

Holotype-based validation, redescription and continental-scale range extension of the South American catfish species *Hypophthalmus oremaculatus* Nani and Fuster, 1947, with additional information on *Hypophthalmus edentatus* Spix and Agassiz, 1829 (Siluriformes, Pimelodidae)

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Holotype-based validation, redescription and continental-scale range extension of the South American catfish species *Hypophthalmus oremaculatus* Nani and Fuster, 1947, with additional information on *Hypophthalmus edentatus* Spix and Agassiz, 1829 (Siluriformes, Pimelodidae)

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ABSTRACT.—The heretofore little-known pimelodid species *Hypophthalmus oremaculatus* Nani and Fuster, 1947, from the río Paraná, Argentina is redescribed and validated based on examination of its recently found holotype and extensive comparative study of specimens of all nominal species of the genus. Specimens of *Hypophthalmus* from the Paraná Basin have often been mistakenly labelled as *H. edentatus* Spix and Agassiz, 1829, and *H. oremaculatus* has occasionally been considered a junior synonym of *H. edentatus*. Examination of the syntypes of *H. edentatus* reveals a long-mistaken concept of its diagnostic features in the original description based on Spix's inaccurate illustration. *Hypophthalmus oremaculatus* is common and widespread in the Paraná Basin, including the Upper Paraná system. This species is also widespread in the Amazon and Orinoco basins.

Hypophthalmus oremaculatus is distinguished from other species of the genus by the following combination of characters: caudal fin shallowly-forked, head broad and short, membrane of skin tying the innermost pelvic-fin ray to the edge of the urogenital-anal region, 55-59 total vertebrae, 3-6 vertebrae with separate and robust neural spines between the Weberian complex and first vertebra with contact between its neural spine and a dorsal-fin pterygiophore, long mental barbels usually extending to pectoral origin or beyond, and dorsal-fin origin approximately in line with anal-fin origin.

RESUMEN.—Se redescrive y valida la especie de pimelódido escasamente conocida hasta ahora, *Hypophthalmus oremaculatus* Nani y Fuster, 1947, del río Paraná, Argentina, basados en el examen del holotipo recientemente encontrado y en el amplio estudio comparativo de ejemplares de todas las especies nominales del género. Ejemplares de *Hypophthalmus* de la cuenca del Paraná, a menudo han sido erróneamente etiquetados como *H. edentatus* Spix y Agassiz, 1829, y *H. oremaculatus* ha sido considerado ocasionalmente un sinónimo junior de *H. edentatus*. El examen de los sintipos de *H. edentatus* revela un concepto largamente equivocado de sus caracteres diagnósticos en la descripción original, basados en la inexacta ilustración de Spix. *Hypophthalmus oremaculatus* es común y esta ampliamente distribuido en la cuenca del Paraná, incluyendo el sistema del Alto Paraná. Esta especie también está ampliamente distribuida en las cuencas del Amazonas y Orinoco.

Hypophthalmus oremaculatus se distingue de otras especies del género por la siguiente combinación de caracteres: aleta caudal suavemente furcada, cabeza ancha y corta, membrana de piel conectando los radios más internos de la aleta pélvica al borde de la región urogenital-anal, 55-59 vértebras totales, 3-6 vértebras con espinas neurales separadas y robustas entre el complejo de Weber y la primera vértebra con contacto entre su espina neural y un pterigióforo de la aleta dorsal, largas barbillas mentonianas, extendiéndose usualmente hasta el origen de la aleta pectoral o mas allá y el origen de la aleta dorsal aproximadamente alineado con el origen de la aleta anal.

INTRODUCTION

In the latest taxonomic catalogues of pimelodid catfishes, the genus *Hypophthalmus* Cuvier, 1829 contains four valid species (Lundberg and Littmann, 2003; Ferraris, 2007; Eschmeyer, 2015): *H. edentatus* Spix and Agassiz, 1829 (the type species); *H. marginatus* Valenciennes, 1840; *H. fimbriatus* Kner, 1857, and *H. oremaculatus* Nani and Fuster, 1947. In the context of an ongoing revision of the genus *Hypophthalmus* (MWL, JGL), we have determined that *H. edentatus* and *H. marginatus* are commonly, and often incorrectly, used names applied to specimens from the Orinoco, Amazon and Paraná basins, and the major rivers of the Guianas. *Hypophthalmus fimbriatus* is a valid, endemic species in the Amazon Basin. *Hypophthalmus oremaculatus* is a valid species that is scarcely known beyond its original description and holotype specimen from the Paraná River in Argentina. Further, we have determined statuses of three species listed in those same catalogues as *species inquirendae*: *H. longifilis* Valenciennes, 1840, is a junior synonym of *H. marginatus*, *H. perporosus* Cope, 1878, is a junior synonym of *H. edentatus*, and *H. dawall* of Röhl (1942) is an unavailable name (Eschmeyer, 2015).

The name *H. oremaculatus* seldom appears in the literature other than in catalogs and lists (e.g. Ringuélet et al., 1967; López et al., 1987; Braga and Piacentino, 1994; Lundberg and Littmann, 2003; Menni, 2004; Ferraris, 2007; Buckup et al., 2007; Eschmeyer, 2015). In his unpublished, but still the most comprehensive taxonomic review of *Hypophthalmus*, Oliveira (1981) recognized one species of the genus in the Paraná Basin that he referred to *H. edentatus*, and he doubted that *H. oremaculatus* is a valid species. Recently, however, the holotype of *H. oremaculatus* (Fig. 1) was located and made available to us for study after its temporary misplacement at the Museo Argentino de Ciencias Naturales in Buenos Aires. Accordingly, we have taken this opportunity to validate and redescribe the species, and to greatly extend its range across cis-Andean South America. *Hypophthalmus oremaculatus* is the common and widespread species of the genus in the Paraná Basin (Fig. 2, 3a), including the Upper Paraná system, an area that was historically isolated from the lower Paraná until inundation of Sete Quedas (Guairá) waterfall following construction of the Itaipú Dam and reservoir (Júlio Jr. et al., 2009). Furthermore, we identify specimens of *H. oremaculatus* in the Amazon and Orinoco basins (Fig. 3 b,c). Unfortunately, the specimen cited as *H. edentatus* by Ringuélet et al. (MLP 14-III-34-8) is lost, but we identify as *H. oremaculatus* the specimen (MACN 3949) attributed to *H. edentatus* by Berg (1898) and Nani and Fuster (1947). We have not personally examined specimens of *H. edentatus* from the Paraná Basin and we doubt that it is present.

