

A review of Venezuelan species of *Hypophthalmus* (Siluriformes: Pimelodidae)

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To date, only one (*H. edentatus*) of the three currently recognized species of the planktivorous catfishes of the genus *Hypophthalmus* has been identified in surveys from Venezuela and the Río Orinoco Basin. Two additional species are now identified and the distributions of all three in Venezuela are mapped. *Hypophthalmus edentatus* is a more robust fish, with a shorter and wider head, and a triangular emarginate caudal fin. In comparison to *H. edentatus*, *H. marginatus* is more slender, with a longer head and forked caudal fin. *Hypophthalmus* cf. *fimbriatus* is distinguished from its congeners by its more elongate body, darker body coloration, and long, flat, black inner mandibular barbels. *Hypophthalmus edentatus* and *H. marginatus* are sympatric in lowland rivers and floodplain habitats of the western llanos, mainstem Río Orinoco, and Orinoco delta. In Venezuela, *H. cf. fimbriatus* is only known to occur in the black waters of the lower Río Casiquiare where the other two species have never been collected.

Hasta hoy, sólo una (*H. edentatus*) de las tres especies reconocidas del género de bagres planctívoros *Hypophthalmus* ha sido señalada para Venezuela y la cuenca del Río Orinoco. Dos especies adicionales son identificadas; también se presenta un mapa de distribución de las tres especies en Venezuela. *Hypophthalmus edentatus* es un pez robusto, con cabeza corta y ancha, y aleta caudal triangular y emarginada. En comparación con *H. edentatus*, *H. marginatus* tiene el cuerpo más fino, con la cabeza más larga y la aleta caudal furcada. *Hypophthalmus* cf. *fimbriatus* se distingue de sus congéneres por su cuerpo más alargado, coloración corporal más oscura y por las barbas mandibulares internas achatadas y de color negro. *Hypophthalmus edentatus* e *H. marginatus* son simpátricos en las planicies y sabanas inundables de los llanos occidentales, el canal principal del Río Orinoco y el delta del Orinoco. En Venezuela, *H. cf. fimbriatus* sólo se conoce de las aguas negras del bajo Río Casiquiare, donde las otras dos especies nunca han sido colectadas.

Introduction

The genus *Hypophthalmus* Cuvier contains three currently recognized species of South American pimelodid catfishes (Carvalho & Goulding, 1985). *Hypophthalmus* are unusual among neotropical fishes in their habit of specialized plankton-feeding. In a manner similar to that used by North

American paddlefish (*Polyodon spathula*), zooplankton are collected from the water column by straining water over the fine sieve created by numerous long, thin gill rakers. Until recently, the genus was assigned to the family Hypophthalmidae based on Cuvier & Valenciennes' (1840: 224-225) interpretation of characters that deviate from the Pimelodidae (absence of teeth on the

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mandible and palate and the large number of branchiostegal rays). Based on more modern systematic analyses, the current consensus is that *Hypophthalmus* belongs to the large neotropical family Pimelodidae (Howes, 1983; Lundberg et al., 1991; de Pinna, 1993).

The genus *Hypophthalmus* can be diagnosed externally by the presence of scaleless skin and three pairs of barbels, one on the maxilla and two on the mandible, and small eyes located lateroventrally in a position approximately the mid-length of the head. The body is laterally compressed, bearing a long-based anal fin that runs from the anus to the anterior margin of the caudal peduncle. The dorsal, pelvic, and pectoral fins have a narrow base and lack spines. The posterior margin of the caudal fin can be deeply forked or emarginate depending on the species.

Currently, *Hypophthalmus* has three recognized species. *Hypophthalmus edentatus* Spix, in Spix & Agassiz, 1829, originally described from Brazil, has been reported subsequently for the Peruvian Amazon (Cope, 1878), the Río Paraná (Nani & Fuster, 1947; Agostinho et al., 1997), the Orinoco Basin in Venezuela (Mago, 1970) and Colombia (Cala, 1986), and the La Plata Basin of Argentina (López et al., 1980), thus being present in all the major cis-Andean basins of South America. *Hypophthalmus marginatus* Valenciennes, 1840 was originally described from Surinam, and according to Oliveira (1981) it could be present in the Río Paraná. However, Carvalho & Goulding (1985) suggested that the species is restricted to the Amazon Basin. *Hypophthalmus fimbriatus* Kner, 1857 apparently is restricted to the Río Negro in Brazil (Carvalho & Goulding, 1985).

Hypophthalmus edentatus is the only member of the genus reported as present in the Orinoco Basin of Venezuela. The first published report of the genus in Venezuela appears to be that of Mago (1970). Subsequent studies report *H. edentatus* as inhabiting floodplains and whitewater caños in some areas of the western and central llanos (Taphorn & Lilyestrom, 1984; Lasso et al., 1995; Rodríguez & Lewis, 1997). Recent captures of several *Hypophthalmus* specimens with different morphology than that of *H. edentatus* motivated our review of the genus in Venezuela. This paper provides the first report of *H. marginatus* and *H. cf. fimbriatus* in Venezuela, a distribution map for all three species within the country, comparisons of morphological differences, and a key for species identification.

