than in other *Hypostomus*) then narrowing posteriorly more quickly than in *Hypostomus* causing body to appear humped. Body of *H. sculpodon* not as deep. Body depth increases from snout to tip of supraoccipital at steep angle, angle of body depth increase decreases from tip of supraoccipital to dorsal-fin spinelet.

Rounded ridge present from anterodorsal corner of orbit to posterior margin of nares; ridge widest and tallest posteriorly. Rounded ridge present from posterodorsal corner of eye to end of pterotic-supracleithrum (additional, sharp ridge of bone and moderately enlarged odontodes present on pterotic-supracleithrum in *H. cochliodon*, *H. hemicochliodon*, and *H. sculpodon*). Space between orbits concave such that dorsal rim of orbit raised above medial surface of head. Nares separated by flap of skin held erect in life.

Dorsal, supramedian, median, and inframedian plate rows complete from head to caudal fin, ventral plate row begins at insertion of pelvic fin and continues to caudal fin. Lateral plates usually with median keels formed from ridge of bone and enlarged odontodes; height of keels vary from absent to tall with odontodes very sharp; keels may be present or absent on any row of lateral plates; keels of first three plates of supramedian plate row

angled dorsally, often confluent with keel of dorsal plate row; keels on first three plates of dorsal row forming angle from tip of supraoccipital to posterolateral corner of nuchal plate, not confluent with keel on dorsal plate row beginning on fourth plate. Base of caudal fin covered in elongate, roughly triangular plates. Entire ventral surface of head and body (including space above pectoral- and pelvic-fin rays) of adults covered in small platelets, platelets often extending onto base of pectoral- and pelvic-fin rays ventrally. Small platelets usually present in skin between dorsal fin and lateral plates of adults. Platelets on abdomen and near fins increase in number with standard length. Head covered in small plates. Frontal, nasal, sphenotic, infraorbitals, pterotic-supracleithrum, suprapreopercle, and supraoccipital supporting odontodes. Opercle supports odontodes in some species. Some odontodes present on posterior margin of preopercle. Platelets that cover anteroventral corner of opercle slightly separated from opercle allowing plates to be marginally everted (angle of eversion less than 30°).

Dorsal fin consisting of small, v-shaped spinelet, fairly strong spine, and seven rays. Caudal fin strongly forked, lower lobe longer than upper. Pectoral-fin spine strong, generally reaches posterior to pelvic-fin rays when depressed ventral to pelvic fin; cleithrum with exposed process dorsal to pectoral-fin rays that tapers posteriorly to point; pectoral-fin inserted on same plane as pelvic fin such that spine, when depressed parallel with body, lies on top of and in contact with pelvic fin. Pelvic-fin spine thin, flexible, generally reaches beyond base of anal fin. Anal fin with relatively strong, unbranched first ray that supports odontodes. Adipose fin (when present) consisting of single median, unpaired preadipose plate and a stout, strong, pointed spine; adipose-fin membrane generally extending to anterior-most procurent caudal-fin spine or just anterior to procurent caudal-fin spines. Dorsal fin II7; pectoral fin I6; pelvic fin I5, anal fin I4, caudal fin I14I.

Jaws strongly angled, dentaries typically forming angle of less than 80°. Teeth few (5-27, mode = 10), generally shorter and wider than most *Hypostomus* (Fig. 1B-C); teeth of most species spoon-shaped (Fig. 1C).

Range: From the Amazon, Aroa, Atrato, Essequibo, La Plata, Magdalena, Orinoco, Sinu, Tocuyo, Tuy, and Yaracuy river drainages and the Lake Maracaibo drainage.

Ecology: Individuals of the *Hypostomus cochliodon* group are most typically collected in slow-flowing, small- to medium-sized rivers, although they may also be collected in piedmont streams. They are typically associated with submerged logs in the flowing portions of the streams.

Key to the species of the *Hypostomus cochliodon* group

- | | | | |
|---|---|--|---|
| 1 | Adipose fin absent..... | <i>Hypostomus levis</i> (Upper Río Madeira in Bolivia) | |
| - | Adipose fin present | | 2 |
| 2 | Opercle supporting few or no odontodes (0-10; Fig. 2B)..... | | 3 |
| - | Opercle supporting a large patch of odontodes (11+; Fig. 2A)..... | | 7 |

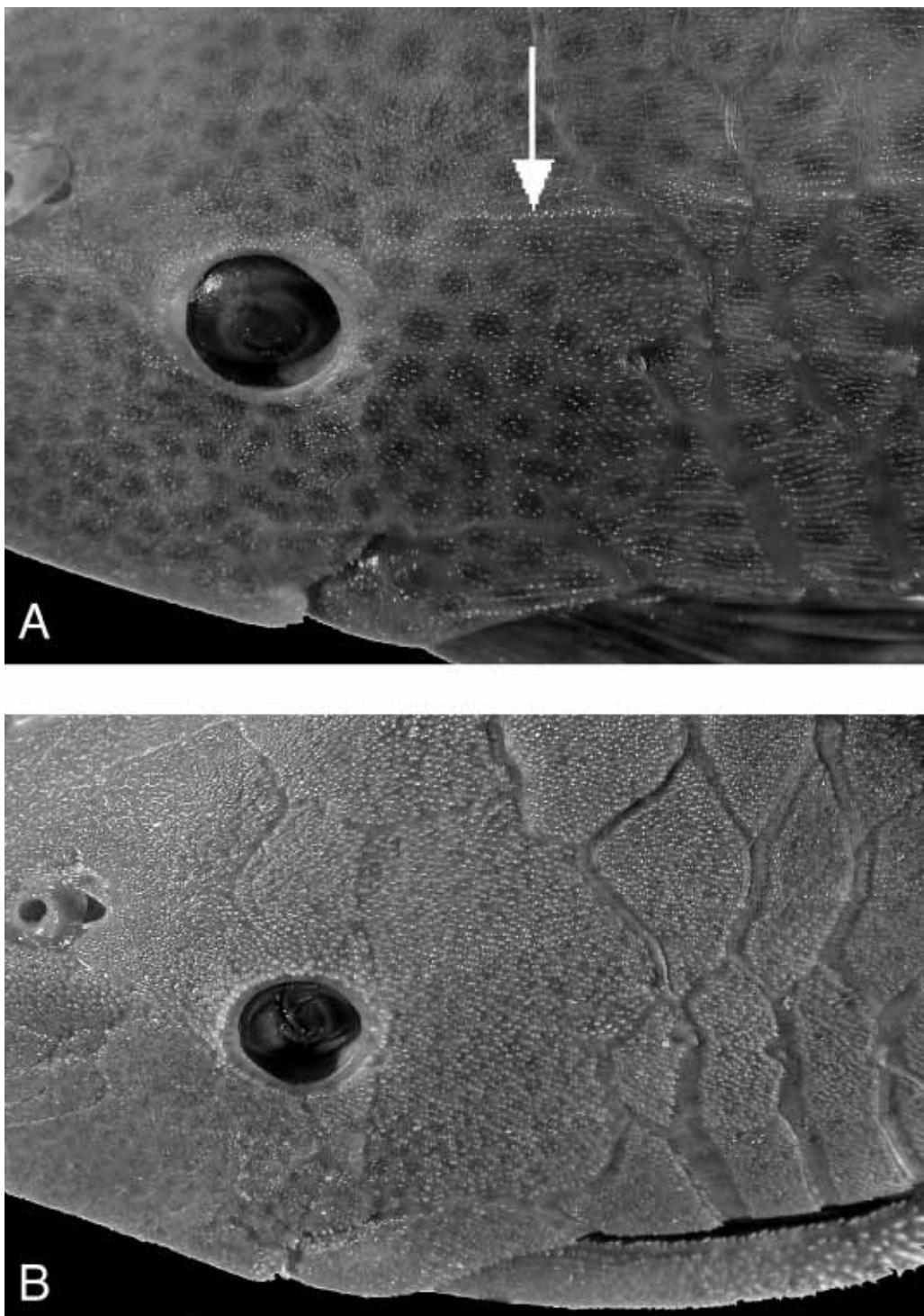


FIGURE 5. Ridge of pterotic-supracleithrum of A. *Hypostomus hemicochliodon*, MUSM 17442 and B. *H. pyrineusi*, LACM 39947-8. Arrow indicates ridge. Anterior is to the left.

- 3 Body typically with wide tan dorsal stripe formed on the ventral half of the plates in dorsal row and dorsal half of plates in supramedian row, spots, if present, few, or body entirely dark brown without spots..... *Hypostomus cochliodon* (Río Paraguay)
- Body without stripes or never entirely dark brown (spots always present) 4
- 4 Keels weak or absent..... *Hypostomus pyrineusi* (Upper Río Amazonas)
- Keels well-developed 5
- 5 Caudal fin bicolored with dorsal lobe light, ventral lobe dark; caudal fin without spots on ventral lobe except on caudal-fin spines. Adult males without modified odontodes on lateral plates (Fig. 2A)..... *Hypostomus taphorni* (Cuyuni River)
- Caudal fin with dorsal and ventral lobes similarly colored; caudal fin with spots at least on ventral lobe. Adult males with modified odontodes on lateral plates (Fig. 2B)....
- 6
- 6 Color tan or gray with dark spots widely spaced (Fig. 9).....
- *Hypostomus ericius* (Upper Río Amazonas of Peru)
- Color dark brown with dark spots closely spaced (Fig. 16).....
- *Hypostomus ocaleus* (Upper Río Amazonas of Peru, Colombia, and Ecuador)
- 7 Body typically with wide tan dorsal stripe formed on the ventral half of the plates in dorsal row and dorsal half of plates in supramedian row, spots, if present, few, or body entirely dark brown without spots. Adult males with modified odontodes on the lateral plates (Fig. 2B). Located only in the Río de La Plata drainage).....
- *Hypostomus cochliodon* (Río Paraguay)
- Body without stripes or never entirely dark brown, spots always present. Adult males without modified odontodes on the lateral plates (Fig. 2A). Río Amazonas drainage and drainages north of Río Amazonas 8
- 8 Buccal papilla tiny or absent (Fig. 3B). Teeth wide with short stalk and with distinctly spoon-shaped cusp (Fig. 1C). Ridge absent on pterotic-supracleithrum (Fig. 5B)
- 9
- Buccal papilla medium to large (Fig. 3A). Teeth narrow with long stalk and not with distinctly spoon-shaped cusp (Fig. 1B). Ridge present on pterotic-supracleithrum (Fig. 5A).....
- 12
- 9 Caudal fin strongly bicolored with dorsal lobe light, ventral lobe dark. Spots on abdomen very small (Fig. 22)..... *Hypostomus taphorni* (Cuyuni River)
- Caudal fin not strongly bicolored with either dorsal lobe light at the base and dark at the tip and ventral lobe dark, or entire fin light, or entire fin with spots that form vertical bands. Spots on abdomen small to large, but never as shown in figure 22..... 10
- 10 Caudal-fin spines lightly colored, generally without spots although juveniles occasionally have some faint spots. Ríos Aroa, Tucuyo, and Yaracuy
- *Hypostomus pagei* (ríos Aroa, Tucuyo, and Yaracuy)
- Caudal-fin spines darkly colored, almost black or with spots. Ríos Orinoco and Tuy and Lago Maracaibo drainages and west of Andes..... 11

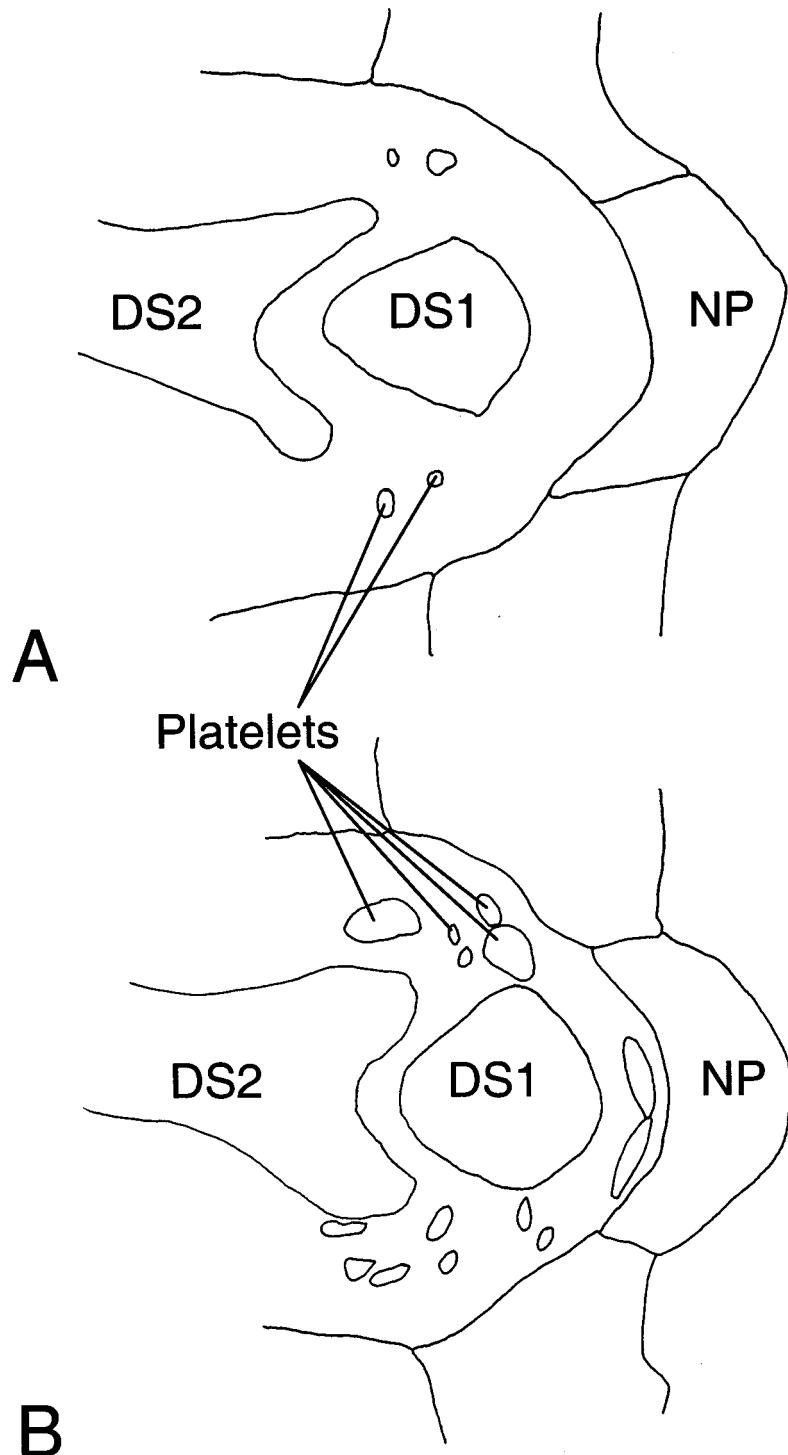


FIGURE 6. Dorsal view of dorsal surface of A. *Hypostomus plecostomoides* and B. *H. hondae* showing the distribution of platelets in the skin. Head is to the right. DS = dorsal spine, NP = nuchal plate.

- 11 Relatively small number of plates in skin between dorsal-fin spine and spinelet and lateral plates (number of plates depends on SL, see Fig. 6A; Table 7).....
..... *Hypostomus plecostomoides* (Río Orinoco)
- Tends to have relatively large number of plates in skin between dorsal-fin spine and spinelet and lateral plates (number of plates depends on SL, see Fig. 6B; Table 7; some specimens from the Rio Atrato lack this trait).....
..... *Hypostomus hondae* (ríos Atrato, Magdalena, and Sinu and Lago Maracaibo)
- 12 Spots on body, if present, not widely-spaced, body color dark brown to black. Buccal papilla small. Dorsal-anal length to anal-fin length ratio 92.5-132.6% (average = $111.1 \pm 8.4\%$). Interorbital width/HL ratio 44.1-55.6% (average = $49.9 \pm 2.7\%$).....
..... *Hypostomus hemicochliodon*
(Ríos Amazonas, Negro, Tapajos, and Xingu and upper Río Orinoco)
- Spots on body widely-spaced, body color reddish brown. Buccal papilla very large. Dorsal-anal length to anal-fin length ratio 69.6-89.7% (average = $79.2 \pm 7.6\%$). Interorbital width/HL ratio 38.5-45.4% (average = $51.4 \pm 3.1\%$).....
..... *Hypostomus sculpodon* (upper ríos Negro and Orinoco)

Hypostomus cochliodon Kner 1853

(Fig. 7)

Hypostomus cochliodon Kner 1853: 265-267, pl. 2 fig. 1.

Hypostomus hypostomus Heckel, in Kner 1853: 265 (name published in synonymy of *Hypostomus cochliodon*).