MATERIAL AND METHODS

In this study MMA and JAVR examined, radiographed and measured the holotype of *H. oremaculatus* and additional specimens of the species collected in the Argentinian Paraná Basin. MWL and JGL examined and measured the available specimens or Xray/photographic images of *H. oremaculatus* from the Paraná Basin in Paraguay and Brazil, and several specimens from the Amazon and Orinoco basins. Prior to or during the course of this work, we examined several thousand specimens representing the four valid species of *Hypophthalmus* plus two species pending formal description. The primary type specimens of all nominal species of South American *Hypophthalmus* were directly examined, except *H. fimbriatus* for which we have recent photographs. There is no specimen of Röhl's (1942) incorrectly used binomen *Hypophthalmus dawall* applied to a Venezuelan catfish of the genus *Brachyplatystoma*. Data, photographic or radiographic images of several important specimens were provided by colleagues: F. Langeani, C. Pavanelli, F. Bockman (material from the Itaipú region, upper Paraná Basin, Brazil), M. Sabaj (Peruvian Amazon, Guyana, Suriname), M. Rocha (rio Parnaíba; INPA fish collection), D. Bastos (INPA fish collection) and C. Bueno (syntypes of *H. edentatus* at MHNN). MWL or JGL examined freshly collected specimens of *Hypophthalmus* while collecting fishes in the Orinoco in Venezuela, the Amazon in Peru and Brazil, and the Surinam River in Suriname. Museum collection codes follow Sabaj et al. (2014).

Twenty linear measurements (Table 1) defined by external landmark points were taken from 49 specimens of *H. oremaculatus* from the Paraná (15 specimens), Amazon (20 specimens), and Orinoco (43 specimens). Measurements were made with dial calipers or needle point dividers and recorded to nearest 0.1 mm. Measurements were not taken from badly distorted or damaged landmarks. For descriptive and comparative purposes ratios and step-measurements are reported using Standard length (SL) or Head length (HL) measured from snout tip to posterior margin of bony opercle.

Vertebral and fin-ray counts (Table 2) were made on cleared and stained specimens, dry skeletons, and radiographs. Vertebral counts include the anteriormost six vertebrae united in the Weberian complex (Lundberg and Luckenbill, in press) and one for the first preural centrum united in caudal skeleton. The first caudal vertebra is immediately posterior to the visceral cavity and has a long hemal spine that is subequal in length to the hemal spine of the following vertebra. Fin-ray counts include all rudimentary and anatomically separate lepidotrichia. Caudal-fin ray counts are given in the sequence: upper procurent rays, upper principal-fin rays, lower principal-fin rays and lower procurent rays.

SYSTEMATICS

Genus *Hypophthalmus* Cuvier, 1829

Type Species.—*Hypophthalmus edentatus* Spix and Agassiz, 1829, by subsequent designation of Bleeker (1862).

Diagnosis.—A genus of Pimelodidae belonging to the “sorubimine group” (Lundberg et al., 2011; Rocha, 2012) that is distinguished from other siluriforms by an exclusive combination of synapomorphies (Howes, 1983; Lundberg and Luckenbill, in press). These distinctive features include: large eyes set laterally and low on the sides of the head; compressed bodies crossed by complexly branched laterosensory canals; wide-mouths with delicate, toothless jaws and expansive branchial chambers with scores of slender gill rakers on all five gill arches; long anal fin with ray counts ranging from 58-71; swim bladder reduced to a pair of bilobed, independent sacs, each doubly encapsulated by outer and inner layers of bone; shortened anterior vertebrae and occipital bones; obsolete first centrum; loss of the claustra and intercalaria from the chain of Weberian ossicles; stout posttemporal-supracleithrum firmly united to a recurved arm of the 4th parapophysis and both reaching far posteriorly to brace the outer swim bladder capsule and articulate with the cleithrum.

Comments.—Within *Hypophthalmus* we find that *H. oremaculatus* and an undescribed species (herein “*Hypophthalmus* n. sp. 1”) comprise an “*Hypophthalmus oremaculatus* species group” characterized by an emarginate or shallowly-forked caudal fin, a broad, short head, and a membrane of skin tying the innermost pelvic-fin ray to the edge of the urogenital-anal region (Figs. 1-3). In contrast, *H. edentatus* (Fig. 4), *H. marginatus*, *H. fimbriatus*, and an undescribed species (herein “*Hypophthalmus* n. sp. 2”) have a deeply-forked caudal fin, a narrowly-compressed, elongated head, and they lack the pelvic-fin membrane.

Centrally important to the foregoing points were the discovery by Maurice Kottelat (1984, 1988) and our assessment of the two syntypes (MHNN 706) of *H. edentatus* in the Museum d’Histoire Naturelle de Neuchâtel, Switzerland. Early in our work on *Hypophthalmus* the MHNN syntypes were examined by MWL who recognized a long standing misconception of the characteristics of the species to which the name *H. edentatus* applies. *Hypophthalmus edentatus* is not a broad and short-headed species with a shallowly-forked caudal fin, but instead is a slender-headed species with a deeply-forked caudal fin (Fig. 4). Then recently, at our request Ms. Celia Bueno at MHNN provided us with high-resolution radiographs of the two syntypes. These X-rays reveal diagnostic characters of the vertebral column that place *H. edentatus* distinctly apart from *H. oremaculatus* and with the slender-headed and deeply-forked tailed *H. marginatus*, *H. fimbriatus* and “*H. n. sp. 2*”. The key points from this finding for the present paper follow and the details, with species redescrptions, will be published in a forthcoming paper revising *Hypophthalmus* (Littmann and Lundberg, in prep.).

Prior to the finding and Kottelat’s study of several type specimens of Spix and Agassiz’s Brazilian fishes in MHNN there is no indication that any ichthyologist working on *Hypophthalmus* examined the syntypes of *H. edentatus*. Also, Whitehead and Myers (1971) and Terofal (1983) reported that, along with other specimens tracing to Spix, the syntypes of *H. edentatus* were presumed destroyed in Munich during World War 2. Without type specimens in hand, and armed only with Agassiz’s description based on Spix’s inaccurate depiction (1829, Plate IX), ichthyologists were left with a vague and incorrect picture of the appearance of the species named *H. edentatus*. Plate IX of *H. edentatus* in Agassiz and Spix (1829; reprinted in Pethiyagoda et al., 1998, p. 382) illustrates a fish in dorsolateral view that has a relatively short head and distinctly forked caudal fin with pointed lobes. This portrayal conflicts with our and other’s



Fig. 1. Holotype of *Hypophthalmus oremaculatus*, MACN 3496, 335 mm SL.

observations of hundreds of specimens, and now with characters presented by the syntypes of *H. edentatus*. Such a combination of external features is not found to exist in the genus *Hypophthalmus*. Before us, Oliveira (1981) pointed out the likely inaccuracies of the illustration and suggested that Spix may have used a poorly preserved or a mixed-species sample of specimens.