Methods

All of the *Hypophthalmus* specimens available in Venezuelan museums (MCNG, MBUCV, MHNLS) were examined for comparison and taxonomic identification. Either all or a portion of each lot was measured to compare morphology and determine diagnostic characters. Fin ray counts were made using transmitted light, and counts included every discernable ray. Measurements were made with dial calipers to the nearest 0.1 mm when <130 mm, and with a metric tape to the nearest 1.0 mm when >130 mm. All measurements were taken as the straight-line distance between two points. Measurements were taken as follows: Standard length (SL): from the tip of the upper jaw to the middle of the base of caudal fin. Predorsal distance: from the tip of the upper jaw to the most anterior point of the base of dorsal fin. Prepelvic distance: from the tip of the upper jaw to the most anterior point of the base of pelvic fin. Preanal distance: from the tip of the upper jaw to the most anterior point of the base of anal fin, without including the anus. Prepectoral distance: from the tip of the upper jaw to the most anterior point of the base of pectoral fin. Body depth: distance from the most anterior point of the base of dorsal fin, vertically to the line where the anal fin rays insert into the body. Caudal peduncle depth: depth vertically at the mid-point between the most posterior point of the base of anal fin and the most anterior point of the insertion of caudal fin. Caudal peduncle length: from the most posterior point of the base of anal fin to the most anterior point of the insertion of caudal fin. Head length (HL): from the tip of the upper jaw to most distal bony point of the opercle, without including opercular membrane. Pectoral, pelvic, and dorsal fin length: from the most anterior point of the base to the tip of the longest ray, following its direction. Anal fin length: from the insertion of the rays to the tip of the longest ray, following its direction. Caudal fin length (dorsal lobe, ventral lobe, median rays): from the middle point of the base to the tip of the longest ray of each lobe. Dorsal and anal fin base: from the most anterior to the most posterior point of the base of the fin. Dorsal to caudal distance: from the most anterior point of the base of the dorsal to the mid-point of the base of the caudal. Eye to dorsal distance: from the most posterior point of the orbit to the most anterior point of the base of the dorsal fin. Maxillary, outer mandibu-

lar, and inner mandibular barbels: the distance from the base to the tip of the extended barbel. Snout length: from the tip of the upper jaw to the most anterior point of the orbit. Orbital diameter: horizontally from the most anterior to the most posterior point of the orbit. Interorbital distance: dorsally between the most internal points of the orbits. Postorbital distance: from the most posterior point of the orbit to the posterior end of the opercle, without including opercular membrane. Inter-nares distance anteriorly/posteriorly: the distance between the anterior/posterior pair of nares. Gill raker length: at the ceratobranchial, from the base to the tip of the raker, following its direction.

Museum abbreviations: ANSP, Academy of Natural Sciences, Philadelphia; MBUCV, Museo de Biología de la Universidad Central de Venezuela, Caracas; MCNG, Museo de Ciencias Naturales, Guanare; MHNLS, Museo de Historia Natural La Salle, Caracas.

Key to the species of *Hypophthalmus* in Venezuela

1. - Caudal fin deeply forked; interorbital distance 25-50 % HL; pectoral fin length 13.2-18.2 % SL.
..... 2
- Caudal fin emarginate, sometimes with dorsal lobe longer than ventral, but never distinctly forked; interorbital distance 54-63 % HL, as narrow as 43.0 % HL in specimens less than 100 mm SL; pectoral fin length 16.4-21.0 % SL.
..... *H. edentatus*
2. - Distance between posterior nares 17-24 % HL; prepelvic distance 29.0-38.9 % SL; inner mandibular barbels not longer than other barbels, black colored only if flattened.
..... *H. marginatus*
- Distance between posterior nares 26-27 % HL; prepelvic distance 27.1-29.0% SL; inner mandibular barbels much longer than other barbels, laterally flattened and black colored.
..... *H. cf. fimbriatus*

Hypophthalmus edentatus Spix

(Fig. 1b)

Material examined. MCNG 30856, 3 ex., 245.0-267.0 mm SL (1 measured); Anzoátegui: Laguna El Venado, beside Río Orinoco, 8°10'N 63°38'W. - MCNG 19624, 9 ex., 127.3-185.0 mm SL (1 measured); Apure: Río Apure, Laguna Remanso, 7°54'N 67°23'W. - MCNG 37237, 3 ex., 334.0-364.0 mm SL; Portuguesa: Canal Cocito, 8°56'09"N 68°59'15"W. - MHNLS 1463, 1 ex., 107.1 mm SL; Apure: Río Apure, Mango Verde. - ANSP 165355.51, 51 ex., 55.4-100.5 mm SL (9 measured); Apure: San Fernando to Puerto Páez Highway, 7°20'N 67°35'W.