Loricaria melanoptera Natterer, in Kner 1853: 265 (name published in synonymy of *Hypostomus cochliodon*)

Material examined: UNKNOWN LOCALITY. AMNH 97884, 2, (80.9-155.5). BRAZIL. Mato Grosso: Rio Cujaba, NMW 46277, 1 (152.9, lectotype) and NMW 44101 (179.3, paralectotype). Near Cuiabá, AMNH 97880, 9, 1 cs, (68.9-124.2). Arroio, Rio do Bugre - Rio Jauru - Rio Paraguai dr. at km 165 on Estrada Porto Esperidião/Pontes e Lacerda (BR 174), ca 48 km de Esperidião, USNM 326357, 4, 1 cs, (75.8-143.6). Arroio Cruzando, Rio Paraguai dr. on estrada Tangara da serra 1, Barra do Bugres, near nova Olimpia, USNM 326319, 2, 1 cs, (70.5-96.6). PARAGUAY. Alto Paraguay: Arroyo Ytyguazu, Río Paraguay dr. Primavera, Caacupe, ANSP 124105, 1, (111.4). Río Apa, Río Paraguay dr. ca 0.5 km upstream (=east) of bridge between Brazil and Paraguay in Bella Vista, $22^{\circ}06'30''S$, $56^{\circ}30'W$, UMMZ 206797, 6, (122.6-211.38). Amambay: Río Aquidaban, Río Paraguay dr. at Paso Horqueta, ca 24 km NNW of Loreto, $23^{\circ}03'48''S$, $57^{\circ}23'W$, UMMZ 207821, 1, (151.4). Río Aquidaban, Río Paraguay dr. in Parque Nacional Cerro Cora ca 32 km WSW of Pedro Juan Caballero, $22^{\circ}38'12''S$, $56^{\circ}03'W$, UMMZ 206767, 1, (130.0). Río Aquidaban, Río Paraguay dr. Parque Nacional Cerro Cora, USNM 232310, 1, (131.1), USNM 232312, 2, (119.4-164.4), and USNM 232311, 1, (146.7). Canendiyu: Río Jejui, Rio Jejui-

Guazu - Río Paraguay dr. ca. 41 km N Curuquaty and 2 km S Ygantini, 24°08'12"S, 55°37'W, UMMZ 206338, 3, 3 cs, (142.2-168). *Concepción*: Río Ypané, Río Paraguay dr. at ferry crossing, ca 2.0 km S by dirt road to Belen (which is ca 18 km ESE Concepcion), 23°29'30"S, 57°15'W, UMMZ 207988, 5, 2 cs, (80.3-113.1) and UMMZ 207989, 3, (66.1-76.3). *Cordillera*: Río La Plata dr. 1.6 km by road S of Tobati, UMMZ 203865, 1, (140.8). Arroyo Tobati, Río Paraguay dr. small river ca. 0.3 km E of dirt road, 1.6 km S of Tobati, 25°18'30"S, 57°04'W, UMMZ 205771, 1, (151.6) and UMMZ 205770, 1, (148.0). Arroyo Tobati, Río Piribebuy - Río Paraguay dr. ca 0.1 km east of Tobati, 25°16'14"S, 57°03'W, UMMZ 205809, 1, (106.5). Arroyo Yaguary-Guazú , Río Aquidaban dr. at bridge on dirt highway (Route #5) ca 26.1 km NE of junction with Route#, ca 68 km WSW of Pedro Juan Caballero, 27°47'24"S, 56°21'W, UMMZ 206691, 1, 147.0). *Paraguari*: Río Tebicuary dr. Salto de Pirareta, ca. 400 m below falls, 5.8 km S. of Piribebuy and 10 km W on dirt road, UMMZ 205673, 3, (112.4-170.5). *San Pedro*: Río Ypané, Río Paraguay dr. on S bank at bridge on dirt highway, 52.7 km S of jct. with highway #5 at Yby-Yau, 23°27'18"S, 56°31'W, UMMZ 208023, 1, (164.0) and UMMZ 208024, 2, (94.9-120.1). *Villa Hays*: no exact locality, FMNH 59735, 1, (151.7).

Diagnosis: *Hypostomus cochliodon* can be distinguished from all other members of the *H. cochliodon* group by its almost entirely brown coloration with ventral half of dorsal plate row and dorsal half of supramedian plate row slightly lighter than lower rows forming a tan stripe, and spots, when present, small and widely placed (vs. spots usually well-developed and closely placed). Unlike most other members of the *H. cochliodon* group, *H. cochliodon* can also be entirely dark brown with no spots anywhere on the body (other members of the *H. cochliodon* group may be very dark, but will retain spots on fins or the abdomen).

Description: See *Hypostomus cochliodon* group description for more details. Morphometric data given in Table 1. Color normally almost entirely dark brown with wide, tan stripes dorsally and ventrally. Tan dorsal stripe on ventral half of dorsal plate row and dorsal half of supramedian plate row; stripe sometimes crossed by dark saddles or with dark spots anteriorly. Tan ventral stripe on ventral half of inframedian plate row and entire ventral plate row. Dorsal stripe forks on nape with one branch continuing straight to eye and other branch ending at posterior tip of supraoccipital. Tan wedge occasionally present at base of supraoccipital crest. Dorsal surface of snout light or mottled. Spots on body often absent, but sometimes present on any part of the body, well separated from one another. Abdomen colored as sides, but usually slightly lighter. Color entirely dark brown without spots in some individuals.

Dorsal fin usually short, not reaching preadipose plate when depressed in most specimens. Depressed pectoral-fin spine ventral to pelvic fin reaches beyond bases of pelvic-fin rays. Tip of pectoral-fin spine of nuptial males with stout, recurved, hypertrophied odontodes.

Keels moderate to well-developed; keel odontodes occasionally sharp. Orbita forming

ridge distinctly raised above medial surface of head; ridges of dorsal and lateral aspect of head well-developed. Longitudinal ridge on pterotic-supracleithrum beginning at postero-dorsal corner of eye formed from raised bone and slightly larger odontodes present. Opercle usually supporting much more than 10 odontodes; in some specimens the opercle does not support odontodes (see Comments). Nuptial body odontodes present (Fig. 2B). Plates in skin anterior to dorsal-fin spines few or absent (Fig. 6A; Table 7).



FIGURE 7. Dorsal, lateral, and ventral views of *Hypostomus cochliodon*, AMNH 97884, 155.5 mm SL.

TABLE 7. Number of plates in the flesh around the dorsal-fin spine and spinelet by size in the *Hypostomus cochliodon* group.

SL (mm)	<i>H. hondae</i>	Other species of <i>H. cochliodon</i> group
<90	Usually 1+	0
90-175	4+	0
175+	6+	0-6

Each jaw with 6-27 teeth (mode = 12). Size of teeth variable (see Comments). Average angle between dentaries 68° ($SD = 14^\circ$; range: 42° - 99° ; $N=30$). Lateral line plates 26-30; dorsal plates 7-8; interdorsal plates 5-7; adipose caudal plates 9-11.

Range: The upper 2/3 of the Río Paraguay basin of Brazil and Paraguay (Fig. 8). *Hypostomus cochliodon* is allopatric to all other species of the *H. cochliodon* group.

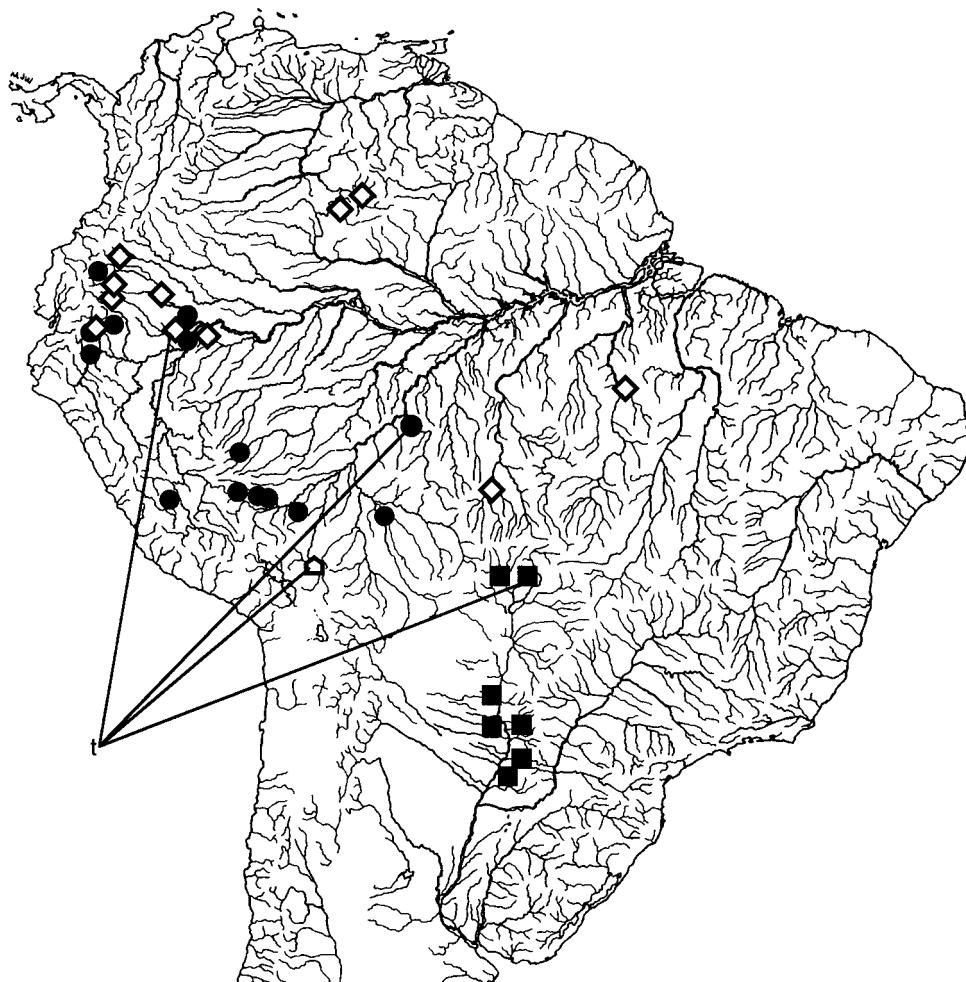


FIGURE 8. Distribution of *Hypostomus cochliodon* (squares), *H. hemicochliodon* (diamonds), *H. levis* (pentagon), and *H. pyrineusi* (dots). Type localities indicated by "t".

Comments: The smallest juveniles often have teeth very similar to algivorous-detritivorous species of *Hypostomus*. As *Hypostomus cochliodon* grow, the teeth apparently are replaced by successively larger, more spoon-shaped teeth, and tooth number decreases. *Hypostomus cochliodon* is variable in color pattern, size of keels, and number of odontodes on the opercle (0 to 30). The variation in number of odontodes may indicate that *H. cochliodon* as presently delimited may represent more than one species; however, the variation in opercular odontode number does not appear to be correlated with variation in other characteristics.

***Hypostomus ericius* new species**

(Fig. 9)

Holotype: PERU. Amazonas: Río Marañon dr. 1 km upstream from Caterpiza, MUSM 17441, 1, (186.8 mm SL).

Paratypes: PERU. Amazonas: Río Marañon dr. 1 km upstream from Caterpiza, MUSM 17441, 1, (186.8). Río Marañon dr. 200 m downstream from Caterpiza, LACM 42004-9, 1, (148.3). Río Marañon dr. Caterpiza, LACM 41893-6, 1, (80.5) and USNM 357392, 1, (93.6). Quebrada Pastazilla, Río Santiago - Río Marañon dr. LACM 39947-7, 1, (120.9). Loreto: Río Amazonas dr. Iquitos, AMNH 218035, 1, (85.1). Río Itaya, Río Amazonas dr. approx. 10 km S Santa Clara, INHS 36876, 1, (80.1). Río Itaya, Río Amazonas dr. upriver of Belém, approx. 4.5 km, Loreto, Peru, 3°47.71'S, 73°17.29'W, SIUC 29195, 1, (94.8). Río Nanay, Río Amazonas dr. sand beach on right bank, 0.25 mi below and across river from Nina Rumi, 03°44'S, 73°20'W, ANSP 176149, 1, (104.5).

Diagnosis: *Hypostomus ericius* can be separated from all other members of the *H. cochliodon* group by coloration: light tan-gray with well-separated spots and no stripes. In addition, *H. ericius* differs from *H. hemicochliodon* by a lack of a buccal papilla and from *H. pyrineusi* by the presence of strong, sharp keels on the lateral plates. *Hypostomus ericius* is most similar to *H. ocaleus* from which it differs mainly in coloration and morphometrics (Fig. 10B).

Description: See *Hypostomus cochliodon* group description for more details. Morphometric data given in Table 1. Coloration generally tan-gray with large, widely-spaced spots. Spots present over entire body and becoming larger posteriorly. Caudal-fin membrane and rays often with black wash distally, and lighter area proximally instead of being spotted. Spots on fin spines and rays occasionally large. Spots less pronounced in juveniles, spots may be absent on abdomen. Juveniles with four faint dorsal saddles: first below anterior rays of dorsal fin, second below posterior rays of dorsal fin and slightly posterior to dorsal fin, third slightly anterior to and ventral to adipose fin, and fourth at base of caudal fin.

Dorsal fin moderately long, usually just barely reaching preadipose plate when depressed. Depressed pectoral-fin spine ventral to pelvic fin reaches beyond bases of pel-

vic-fin rays. Pectoral-fin spine supporting numerous stout, recurved, hypertrophied odontodes in nuptial males.

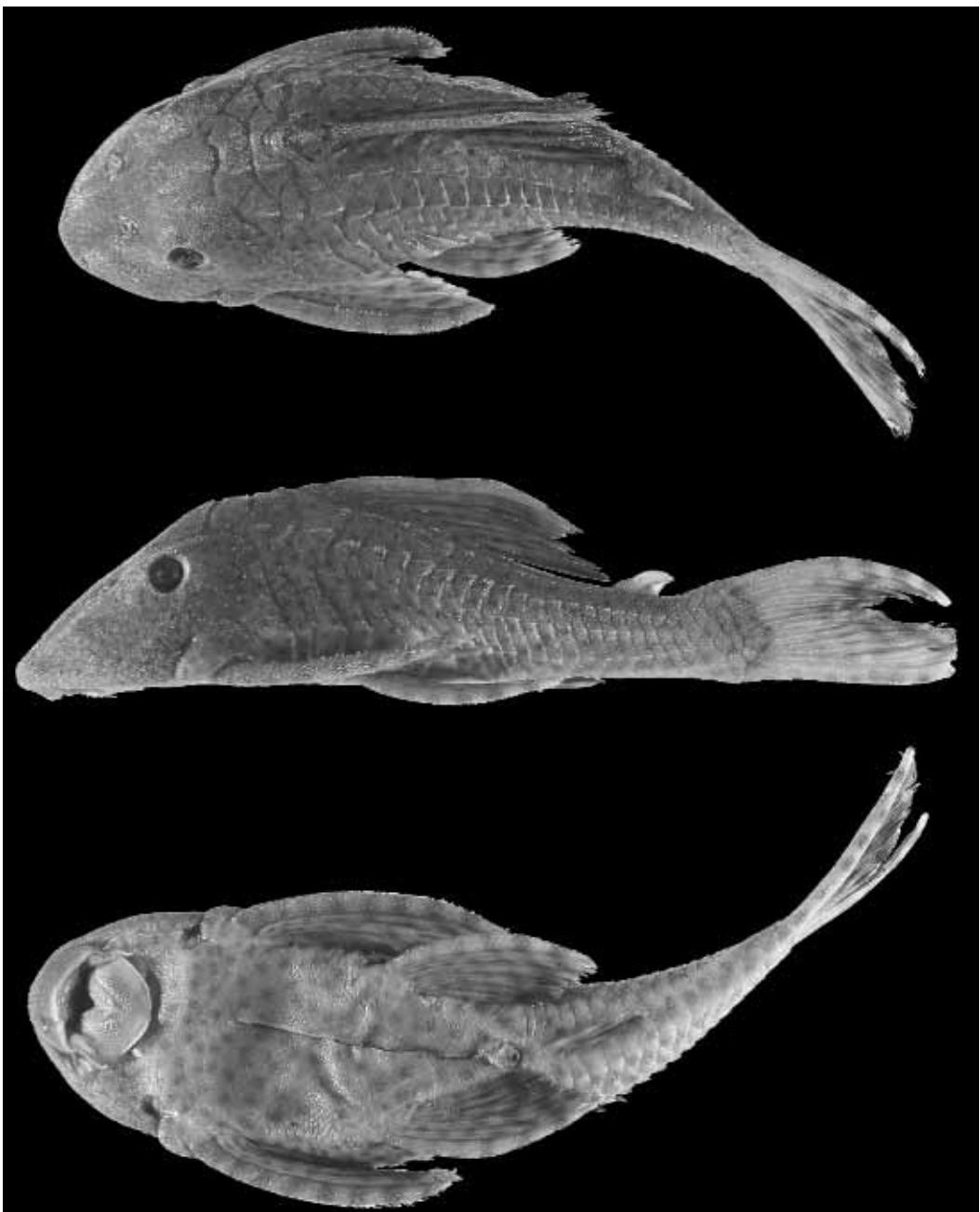


FIGURE 9. Dorsal, lateral, and ventral views of *Hypostomus ericius*, new species, LACM 42004-9, paratype, 148.3 mm SL.

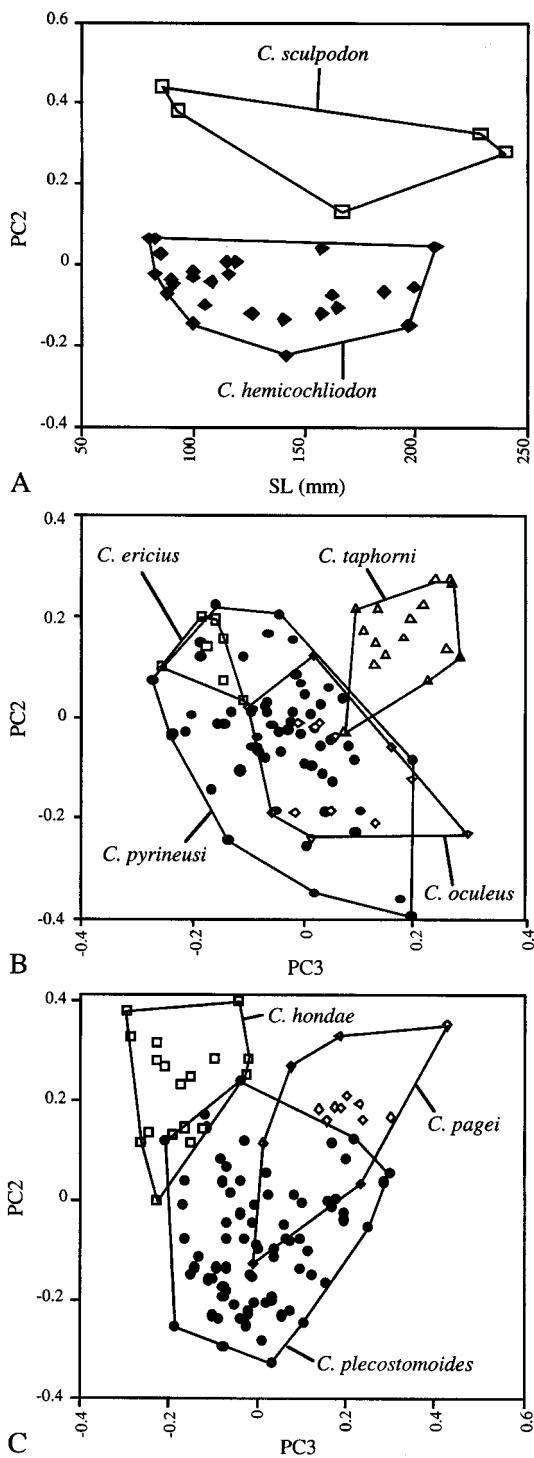


FIGURE 10. Results of principal components analysis. A. PC2 vs. SL for intermediate group, B. PC2 vs. PC4 for the odontodeless opercle group, C. PC2 vs. PC3 for the northern group.