During the 19th century additional species of *Hypophthalmus* were described: Valenciennes, *H. marginatus* and *H. longifilis* (1840); Kner, *H. fimbriatus* (1857); and Cope, *H. perporosus* (1878). In his master's dissertation, Oliveira (1981) reviewed the taxonomic history of *Hypophthalmus*, noting that in these works, few specimens were consulted and comparisons were superficial and incomplete. Eigenmann and Eigenmann (1890) examined specimens from the lower Amazon, compared the published species descriptions and concluded that *Hypophthalmus* contained a single variable species. With the exception of Nani and Fuster's 1947 description of *H. oremaculatus*, the assertion of monotypy of *Hypophthalmus* by Eigenmann and Eigenmann largely prevailed from the late 19th and through most of the 20th century.

Departing from the foregoing view of monotypy, Oliveira (1981) concluded, based on his study of over 350 specimens in the Museu de Zoologia of the Universidade de São Paulo, that there are three valid species overall: *H. edentatus*, *H. marginatus* and *H. fimbriatus*. Of these, Oliveira's description and illustration of *H. edentatus*, lacking the benefit of direct examination of the types, continued to present this species with broad, short head and shallowly forked or emarginate caudal fin. Consistent with his view of *H. edentatus*, Oliveira recommended placement of *H. oremaculatus* in synonymy with *H. edentatus*. Since the 1980s, *H. edentatus*, *H. marginatus* and *H. fimbriatus* have been recognized as valid, but with the ongoing misapplication of *H. edentatus*. With the new information on the syntypes of *H. edentatus* we see that this is incorrect, and we find that *H. oremaculatus* is an available name for the species treated in detail herein. Further, through examination of the type specimens, we have determined that the names *H. longifilis* Valenciennes, 1840, and *H. perporosus* Cope, 1878, are respectively synonyms of *H. marginatus* and *H. edentatus*. *Hypophthalmus dawall* of Röhl (1942), used only and erroneously for *Brachyplatystoma filamentosum*, is an unavailable name in taxonomy (Eschmeyer, 2015).

Hypophthalmus oremaculatus Nani and Fuster, 1947

Figures 1-3, Tables 1, 2

Hypophthalmus oremaculatus.—Nani and Fuster, 1947: 3, Fig. 2-3 (original description, single specimen). Ringuelet and Arámburu, 1957 (listed, Paraná-La Plata), Ringuelet

and Arámburu, 1961 (listed, Paraná-La Plata), Ringuelet et al., 1967 (listed, characters, Argentina); Liotta, 2005 (listed, name only, Argentina); López et al., 2003 (listed, name only, Argentina); Menni, 2004 (listed, questions validity, Argentina); Buckup et al., 2007 (listed, name, Brazil).

Hypophthalmus edentatus.—Misapplications of the name of an extralimital species to *H. oremaculatus* in the Paraná Basin – Berg, 1898, and Nani and Fuster, 1947 (MACN 3949 [not 3049], río Paraná, Zárate); Ringuelet et al., 1967 (listed, Argentina); López et al., 1980 (Ensenada, Río de la Plata); Oliveira, 1981 (MZUSP 15368, 15369, río Paraná, Brazil); Nakatani et al., 1998 (larval morphology and growth); Ambrósio et al., 2003 (age and growth); Liotta, 2005 (listed, name only, Argentina); López et al., 2003 (listed, name only, Argentina); Menni, 2004 (listed, Argentina); Demonte and Arias, 2005 (arroyo Feliciano, Argentina); Neris et al., 2010 (listed, name only, Paraguay); Britski et al. 1997, 2007 (listed, name only, Pantanal); da Graça and Pavanelli, 2007 (listed, discussion of *H. oremaculatus*, Alto Paraná, Brazil); Brancolini et al., 2014 (río Pilcomayo, Argentina, first record from the basin with new material).

Hypophthalmus edentatus.—Misapplications of the name to specimens of *H. oremaculatus* in the Amazon Basin: Oliveira, 1981 (from Brazil: MZUSP 5644, 13360, 14909, 14920, 14931, 14933, 14935, 14980; from Peru MZUSP 14942; listed, measurements and description combined with data from specimens of "*Hypophthalmus* n. sp.1" as used herein).

Hypophthalmus edentatus.—Misapplications of the name to specimens of *H. oremaculatus* in the Orinoco Basin: López-Fernández and Winemiller 2000: 37 (at least in part, from Venezuela ANSP 165355, MCNG 30856, MHNLS 1463; listed and description possibly combined with data from specimens of "*Hypophthalmus* n. sp.1" as used herein).

Holotype.—MACN 3496, 335 mm SL (our measurement; original description inconsistently reported SL as 335 mm and 355 mm), Argentina, Prov. Sante Fe, río Paraná lower course at Puerto Gaboto, 32°25'58"S, 060°48'33"W.

Other Specimens.—Paraná Basin, Argentina: MLP 8264 (142 mm SL), Prov. Buenos Aires, río de la Plata at Ensenada, 34°51'42"S, 057°54'40"W, Aug 1973, R. Arámubru; MACN 5464 (288 mm SL) Prov. Santa Fé, río Paraná at Rosario, 32°57'S, 60°40'W, MLP 10754 (5, 254-283 mm SL), CI-FML 6118 (2, 229-251 mm SL) Prov. Misiones, Dep. Candelaria, río Paraná at

Candelaria, 27°26'45"S, 055°44'53"W, 1990, Proyecto Biología Pesquera Regional; CI-FML 6191 (255 mm SL), Prov. Corrientes, río Paraná at Ita-Ibate near Corrientes, 27°28'39"S, 57°58'33", Nov. 2004, S. Sánchez et al.; CI-FML 5923 (2, 136.2-142.0 mm SL), Prov. Salta, Dep. Rivadavia, secondary channel of río Bermejo near Rivadavia City, 24°6'33"S, 062°40'20"W, 20 Jan 2014, M. Mirande, G. Terán and F. Alonso (first record in the basin). CI-FML 6191 (260 mm SL), Prov. Corrientes, Dep. General Paz, río Paraná near Ita Ibaté (27°28'39" S, 57°58'33"),