Diagnosis. *Hypophthalmus edentatus* is distinguished from the other species in the genus by the following combination of characters: caudal fin emarginate, in contrast to deeply forked in the other two species; pectoral fin long (length 4.9-6.0 times in SL), body tall (depth 3.6-4.9 times in SL), short and broad head (length 3.9-4.6 times in SL, interorbital distance 1.6-2.1 times in HL). Size up to 364 mm SL.

Description. See Figure 1b for general appearance, Figure 2 for detail of the head, and Table 1 for morphometrics of 15 specimens 73.8-364.0 mm SL.

Fusiform, head dorsal contour straight, slightly ascending; predorsal profile ascending and moderately convex from postero-occipital to origin of dorsal fin; dorsal fin straight, inclined over dorsum and slightly sloped at tip; prepelvic contour more convex than dorsal, lower end of opercle not completely covering isthmus; posterior to isthmus, body line abruptly convex, and then almost straight to origin of pelvic fin. Head flat anteriorly, wider than longer, profile triangular; eye slightly in anterior half of head length; snout short; ventrally, opercular membrane covering anterior part of isthmus; opercle rounded, its posterior end barely reaching anterior end of pectoral base; isthmus short, significantly wider near base of pectoral fin. Barbels approximately the same length, sometimes moderately flattened laterally.

Dorsal origin slightly anterior to anal origin. D I/5 (4 ex.), I/6 (11). Pectoral triangular, distal edge curved, posterior edge curved and longer than distal. P I/12 (1), I/13 (1), I/14 (5), I/15 (5), I/16 (3). Pelvic diminute, triangular. V 5 (1), 6



Fig. 1. Three Venezuelan *Hypophthalmus* species: **a**, *H. marginatus*, MCNG 37238, 416 mm SL, Caño Cocito/Río Portuguesa; **b**, *H. edentatus*, MCNG 37237, 364 mm SL; Caño Cocito/Río Portuguesa (caudal fin nipped by piranhas); and **c**, *H. cf. fimbriatus*, MCNG 37236, 374 mm SL, Río Casiquiare.

(14). Anal straight, partially covered by muscle tissue at base of rays. A 58 (1), 59 (1), 60 (3), 61 (3), 62 (1), 63 (4), 67(1). Posterior margin of caudal fin emarginate in undamaged and small specimens (SL<100 mm), upper lobe slightly longer, sometimes with a sharply tapering tip.

Coloration. In alcohol. Ground color light gray. In adults, dorsal portion of body generally darker, but with no precise separation from whiter ventrum. Poorly preserved specimens and juveniles (SL<120 mm) usually dirty pink or whitish yellow. Dorsal and adipose gray. Pectoral, pelvic, and anal fin light gray. Specimens smaller

than 120 mm SL sometimes with black dorsal tip. Barbels slightly darker than body, even darker if flattened.

In life. Ground color light gray with shiny yellowish veneer on flanks and steel blue cast on dorsum and head. Ventrums white. Fins with color of body, caudal and anal fin may have reddish color produced by vascular tissues. Barbels light grey dorsally, white ventrally.

Distribution. *Hypophthalmus edentatus* is the most commonly collected of the three species of the genus. Its distribution includes both white and clearwater rivers of the lower Orinoco basin

(Fig. 3). The species is widely distributed in the western llanos. The most abundant records correspond to the Río Apure drainage, where this species is captured in flooded savannas or permanent and seasonal lagoons. It also occurs in the central llanos, and the species is recorded for the Río Apurito and for the Orinoco, near the mouth of Caño Cuchivero. The most eastern collection in the Orinoco corresponds to a seasonal lagoon in Anzoátegui State. The southernmost record for the species in Venezuela is the Río Paragua in Bolívar State. No records of *H. edentatus* are available for the Orinoco delta or for the middle to upper reaches of the river. The wide continental distribution of the species suggests that it is probably present in these areas.

Ecology. Although reported for several river main channels, most collections of *H. edentatus* have been made during the dry season in lagoons and floodplains. This suggests that the fish inhabits the flooded savanna during the rainy season. Available records suggest that *H. edentatus* is most common in whitewater habitats (Fig. 4), and its presence in black waters appears to be extremely limited (a single record from the Río Paragua in Bolívar state within the Río Caroní drainage). Brazilian studies (Carvalho et al., 1978; Carvalho, 1980) showed that this is a pelagic species that feeds primarily on zooplankton, especially Cladocera, Copepoda, and Ostracoda.