Keels sharp, very strongly developed. Orbita forming ridge distinctly raised above medial surface of head; ridges of dorsal and lateral aspect of head well-developed. Longitudinal ridge formed of raised bone and slightly larger odontodes absent on pterotic-supraclerithrum beginning at postdorsal corner of orbit. Opercle usually not supporting odontodes, but sometimes up to 10 odontodes may be present on opercle (Fig. 2B). Nuptial body odontodes present (Fig. 2B). Plates in skin anterior to dorsal-fin spine usually absent or not numerous (Fig. 6A; Table 7). Cheek plates generally support several stout odontodes slightly larger than surrounding odontodes. Head appears wider and taller than in other species of *Hypostomus*.

Each jaw with 5-9 teeth (mode = 7), teeth large and spoon-shaped. Average angle between dentaries 53° (SD = 9°; range: 40°-69°; N=7). Lateral line plates 27-28; dorsal plates 7-9; interdorsal plates 5-7; adipose caudal plates 9-10.

Range: Currently known from the Ríos Marañon, Itaya, and Nanay of the Upper Río Amazonas drainage of Peru (Fig. 11). *Hypostomus ericius* is sympatric with *H. hemicochliodon*, *H. oculatus*, and *H. pyrineusi*.

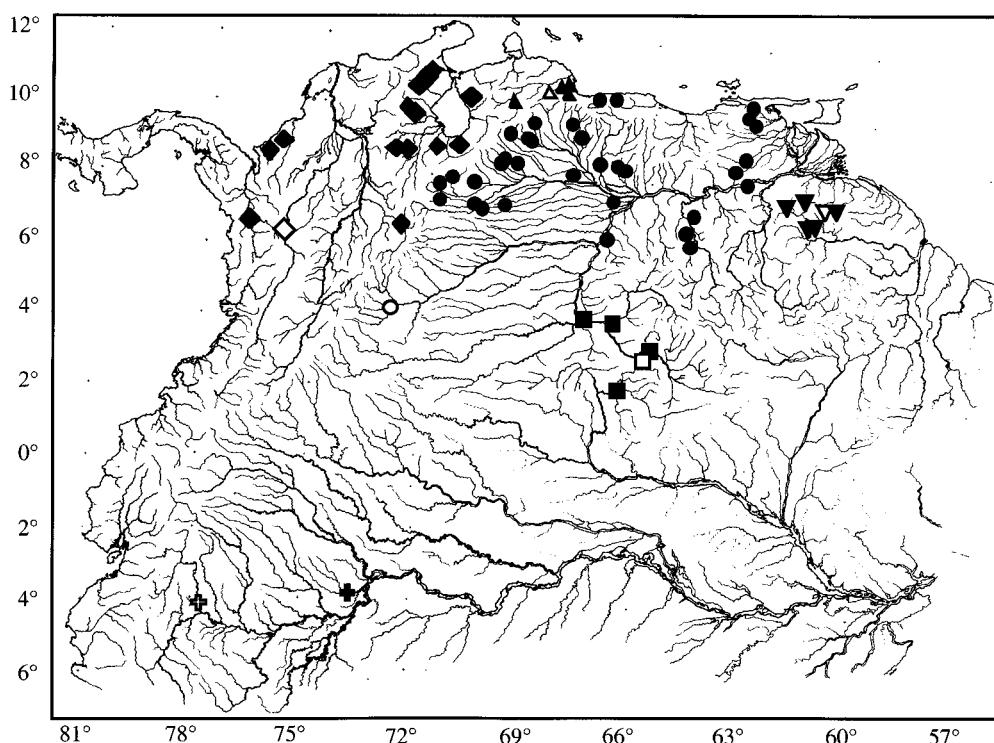


FIGURE 11. Distribution of *Hypostomus ericius* (pluses), *H. hondae* (diamonds), *H. pagei* (triangles), *H. plecostomoides* (dots), *H. sculpodon* (squares), and *H. taphorni* (inverted triangles). Open symbols are type localities.

Etymology: From the Latin, *ericius*, for hedgehog in reference to the many sharp odontodes on the keels.

***Hypostomus hemicochliodon* new species**

(Fig. 12)

Holotype: PERU. Río Nanay, Río Amazonas dr. at Pampa Chica, 4.54 km from Iquitos center, 269° bearing, 03°45'07"S, 73°16'59"W, MUSM 17442, 1, (126.2 mm SL).

Paratypes: PERU. *Amazonas*, Río Marañon dr. 500 m upstream from Caterpiza, LACM 42013-4, 1, (87.8). Río Marañon dr. Caterpiza, LACM 41886-2, 1, (100.3) and LACM 41893-4, Amazonas, Quebrada, Río Santiago - Río Marañon dr. quebrada enters Río Santiago from east, 2/3 length of island downstream of La Poza, LACM 39862-5, 1, (80.1). Quebrada Kayamasa, Río Marañon dr. 40 km upstream from Caterpiza, LACM 41853-3, 1, (206.9). Quebrada Pastazilla, Río Santiago - Río Marañon dr. LACM 39947-5, 2, (109.7-118.9) and LACM 39937-6, 1, (162.6). Río Santiago, Río Marañon dr. at La Poza, FMNH 97010, 1, (115.1) and LACM 41729-34, 1, (91.3). *Loreto*, Caño Sacarito, Río Orosa - Río Amazonas dr. about 35 min by boat upstream from mouth of Tonche Caño, 67.1 mi ENE Iquitos, 03°36'50"S, 72°16'55"W, INHS 39690, 1, (84.6), AUM 28907, 1 (82.8). Río Itaya, Río Amazonas dr. approx. 10 km S Santa Clara, INHS 36878, 1, 1 cs, (99.8) and SIUC 36690, 1, (93.8). Río Itaya, Río Amazonas dr. ca. 4-5 km upstream from Iquitos (Belém) above and below mouth of Quebrada Manzana, 03°47'71"S, 73°17'29"W, INHS 39962, 1, (100.5). Río Itaya, Río Amazonas dr. near Iquitos, AMNH 218019, 1, (82.1). Río Nanay, Río Amazonas dr. at Pampa Chica, 4.54 km from Iquitos center, 269°bearing, 03°45'07"S, 73°16'59"W, INHS 50131, 2, 1 cs, (80.6-107.8).

Nontype material: BRAZIL. *Mato Grosso*, Rio Juruena, Rio Tapajos dr. upper Rio Juruena, USNM 199225, 1, (119.3). Rio Xingu, Rio Amazonas dr. São Felix, USNM 207509, 1, (82.7). ECUADOR: *Napo*, Río Jivino, Río Napo dr. lower 4 km (mostly) to 0.6 km upstream from mouth (most between the two ports of Limoncocha), 00°24'36"S, 76°39'00"W, FMNH 106021, 1, (105.3). Río Shushufindi, Río Aguarico dr. lower reaches, about 2 km from mouth in Río Aquarico, 00°17'30"S, 76°25'36"W, FMNH 106025, 2, (141.5-157.9). Tributary, Río Payamino dr. few km upstream from San Jose de Payamino, 00°20'12"S, 77°18'W, FMNH 106024, 1, (158.0). Tributary, Río San Miguel dr. km 50, 4.5 km S of Tipischa, FMNH 106022, 1, (208.7). Tributary, Río Churuyacu - Río Payamino dr. Tiuyacu, first tributary of Río Churuyacu upstream from mouth in Río Payamino and near mouth of Río Churuyacu, 00°29'30"S, 77°18'W, FMNH 106023, 3, (112.6-197.2). Río Corrientes, Río Napo dr. eastern Ecuador, FMNH 92633, 3, 1 cs, (78.6-89.8). VENEZUELA. *Amazonas*, Caño Jenita, Río Ocamo dr. Oramo department, in an old meander 1 km river km above the Río Ocamo, 02°46'N, 64°54'W, MCNG 24332, 1, (142.3). Laguna Pacón, Río Orinoco dr. in pools behind beach along Río Ventuari about 0.5 hr above mouth, MBUCV V-23092, 1, (165.2). Río Cataniapo, Río Orinoco dr. in Las Palvas, MBUCV V-24501 (none measured). Río Mavaca, Río Orinoco dr. river above camp base, MBUCV V-19239, 1, (186.1). Río Siapa, Rio Casiquiare - Río Negro dr. Departamento Río Negro, at campsite near Laguna Cumicapi between Río Emoni and Río

Manipitare, MCNG 37041, 1, (100.3). Río Siapa, Río Casiquiare dr. near and downstream of confluence with Río Manipitare, 01°54'06"N, 65°57'05"W, MCNG 37032, 1, (199.5).

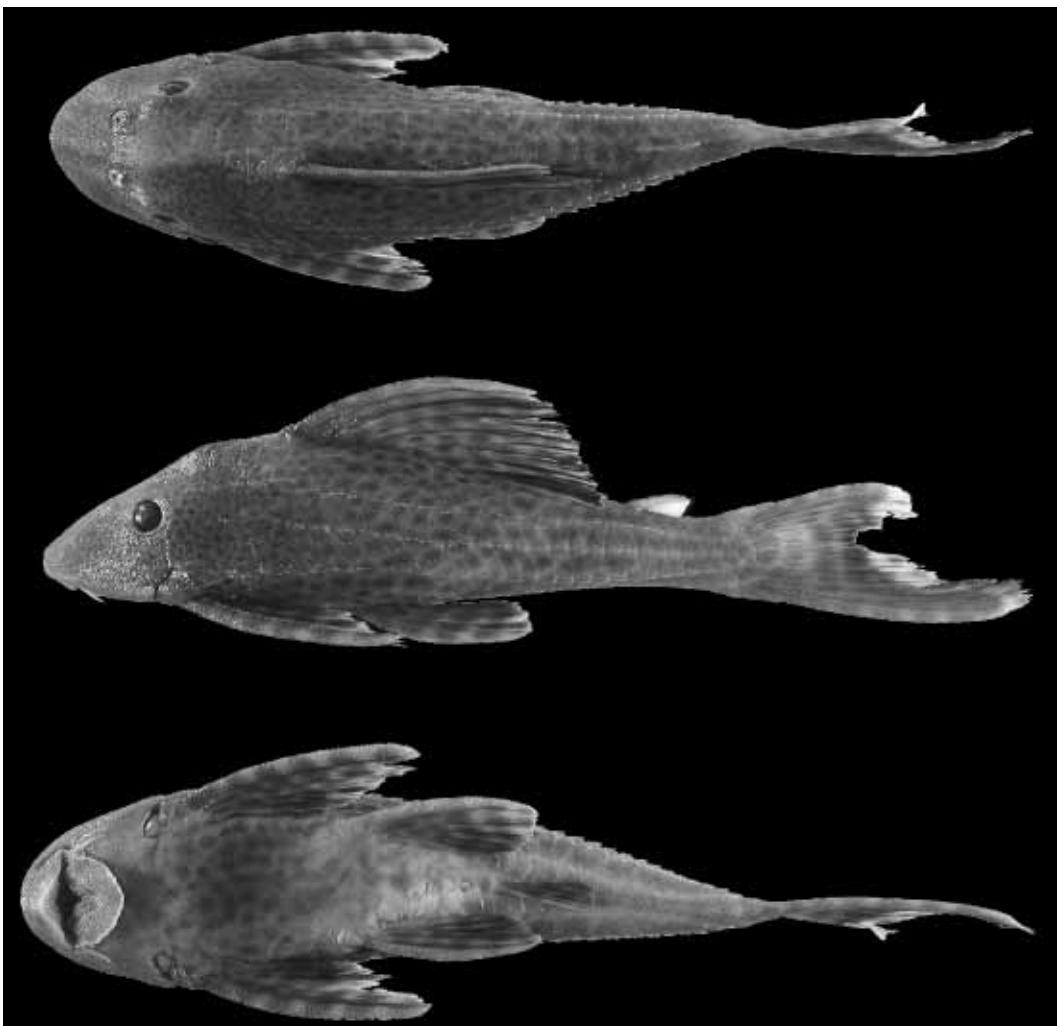


FIGURE 12. Dorsal, lateral, and ventral views of *Hypostomus hemicochliodon*, new species, MUSM 17442, holotype, 126.2 mm SL.

Diagnosis: *Hypostomus hemicochliodon* differs from all other members of the *H. cochliodon* group except *H. sculpodon* by the presence of a medium-sized buccal papilla (condition intermediate between those shown in figures 4A and 4B), intermediately developed teeth (Fig. 1B; juvenile *H. cochliodon* also occasionally have intermediate teeth), and a large patch of odontodes on the opercle. *Hypostomus hemicochliodon* differs from *H. sculpodon* by coloration (dark brown with closely spaced spots vs. brownish-red with

widely spaced spots), by having a greater dorsal-anal length to anal-fin length ratio (average = $111.1 \pm 8.4\%$, 92.5-132.6% vs. average = $79.2 \pm 7.6\%$, 69.6-89.7%), and almost completely by having a larger interorbital width/HL ratio (average = $49.9 \pm 2.7\%$, 44.1-55.6% vs. average = $51.4 \pm 3.1\%$, 38.5-45.4%).

Description: See description of the *Hypostomus cochliodon* group for more details. Morphometric data given in Table 2. Color brown with medium to large spots. Spots become larger posteriorly, often coalescing on caudal peduncle to form large, longitudinally oval dashes or stripes. Some adults with spots on body absent. Spots on abdomen variable; fairly large specimens often have few or no spots on the abdomen; abdomen often significantly lighter than sides, almost white. Four faint dorsal saddles often present: first below anterior rays of dorsal fin, second below posterior rays of and slightly posterior to dorsal fin, third slightly anterior to and ventral to adipose fin, and fourth at base of caudal fin. One captive *Hypostomus hemicochliodon* demonstrated well-developed ability to change color, particularly ability to lighten coloration of abdomen and intensify lateral spots or dorsal saddles (either spots or the saddles dominant, but never both dark at same time).

Dorsal fin fairly short, usually falls short of preadipose plate when depressed. Depressed pectoral-fin spine ventral to pelvic fin reaches 2-3 plates beyond bases of pelvic-fin rays. Tip of pectoral-fin spine of nuptial males with stout, recurved, hypertrophied odontodes.

Keels strong, sharp. Orbit forming ridge distinctly raised above medial surface of head; ridges of dorsal and lateral aspect of head well-developed. Longitudinal ridge formed of raised bone and slightly larger odontodes present on pterotic-supracleithrum beginning at postdorsal corner of orbit. Opercle broadly exposed, always supporting much more than ten odontodes. Nuptial body odontodes absent (Fig. 2A). Plates in skin anterior to dorsal-fin spine absent or few (Fig. 6A; Table 7).

Each jaw with 7-23 teeth (mode = 15), teeth of intermediate size (Fig. 1B). Average angle between dentaries 63° ($SD = 7^\circ$; range: 45° - 75° ; $N=23$). Lateral line plates 28-30; dorsal plates 8-9; interdorsal plates 6-8; adipose caudal plates 8-10.

Range: Has a wide range across central South America in the Ríos Marañon, Itaya, Nanay, Napo, and Orosa of the upper Río Amazonas of Peru, the Río Napo drainage of the Upper Río Amazonas drainage of Ecuador, the Ríos Tapajos and Xingu of the lower Río Amazonas drainage of Brazil, and the upper Río Negro drainage (middle Río Amazonas drainage) and upper Río Orinoco drainage of Venezuela. (Fig. 8). *Hypostomus hemicochliodon* is sympatric with *H. ericius*, *H. oculatus*, *H. pyrineusi*, and *H. sculpodon*.

Etymology: From the Latin, *hemi*, for half, the Latin, *coclea* (*coch-*), for spoon, and the Greek, *odon*, for tooth in reference to the fact that the teeth are about half as spoon-shaped as those of wood-specializing members of the *Hypostomus cochliodon* group.

***Hypostomus hondae* (Regan 1912)**

(Figs. 13, 14A)

Plecostomus hondae Regan 1912: 666, pl. 76 Fig. 4.
Hypostomus pospisili Schultz 1944: 312-313, pl. 11 C-D.