Nov.2004, coll. S. Sánchez et al. Brazil: MZUSP 40082 (3, 139-252 mm SL), Est. Mato Grosso do Sul, Aquidauana, río Paraguay (río Aquidauana), Baía da Onça ou Jatobá, Faz. Alegrete, 19°44'30"S, 056°50'42"W, A. C. Catella; NUP 11396 (4), Est. Mato Grosso, río Paraguai (río Quilombo), Chapada dos Guimaraes, 15°07'04"S, 055°32'11"W, 12 Nov 2003, NUPELIA; MZUSP 15368 (358 mm SL), Est. Paraná, río Paraná below Sete Quedas, 24°09'55"S, 054°20'14"W, 22 Feb 1977, CETESB; MZUSP 13360 (387 mm SL), MZUSP 15369 (373 mm SL, ♀), Est. Paraná, río Paraná,

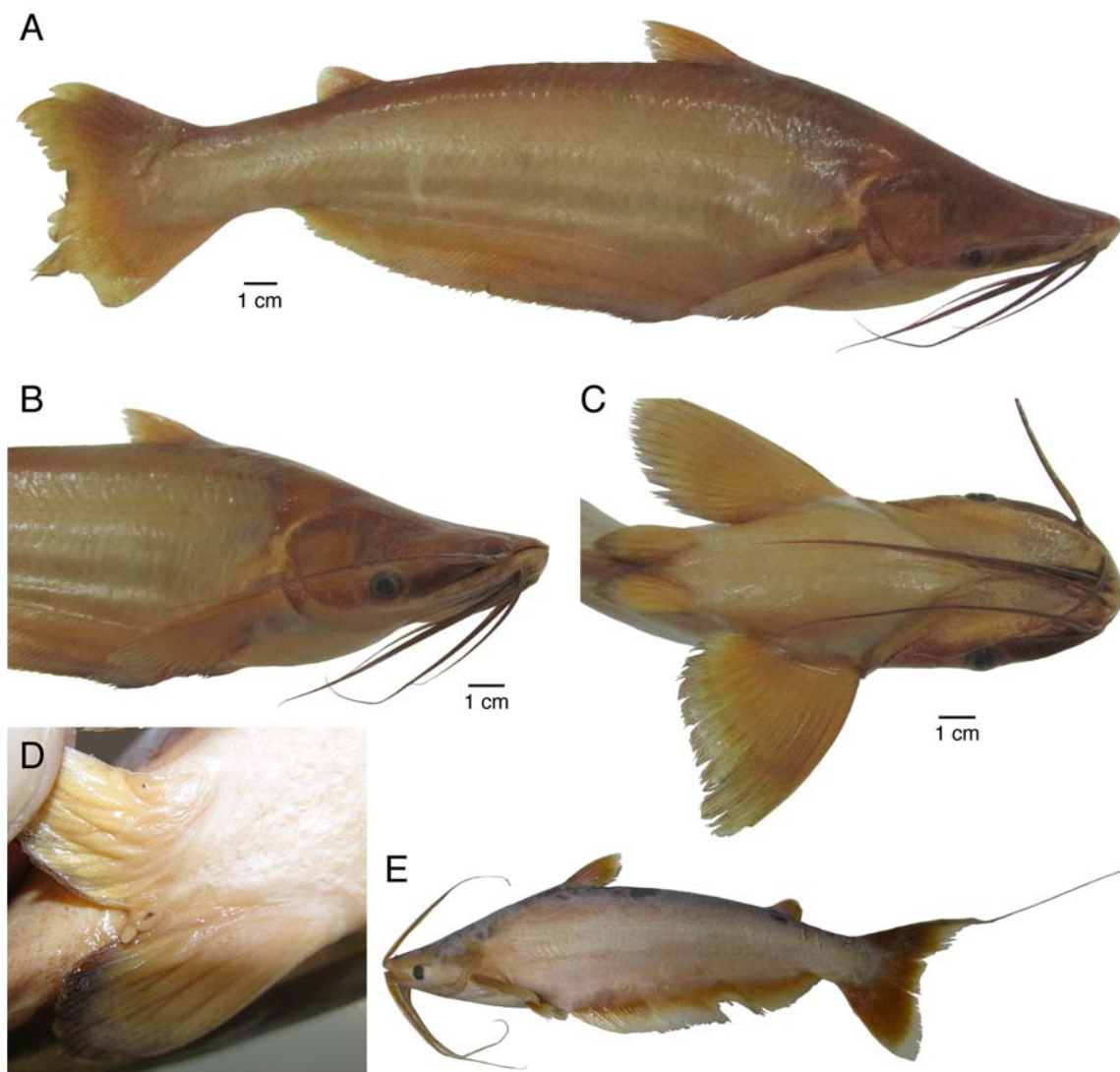


Fig. 2. *Hypophthalmus oremaculatus* A-D. MACN 5464, 288 mm SL. A. Lateral view of whole fish, B. Lateral view of head and trunk, C. Ventral view of head and trunk, D. Pelvic-fin membrane adnate to ano-urogenital region. E. Lateral view of fresh whole fish (disposition unknown) with filamentous upper principal caudal-fin ray, San Fernando de Apure, Orinoco Basin, Venezuela.