Hypophthalmus marginatus Valenciennes
(Fig. 1a)

Material examined. MCNG 19573, 1 ex., 114.0 mm SL; Apure: Río Apure Viejo, in front of slaughter house. – MCNG 32953, 1 ex., 286.0 mm SL; Guárico: Aguaro-Guariquito National Park, Río Guariquito, 7°52'N 66°33'W. – MCNG 37238, 3 ex., 396.0–416.0 mm SL; Portuguesa: Canal Cocito at 8°56'09" 68°59'15"W. – MHNLS 6018, 1 ex., 233.0 mm SL; Territorio Federal Delta Amacuro: Caño Macareo. – MHNLS 9525, 1 ex., 288.0 mm SL; Territorio Federal Delta Amacuro: Caño Manamo. – MHNLS 7133, 1 ex., 283.0 mm SL; Bolívar: Río Orinoco at Polvorín. – MHNLS 4679, 11 ex., 74.9–141.0 mm SL (3 measured); Territorio Federal Amazonas: Caño Macareo. – MBUCV 15201, 1 ex., 218.0 mm SL; Bolívar: Río Orinoco, near mouth of Río Caura, 7°38'N 64°52'W. – MBUCV 9336, 1 ex., 139.0 mm SL; Apure: Río



Fig. 2. Comparison of the head in profile of *H. marginatus*, MCNG 37237, 416 mm SL (top) and *H. edentatus*, MCNG 37238, 364 mm SL (bottom).

Apure in front of the mouth of Río Portuguesa, 7°57'N 67°32'W. – MBUCV 17973, 1 ex., 104.0 mm SL; Bolívar: Río Orinoco, near mouth of Río Caura, 7°38'N 64°54'W. – MBUCV 11727, 4 ex., 61.9–65.7 mm SL (1 measured); Guárico: Highway from Calabozo to San Fernando de Apure, 8°6'N 67°36'W.

Diagnosis. Distinguished from other species of the genus in having a long and narrow head (length 3.5–5.1 times in SL, interorbital distance 2.0–3.9 times in HL). Body depth 4.5–5.7 times in SL. Distinguishable from *H. edentatus* by strongly forked caudal fin in all size classes, and from *H. fimbriatus* by the lack of enlarged and flattened inner-mandibular barbels. Size up to 416 mm SL.

Description. See Figure 1a for general aspect, Figure 2 for detail of the head, and Table 1 for morphometrics of 15 specimens 61.9–416.0 mm SL.

Fusiform, head and predorsal contour ascending almost straight, slightly convex near origin of dorsal fin; dorsal fin almost vertical, slightly sloped at tip; prepelvic contour straight, lower

end of opercle covering isthmus and anterior part of head, line of body slightly convex near origin of pelvic fins. Head flat, much longer than wide, eye in middle of its length; snout long; ventrally, opercle membrane extending to near base of pectoral fin, partially covering isthmus; isthmus long and thin; opercle elongate and slightly longer in upper half posteriorly, tip rounded and slightly overlapping pectoral fin base; barbels of approximately same length, sometimes slightly laterally flattened.

Dorsal origin opposite to anal origin. D I/6 (15 ex.). Pectoral triangular, distal edge slightly curved, posterior edge straight. P I/12 (2), I/13 (2), I/14 (5), I/15 (5), I/16 (1). Pelvic small, triangular. V 5 (1), 6 (11), 7 (1). Anal straight, rays

slightly longer near the anus. A 56 (1), 59 (4), 60 (2), 61 (1), 62 (1), 63 (1), 64 (1), 66 (1), 67 (2). Caudal deeply forked, dorsal lobe longer than ventral.

Coloration. In alcohol. Ground color light gray or white. In adult specimens, head and dorsal half of body dark gray, clearly distinguishable from white ventrum. Juveniles (SL<100 mm) pale, dirty yellowish or white, probably depending on preservation. Dorsal and adipose gray. Pectoral fin gray dorsally and white ventrally. All fins with black distal edge in adults. Barbels generally darker gray than body, sometimes black, especially if flattened.

In life. Ground color light gray with blue-

Table 1. Morphometric data of Venezuelan species of *Hypophthalmus*. (ant.= anteriorly; post.=posteriorly).