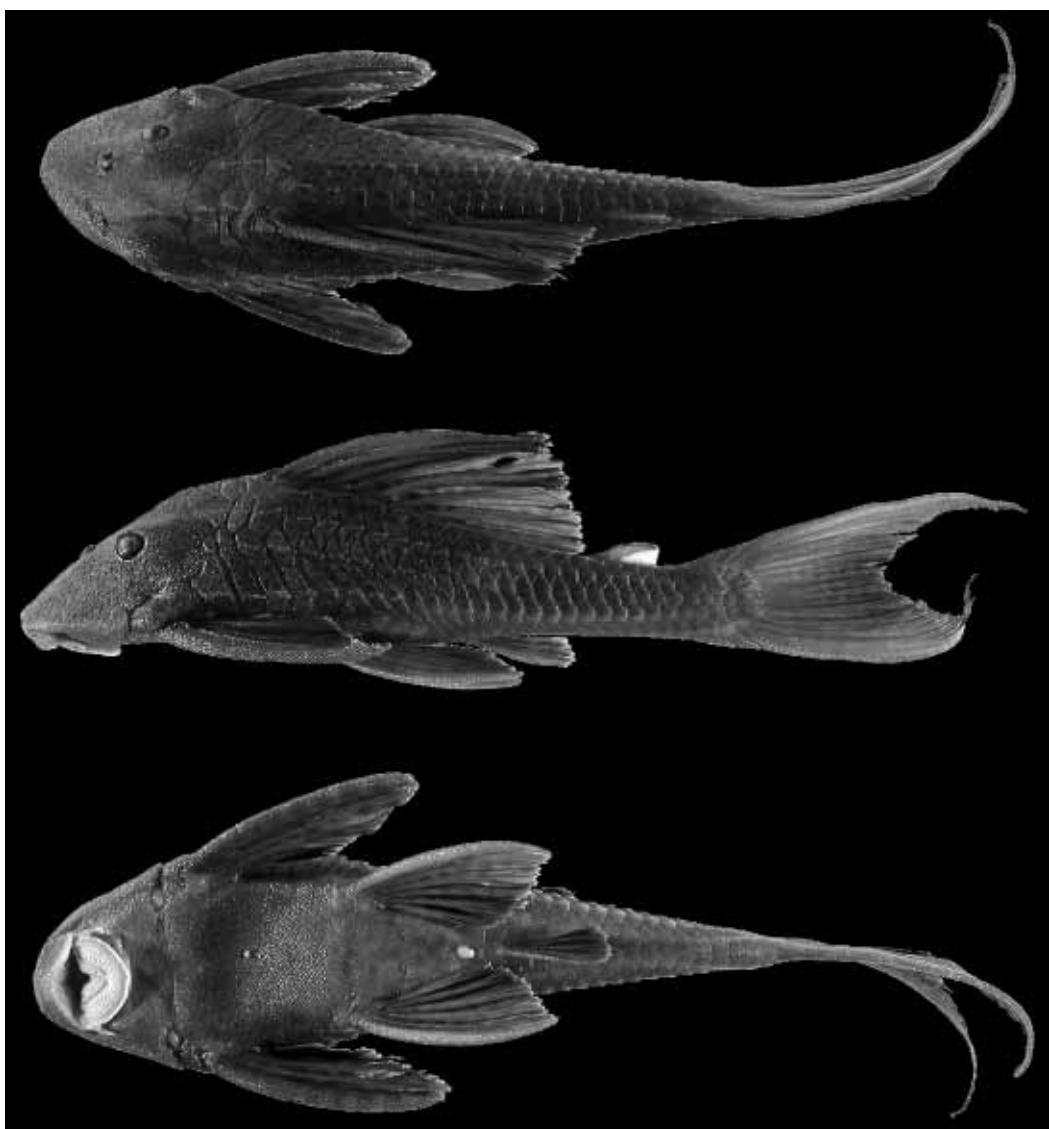


FIGURE 13. Dorsal, lateral, and ventral views of *Hypostomus hondae*, AUM 22135, 143.8 mm SL.

Material examined: COLOMBIA. Río Sinu dr. Lorica, CAS 149472, 1, 1 cs, (81.7). Probably Río Sinú, Lorica, CAS 6417, 1, (177.0). Atrato: Quibdo market, STRI 1530, 1,

(207.9) and STRI 1531, 1, (205.9). *Caldas*: Río Samana La Miel, Río Magdalena dr. at or near junction of Río Samana La Miel near La Dorada, CAS 150373, 1, (104.7). *Santander*: caño Tigre, Río Sogamosa - Río Magdalena dr. SIUC 34909, 1, (119.0). *Sucre*: Pozo del Chorro, Sinclejo, CAS 149472, 4, (81.7-107.4) and USNM 175305, 2, (79.5-102.1). *Tolima*: Honda, Colombia, BMNH 1909.7.23.43 (60.8, holotype) and BMNH 1909.7.23.44 (58.4, paratype). *VENEZUELA*. *Merida*: Río Escalante, Lago Maracaibo dr. at bridge of highway 1, 08°31'N, 71°47'W, MCNG 24843, 3, (75.0-81.4) and INHS 59864. Tributary, Río Gavilan - Lago Maracaibo dr. 3 km E Capazon, 08°49'75"N, 71°25'61"W, INHS 59881. *Zulia*: Maracaibo Expedition, MBUCV V-23883, 3, (92.5-110.5). Caño La Playa, Lago Maracaibo dr. Hacienda San Jose, MCNG 33504, 1, (85.5). Lagunas de Tule, Río Cachiri dr. MCNG 7487, 1, (226.6). Río Cachiri, Lago Maracaibo dr. MCNG 7419, 1, (92.6). Río Cachiri, Lago Maracaibo dr. at Santa Marta bridge, MCNG 33526, 1, (119.8). Río Catatumbo, Lago Maracaibo dr. at bridge on road to Machiques, MBUCV V-18491, 1, (81.0). Río Machango, Lago Maracaibo dr. 20 km above bridge, S Of Lagunillas, UMMZ 142488, 1, (57.4, paratype *H. pospisili*). Río Negro, Río Santa Ana - Lago Maracaibo dr. 12 km S Machiques on road to Tucuco, INHS 59945. Río Negro, Río Santa Ana - Lago Maracaibo dr. Bridge ca. 8 km SW Alturnitas, 09°41'30"N, 72°25'47"W, INHS 35436, 1, (130.7). Río Palmar, Lago Maracaibo dr. in Hacienda el Milagro NW of the village of Rosario, MBUCV V-18206, 2, (153.2-188.0). Río Palmar, Lago Maracaibo dr. Sierra de Perija, NW Lago Maracaibo, Hacienda el Milagro, MBUCV V-18411, 1, (168.6). Río Santa Rosa, Río Santa Ana - Lago Maracaibo dr. Highway 6 bridge, 09°39'06"N, 72°35'00"W, INHS 35466, 1, (75.9). Río Yasa, Lago Maracaibo dr. 5 km S Machiques, INHS 60463, 1, 1 cs, (102.2) and MCNG 25011, 1, (82.0). Río Zulia, Lago Maracaibo dr. MCNG 7486, 1, (237.9). Zulia, Tulé Reservoir, Lago Maracaibo dr. lagoon, 10°53'N, 71°12'W, MCNG 746.

Diagnosis: Most *Hypostomus hondae* can be distinguished from all other members of the *H. cochliodon* group by the presence of more plates in the skin between the dorsal fin and the lateral plates anterior of the dorsal-fin spine (Fig. 6B; Table 7; some Colombian specimens do not have a large number of plates around the dorsal fin). The number of plates in this area depends on the size of the fish, some very small specimens lack plates in this region, but most small specimens have at least one or more isolated odontodes present. *Hypostomus hondae* is most similar to *H. pagei* and *H. plecostomoides*. *Hypostomus hondae* further differs from *H. pagei* by having spots on the caudal-fin spines (except in very melanistic specimens), by having darker coloration, a different juvenile coloration (Fig. 14A vs. Fig. 14B; see description of *H. pagei*), and by having the pectoral-fin spine reach 2-3 plates beyond the pelvic fin when depressed ventral to the pelvic fin (vs. 0-1). No additional characters can distinguish *H. hondae* from *H. plecostomoides*.

Description: See *Hypostomus cochliodon* group description for more details. Morphometric data given in Table 2. Body dark brown with round spots present almost everywhere; most specimens with spots fading posteriorly with none present on caudal

peduncle. Size of spots on body from medium to large, size increases posteriorly. Some specimens (particularly juveniles) with four dorsal saddles visible: first below anterior rays of dorsal fin, second below posterior rays of dorsal fin and slightly posterior to dorsal fin, third below adipose fin and slightly anterior to adipose fin, and fourth at base of caudal fin; dark bar also present between the eyes. Caudal fin always with spots except in strongly melanistic specimens in which caudal fin appears almost black. Caudal fin often lighter basally than distally. Abdomen slightly lighter than sides in adults; in juveniles, abdomen much lighter than sides and spots may be faint or absent.



FIGURE 14. Lateral views of juveniles of A. *Hypostomus hondae*, 32.2 mm SL and B. *H. pagei*, paratype, 30.7 mm SL.

Dorsal fin usually short, when depressed in most specimens, not reaching preadipose plate. Depressed pectoral-fin spine ventral to pelvic fin reaches 2-3 plates beyond pelvic-fin rays. Tip of pectoral-fin spine of nuptial males with stout, recurved, hypertrophied odontodes.

Keels weak to moderately developed. Orbit forming ridge distinctly raised above medial surface of head; ridges of dorsal and lateral aspect of head well-developed. Longitudinal ridge on pterotic-supracleithrum beginning at posterodorsal corner of eye formed from raised bone and slightly larger odontodes absent. Opercle distinctly exposed, always supporting much more than ten odontodes. Nuptial body odontodes absent (Fig. 2A). Plates in skin anterior to dorsal-fin spine almost always present and more numerous than in comparatively-sized specimens of other species of the *H. cochlodon* group (Fig. 6B; Table 7). Most specimens less than 70 mm SL with at least one or two free odontodes in skin anterior to dorsal-fin spine; some Colombian specimens lack this characteristic.

Each jaw with 8-22 teeth (mode = 11), teeth almost always large and spoon-shaped, some individuals with smaller, more numerous teeth. Average angle between dentaries 65° (SD = 8°; range: 48°-86°; N=27). Lateral line plates 27-29; dorsal plates 8-10; interdorsal plates 6-8; adipose caudal plates 8-10.

Range: Lago Maracaibo drainage of Colombia and Venezuela, and the Río Magdalena, Río Sinú, and Río Atrato drainages of Colombia (Fig. 11). *Hypostomus hondae* is allopatric to all other species of the *H. cochliodon* group.

***Hypostomus levis* (Pearson 1924)**
(Fig. 15)

Rhinelepis levis, Pearson 1924: 22-23, pl. 5 figs. 1-3.

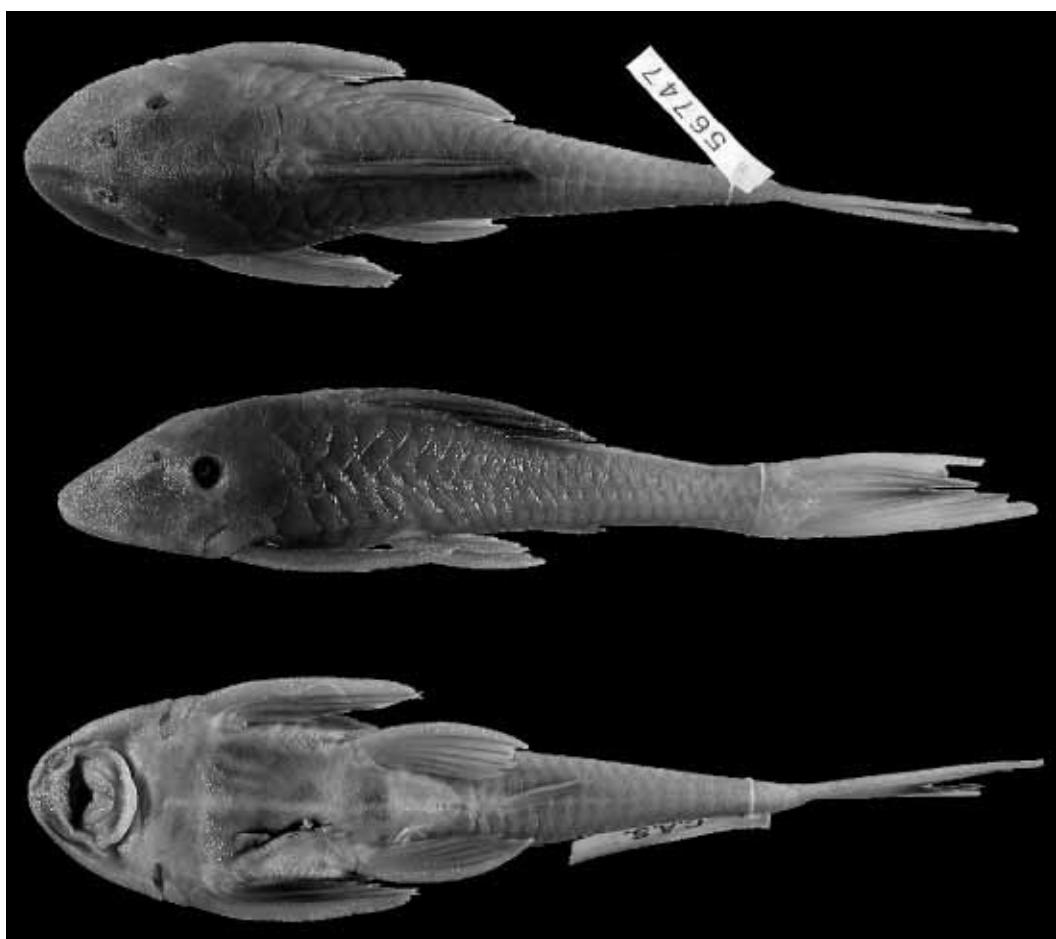


FIGURE 15. Dorsal, lateral, and ventral views of *Hypostomus levis*, CAS 56747, topotype, 92.2 mm SL.

Material examined: BOLIVIA. *La Paz*: Río Cochabamba, Río Beni dr. Huachi, at junction of Río Bopi and Río Cochabamba, CAS 77349, 1, (152.9), Holotype and CAS 77350, 2, (115.0-150.8), Paratypes: Río Popoi, Río Beni dr. CAS 56747, 2, 1 cs, (77.1-92.2) and UMMZ 66492, 1, (57.6).

Diagnosis: *Hypostomus levis* can be separated from all other members of the *H. cochliodon* group by the lack of an adipose fin.

Description: See *Hypostomus cochliodon* group description for more details. Morphometric data given in Table 3. Available specimens probably faded considerably; light brown; pectoral and pelvic fins and occasionally head spotted; spots absent elsewhere except for some faint ones in dorsal fin. Abdomen considerably lighter than sides, without spots. Caudal fin with dark wash distally, base of caudal fin significantly lighter than distal margin.

Dorsal fin short. Adipose fin and pre-adipose plate absent. Depressed pectoral-fin spine ventral to pelvic fin reaches beyond bases of pelvic-fin rays.

Keels absent; lateral plates almost perfectly smooth. Orbita forming slight ridge slightly raised above medial surface of head; ridges of dorsal and lateral aspect of head fairly smooth. Longitudinal ridge on pterotic-supracleithrum beginning at posterodorsal corner of eye formed from raised bone and slightly larger odontodes absent. Opercle usually supporting no odontodes, but occasionally with one or two odontodes present. Presence of unique nuptial body odontodes (Fig. 2B) in *H. levis* unknown (see Discussion below). Plates in skin anterior to dorsal-fin spine absent in specimens examined.

Each jaw with 11-17 teeth (mode = 14), teeth relatively small, but distinctly spoon-shaped (Armbruster & Page 1997). Average angle between dentaries 63° (SD = 9°; range: 53°-68°; N=3). Lateral line plates 28-30; dorsal plates 8; dorsal-caudal plates 16-18.

Range: Only known from the Ríos Cochabamba and Popoi of the upper Río Beni - Upper Río Madeira drainage of Bolivia (Fig. 8). *Hypostomus levis* is allopatric to all other members of the *H. cochliodon* group, but is potentially sympatric with *H. pyrineusi*.

Hypostomus ocaleus (Fowler 1943)

(Fig. 16)

Panaque ocaleus Fowler 1943: 256-258, figs. 48-51.

Material examined: AQUARIUM SPECIMEN: AUM 16090, 1 cs. COLOMBIA. Caqueta: Río Orteguasa - Río Amazonas dr. Florencia, Caqueta, ANSP 70518, 1, (140.5), Holotype, ANSP 70519, 2, (91.8-126.3), Paratypes, and USNM 100773, 1, (143.9). ECUADOR. State unknown: Quebrada, Río Jivino - Río Napo dr. ANSP 120350, 1, (163.6). Río Catapino, Río Corrientes - Río Napo dr. MCNG 9724, 2, (145.8-161.3). Río Catapino, Río Corrientes - Río Napo dr. Panayaco, MCNG 9725, 2, (149.1-190.6). Napo: Río Aguarico, Río Napo dr. at campamento Guarimo CEPE, 00°01'S, 76°37'30"W, FMNH

106015, 1, (129.35). Río Due, Río Aguarico dr. at site of bridge under construction 8.8 km SW Lumbaqui by road and 0.4 km N of the road, 00°00'12"S, 77°23'48"W, FMNH 106014, 1, (90.8). Río Lushanta, Río Napo dr. 4 km E Archidona, AUM 28229, 3, 3 cs, (3). Río Lushian, Río Napo dr. 2 km N Archidona, AUM 28221, 1, 2 cs, (1). Río Lushian, Río Napo dr. 3 km N Archidona, AUM 28342, 2, (211.9-216.9). Río Pano, Río Napo dr. 5.5 km NW Tena, elev. 550 m, AUM 28216, 2, (82.9-100.1). Tributary, Río Payamino dr. few km upstream from San Jose de Payamino, 00°20'12"S, 77°18'W, FMNH 106016, 3, (152.2-185.4). PERU. Amazonas: Río Marañon dr. Caterpiza, LACM 41873-5, 1, (175.7). Río Cenepa, Río Marañon dr. near Río Tujushiku, LACM 39647-2, 2, (161.4-167.6). Río Santiago, Río Marañon dr. at La Poza, LACM 41724-16, 1, (112.3).

Diagnosis: *Hypostomus ocaleus* can be distinguished from all other members of the *H. cochliodon* group except *H. ericius*, *H. hemicochliodon*, and *H. sculpodon* by having well-developed keels. *Hypostomus ocaleus* differs from *H. hemicochliodon* and *H. sculpodon* by a lack of a buccal papilla, by having 0-10 odontodes on the opercle (versus more than 10), and the presence of nuptial body odontodes (Fig. 2B); and from *H. ericius* by being dark brown with closely-placed spots (vs. tan to gray with widely separated spots) and by the following ratios: anal-fin length/SL (10.8-13.9% vs. 13.4-17.0%) and interorbital width/head length (42.4-50.2% vs. 50.5-56.6%).

Description: See *Hypostomus cochliodon* group description for more details. Morphometric data given in Table 3. Body almost entirely dark brown with medium to large spots present. Spots increasing in size posteriorly and almost coalescing to form stripes on caudal peduncle. Spots on abdomen large, often confluent with one another and forming crescents and rings. Abdomen slightly lighter than sides, particularly in juveniles. Individuals below 100 mm SL often entirely dark brown except for faint spots on dorsal and paired fins and with lighter abdomen.