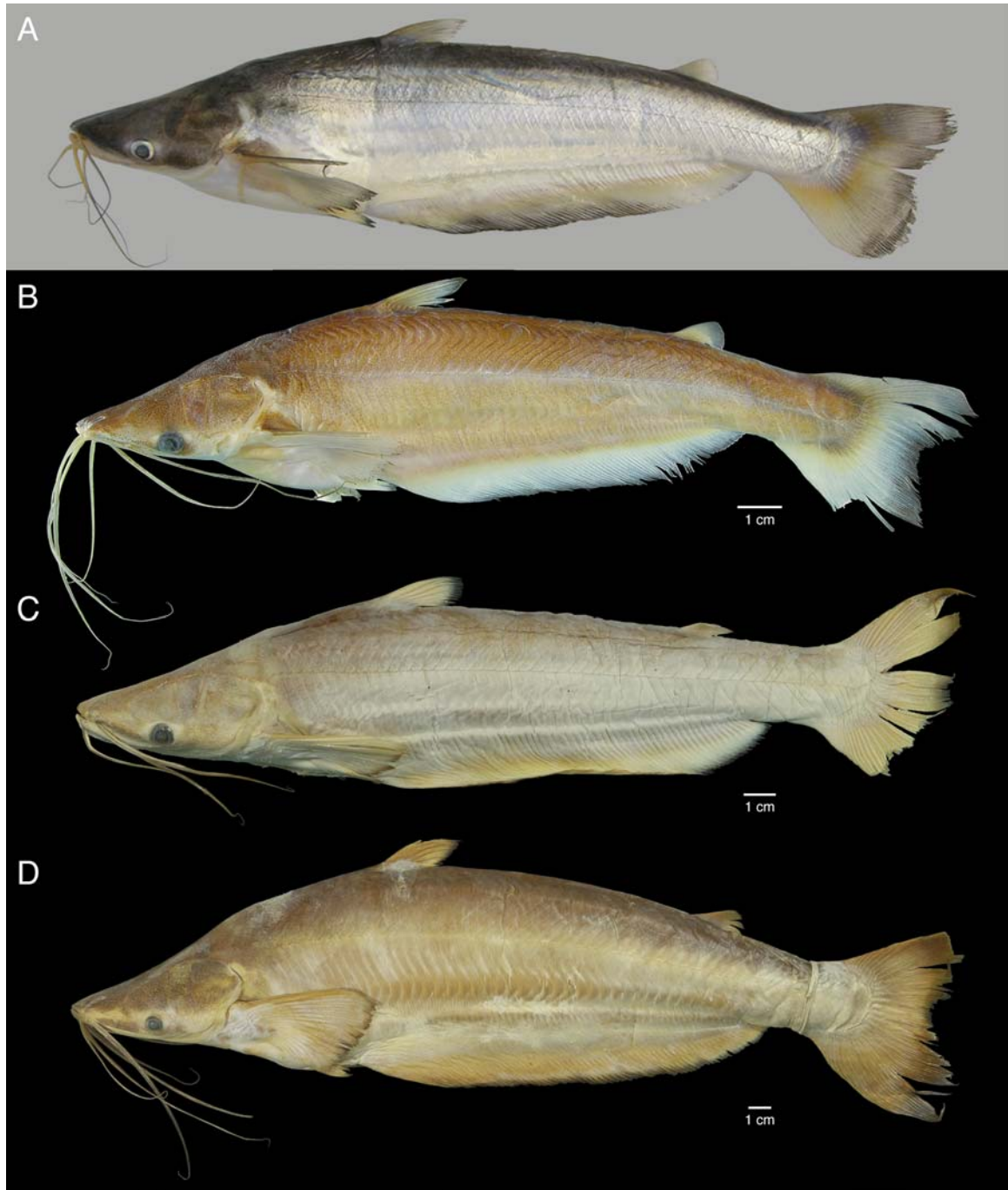


Fig. 3. Representative specimens of *Hypophthalmus oreamaculatus* from the Paraná, Amazon, Orinoco basins. A. CI-FML 6191, 255 mm SL, Argentina, Paraná River, Ita-Ibaté near Corrientes; B. NRM 31522, 183 mm SL, Paraná, Paraguay. C. ANSP 120650, 245 mm SL, Amazon, Colombia, Market at Leticia; D. ANSP 128136, 366 mm SL, Orinoco Basin, Colombia, río Meta, Lago Mozambique.

Porto Verde, 25°09'S, 054°25'W, CETESB; NUP 520 (1), Est. Paraná, Rio Ocoí, tributary of Itaipú reservoir, town of São Miguel do Iguacu, 25°14'16"S, 054°22'58"W, 18 Nov 1988, NUPELIA; NUP 1730 (273 mm SL), Est. Paraná, County Porto Rico, tributary of rio Paraná, 22°46'04"S, 053°16'06"W, 1990-1995, NUPELIA; MZUSP 63592 (4, 126-265 mm SL), MZUSP 63593 (16, 154-227 mm SL), Est. Paraná, probably multiple sites (Iguaçu, Santa Helena, Guairá) on/near Itaipú Reservoir, NUPELIA. Paraguay: NRM 31522 (183 mm SL), Dep. Paraguari, Lago Ypoá, Estancia Ypoá, 25°54'33"S, 057°25'34"W, 5-7 Oct 1994, Kullander et al.; NRM 31890 (4, 298-308 mm SL), Dep. Cordillera, Lago Ypacaraí, San Bernardino, Club Náutico, 25°18'47"S, 057°18'02"W, 20 Oct 1994, B. Dellling et al.; USNM 232309 (180 mm SL), Dep. Central, Lago Ypacaraí, 6 km SE of Aregua, 25°19'22"S, 057°21'18"W, 5 Dec 1980, L. Naylor and R. White.

Amazon Basin. Amazon River (Solimões and Amazonas): Brazil: MZUSP 14924 (1), MZUSP 14925 (330 mm SL), MZUSP 14926 (351 mm SL, ♂), Est. Amazonas, Janauacá, Lago Janauacá area, 03°25'S, 61°17'W, Nov 1967-Jan 1968, Alpha Helix Amazon Expedition; MZUSP 14927 (277 mm SL, ♂), MZUSP 14928 (320 mm SL, ♀), MZUSP 14929 (323 mm SL), MZUSP 14930 (348 mm SL, ♀), MZUSP 14931 (1), MZUSP 14932 (305 mm SL, ♂), MZUSP 14933 (340 mm SL, ♂), MZUSP 14934 (314 mm SL, ♀), MZUSP 14935 (378 mm SL, ♀), Est. Ama-

zonas, Salgada, Lago Janauacá, 03°25'S, 61°17'W, 7-25 Jan 1977, Alpha Helix Amazon Expedition; MBUCV 2073 (2, 236-253 mm SL), Manaus, 24 Feb 1964, local fishermen; MZUSP 57142 (1 of 2, 110 mm SL), just above Vila de Careiro, 03°14'08"S, 59°56'W, 20 July 1996, Zanata et al.; SIUC 12638 (2, 202-205 mm SL), Est. Amazonas, slough ca. 10 km E of Manaus, 9 Oct 1985, T.E. Shepard and M.T. Barton; USNM 52560 (252 mm SL); between Para and Manaus, 1901, J.B. Steere. Colombia: ANSP 120650 (245 mm SL), Amazonas Dept., Río Amazonas, Leticia market, 04°13'03"S, 069°56'57"W, 27 Jun 1968, Huggins. Peru: ANSP 182743 (1 of 2, 168 mm SL), río Amazonas, Loreto, Maynas, near Iquitos, reportedly from lower río Itaya, 03°44'14"S, 073°13'40"W, 5 Aug 2005, M.H. Sabaj et al.; FMNH 92889 (1), Iquitos market, 03°44'42"S, 073°14'06"W, Jul 1975, local fisherman and D.W. Greenfield et al. Ucayali River Basin. Peru: USNM 284887 (120 mm SL), Dept. Loreto, Coronel Portillo, side caño, 08°22'59"S, 074°33'W, 26 Aug 1986, R.P. Vari; MZUSP 14942 (166 mm SL, ♂), Pucallpa, 08°22'59"S, 074°33'W, 9 Mar 1980, I. Samanez; MZUSP 15129 (89 mm SL), Pucallpa, 08°22'59"S, 074°33'W, 29 Oct 1979, H. Ortega; USNM 273616 (2, 143-153 mm SL), Dept. Loreto, Pucallpa, Puerto Ucayali, 08°22'59"S, 074°33'W, 15 Feb 1983 H. Ortega. Jurura River Basin. Brazil: USNM 196711 (1 of 2, 262 mm SL), Est. Amazonas, Rio Envira, trib of Rio Tarauacá, 07°26'S, 70°1'W, no date. Tefé River and Lake Basin: Brazil: MZUSP



Fig. 4. A representative specimen of *Hypophthalmus edentatus* ANSP 179219, 227 mm SL, from the Brazilian Amazon showing the elongate, narrow head and deeply forked caudal fin that is characteristic of *Hypophthalmus* species not included in the *Hypophthalmus oremaculatus* species group.