	<i>H. edentatus</i> (n=15)				<i>H. marginatus</i> (n=15)				<i>H. cf. fimbriatus</i> (n=5)			
	mean	SD	min.	max.	mean	SD	min.	max.	mean	SD	min.	max.
Standard length (mm)	152.8				218.6		61.9	416.0	343.2			
Percentages of SL												
Predorsal distance	43.5	2.9	39.0	46.5	44.0	2.0	39.7	48.1	40.2	0.7	39.0	40.9
Prepelvic distance	32.0	7.1	30.2	36.0	33.9	3.5	29.1	43.3	27.9	0.6	27.1	28.7
Preanal distance	40.1	1.7	37.2	43.1	38.7	2.6	33.9	46.0	33.5	0.7	32.5	34.3
Prepectoral distance	25.9	2.8	20.6	29.5	24.1	2.4	19.5	27.9	20.7	0.5	20.2	21.4
Body depth	21.0	2.7	18.1	27.7	19.8	1.6	17.5	22.3	17.3	0.6	16.7	18.0
Caudal peduncle depth	8.2	1.0	7.0	10.3	7.9	0.6	7.0	9.2	7.5	0.4	6.9	7.8
Caudal peduncle length	12.9	2.6	4.0	14.6	9.0	4.7	4.5	16.7	7.5	0.6	6.7	8.1
Head length	25.6	2.2	21.5	28.5	24.6	2.1	19.5	28.1	21.3	0.4	20.7	21.9
Pectoral fin length	18.9	1.2	16.4	21.0	15.7	1.6	13.2	18.2	15.5	0.5	15.0	16.4
Pelvic fin length	7.5	1.0	5.6	9.5	6.1	0.6	4.8	6.9	5.5	0.5	4.7	5.9
Dorsal fin length	12.1	1.7	9.7	14.2	12.0	2.1	9.3	16.0	7.4	0.7	6.7	8.2
Anal fin length	10.2	2.2	6.3	13.1	8.0	1.4	5.7	10.4	7.1	0.8	6.0	8.0
Caudal fin length												
(dorsal lobe)	21.5	12.2	20.3	26.6	23.5	5.1	13.1	29.5	18.2	3.3	12.6	21.4
(ventral lobe)	23.3	11.5	18.7	24.7	21.7	4.8	12.0	27.7	15.2	0.7	14.6	16.2
(median rays)	10.3	5.3	9.3	13.0	7.3	2.2	5.1	13.4	5.6	0.6	5.0	6.2
Dorsal fin base	4.7	0.5	3.7	5.6	4.8	0.5	3.6	5.4	3.2	0.3	2.9	3.5
Anal fin base	47.4	1.3	45.5	50.6	46.0	2.2	41.4	50.3	51.0	1.6	48.9	52.7
Dorsal-caudal distance	59.4	1.4	56.5	61.4	57.3	3.4	48.0	61.9	61.6	1.2	60.5	63.4
Eye-dorsal distance	31.7	3.8	18.6	34.6	33.6	6.9	29.4	58.0	30.9	0.1	30.8	31.0
Maxillary barbel length	40.7	8.9	26.1	52.2	40.3	15.1	21.6	72.0	24.5	0.7	23.4	25.4
Outer mandibular barbel	33.1	9.0	18.4	44.0	33.1	11.5	18.9	52.3	21.5	1.4	20.6	23.9
Inner mandibular barbel	38.7	8.0	25.8	50.0	36.7	11.8	21.3	58.6	37.5	1.3	35.4	38.8
Percentages of HL												
Snout length	42.8	3.1	37.0	46.9	44.7	7.3	22.3	52.8	44.8	2.0	42.4	47.6
Orbital diameter	15.9	4.3	8.8	20.6	11.8	4.1	6.9	20.6	10.2	0.3	9.9	10.7
Interorbital distance	53.1	22.7	43.0	62.7	41.5	7.0	25.2	49.8	44.0	2.4	41.3	47.8
Postorbital distance	44.7	2.7	39.7	51.7	39.0	4.8	24.4	45.0	43.9	1.4	42.4	45.4
Inter-nares distance ant.	25.7	7.5	21.8	31.2	24.9	2.2	21.2	28.0	27.6	1.3	26.4	29.4
Inter-nares distance post.	25.7	7.5	21.0	31.5	20.4	4.7	6.0	24.1	26.3	0.6	25.9	27.0
Gill raker length	26.8	9.7	17.7	37.2	18.0	3.8	13.5	25.8	20.6	1.1	18.8	21.5

gray cast on dorsum and head. Flanks and ventrum white. Fins with color of body, except caudal fin blue-gray with black distal edge. Caudal and anal may have a reddish color produced by vascular tissues. Barbels black.

Distribution. *Hypophthalmus marginatus* has been collected in whitewater rivers and caños along the lower Orinoco Basin (Fig. 3). The species is widespread in the western llanos, where it has been collected in abundance. The Río Apure and its tributaries are some of the most frequently sampled areas in Venezuela, and consequently a considerable part of the records come from this area. The eastern limit of the distribution range of the species is the Orinoco Delta. No records exist from the southern Orinoco region.

Ecology. *Hypophthalmus marginatus* appears to be restricted to habitats in or near the primary channels of whitewater rivers (Fig. 4). No records from blackwater rivers currently exist. Almost no collections have been made in seasonal lagoons, suggesting that the species may prefer larger, permanent water bodies. Nothing is known of the habits of this species in Venezuela, as it has been confused with *H. edentatus* until now. Studies in Brazil indicate that *H. marginatus* feeds on phytoplankton (Carvalho et al., 1978, cited by Carvalho & Goulding, 1985).