Dorsal fin occasionally large, reaching beyond adipose fin when depressed, but dorsal fin generally reaching preadipose plate or slightly beyond when depressed. Pectoral-fin spine when depressed ventral to pelvic fin reaches beyond bases of pelvic-fin rays. Pectoral-fin spine supporting numerous stout, recurved, hypertrophied odontodes in nuptial males.

Keels sharp, strongly developed. Orbita forming ridge distinctly raised above medial surface of head; ridges of dorsal and lateral aspect of head well-developed. Longitudinal ridge on pterotic-supracleithrum beginning at posterodorsal corner of eye formed from raised bone and slightly larger odontodes absent. Opercle usually not supporting odontodes, but one to ten odontodes may be present, and odontodes on opercle more numerous in juveniles. Nuptial body odontodes present (Fig. 2B). Platelets in skin anterior to dorsal-fin spine usually absent or not numerous (Fig. 6A; Table 7).

Each jaw with 7-18 teeth (mode = 8), teeth large and spoon-shaped. Average angle between dentaries 65° (SD = 10°; range: 48°-89°; N=23). Lateral line plates 27-30; dorsal plates 7-9; interdorsal plates 5-7; adipose caudal plates 9-11.

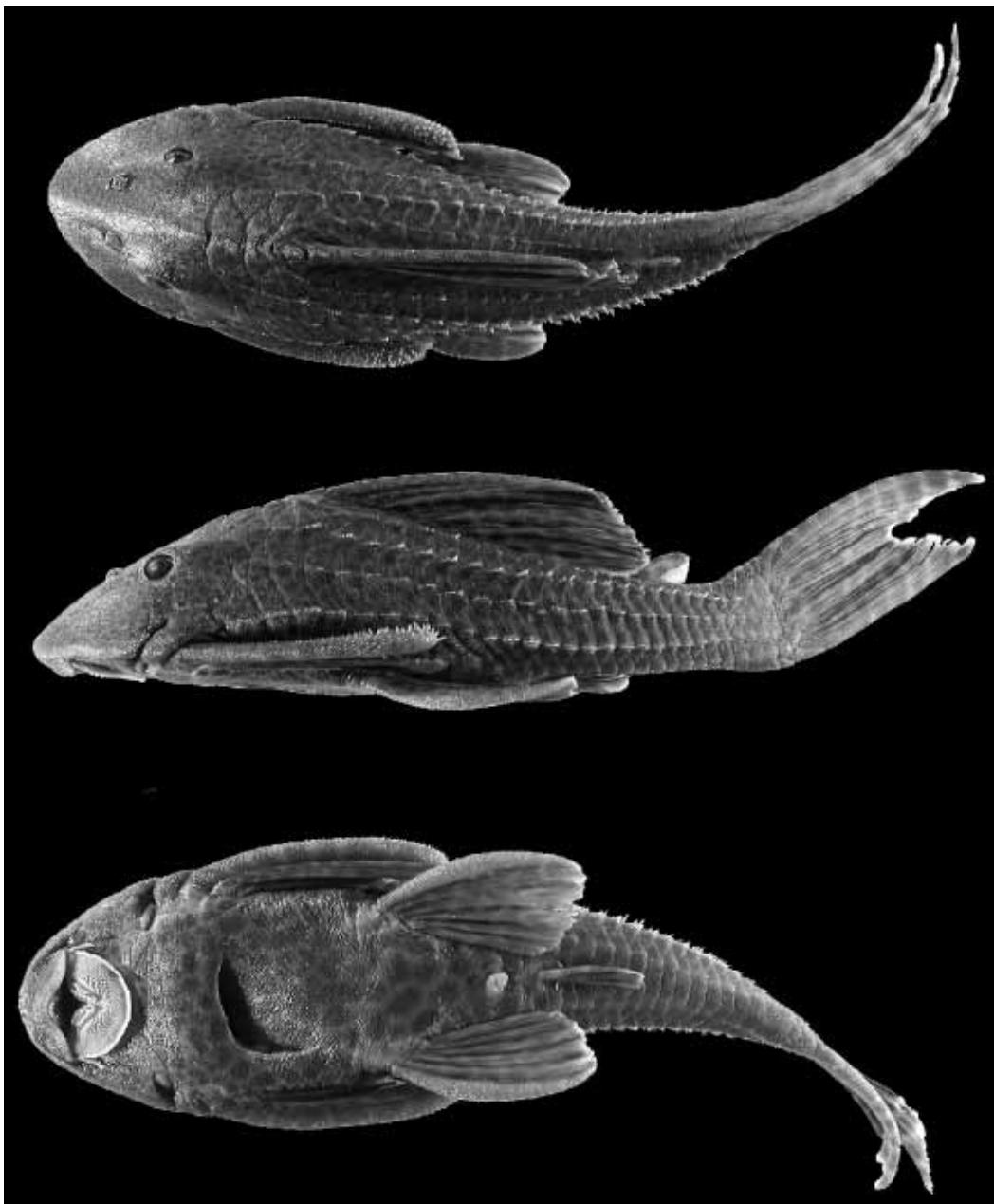


FIGURE 16. Dorsal, lateral, and ventral views of *Hypostomus ocaleus*, FMNH 106016, 185.4 mm SL.

Range: Found in the Río Marañón drainage of Peru, the Río Napo drainage of Ecuador, and the Río Orteguasa drainage of Colombia, all tributaries of the Upper Río Amazonas drainage (Fig. 17). *Hypostomus ocaleus* is sympatric with *H. ericius*, *H. hemicochliodon*, and *H. pyrineusi*.

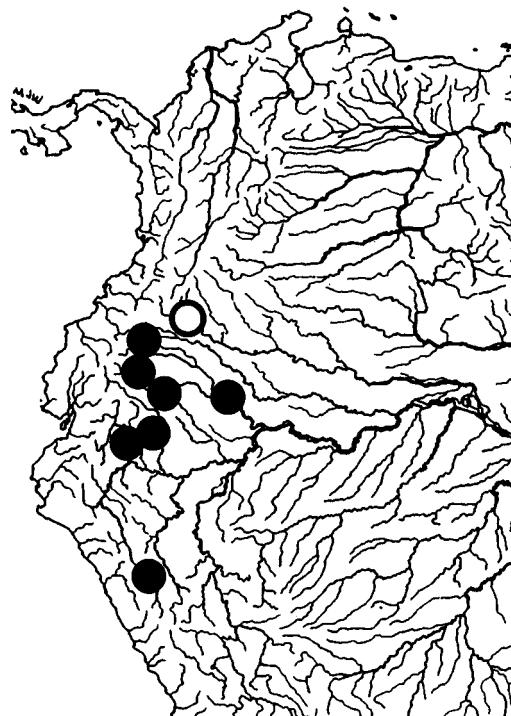


FIGURE 17. Distribution of *Hypostomus ocaleus*. Open symbol is type locality.

***Hypostomus pagei* new species**
(Figs. 14B, 18)

Holotype: VENEZUELA, Yaracuy, Río Tupe, Río Aroa dr. ca. 12 km N Aroa on Highway 3, 10°30'31"N, 68°52'55"W, MCNG 24696, 1, (158.6 mm SL).

Paratypes: VENEZUELA. *Falcón*: Caño El 26, Río Aroa dr. 4 km N Palma Sola, 10°36'48"N, 68°33'46"W, USNM 363172, 1, (84.0) and MCNG 32097, 1. Río Aroa, Caribbean Sea dr. 8 km W Boca de Aroa, 10°39'53"N, 68°22'15"W, INHS 34946, 1, (37.4). Río Aroa, Caribbean Sea dr. Palma Sola, 10°35'58"N, 68°33'03"W, INHS 34952, 4, (18.7-24.7). *Yaracuy*: Caño Caripal, Río Aroa dr. 13 km SE Yumare, 10°33'42"N, 68°37'37"W, INHS 34921, 1, (91.8). Same data as holotype, AUM 30833, 2, (32.6-65.7), INHS 60098, 9, 1 cs, (66.4-73.0), MCNG 43794, 5, (19.6-64.8). Río Yumare, Río Aroa dr. 7 km NW Yumare, 10°38'N, 68°43'W, INHS 60110, 1, (156.7).

Nontype material: VENEZUELA. *Lara*: Río Curarigua, Río Tucuyo dr. Paso San Antonio, pozo de la Iguana near Curarigua, MBUCV V-18450, 4, (83.4-187.7). Río Curarigua, Río Tucuyo dr. Puente Torres at bridge, INHS 28867, 1, (172.5). *Yaracuy*: Río Yurubi, Río Yaracuy dr. ca. entrance to Guayabito, 10°29'08"N, 68°39'40"W, MCNG 27617, 1, (88.0). Tributary, Río Yaracuy dr. E Marin, INHS 28902, 2, (84.9-91.8).

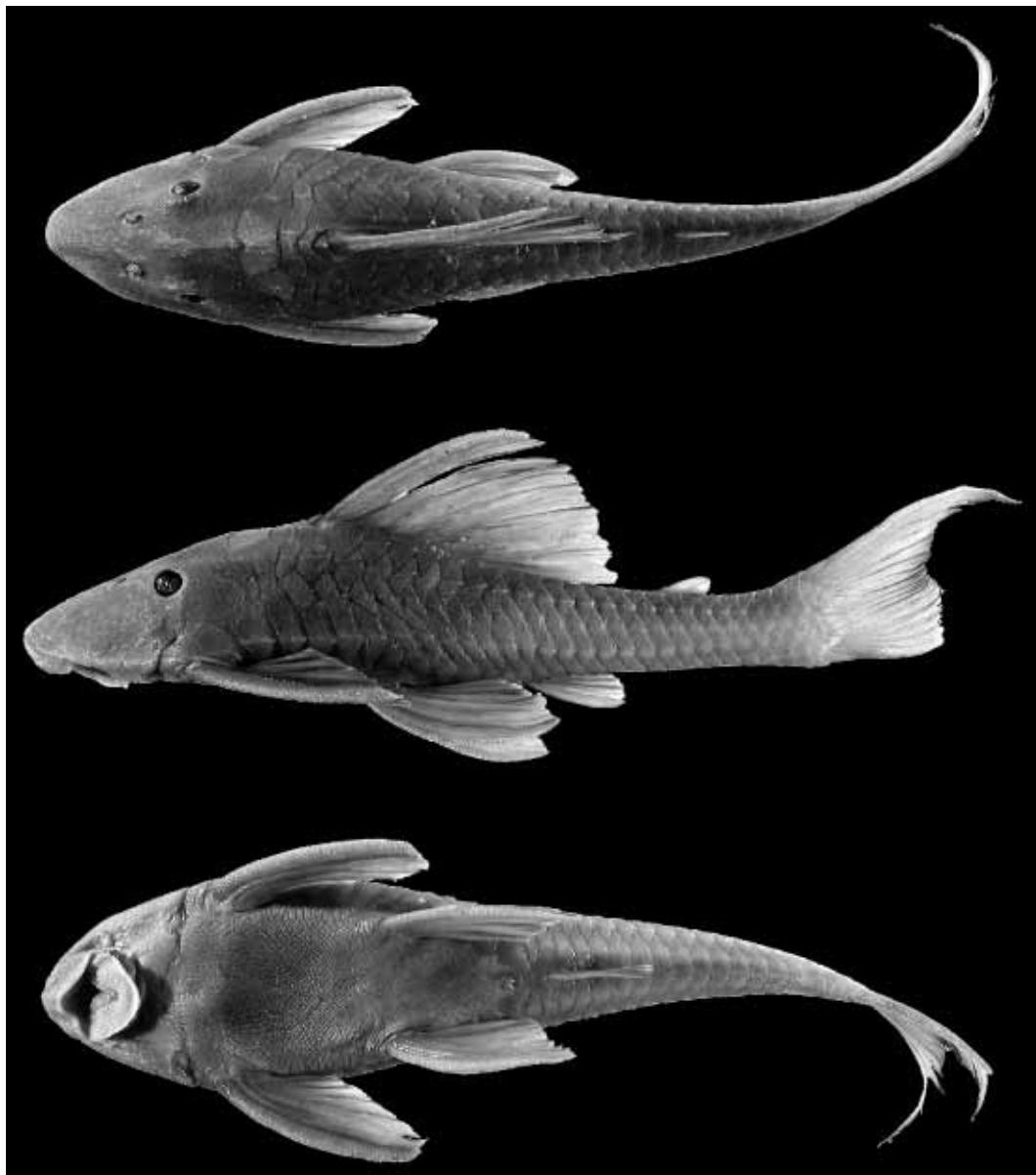


FIGURE 18. Dorsal, lateral, and ventral views of *Hypostomus pagei*, new species, INHS 60110, paratype, 156.7 mm SL.

Diagnosis: *Hypostomus pagei* differs from most other members of the *H. cochliodon* group mainly in coloration: a light, gray-brown with the spots considerably faded or absent (vs. a deep, dark brown with the spots well-developed). Juvenile *H. pagei* additionally have the caudal fin darkest along both spines and at the base, clear medially (Fig. 14B), a

color pattern not found in any other members of the *H. cochliodon* group. *Hypostomus pagei* is most similar to *H. hondae* and *H. plecostomoides*. *Hypostomus pagei* differs from *H. hondae* and *H. plecostomoides* by the general absence of spots on the caudal fin and/or caudal-fin spines (*H. pagei* may have some very faint spots on the caudal-fin spines; some *H. plecostomoides* lack spots on the caudal-fin spines, but the spines are almost black instead of light gray-brown) and by having shorter pectoral-fin spines (reaching 0-1 plates beyond pelvic fin when depressed below the pelvic fin vs. 2-3 plates with the exception of one specimen of *H. pagei* that has pectoral-fin spines that reach two plates beyond the pelvic fin and the one specimen of *H. plecostomoides* examined from the Lago Valencia drainage that has pectoral-fin spines that do not reach beyond the pelvic fin).

Description: See description of the *Hypostomus cochliodon* group for more details. Morphometric data given in Table 4. Color gray-brown. Spots, if present, usually very faint and restricted to paired fins, dorsal fin, head, anterior part of body and/or abdomen. Spots particularly faint in adults. Caudal fin darkest distomedially. Spots absent from entire caudal fin in adults. Juveniles with faint spots on caudal-fin spines and dark brown along spines and base (Fig. 14B). Caudal fin coloration darker than body color in juveniles, lightens ontogenetically until equal to body color. Juveniles typically slightly darker overall than adults.

Dorsal fin short, falling short of preadipose plate. Depressed pectoral-fin spine ventral to pelvic fin reaches beyond bases of pelvic-fin rays, but to a lesser extent than in other species of the *H. cochliodon* group (0-1 plate vs. 2-3 plates in most other specimens of the *H. cochliodon* group).

Keels weak, almost absent. Orbita forming slight ridge slightly raised above medial surface of head; ridges of dorsal and lateral aspect of head fairly smooth. Longitudinal ridge formed of raised bone and slightly larger odontodes absent on pterotic-supracleithrum beginning at postdorsal corner of orbit. Opercle usually broadly exposed, always supporting much more than ten odontodes. Plates in skin anterior to dorsal-fin spine absent or few (Fig. 6A; Table 7).

Each jaw with 7-17 teeth (mode = 11), teeth large and spoon-shaped. Average angle between dentaries 63° (SD = 5° ; range: 53° - 73° ; N=14). Lateral line plates 27-29; dorsal plates 8-9; interdorsal plates 6-8; adipose caudal plates 9-10.

Range: Found in northwestern Venezuela in the Río Aroa, Río Tocuyo, and Río Yaracuy basins, short rivers that drain directly into Caribbean Sea (Fig. 11). *Hypostomus pagei* is allopatric to all other species of the *H. cochliodon* group.

Etymology: Named for Dr. Lawrence M. Page for his help and guidance during my career, and to honor the fact that he helped to collect a majority of the specimens of this species.

***Hypostomus plecostomoides* Eigenmann 1922**
(Fig. 19)

Hypostomus plecostomoides Eigenmann 1922: 225-226. Holotype is lost.

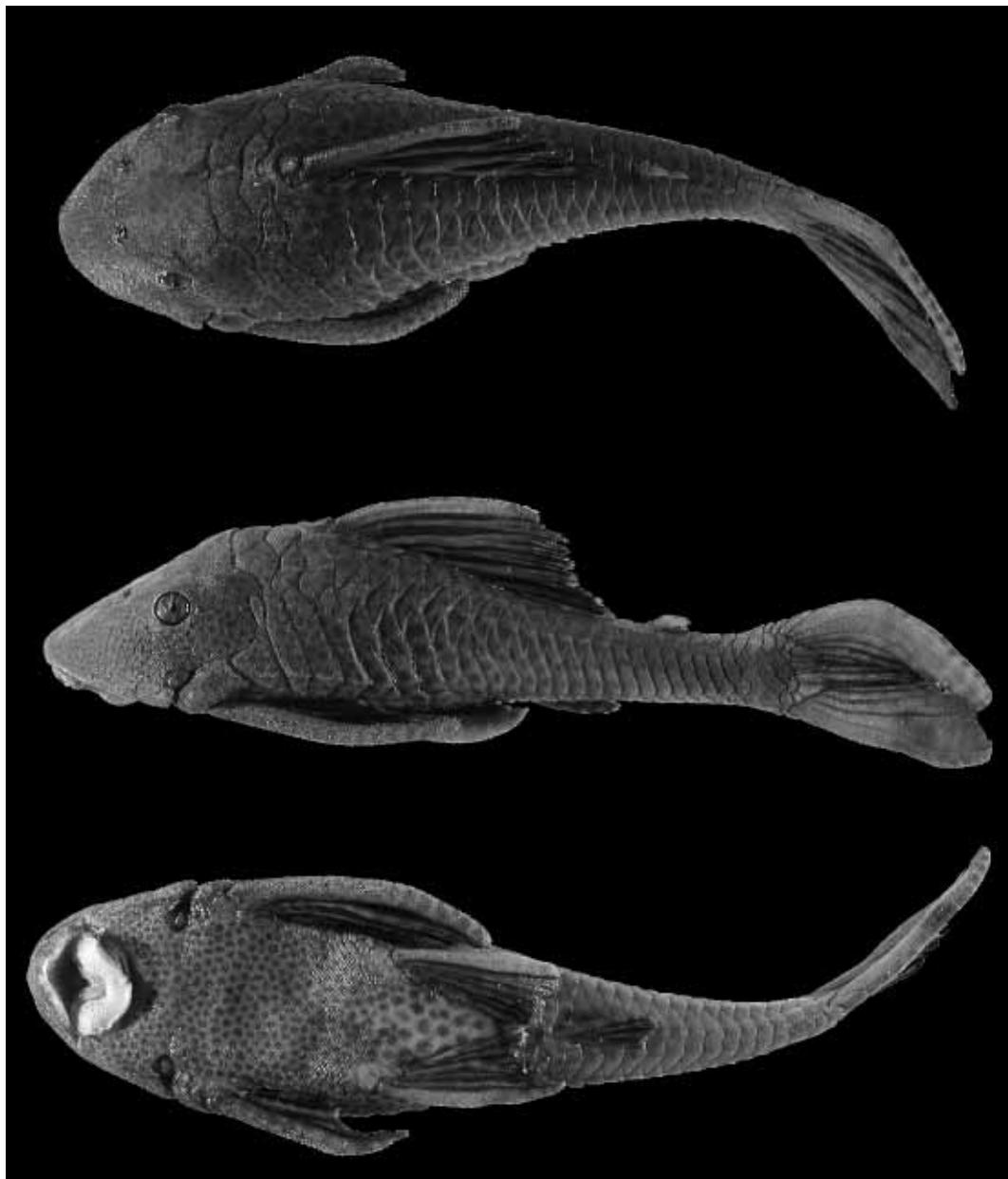


FIGURE 19. Dorsal, lateral, and ventral views of *Hypostomus plecostomoides*, AUM 22555, 186.3 mm SL.