- 32107 (29, 255-311 mm SL), Est. Amazonas, Tefé, Supia-Pucu (Xavascal), 03°22'34"S, 064°49'40"W, 28 Aug 1979, M. Goulding; MZUSP 32108 (269 mm SL), Est. Amazonas, Mucura, Tefé, Lago at night, 03°22'34"S, 064°49'40"W, 30 Jul 1979, M. Goulding; MZUSP 32109 (2 of 3, 194-302 mm SL), Est. Amazonas, Tefé, Rio Tefe, mastro, 03°22'34"S, 064°49'40"W, 5 Aug 1979, M. Goulding. Purus River Basin. Brazil: MZUSP 67928 (3, 242-251 mm SL), Est. Acre, town of Rio Branco, Lago Amapá, margin edge of rio Acre, 14 Feb 2001, W.M. Aiache; MZUSP 6021 (263 mm SL), MZUSP 14919 (279 mm SL, ♂), MZUSP 14920 (248 mm SL), MZUSP 14921 (268 mm SL), MZUSP 14922 (244 mm SL), MZUSP 14923 (291 mm SL, ♀), Est. Amazonas, Coari, Lago Beruri, 03°50'S, 61°20'W, 7-8 Apr 1967, Expedição Permanente à Amazônia; MZUSP 57767 (98 mm SL), rio Purus above Solimões, 03°59'27"S, 61°29'38"W, 27 July 1996, M. Toledo Piza et al. Negro River Basin. Brazil: MZUSP 14909 (255 mm SL), MZUSP 14910 (262 mm SL, ♀), Est. Amazonas, Igarepé Jaraqui, left margin of river, above Manaus, 03°00'24"S, 60°24'W, 22-24 Apr 1967, Expedição Permanente à Amazônia; MZUSP 32113 (1 of 2, 235 mm SL), MZUSP 31272 (244 mm SL), Est. Amazonas, Anavilhanas, igapó, 02°7'S, 60°75'W, Mar-Apr 1980, M. Goulding; MZUSP 38762 (250 mm SL), Est. Amazonas, mouth of rio Cuieiras, 02°50'S, 60°5'W, 27-31 Jan 1977, Alpha Helix Expedition; MZUSP 42387 (2, 187-269 mm SL), Est. Amazonas, S. Gabriel Cachoeira, 00°07'S, 67°05'W, no date, M. Goulding; INPA 9634 (1 of 3, 109 mm SL), INPA 10304 (2 of 59, 63-66 mm SL), Est. Amazonas, Novo Airão, next to the mouth of the rio Jaú, 02°62'S, 60°94'W, M. Garcia et al.; MZUSP 55695 (4, 73-155 mm SL), Est. Amazonas, rio Negro, 10.6 km below Tacuma-acu, 03°08'24"S, 60°07'20"W, J. Lundberg et al. Branco River Basin. Brazil: MZUSP 32111 (1 of 6, 240 mm SL), Est. Roraima, Ilha Cantagalo, Marará, rio Camanau, 01°30'S, 61°16'W, 28 Oct 1979, M. Goulding. Madeira River Basin. Bolívia: MZUSP 27837 (2, 226-245 mm SL), Madre de Dios: Laguna San Luis, Conv. Piscic. ORSTOM-UTB. Brazil: INPA 25093 (7, 170-184 mm SL), INPA 25096 (307 mm SL), Est. Amazonas, Manicoré, 05°48'42"S, 061°17'29"W; INPA 25094 (1), Est. Amazonas, Novo Aripuanã, 05°07'13"S, 060°23'22"W; MZUSP 14980 (321 mm SL, ♂), MZUSP 28376 (350 mm SL), Est. Rondônia, Lago Piauí, mouth of Rio Jamari, 08°26'55"S, 063°30'17"W, 29 Nov 1975, Expedição Permanente à Amazônia; MZUSP 32100 (17 of 22, 207-287 mm SL), MZUSP 32101 (3, 221-295 mm SL), MZUSP 32102 (13 of 15, 216-293 mm SL), MZUSP 32104 (4, 212-237 mm SL), MZUSP 32105 (3, 270-255 mm SL), MZUSP 82308 (257 mm SL), Est. Rondônia, Calama, 08°03'03"S, 062°54'01"W, Aug-Sep 1980, M. Goulding. Trombetas River Basin: Brazil: Pará, MZUSP 5644 (333 mm SL, ♀), Oriximiná, Lago Paru, 01°53'14"S, 055°52'38.19"W, 28 Feb 1967, Expedição Permanente à Amazônia; MZUSP 14936 (1), MZUSP 14937, (295 mm SL, ♀), MZUSP 14938, (298 mm SL, ♀), MZUSP 14939, (1, ♀), MZUSP 14940, (1), MZUSP 14941, (287 mm SL, ♀), Oriximiná, Lago Paru, 01°53'14"S, 055°52'38"W, 28 Feb-5 Mar 1967, Expedição Permanente à Amazônia; MZUSP 31505 (267 mm SL), Pará, Cuminá, Beira do rio, 01°31'12"S, 056°12'W, Oct-Nov 1983, M. Goulding; MZUSP 15523 (~260 mm SL), MZUSP 15524 (1), MZUSP 15525 (1), MZUSP 15971 (270 mm SL), MZUSP 15972 (275 mm SL), MZUSP 15973 (279 mm SL), Pará, mouth of Lago Jacaré, Reserva Biológica de Trombetas, 01°19'59"S, 056°51'W, 14 Jul 1979, R.M.C. Castro. Amazon Basin, Brazil: INPA 17403 (2, 253-255 mm SL) no data.
- Orinoco Basin. Colombia: ANSP 128136 (366 mm SL), Meta Dept, rio Meta drainage, Hacienda Mozambique; Lake Mozambique, 03°57'54"N, 073°03'02"W, 27 Mar 1971, J.E. Bohlke et al. Venezuela, Est. Cojedes: MHNLS 3144 (9, 145-178 mm SL), Cojedes, Pao de San Juan, rio Pao, Hato Laguna? between km 78 and 80 on highway Tinaco-El Baul, 09°11'32"N, 068°07'35"W, 20 Apr 1980, F. Ramon and G. Alejandro. Est. Portuguesa: MBUCV 12847 (7 of 16, 127-150 mm SL), rio Boconó, in San Marcos, 29 July 1981, F. Provenzano, O. Castillo y Aguana; UF 80465 (129 mm SL), Laguna Flor Amarilla, 08°43'30"N, 069°34'09"W, 4 Apr 1984, D.C. Taphorn et al. Est. Apure: ANSP 165355 (4, 752.3-98.4 mm SL), rio Cunaviche: ca 20 km SW of Cunaviche on S. Fernando de Apure-Pto. Paez Hwy, 07°19'57"N, 067°44'08"W, 6 Nov 1989, S. Schaefer et al.; MBUCV 598 (142 mm SL), Laguna del Pavoncito, old course of the rio Apure, 07°52'46"N, 067°29'51"W, 16 Jan 1963, J.A. Fernández and J.A. Luengo; MBUCV 8254 (236 mm SL), old course of the rio Apure, (Merecure), near San Fernando de Apure, 07°52'47"N, 067°29'51"W, 16 July 1975, A. Machado et al.; MCNG 5150 (159 mm SL), Modulos Fernando Corrales UNELLEZ, 7 Feb 1982, D. Taphorn and C. Lilyestron; MHNLS 1463 (117 mm SL), rio Apure, Mango Verde, 18 Aug 1951, A. Fernández-Yépez; MHNLS 2826 (1), 11.4 km N of new dike, Módulo UNELLEZ, 07°34'N, 069°09'W, 14 Feb 1979, F. Guillermo et al. MHNLS 11012 (8), Caño Macanillal, Hato El Frío, ; 07°49'N, 068°54'W, 3 Aug 1989, C. Lasso; MHNLS 11014 (9), Caño Rabo de Iguana, Hato El Frío, in the road to Manirito, 07°49'N, 068°54'W, 1 Aug 1989, C. Lasso; MHNLS 11015 (19), Caño Rabo de Iguana, Hato El Frío, 07°49'N, 068°54'W, 29 Aug 1989, C. Lasso; MHNLS 11016 (9), Laguna La Ramera, Hato El Frío, 07°49'N, 068°54'W, 27 Nov 1989, C. Lasso; MHNLS 11017 (23), Estero de Manirito, before the bridge, Hato El Frío, 07°49'N, 068°54'W, 30 Dec 1989, C. Lasso; MHNLS 11027 (20, 86-140 mm SL), Hato El Frío, between Caño Rabo de Iguana and Estero de Manirito, 07°49'N, 068°54'W, 14 Sep 1989, C. Lasso; MHNLS 11018