Hypophthalmus cf. fimbriatus Kner
(Fig. 1c)

Material examined. MCNG 37236, 5 ex., 311.0-374 mm SL; Amazonas: Río Casiquiare at 1°71'N 66°56'W.

Diagnosis. *Hypophthalmus cf. fimbriatus* is distinguishable from other species in the genus by its long, black, and flattened inner mandibular barbels; slender body (body depth 5.5-6.0 times in SL), head dorsoventrally compressed, and general dark coloration in alcohol. Distinguishable from *H. edentatus* by the forked tail and from *H. marginatus* by the short and wide head. Size up to 343 mm SL.

Description. See Figure 1c for general appearance and Table 1 for morphometrics of five specimens 311.0-374 mm SL.

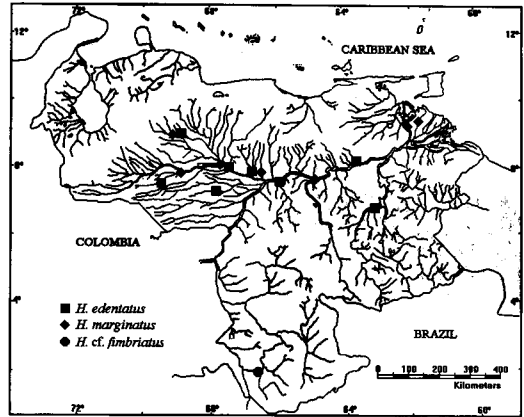


Fig. 3. Known distribution of *Hypophthalmus* species in Venezuela.

Fusiform, elongate. Predorsal contour straight from tip of the snout to origin of the dorsal fin; one specimen shows slightly convex profile from occipital to origin of dorsal; dorsal fin short, straight, inclined over body dorsum; prepelvic contour straight to moderately convex, especially behind opercle posterior end to pelvic fin origin. Head flat, relatively long and wide, eye in middle of its length, more ventrally than dorsally positioned; snout moderately long; ventrally, opercle membrane covering isthmus slightly farther than posterior margin of eye; isthmus long and thin; opercle rounded at lower edge, elongate at upper-posterior end, slightly overlapping pectoral fin origin. Barbels black, maxillary and outer mandibular visibly shorter than inner mandibular, the latter distinctively flattened proximally, tapering to a point distally.

Dorsal origin slightly posterior to anal origin. D I/6 (5 ex.). Pectoral triangular, elongate, sometimes reaching most anterior end of anal fin, distal edge moderately curved, posterior edge straight or slightly curved. P I/13 (1), I/14 (2), I/15 (2). Pelvic small, triangular. V 5 (1), 6 (4). Anal straight, rays diminishing in length near base of caudal peduncle. A 64 (1), 65 (2), 68 (1), 69 (1). Caudal forked, ventral lobe slightly deeper than dorsal, both sharply tipped, sometimes with a filament.

Coloration. In alcohol. Ground color ash gray; dorsal portion of body almost black gray, lighter gray in flanks and ventrum. Dorsal and adipose same color as dorsum; pectoral light gray; pelvic



Fig. 4. Río Portuguesa in Estado Portuguesa, a typical whitewater river of the western llanos and habitat of *Hypophthalmus edentatus* and *H. marginatus*.

uncolored; anal darker at base; caudal black near base, not reaching tip of rays. Barbels black.

In life. Ground color light gray, shiny metallic-green veneer on head and flanks; dorsum almost black gray; ventrum white. Dorsal and adipose dark gray; caudal and anal dark gray or black proximally, clear distally; pectoral dark gray on anterior rays, clear posteriorly; pelvic white. Barbels black.

Distribution. Until now, *H. fimbriatus* has been collected only from the Río Negro, Brazilian Amazon (Carvalho & Goulding, 1985). If it is the same species, our report extends its range northward into the upper Río Negro and Orinoco basins (Fig. 3). The fish were taken from the Río Casiquiare channel (Fig. 5), which receives waters from the upper Orinoco and delivers them to the upper Río Negro. The upper Orinoco channel has not been extensively collected, and further collections in this area are needed to clarify the distributional boundaries of *H. cf. fimbriatus*.

Ecology. Given limited records and a limited geographical range, little can be said of the eco-

logical preferences of *H. cf. fimbriatus*, except that the species appears to be restricted to black waters (Fig. 5). Carvalho & Goulding (1985) described a diet comprised primarily of zooplankton in the lower Río Negro.

Remarks. Our specimens agree with the description given by Oliveira (1981) and the photograph of lower Río Negro *H. fimbriatus* shown in Carvalho and Goulding (1985). However, some specimens from the Río Negro have greatly enlarged mandibular barbels (J. Lundberg, pers. com.), not observed in our material. For this reason, we refer to Venezuelan specimens as *H. cf. fimbriatus* pending completion of further study.