Material examined: COLOMBIA. *Meta*: Caño Rico, Río Meta dr. at Brasilia, ca. 03°59'N, 73°08'W, ANSP 133235, 2, 1 cs, (83.6-98.8). Quebrada Venturosa, Río Meta dr. between La Balsa and Puerto Lopez, ca. 04°05'N, 72°58'W, ANSP 133365, 1, (94.4). Río Negrito, Río Meta dr. downstream of bridge at La Balsa, ca. 04°04'N, 73°04'W, ANSP 131658, 1, (101.7). VENEZUELA. *Anzoategui* Atapirire, Río Orinoco dr. Atapirire road, Manasma, MBUCV V-16944, 1, (97.2). Río Moquete, Río Orinoco dr. Paso bajito, MBUCV V-16922, 1, (167.0). Río Tigre, Caño Manamo dr. near El Tigre, 08°55'38"N, 64°11'11"W, INHS 31412, 2, (69.4-105.8). *Apure*: caño, Río Apure dr. 07°16'26"N, 71°05'20"W, INHS 28385, 2, (113.1-113.2). Caño Las Mercedes, Río Apure dr. dique via Apurito, cerca San Fernando de Apure-Biruaca, 07°51'30"N, 67°22'30"W, MCNG 13923, 1, (173.4). Caño Maporal, Río Apure dr. at the metal bridge near the Module (a field station of UNELLEZ), 07°25'30"N, 69°35'40"W, MCNG 9134, 1, (222.7). Río Apure, Río Orinoco dr. side channel along dike opposite municipal slaughter house, 07°35'N, 67°29'W, USNM 258264, 2, (136.1-193.8). Río Aruaca, Río Apure dr. in floodplain, paso Aruaca, 07°26'55"N, 68°26'00"W, MCNG 20655, 1, (142.8). *Aragua*: Río Bue, Lago Valencia dr. Maracay, CAS 12694, 1, (218.8). *Barinas*: Caño Arenosa, Río La Yuca - Río Masparro dr. 14 km N Barinas, 08°46'14"N, 70°15'30"W, INHS 31837, 3, 1 cs, (105.6-119.4). Caño Capa, Río Masparro - Río Apure dr. 2 mi E El Tombor, 08°21'35"N, 69°46'07"W, INHS 35487. Caño Guanaparo, Río Apure dr. N of Apurito, 08°07'40"N, 68°20'40"W, MCNG 13025, 1, (183.2). Caño Hondo, Río Apure dr. Agua Negra, INHS 30000, 3, 1 cs, (112.7-218.4). Río Chiri Chiri, Río Apure dr. 0.5 km above mouth, 07°39'40"N, 71°29'01"W, MCNG 10572, 1, (169.5). Río Mitado-seco, Río Apure dr. USNM 194210, 1, (205.4). Río Santa Barbara, Río Apure dr. at bridge on Barinas to San Cristobal road, km 504, 07°50'10"N, 71°11'00"W, MCNG 11720, 1, (153.8). Río Santo Domingo, Río Apure dr. in Torunos, Hacienda La Isla, 08°30'32"N, 70°05'03"W, INHS 28710, 1, (87.1). Tributary of Río Suripa - Río Apure dr. 36 km NE La Pedrera on route 5, INHS 28284, 1, (106.4). Tributary of Río Caipe, Río Apure dr. 6 km NE Torunos, INHS 28744, 2 cs. *Bolivar*: Caño Brande, Río Orinoco dr. Ciudad Bolívar, 08°14'50"N, 63°15'55"W, ANSP 166889, 1, (211.9). Caño Caiman, Río Orinoco dr. at crossing of Caicara to Puerto Ayacucho highway 191, 2 km W of Ciudad Bolívar to Caicara highway, ANSP 162345, 1, (211.1) and MBUCV V-16855, 1, (192.0). Caño Garrapáta, Río Orinoco dr. at bridge between Río Paguaza and Villacoa, 06°19'20"N, 67°07'00"W, MCNG 11176, 1, (125.4). Caño Tabara, Río Nichare - Río Orinoco dr. 3 km above mouth with Río Nichare, 06°22'N, 64°58'W, MCNG 22931, 1, (188.6). Isolated lagoon, Río Orinoco dr. 200 yards N of Jubillal, 06°57'N, 64°50'W, ANSP 141559, 1, (131.5). Salto Icutu, Río Orinoco dr. Cedeno district, in front of camp, 05°53'N, 64°51'W, MCNG 21160, 1, (199.8). *Cojedes*: Río Camoruco, Río Cojedes - Río Portuguesa dr. about 10 km NW Libertad, INHS 29061, 1, (110.1). Río Tinaco, Río Portuguesa dr. El Baul, INHS 59831, 1, (116.4). *Guarico*: Río Guarico, Río Orinoco dr. at Flores Morada's ranch, ca. 3-4 km E of road from Calabozo to San Fernando, USNM 260217, 1, (109.6). Río Guarquito, Río

Orinoco dr. in front of Medana de Gomez, MCNG 32975, 1, (188.8). Río San Bartolo, Río Orinoco dr. Parque Nacional Aguaro-Guariquito, Aguas Muertes, 08°04'40"N, 66°40'00"W, MCNG 15027, 1, (140.5). Río San Bartolo, Río Orinoco dr. Parque Nacional Aguaro-Guariquito, Aguas Muertes, 08°06'30"N, 66°40'19"W, INHS 34862, 2, (175.7-187.1) and MCNG 31701, 2, (149.0-248.5). Río San Bartolo, Río Orinoco dr. Parque Nacional Aguaro-Guariquito, Aguas Muertes in the Payares, 08°08'01"N, 66°40'53"W, MCNG 31792, 1, (230.9). Río San Jose, Río Guariquito - Río Orinoco dr. Parque Nacional Aguaro-Guariquito, 08°28'55"N, 66°53'19"W, INHS 34614, 1, (107.1). *Miranda*: Río Cuira, Río Tuy dr. FMNH 84616, 1, (69.7) and MBUCV V-3756, 1, (140.1). Río Tuy, Caribbean Sea dr. in pool isolated from main stream near Ocumaro de Tuy, MBUCV V-3701, 10, (96.4-103.2). *Monagas*: Río Amana, Río Guanipa dr. 7 km NNW Santa Barbara, INHS 31263, 1, 2 cs, (139.7) and MCNG 29159, 1, (124.4). Río Amana, Río Guanipa dr. Las Cañitas near El Tefero, MBUCV V-6755, 1, (107.2). Río de Oro, Río Guarapiche - Río San Juan dr. 4 km SW Jusepin, INHS 31448, 1 cs. Río Guanipa, Caribbean Sea dr. Highway 5 bridge, 09°22'06"N, 63°46'47"W, INHS 31365, 3, 2 cs, (79.2-96.6). Río Guarapiche, Río Orinoco dr. Caicara, USNM 163168, 1, (102.9). *Portuguesa*: Caño El Mamon, Río Portuguesa dr. 9 km SE of highway 5 on the road to La Quebrada, 09°07'20"N, 69°31'20"W, MCNG 12648, 2, (171.2-185.2). Caño Iguecito, Río Portuguesa dr. on the road to Moritas, 08°38'00"N, 69°29'56"W, MCNG 30207, 1, (107.2). Caño Igues, Río Portuguesa dr. 2 km from bridge at Paplón, 08°38'15"N, 69°59'45"W, MCNG 30163, 1, (164.8). Caño Igues, Río Portuguesa dr. La Capilla, INHS 31966, 1, (97.4). Caño Maraca, Caño Igues - Río Portuguesa dr. on road from Guanare to Guanarito at 60 km marker, 08°49'34"N, 69°20'45"W, INHS 35667, 2, (103.7-182.6), MCNG 15696, 1, (131.0), MCNG 8603, 2, (158.6-183.5), and MCNG 27275, 1, (135.7). Río Guanare, Río Portuguesa dr. Guanarito, INHS 31991, 1, (82.3). Río Guanare, Río Portuguesa dr. on S side in Finca Merecure, approximately 45 min from Guanare on the road to Las Moritas, MCNG 33951, 1, (191.66). Río Orape, Río Portuguesa dr. 45 km E of San Rafael de Onoto, 09°43'40"N, 68°30'10"W, MCNG 18716, 1, (108.0). *Tachira*: Río Teteo, Río Apure dr. on road to El Nula, 07°28'40"N, 71°55'40"W, MCNG 8086, 2, (122.3-154.0). Tributary to Río Doradas, Río Apure dr. La Pedrera, INHS 28153, 1, (87.2).

Diagnosis: *Hypostomus plecostomoides* is the most difficult species of the *H. cochliodon* group to identify as it is without any known synapomorphies. The most similar species are *H. hondae*, *H. pagei*, and *H. taphorni*. *Hypostomus plecostomoides* differs from *H. pagei* by having spots on the caudal-fin spines (except in very melanistic specimens), by having darker overall coloration, a different juvenile coloration (Fig. 14A vs. Fig. 14B; see description of *H. pagei*), and by generally having the pectoral-fin spines reaching 2-3 plates beyond the pelvic fin when depressed ventral to the pelvic fin (vs. 0-1; one specimen of *H. pagei* has the pectoral fin reaching two plates beyond the pelvic fin, and the single specimen of *H. plecostomoides* examined from the Lago Valencia drainage has the pectoral fin not extended beyond the pelvic fin); from *H. hondae* by having a lower num-

ber of plates in the skin around the dorsal-fin spine (Fig. 6A; Table 7); and from *H. taphorni* by lacking a bicolored caudal fin and by having no or medium to large spots on the abdomen (vs. small spots; Fig. 22; see Comments). *Hypostomus plecostomoides* can be distinguished from *H. cochliodon* by having a different color pattern (lacking a dorsal stripe and generally being well-spotted), from *H. ericius* and *H. oculatus* by lacking sharp keels, and from *H. ericius*, *H. oculatus*, and *H. pyrineusi* by having greater than 10 odontodes on the opercle.

Description: See *Hypostomus cochliodon* group description for more details. Morphometric data given in Table 4. *Hypostomus plecostomoides* is variable in coloration. Typically, body almost entirely dark brown with medium to large spots usually present. Spots on head fairly large compared to *H. hondae*, *H. pagei*, and *H. taphorni*. Spots increasing in size but fading posteriorly, spots absent on caudal peduncle (Figs. 21). Spots on abdomen typically large, but some specimens with medium-sized spots, spots never as small as in *H. taphorni* (Fig. 22). Spots occasionally entirely absent and entire fish dark brown (almost black). Caudal fin may be entirely spotted, but caudal-fin membrane and rays typically black or black distally and light proximally. Caudal-fin spines typically spotted although some specimens with entirely black spines; caudal fin not bicolored. Specimens from particularly muddy streams gray-brown, but not to extent seen in *H. pagei*. Abdomen colored as sides, sometimes slightly lighter; adults almost always with well-developed spots on abdomen. Color in juveniles as in adults, but spots comparatively larger and abdomen generally white and unspotted.

Dorsal fin short, rarely reaching preopercular plate when depressed. Depressed pectoral-fin spine ventral to pelvic fin reaches 2-3 plates beyond pelvic-fin rays (only one specimen reached just to posterior edge of pelvic fin). Tip of pectoral-fin spine of nuptial males with stout, recurved, hypertrophied odontodes.

Keels weak to moderately developed. Orbita forming moderate ridge slightly raised above medial surface of head; ridges of dorsal and lateral aspect of head fairly well-developed. Longitudinal ridge on pterotic-supracleithrum beginning at posterodorsal corner of eye formed from raised bone and slightly larger odontodes absent. Opercle always supporting much more than ten odontodes. Nuptial body odontodes absent (Fig. 2A). Plates in skin anterior to dorsal-fin spine absent or few (Fig. 6A; Table 7).

Each jaw with 5-16 teeth (mode = 9), teeth large and spoon-shaped. Average angle between dentaries 57° ($SD = 10^\circ$; range: 41° - 82° ; $N=30$). Lateral line plates 27-30; dorsal plates 7-9; interdorsal plates 6-8; adipose caudal plates 8-11.

Range: Found in the Río Orinoco basin of Colombia and Venezuela, and the Río Tuy and Lago Valencia drainages of Venezuela (Fig. 11). *Hypostomus plecostomoides* is allopatric to all other species of the *H. cochliodon* group (see Comments).

Comments: Specimens most appropriately identified as *Hypostomus plecostomoides* from the Orinoco drainage in northwestern Bolívar state, Venezuela (ANSP 162345, MBUCV V-16855, MCNG 11176, and MCNG 22931), may provide evidence for intergra-

dation between *H. plecostomoides* and *H. taphorni*. Some specimens from this region have the bicolored caudal fin diagnostic for *H. taphorni*, and few or no odontodes on the opercle and relatively smaller spots on the head than typical in *H. plecostomoides*. However, the specimens lack the second synapomorphy for *H. taphorni*, small spots on the abdomen. Alternatively, it is possible that these specimens represent an undescribed species. Additional specimens will have to be examined before the status of the members of the *H. cochliodon* group from northern Bolívar state can be assessed. For the purposes of this study, specimens from northern Bolívar were excluded from the description above and from Table 4.

***Hypostomus pyrineusi* Miranda-Ribeiro 1920**
(Fig. 20)

Hypostomus pyrineusi Miranda-Ribeiro 1920: 9, pls. 3-4.

Material examined: BOLIVIA. Beni: Río Curiraba, Río Madeira dr. Campamento Trapi-che, USNM 305281, 1, (119.8). Río Itenez, Río Beni - Río Madeira dr. 5 km S Costa Marques, Brasil, 1 km above mouth of Río Baures, AMNH 39941, 1, (210.1). Río Itenez, Río Beni dr. 9 km SE of Costa Marques, Brasil, UMMZ 204399, 5, (139.9-226.7). Río Itenez, Río Beni - Río Madeira dr. opposite Costa Marques, Brasil, AMNH 39758, 2, (92.0-213.4). Río Itenez, Río Beni - Río Madeira dr. playa pond, 9 km SE Costa Marques, Brasil, AMNH 40108 (none measured). Río Maniqui, Río Marmore - Río Madeira dr. San Borja, INHS 36995, 2, (162.7-176.0). BRAZIL. Acre: Rio Macauhan, Rio Yaco - Rio Purus dr. vicinity of Rio Macauhan, USNM 94653, 1, (122.5). Rio Macaua, Rio Iaco dr. near Sena Madueira, 09°20'S, 68°45'W, AMNH 12599, 1, (113.5). Amazonas: Rio Jamari, MNRJ 863, 1, (204.0), Holotype: ECUADOR. Napo: Río Catapino, Río Corrientes - Río Napo dr. MCNG 9724, 1, (174.8). Río Pucuno, Rio Suno - Rio Napo dr. 00°47'S, 77°16'W, USNM 177222, 1, (71.3). Río Lushian, Río Misahuali dr. at bridge E of Rucul-lacta, 00°54'42"S, 77°48'48"W, CAS 106013. Shansho Caño, USNM 124875, 1, (100.5). PERU. Amazonas: Río Marañon dr. 1 km upstream from Caterpiza, LACM 42005-13, 2, (84.1-89.5) and LACM 42003-8, 2, (150.6-174.3). Río Marañon dr. 100 m downstream from Caterpiza, LACM 41996-9, 1, (137.1) and LACM 41972-3, 1, (140.9). Río Marañon dr. 300 m upstream from Caterpiza, LACM 41813-1, 1, (207.7). Río Marañon dr. 500 m upstream from Caterpiza, LACM 41992-7, 4, 1 cs, (162.4-190.1) and LACM 42010-8, 1, (108.0). Río Marañon dr. 800 m upstream from Caterpiza, LACM 41834-1, 1, (131.2). Río Marañon dr. Caterpiza, LACM 41873-7, 1, (180.7), LACM 41882-4, 1, (180.9), LACM 41884-1, 1, (198.9), LACM 41887-5, 1, (160.3), LACM 42009-10, 1, (133.9-164.9), LACM 41898-2, 1, (140.0), LACM 41893-9, 2, 1 cs, (152.8-163.2), LACM 42115-8, 1, (104.7), LACM 41895-6, 1, (152.8-163.2), and LACM 42116-4, 1, (93.0). Quebrada Kayamasa, Río Marañon dr. 40 km upstream from Caterpiza, FMNH 97016, 1, (140.9),