(55), Caño Macanillal, Hato El Frío, 07°49'N, 068°54'W, 13 Feb 1989, C. Lasso; MHNLS 11023 (15), Caño Macanillal, Hato El Frío, 07°49'N, 068°54'W, 18 Mar 1990, C. Lasso; MHNLS 11025 (140), Caño Macanillal, between La Tapa and El Gabanal, Hato El Frío, 07°49'N, 068°54'W, 26 Apr 1989, C. Lasso; MHNLS 11031 (3), Caño Macanillal, Hato El Frío, 07°49'N, 068°54'W, 28 Nov 1989, C. Lasso; MHNLS 11019 (6, 68-147 mm SL), Caño Guaritico, between Las Ventanas and Divi-Divi, Hato El Frío, 07°49'00.012"N, 068°54'W, 16 May 1989, C. Lasso; MHNLS 11020 (5), Caño Mucurita, near biological station, Hato El Frío, 07°49'N, 068°54'W, 24 Jan 1990, C. Lasso; MHNLS 11026 (9), Caño Mucurita, near biological station, Hato El Frío, 07°49'N, 068°54'W, 28 Aug 1989, C. Lasso; MHNLS 11028 (10, 107-175 mm SL), Caño Mucurita, near biological station, Hato El Frío, 07°49'N, 068°54'W, 27 Oct 1989, C. Lasso; MHNLS 11021 (18), caño Guaritico, waters above the old course of the La Madre below Divi-Divi, Hato El Frío, 07°49'N, 068°54'W, 25 Jan 1990, C. Lasso; MHNLS 11022 (3), Caño Mucuritas, near biological station, Hato El Frío, 07°49'N, 068°54'W, 17 Mar 1990, C. Lasso; MHNLS 11032 (5, 100-153 mm SL), Apure, Caño Mucuritas, near biological station, Hato El Frío, 07°49'N, 068°54'W, 28 Nov 1989, C. Lasso; MHNLS 11030 (6), next to road between Caño Mucurita and Laguna La Carmera, Hato El Frío, 07°49'N, 068°54'W, 12 Feb 1989, C. Lasso; MHNLS 11033 (9), road to Fundación La Morita, Hato El Frío, 07°49'N, 068°54'W, 20 Mar 1990, C. Lasso; UF 80841 (150 mm SL), Muñoz, Barrow pit canal E side of UNELLEZ module, 3 km before new dike, ca. 07°49'N, 068°52'00.012"W, 14 Feb 1979, D.C. Taphorn et al. Est. Guárico: INHS 35412 (4, 190-208 mm SL), Laguna Larga Ii, 07°39'58"N, 066°13'25"W, 19 May 1987, M.A. Rodriguez and S. Richardson; INHS 35725 (1), Laguna Larga Ii, 07°39'58"N, 066°13'25"W, 19 May 1987, M.A. Rodriguez and S. Richardson; MBUCV 10965 (1 of 2, 145 mm SL), Guárico, on the side of the highway San Fernando de Apure-Calabozo, Caño Falcón, 23 Nov 1979, J.A. Luenigo and L. Aguana; MBUCV 11467 (2, 233-260 mm SL), Guárico, Laguna La Rompia, connected with the río Apurito, 07°39'11.2068"N, 066°20'04.398"W, 18 July 1980, Francisco Mago L. et al.; MBUCV 21798 (133 mm SL), Guárico, río Orituco via Pirito, west of Calabozo-Cazorla, 29 Nov 1991, H. Moreno, F. Gil, A. Machado and F. Provenzano; MCNG 32953 (277 mm SL), río Guariquito approx. 4 km upstrm of Medanos de Gomez, 07°48'57"N, 066°31'47"W, 9 Jun 1995; MHNLS 5945 (1), Guárico, río Portuguesa, Hato Terecai, Camaguan, 08°06'01"N, 067°36'31"W, 27 Feb 1982, B. Ramon; MHNLS 7844 (1 of 6), Guárico, río Portuguesa, Camaguan, 08°06'01"N, 067°36'31"W, 6 May 1984, B. Ramon. Est. Anzoátegui: INHS 33960 (1 of 2, 230 mm SL), Anzoátegui, Laguna