Discussion

Although overlooked in field collections for several decades, at least three species of *Hypophthalmus* exist in Venezuela. *Hypophthalmus edentatus* is sympatric with *H. marginatus* in a variety of lowland habitats of the Venezuelan llanos and other areas lying to the east within the Orinoco



Fig. 5. Rio Casiquiare in Estado Amazonas, a blackwater tributary of the Río Negro and habitat of *Hypophthalmus* cf. *fimbriatus*.

Basin. These two species are readily distinguished from each other by a series of morphometric and external anatomical features, most notably the differences in head and caudal fin shape. Among juveniles, head features are very similar (Fig. 6) and the caudal fin provides the most reliable character for species identification. In Venezuela, *H. cf. fimbriatus* appears to be restricted to the acidic, black waters of the lower Río Casiquiare where the other two species are not known to occur.

The morphological characters of Venezuelan *H. edentatus* specimens coincide with those described by Nani & Fuster (1947) and by Oliveira (1981) as diagnostic for the species. These results suggest that *H. edentatus* is a continentally distributed species, that ranges from the Orinoco and Guyana coastal drainages in northern South America throughout the Amazon to the Paraná Basin in the south of the continent.

Using the characters given by Oliveira (1981), Venezuelan *H. marginatus* specimens appear to be conspecific with fish from Surinam and the Amazon. The wide distribution of this species in the western llanos of Venezuela suggests that it

also could occur in lowland rivers of the Orinoco Basin within Colombian territory.

The five Casiquiare specimens of *H. cf. fimbriatus* that we examined agree with the description given by Oliveira for Río Negro specimens. They are also similar in appearance with the photograph in Carvalho & Goulding (1985). The one exception is the shape of the barbels, with the Casiquiare specimens having somewhat narrower fimbria on the inner mandibular barbels. Detailed comparison with Río Negro specimens would be necessary for confirmation of *H. cf. fimbriatus* identity, or for suggesting a distinct taxonomic entity, as the degree of fimbriation varies considerably in the other two species as well (J. Lundberg, pers. com.; pers. observ.).

The habitats from which *H. edentatus* and *H. marginatus* have been captured suggest habitat partitioning. Although both species were captured in the same gillnet at one location (Caño Cocito near its confluence with the Río Portuguesa in August, 1996), most of the *H. marginatus* specimens were captured from river and creek channel habitats, whereas most specimens of *H. edentatus* were captured from aquatic flood-