LACM 41872-4, 2, (150.9-187.7), LACM 41846-4, 1, (199.7), LACM 41852-1, 1, (173.6), and LACM 41853-4, 2, (136.7-156.4). Quebrada Pastazilla, Río Santiago - Río Marañon dr. LACM 39947-8, 2, (208.5-215.1). Quebrada Yutupiza, Río Marañon dr. LACM 36337-10, 1, (159.4). Río Cenepa, Río Marañon dr. near San Antonio, LACM 39638-3, 3, 1 cs, (94.2-202.8). Río Huampani, Río Marañon dr. Maja Quebrada, LACM 36359-2, 1, (228.0). Río Marañon, Río Amazonas dr. at and across from Sta. Maria de Nieva and confluence of Río Nieva, FMNH 97017, 2, (110.6-131.9). Río Santiago, Río Marañon dr. at La Poza, LACM 41724-17, 1, (131.5), LACM 41723-10, 1, (130.5), LACM 41729-39, 1, (147.7), LACM 41730-11, 1, (128.8), LACM 39883-11, 3, 1 cs, (137.9-170.8). *Huanaco*: Río Huallaga, Río Ucayali dr. at Tingo Maria, CAS 56754, 2, 1 cs, (79.6-86.1) and CAS 95117, 2, 1 cs, (69.7-160.5). Río Rondos, Río Monzon dr. vicinity of Tingo Maria, just above new bridge site, ANSP 38873 (none measured). *Loreto*: Río Amazonas, Atlantic Ocean dr. INHS 39358 (none measured). Río Amazonas, Atlantic Ocean dr. 21.1 mi NE Iquitos bearing 22°, 03°30'30"S, 73°03'28"W, INHS 39122 (65.2). Río Amazonas, Atlantic Ocean dr. at Pueblo Gallito, INHS 36939, 1, (80.3). Río Itaya, Río Amazonas dr. approx. 10 km S Santa Clara, INHS 36877, 1, (94.8). Río Nanay, Río Amazonas dr. well above Morona cocha, ANSP 38874 (none measured). Río Napo, Río Amazonas dr. at Mazan, INHS 36565 (none measured). *Madre de Dios*: Caño Pachija, Río Madre de Dios dr. Manu National Park, Pakitza, from mouth to 7 km upstream, USNM 319601, (81.2). Caño Picaflor, Río Madre de Dios dr. Pakitza, Caña Brava Trail #19, USNM 319353, 1, (114.1). Tributary, Río Tambopata - Río Madre de Dios dr. stream enters Río Tambopata from S bank approximately 500 m downstream of Explorer's Inn boat landing, 12°49'35"S, 69°17'30"W, USNM 264049, 1, (178.5). Tributary to Río Madre de Dios, on S side about 10 km downstream of junction of Río Tambopata and Río Madre de Dios, 12°30'S, 69°10'W, USNM 263911, 1, (130.1). Tributary, Río Tambopata - Río Madre de Dios dr. second stream entering Río Tambopata on SW shore upstream of mouth of Río La Torre, 12°49'40"S, 69°18'W, USNM 264050, 2, (143.0-202.6).

Diagnosis: *Hypostomus pyrineusi* is distinguished from most members of the *H. cochliodon* group except some *H. cochliodon*, *H. levis*, *H. ericius*, *H. ocaleus*, and *H. taphorni* by having 0-10 (usually 0; Fig. 2B) odontodes on the opercle (vs. 11 or more). *Hypostomus pyrineusi* further differs from *H. hemicochliodon* and *H. sculpodon* by lacking a ridge on the pterotic-supracleithrum (Fig. 5B), by the presence of large, spoon-shaped teeth (vs. teeth intermediate; Fig. 1C vs. B), and a lack of a buccal papilla; from *H. ericius*, *H. hemicochliodon*, *H. ocaleus*, and *H. sculpodon* by lacking strong, sharp keels on the lateral plates; from *H. levis* by having an adipose fin; from *H. cochliodon* by having the spots more numerous and close-set on the body (vs. spots absent or widely spaced); and from *H. taphorni* by having pigmentation on the lobes of the caudal fin equally distributed (vs. lower lobe darker than upper).

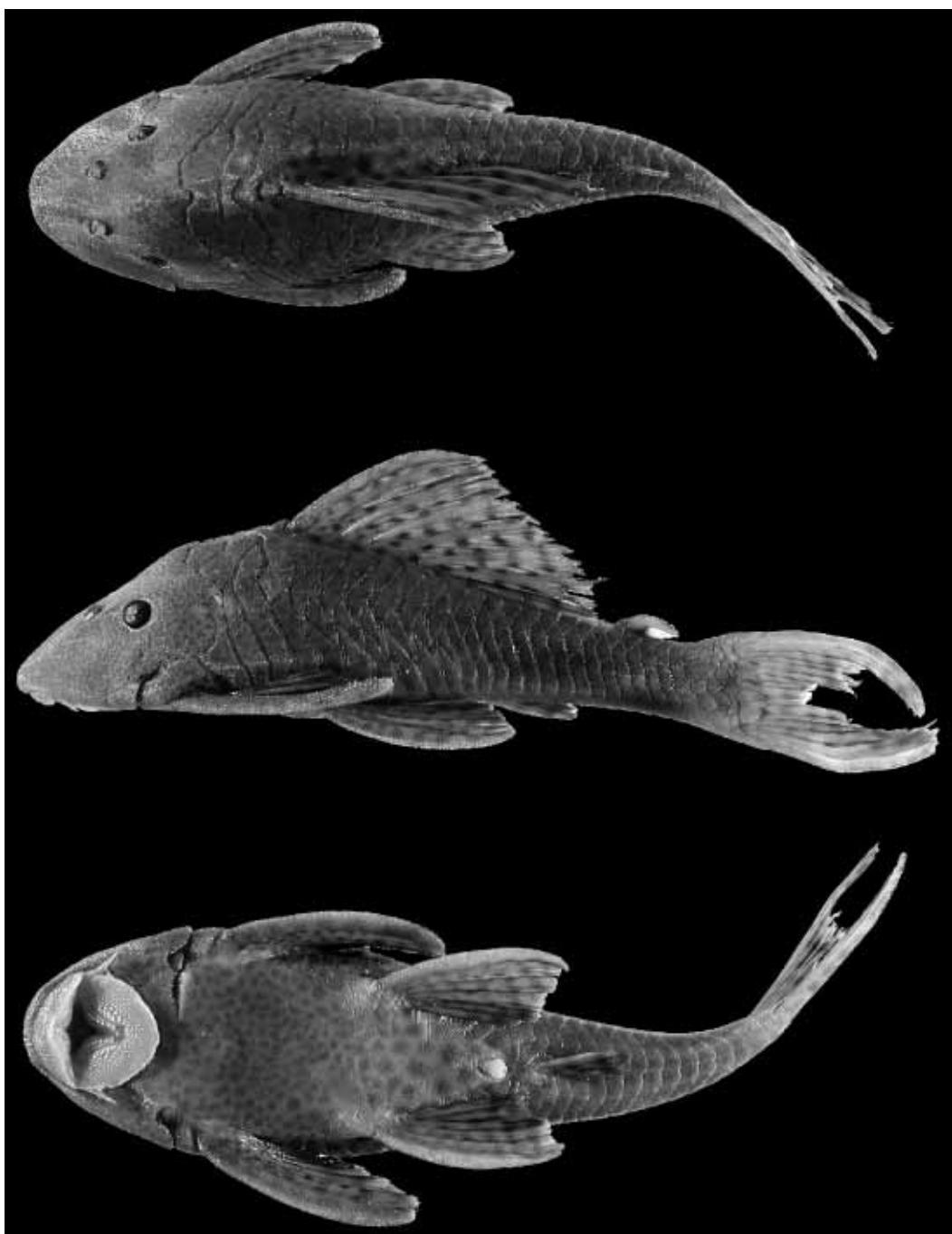


FIGURE 20. Dorsal, lateral, and ventral views of *Hypostomus pyrineusi*, INHS 36995, 176.0 mm SL.

Description: See *Hypostomus cochliodon* group description for more details. Morphometric data given in Table 5. Body typically almost entirely dark brown with medium

to large spots present. Spots on head fairly large when compared to those of *H. hondae*, *H. pagei*, and *H. taphorni*. Spots increasing in size and fading posteriorly, absent on caudal peduncle. Spots on abdomen typically large, some specimens with medium-sized spots, spots never as small as in *H. taphorni*; (Fig. 22). Spots occasionally absent and entire fish dark brown (almost black). Caudal fin may be entirely spotted, but caudal-fin membranes and rays typically black or black distally and light proximally; caudal-fin spines typically spotted although some specimens with entirely black caudal-fin spines; caudal fin not bicolored. Abdomen colored as sides, sometimes slightly lighter. Color in juveniles as in adults, but spots comparatively larger and abdomen generally white and unspotted.

Dorsal fin short, rarely reaching preopercular plate when depressed. Depressed pectoral-fin spine ventral to pelvic fin reaches 2-3 plates beyond pelvic-fin rays. Tip of pectoral-fin spine of nuptial males with stout, recurved, hypertrophied odontodes.

Keels weak to moderately developed. Orbita forming moderate ridge slightly raised above medial surface of head; ridges of dorsal and lateral aspect of head fairly well-developed. Longitudinal ridge on pterotic-supracleithrum beginning at posterodorsal corner of eye formed from raised bone and slightly larger odontodes absent. Opercle usually supporting no odontodes, but occasionally one to three odontodes are present. Nuptial body odontodes present (Fig. 2B). Plates in skin anterior to dorsal-fin spine absent or few (Fig. 6A; Table 7).

Each jaw with 5-14 teeth (mode = 8), teeth large and spoon-shaped. Average angle between dentaries 55° (SD = 7°; range: 43°-69°, N=30). Lateral line plates 26-31; dorsal plates 8-9; interdorsal plates 4-7; adipose caudal plates 9-16.

Range: Found in the Río Madeira drainage of Bolivia and Brazil, the Ríos Napo, Ucayali, Marañon and upper Río Amazonas drainage of Peru, and the Río Napo drainage of Ecuador, (Fig. 8). *Hypostomus pyrineusi* is sympatric with *H. ericius*, *H. hemicochliodon*, and *H. oculatus* and is potentially sympatric with *H. levis*.

Hypostomus sculpodon new species (Fig. 21)

Holotype: VENEZUELA, Amazonas, Río Casiquiare, Río Negro dr. Departamento Río Negro, at Piedra Caruana (at second camp, left descending bank of river in portion of river between mouths of Río Siapa and Río Pasimoni), 01°58.611'N, 66°32.359'W, MCNG 37042, 1, (239.7 mm SL).

Paratypes: VENEZUELA. Amazonas: Caño Cascacadura, Río Orinoco dr. 7 km E of San Fernando de Atabapo, MBUCV V-8151, 2, (85.8-93.0). Río Casiquiare, Río Negro dr. Departamento Casiquiare, lake adjacent to area approximately 15 river miles above mouth, of Río Casiquiare, 01°58'N, 66°55'W, MCNG 12148, 1, (166.8). Río Casiquiare, Río Negro dr. Departamento Río Negro, 25 km from confluence with Río Negro, MCNG 37031, 1, (229.4), Paratype.

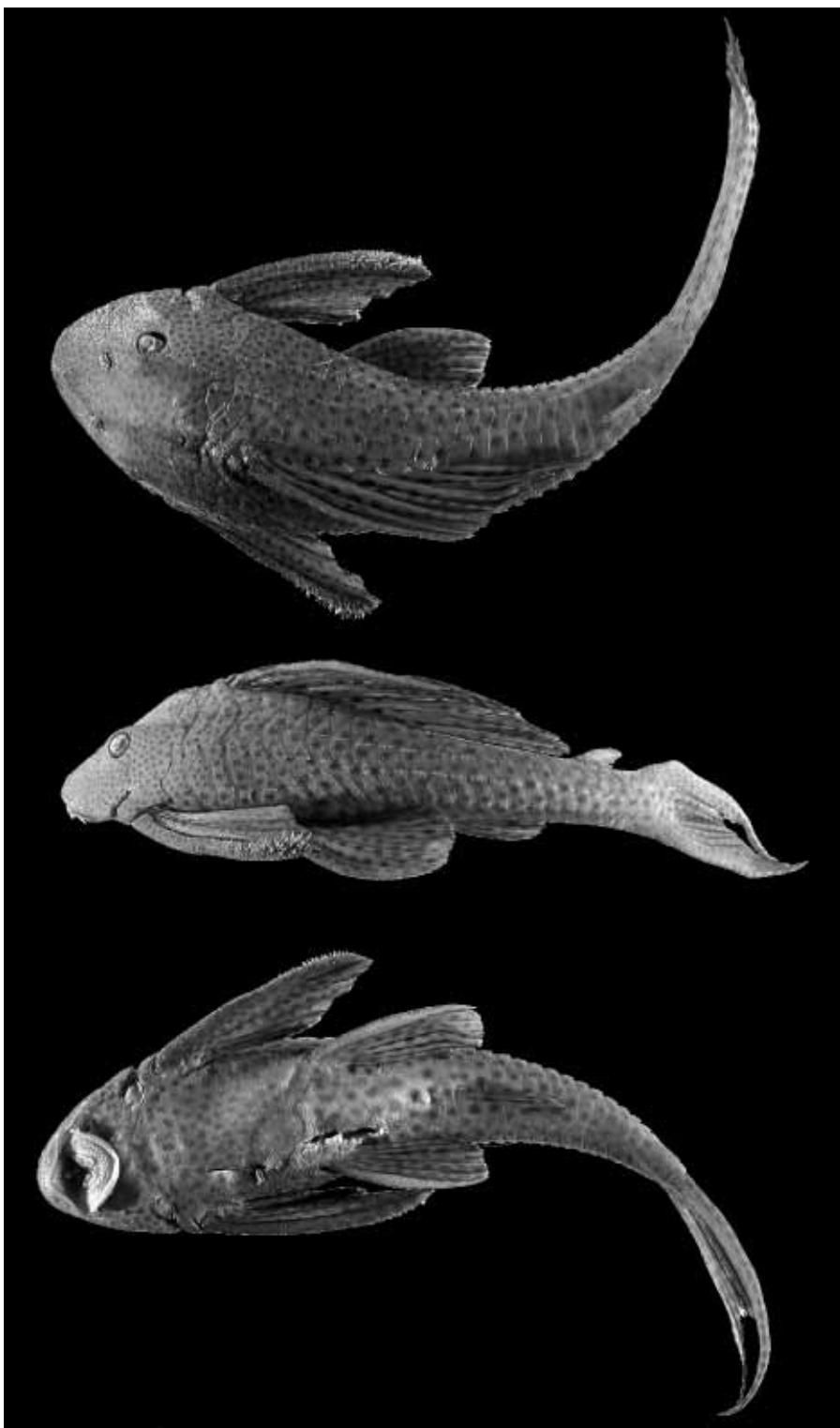


FIGURE 21. Dorsal, lateral, and ventral views of *Hypostomus sculpodon*, new species, MCNG 37042, holotype, 239.7 mm SL.

Diagnosis: *Hypostomus sculpodon* differs from all other members of the *H. cochliodon* group except *H. hemicochliodon* in the presence of a buccal papilla and intermediate developed teeth (Fig. 1B; juvenile *H. cochliodon* and *H. taphorni* occasionally also have intermediate teeth). *Hypostomus sculpodon* differs from *H. hemicochliodon* in coloration (brownish-red with widely spaced spots vs. dark brown with closely spaced spots), by having a smaller dorsal-anal length to anal-fin length ratio (average = $79.2 \pm 7.6\%$, 69.6-89.7% vs. average = $111.1 \pm 8.4\%$, 92.5-132.6%), and almost completely by having a smaller interorbital width/HL ratio (average = $51.4 \pm 3.1\%$, 38.5-45.4% vs. average = $49.9 \pm 2.7\%$, 44.1-55.6%).

Description: See description of the *Hypostomus cochliodon* group for more details. Morphometric data given in Table 5. Color red-brown. Body and fins well spotted, spots widely spaced. Spots on head and anterior portion of body (to about anterior third of dorsal fin) medium-sized, then shifting abruptly to large spots on posterior part of body. Spots on posterior part of body not progressively increasing in size, generally longitudinally ovoid. Abdomen significantly lighter than sides with spots large. Juveniles colored similarly to adults, but all spots of about the same size (except small spots at anterior margin of head), and abdomen much lighter with spots faint or absent.

Dorsal fin fairly large, usually reaching preopercle plate when depressed. Pectoral-fin spine, when depressed ventral to pelvic fin, reaching 2-3 plates beyond pelvic-fin rays. Tip of pectoral-fin spine of nuptial males with stout, recurved, hypertrophied odontodes.

Keels strong with sharp odontodes. Orbita forming ridge distinctly raised above medial surface of head; ridges of dorsal and lateral aspect of head well-developed, particularly supraoccipital crest. Longitudinal ridge formed of raised bone and slightly larger odontodes present and very well developed on pterotic-supracleithrum beginning at postdorsal corner of orbit. Opercle broadly exposed, always supporting much more than 10 odontodes. Nuptial body odontodes absent (Fig. 2A). Plates in skin anterior to dorsal-fin spine absent or few (Fig. 6A; Table 7). Head and body not particularly deep, body more sleek than other members of the *H. cochliodon* group.

Each jaw with 12-19 teeth (mode = 14), teeth intermediate in size (Fig. 1B). Average angle between dentaries 67° (SD = 11° ; range: 56° - 83° ; N=5). Lateral line plates 30; dorsal plates 9-10; interdorsal plates 7-8; adipose caudal plates 9.

Range: Found in the upper Río Negro and upper Río Orinoco basins of Venezuela (Fig. 11). *Hypostomus sculpodon* is sympatric with *H. hemicochliodon*.

Etymology: From the Latin, *sculpo*, meaning to carve, cut, grave, or chisel in stone, brass, or wood and from the Greek, *odon*, for tooth in reference to the ability of the species to chisel wood with the teeth.

***Hypostomus taphorni* (Lilyestrom 1984)**

Fig. 22

Cochliodon taphorni Lilyestrom 1984:43, figs. 8-9.