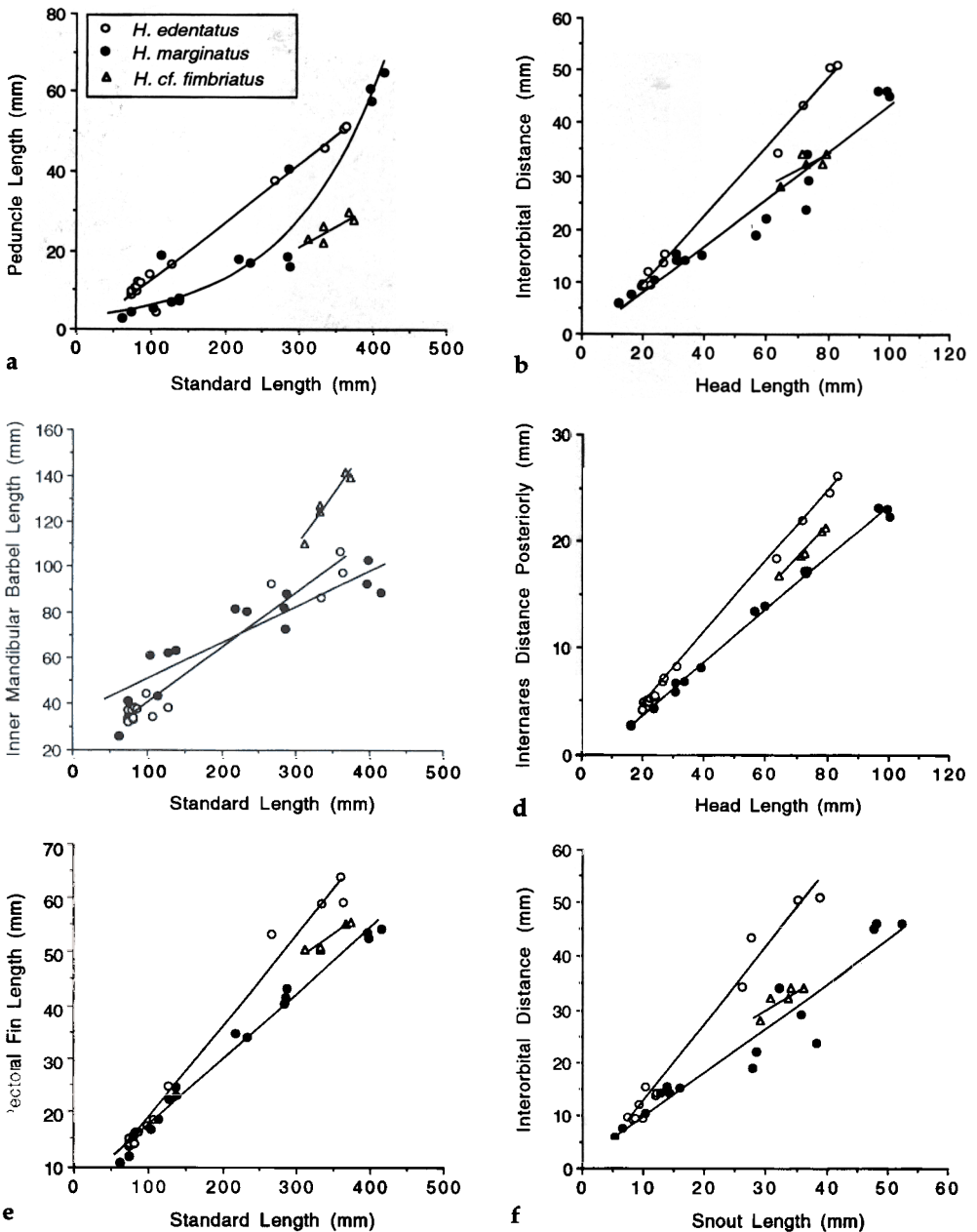


Fig. 6. Graphs showing bivariate relationships between morphometric attributes distinguishing *Hypophthalmus* species in Venezuela. The equation for the curvilinear regression for Peduncle Length \times SL for *H. marginatus* is $Y = 2.79 \times 10^{0.003x}$. The slope, intercept, and coefficient of determination for each linear regression equation are as follows: **a**, peduncle length \times SL: *H. edentatus*: 0.14, -1.74, 0.97; *H. cf. fimbriatus*: 0.10, -7.59, 0.66; **b**, interorbital distance \times HL: *H. edentatus*: 0.65, -3.66, 0.99; *H. marginatus*: 0.44, -0.94, 0.94; *H. cf. fimbriatus*: 0.32, 8.83, 0.57; **c**, inner mandibular barbel length \times SL: *H. edentatus*: 0.24, 15.85, 0.93; *H. marginatus*: 0.16, 34.34, 0.81; *H. cf. fimbriatus*: 0.47, -34.15, 0.93; **d**, internares distance posteriorly \times HL: *H. edentatus*: 0.34, -2.37, 0.99; *H. marginatus*: 0.25, -1.34, 0.99; *H. cf. fimbriatus*: 0.32, -4.26, 0.98; **e**, pectoral fin length \times SL: *H. edentatus*: 0.17, 1.85, 0.99; *H. marginatus*: 0.12, 5.50, 0.98; *H. cf. fimbriatus*: 0.09, 20.92, 0.91; **f**, interorbital distance \times snout length: *H. edentatus*: 1.46, -2.34, 0.98; *H. marginatus*: 0.83, 1.53, 0.92; *H. cf. fimbriatus*: 0.76, 7.17, 0.75.

plain habitats, including seasonally inundated lagoons. These observations suggest that *H. edentatus* spends the rainy season in the flooded savanna, whereas *H. marginatus* probably migrate from the permanent channels only rarely. Although this issue requires further research, differences in certain morphological features also indicate that these species use different habitats. The forked tail and more slender head and body of *H. marginatus* would be advantageous for a fish that occupies the water column in lotic habitats. Under flowing water conditions, low body drag and a caudal fin with a high aspect ratio (shaped to reduce the force of drag in water) would enhance swimming efficiency, which would be important during sieve foraging. Patterns of habitat use also influence predation threat. The lobes of a deeply forked caudal fin probably would be more attractive and vulnerable to fin-nipping piranhas (Winemiller & Kelso-Winemiller, 1993). Residence in the main channels would be associated with less exposure to these small piranhas which tend to be most abundant in lentic or slow moving water (Nico & Taphorn, 1988; Winemiller, 1990). In contrast to *H. marginatus*, most of the specimens of *H. edentatus* from the llanos had caudal fins damaged by piranhas.

Existing diet information from studies in Brazil indicates that the two sympatric *Hypophthalmus* species may feed on different kinds of plankton. In an Amazon floodplain lake, *H. edentatus* consumed a variety of zooplankton taxa (Carvalho, 1980). However, *H. marginatus* from the Río Tocantins mouth-lake was described as feeding primarily on phytoplankton (Carvalho et al., 1978, cited in Carvalho & Goulding, 1985). This species' apparent restriction to whitewater habitats might be associated with the lack of phytoplankton standing biomass that has been noted for nutrient-impooverished black waters (Sioli, 1984). *Hypophthalmus fimbriatus* in the lower Río Negro fed primarily on zooplankton, especially Cladocera and Copepoda (Carvalho & Goulding, 1985).

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