Material examined: VENEZUELA. Bolívar: Río Botanmo, Río Cuyuni dr. on the road to Bochinche, 07°25'N, 61°11'W, MCNG 8048, 1, (184.8, holotype), MCNG 8049, 1, (76.2, paratype). Caño Negro, Río Cuyuni dr. caño a little above Isla de Anacoco, 06°47'N, 61°12'W, MCNG 1452, 1, (181.7, paratype). Caño, Río Cuyuni dr. Highway 1, 20 river km above km 88 of El Dorado - Santa Elena road, MBUCV V-16491, 1, (151.6). Caño Negro, Río Cuyuni dr. primary tributary of the Río Cuyuni above Isla Anacoco, 06°44'N, 61°09'W, MCNG 928. Caño Quebrada Clara, Río Cuyuni dr. at the mouth of Quebrada Clara at Anacoco, cerca the confluence with the Río Cuyuni, approx. 1 km up, 06°47'N, 61°10'W, MCNG 16901, 1, (149.1). Caño Quebrada Clara, Río Cuyuni dr. below bridge cerca isla Anacoco, 06°42'N, 61°09'W, MCNG 16450, 1, (83.5). Río Corumo, Río Botanmo - Río Cuyuni dr. 10 km E Tumeremo on road from Tumeremo to Bochinche (just after Fort Terembay), 07°25'00"N, 61°28'00"W, ANSP 168195, 7, 2 cs, (120.4-158.7), MBUCV V-26824, 9, 2 cs, (115.9-197.1), INHS 31768, MCNG 29566, 1, (72.3), and MCNG 16038, 1, (80.8). Río Cuyuni, Río Essequibo dr. 10 km W km 88 of El Dorado - Santa Elena road, MBUCV V-16601, 1, (130.4). Río Cuyuni, Río Essequibo dr. cerca de la Chalana de Anacoco, 06°43'N, 61°09'W, MCNG 11066, 1, (228.0). Río Cuyuni, Río Essequibo dr. near Isla Anacoco, MCNG 7535, 1, (219.2). Río Yuruari, Río Cuyuni dr. just E El Manteco, INHS 31600, 1, (87.2).

Diagnosis: *Hypostomus taphorni* can be distinguished from all other members of the *H. cochliodon* group by the combination of having a bicolored caudal fin (light above, dark below) and small spots on the abdomen. Some specimens tentatively identified as *H. plecostomoides* from northern Bolívar State, Venezuela, have a bicolored caudal fin, but have medium to large spots on the abdomen (See Comments in *H. plecostomoides*).

Description: See *Hypostomus cochliodon* group description for more details. Morphometric data given in Table 6. Body typically almost entirely dark brown with medium to large spots present. Spots on head fairly small when compared to *H. plecostomoides*, fading posteriorly and absent on caudal peduncle. Spots on abdomen very small (Fig. 22). Caudal fin bicolored, upper lobe tan and without spots, lower lobe black. Color in juveniles as in adults, but spots comparatively larger with spots on abdomen very light or absent.

Dorsal fin short, rarely reaching preadipose plate when depressed. Depressed pectoral-fin spine ventral to pelvic fin reaches 2-3 plates beyond pelvic-fin rays. Tip of pectoral-fin spine of nuptial males with stout, recurved, hypertrophied odontodes.

Keels weak to moderately developed. Orbita forming ridge moderately raised above medial surface of head; ridges of dorsal and lateral aspect of head fairly well-developed. Longitudinal ridge on pterotic-supracleithrum beginning at posterodorsal corner of eye

formed from raised bone and slightly larger odontodes absent. Opercle supporting up to 10 odontodes in juveniles; number of odontodes on the opercle decreases with age and many adults have no odontodes on the opercle. Nuptial body odontodes present (Fig. 2B). Plates in skin anterior to dorsal-fin spine absent or few (Fig. 6A; Table 7).

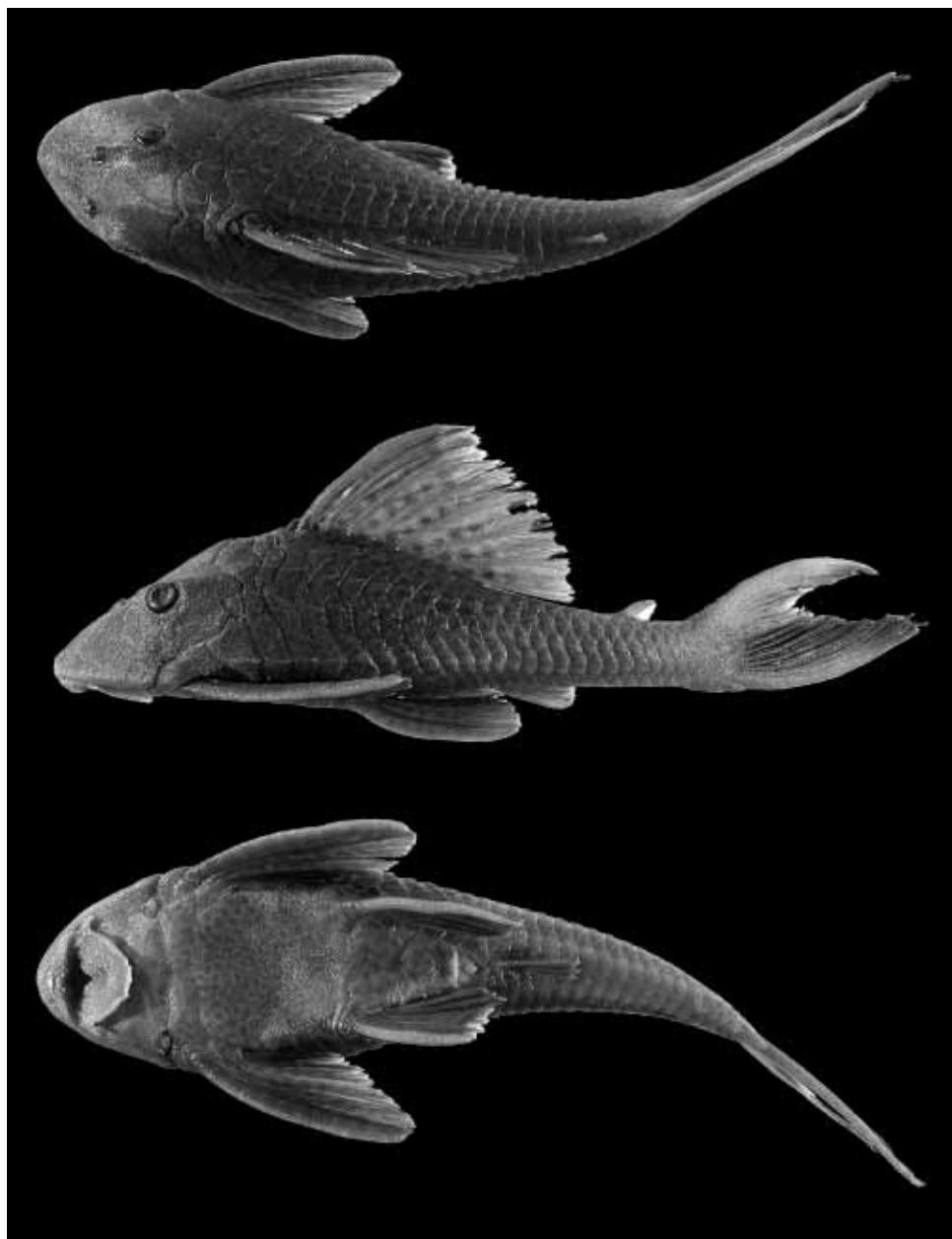


FIGURE 22. Dorsal, lateral, and ventral views of *Hypostomus taphorni*, ANSP MBUCV V-26824, 136.8 mm SL.

Each jaw with 6-12 teeth (mode = 10), teeth large and spoon-shaped. Average angle between dentaries 56° ($SD = 7^\circ$; range: 44° - 66° ; $N=13$). Lateral line plates 27-29; dorsal plates 8-9; interdorsal plates 6-8; adipose caudal plates 8-10.

Range: From the Río Cuyuni drainage of Venezuela (Fig. 11). Recent collecting in Guyana suggests that *H. taphorni* is limited to the Cuyuni drainage and replaced by two undescribed species in the rest of the Essequibo river drainage. *Hypostomus taphorni* is allopatric to all other members of the *H. cochliodon* group (see Comments on page 43).

Discussion

Delimiting the species of the *Hypostomus cochliodon* group is made difficult by the fact that the species vary little in morphometrics or meristics, and the species have a well-developed ability to alter color pattern. However, the species can be divided into four groups and from those groups it is possible to distinguish the species. The four groups are the intermediate group (*H. hemicochliodon* and *H. sculpodon*), *H. cochliodon* with a unique color pattern, the odontodeless opercle group (*H. ericius*, *H. levis*, *H. oculatus*, *H. pyrineusi*, and *H. taphorni*), and an undifferentiated northern group (*H. hondae*, *H. pagei*, and *H. plecostomoides*). The odontodeless opercle group can be further subdivided into a highly keeled group (*H. ericius* and *H. oculatus*) and a weakly to non-keeled group (*H. levis*, *H. pyrineusi*, and *H. taphorni*). Once in these groups, it is fairly simple to separate the species. Principal components analysis is provided for each of the groups although *H. levis* is excluded from the analysis because it lacks many of the measurements because of its absence of an adipose fin.

The PCA of the intermediate group showed a 100% separation of the species on principal component 2 (Fig. 10A). PC2 is most strongly and negatively effected by dorsal-anal length and anal-fin width and most strongly and positively effected by anal-fin length and folded dorsal-fin length. A ratio of dorsal-anal length to anal-fin length completely separates the two species from one another: average = $111.1 \pm 8.4\%$, 92.5-132.6% in *Hypostomus hemicochliodon* and average = $79.2 \pm 7.6\%$, 69.6-89.7% in *H. sculpodon*).

The PCA of the odontodeless groups showed two trends, a complete or almost complete separation of *H. taphorni* from *H. ericius*, *H. oculatus*, and *H. pyrineusi* and a complete separation of *H. ericius* and *H. oculatus* on a graph of PC2 vs. PC3 (Fig. 10B). PC2 is most strongly and negatively effected by adipose-caudal length and mouth width and most strongly and positively effected by interdorsal length, eye-nare length and orbit length. PC3 is most strongly and negatively effected by base of anal-fin length, anal-fin length, and adipose-spine length and most strongly and positively effected by interdorsal length, adipose-caudal length, and postanal length. Although there is no morphometric evidence suggesting that *H. ericius* and *H. oculatus* are distinct from *H. pyrineusi* there are morphological differences (well-developed keels in *H. ericius* and *H. oculatus* vs. no or weak keels in *H. pyrineusi*).

The PCA of the northern group showed some general trends separating *H. hondae* and *H. pagei* from *H. plecostomoides* and a complete separation of *H. hondae* from *H. pagei* on PC2 vs. PC3 (Fig. 10C). PC2 is most strongly and negatively effected by eye-nare length and interorbital width and most strongly and positively effected by anal-fin length and interdorsal length. PC3 is most strongly and negatively effected by anal-fin length and folded dorsal-fin length and most strongly and positively effected by adipose-caudal length and interdorsal length.

For the most part, the species of the *Hypostomus cochliodon* group are allopatric (Figs. 8, 11, 17). It is only in the Amazon basin that several species coexist. *Panaque*, the other wood-eating genus of loricariid catfishes, also reaches its peak of diversity in the Amazon basin (Schaefer & Stewart 1993; Schaefer & Stewart 2002). In the upper Río Marañon drainage of Peru, there are at least nine species of wood-eaters: *H. ericius*, *H. hemicochliodon*, *H. oculatus*, *H. pyrineusi*, *P. albopunctatus*, *P. dentex*, *P. gnomus*, *P. nocturnus*, and probably at least one species of the *P. nigrolineatus* clade (distributions based on this study and Schaefer & Stewart 1993). How these species subdivide the wood-eating niche is unknown, and ecological studies on wood-eating by fishes in the upper Río Marañon would represent a very interesting study.

Weber and Montoya-Burgos (2002) recently described *Hypostomus fonchii* and suggested that the species was derived from the *H. cochliodon* group. The teeth described for *H. fonchii* are elongate and unicuspид and it is suggested that the unicuspид teeth represent a synapomorphy for *H. fonchii* and the *H. cochliodon* group. This is problematic in that I have not observed truly unicuspид teeth in any members of the *H. cochliodon* group. In all specimens of the *H. cochliodon* group that I have examined, the medial cusp remains present, but is generally fused with the lateral cusp. The mesial cusp remains visible as a slightly darker, thicker ridge on the medial side of the tooth. I have not examined any specimens of *H. fonchii*, and I cannot determine whether or not this is the case with this species. The only truly unicuspид teeth that have been reported for the Hypostominae are the teeth found in nuptial male *Aphanotorulus* (Armbruster & Page 1996). I do not consider *H. fonchii* as a member of the *H. cochliodon* group as its body shape is that of a generalized, fast-water dwelling *Hypostomus* and not the derived shape of *H. cochliodon*. Exact placement of *H. fonchii* awaits an analysis of its diet, osteology, and external anatomy for the synapomorphies of the *H. cochliodon* group.

Recent expeditions into poorly collected regions where no members of the *Hypostomus cochliodon* group have been reported from in the past are finding more species of the *H. cochliodon* group. Two undescribed species are now known from the Essequibo and Takutu River drainages of Guyana (pers. obs.) and one species from the Rio Tocantins in Brazil (Reis, pers. comm.). These species and a revised key will be presented in future publications.

Phylogeny

- Character 1: Teeth – 0: elongate (Fig. 1A); 1: intermediate throughout life (Fig. 1B); 2: spoon-shaped at least in adults (Fig. 1C).
- Character 2: Maxilla – 0: straight to moderately curved (Fig. 3A); 1: greatly curved, almost forming right angle (Fig. 3B).
- Character 3: Odontodes on opercle – 0: 11+ (Fig. 2A); 1: 0-10 (Fig. 2B).
- Character 4: Longitudinal ridge formed from bone and slightly enlarged odontodes on pterotic-supracleithrum – 0: present (Fig. 5A); 1: absent (Fig. 5B).
- Character 5: Nuptial body odontodes – 0: absent (Fig. 2A); 1: present (Fig. 2B).
- Character 6: Notch between the hyomandibula and metapterygoid – 0: present (Fig. 3A); 1: absent (Fig. 3B).
- Character 7: Buccal papilla – 0: present (Fig. 4A); 1: absent or extremely small (Fig. 4B).
- Character 8: Dentary angle – 0: averaging greater than 90°; 1: averaging less than 80°.
- Character 9: Sharp keel odontodes – 0: present; 1: absent.
- Character 10: Body shape deep and narrow with the head taller than wide – 0: absent; 1: present.

TABLE 8. Character state matrix for phylogenetic analysis.

Species	Character									
	1	2	3	4	5	6	7	8	9	10
<i>H. plecostomus</i>	0	0	0	0	0	0	0	0	0	0
<i>H. cochlodon</i>	2	1	0&1	0	1	1	1	1	0	1
<i>H. ericius</i>	2	?	1	1	1	?	1	1	1	1
<i>H. hemicochlodon</i>	1	0	0	0	0	1	0	1	0	1
<i>H. hondae</i>	2	1	0	1	0	1	1	1	0	1
<i>H. levis</i>	2	1	1	1	?	1	1	1	0	1
<i>H. oculatus</i>	2	1	1	1	1	1	1	1	1	1
<i>H. pagei</i>	2	1	0	1	0	1	1	1	0	1
<i>H. plecostomoides</i>	2	1	0	1	0	1	1	1	0	1
<i>H. pyrineusi</i>	2	1	1	1	1	1	1	1	0	1
<i>H. sculpodon</i>	1	?	0	0	0	?	0	1	0	0
<i>H. taphorni</i>	2	1	1	1	0	1	1	1	0	1

Very few morphological characters are useful in elucidating the relationships of the species of the *Hypostomus cochlodon* group. Based on the ten characters found, a phylogeny is produced for the species of the *H. cochlodon* group (Fig. 23). The single tree found

has 12 steps and CI = 1.00. Character state data is in Table 8. No skeletal material is available for *H. sculpodon* or *H. ericius*; however, external evidence does provide information as to the potential relationships of these species with other members of the *H. cochliodon* group. Considering there are so few characters available for analysis, the phylogeny should be considered tentative.

Also providing support for the basal position of *Hypostomus hemicochliodon* and *H. sculpodon* is diet. In all of the specimens of the *H. cochliodon* group examined, almost the entire intestine is filled with small wood chips suggesting that the fishes consume little other than wood. In *H. hemicochliodon* and *H. sculpodon* the intestine mostly contains wood, but other organic matter makes up a major portion of the diet (not greater than 50%). It is apparent that *H. hemicochliodon* and *H. sculpodon* are wood eaters but not wood specialists.

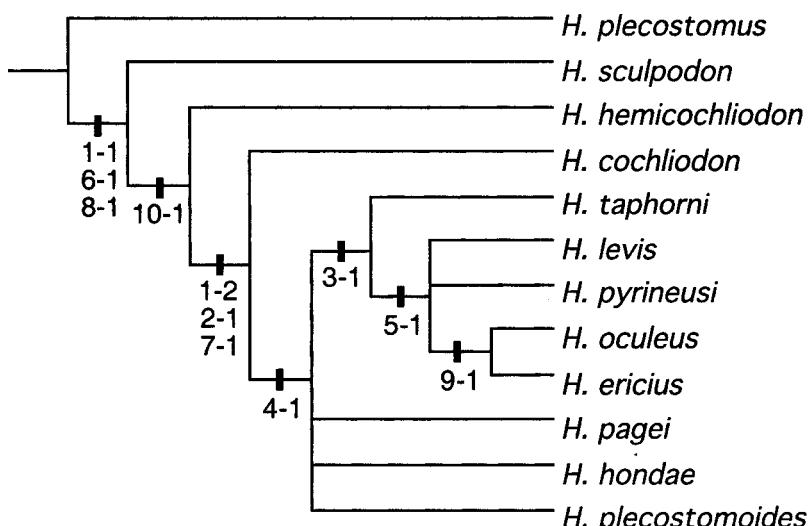


FIGURE 23. Single most parsimonious tree of 9 steps, CI = 1.00. Skeletons of *Hypostomus ericius* and *H. sculpodon* are not available thus placement of osteological characters for these taxa is based on speculation (see Phylogeny section).

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