Aguilera, 08°10'59"N, 063°25'59"W, 28 Apr 1988, M.A. Rodriguez; INHS 29294 (2, 164-200 mm SL), Laguna Curita, 1987, M.A. Rodriguez; INHS 34451 (223 mm SL), Laguna La Jobera, 1987, M.A. Rodriguez; INHS 35612 (223 mm SL), Anzoátegui, Laguna Aguilera, 08°10'59"N, 063°25'59"W, 20 Jan 1988, M.A. Rodriguez; MBUCV 17185 (6 of 11, 173-193 mm SL), Anzoátegui, Laguna Terecaya near Soledad, ca. 08°10'05"N, 063°34'01"W, 22 May 1986, M. A. Rodríguez and S. Richardson; MCNG 30856 (3, 245-265 mm SL), Anzoátegui, Independencia, Laguna El Venado Caramacatico, Caño Mato, 08°10'00"N, 063°37'59"W, 6 Jan 1987, M.A. Rodriguez. Est. Bolívar: INHS 35304 (242 mm SL), Bolívar, Laguna Caño Largo, 08°05'47"N, 063°45'56"W, 26 Apr 1988, M.A. Rodriguez; INHS 35740 (296 mm SL), Bolívar, Laguna Caño Largo, 14 Apr 1988, M.A. Rodriguez; MHNLS 12878 (130 mm SL), Bolívar, río Caura, Laguna Caramacatico, Caño Mato, 28 August 1998, C. Vispo; USNM 270112 (1 of 3, 164 mm SL), Bolivar, small caño connecting with río Orinoco, immediately S of El Burro, 06°10'48"N, 067°25'12"W, 9 Dec 1984, Vari, Castillo, Ferraris. Est. Delta Amacuro: MBUCV 13139 (173 mm SL), shallow lagoon with muddy bottom, north coast of río Orinoco, west of caño Araguaita, 08°40'00"N, 062°00'W, 14 Nov 1979, E.C. Marsh et al.

New Diagnosis.—*Hypophthalmus oremaculatus* is member of the *Hypophthalmus oremaculatus* species group by having an emarginate to shallowly-forked caudal fin, a relatively broad, short head, and a membrane of skin joining the innermost pelvic-fin ray to the edge of the urogenital-anal region. Within the *Hypophthalmus oremaculatus* species group, *H. oremaculatus* is distinguished from "*Hypophthalmus* n. sp.1" (Littmann and Lundberg, in preparation) by having low numbers of vertebrae, 55-59 total vertebrae (vs. 62-65); 3-6 vertebrae with separate and robust neural spines between the Weberian complex and the first vertebra with its neural spine articulating with the dorsal-fin pterygiophores (vs. 5-6 separate and slender neural spines before the first vertebra contacting the dorsal-fin pterygiophores); long mental barbels extending to pectoral origin or beyond (vs. short mental barbels barely passing the eye); and the dorsal-fin origin approximately in line with anal-fin origin (vs. dorsal-fin origin posterior to anal-fin origin).

Redescription.—Maximum observed size approaching 390 mm SL. In lateral view dorsal profile abruptly convex from upper lip onto snout, then scarcely concave to occipital roof or onto nape and rising convexly to dorsal-fin origin; horizontal or a little convex below and behind dorsal fin to adipose-fin origin, then falling in a straight to gently convex line below adipose to caudal-

fin base. Ventral profile convex from chin to below rictus, then gently convex or nearly straight along head, pectoral girdle and abdomen to anal-fin origin; slightly concave to nearly straight along base of anal-fin and caudal peduncle to caudal-fin base. Cross-sectional shape domed at vertical through middle of eye, becoming narrowly triangular behind occiput to pelvic-fin insertions, increasingly compressed posteriorly to caudal peduncle and fin.

Head length contained 1.6-1.8 times in predorsal length and 3.6-4.5 times in SL. Head depth at mid-eye less than head width at same level, about equal to distance between ventral margins of orbits, contained ca. 2.6 in HL. Head depth at base of supraoccipital process contained about twice in HL. Sides of head nearly parallel behind level of posterior nostrils, maximum head width about equal to maximum body width across cleithra at pectoral-spine insertions and width contained 1.7-2.2 times in head length.

Snout anterior to insertions of maxillary barbels smoothly rounded in dorsoventral views, slightly overlapping but not projecting beyond mandibular symphysis. Snout length contained 1.8-2.2 times in HL. Mouth terminal, opening anteriorly; toothless premaxillaries not exposed with mouth closed; rictal corner of closed mouth at a vertical midway between posterior naris and eye; gape length (snout tip to rictus) greater than distance from snout tip to posterior rim of posterior naris, contained 1.5-2.1 times in snout length. Lips smooth, not set off from premaxillary or mandible by grooves or accessory folds. Post-rictal fold of smooth, non-fleshy skin, forming a shallow groove behind corner of mouth, terminating before eye by a distance equal to half eye diameter; no shallow grooves extending dorsal or ventral to rictus to post-rictal fold.

Jaws and palate edentulous. Most of skull roofing bones hidden by moderately thick skin. Lateralmost margins of sphenotic and pterotic visible; posterior parts of frontals and supraoccipital flanking obscure posterior cranial fontanelle. Supraoccipital posterior process with a median sulcus filled with integument and adipose tissue and visibly projecting well onto nape but remote from posteriorly-displaced dorsal fin.

Three pairs of barbels, each proximally compressed and with membranous posterior margins increasingly developed in larger specimens. Maxillary barbels inserted a little posterior to a vertical through anterior nostril; reaching to a vertical near posterior margin of pelvic fins or insertion of anal fin. Inner mental barbels insert close together immediately behind mandibular symphysis; reaching to or a little beyond posterior (inner) insertion of pectoral fin. Outer mental barbels inserted on the mandible midway between insertions of inner mental and maxillary barbels; reaching to or a little beyond pectoral-fin origin.

Gular fold defining a V-shaped groove in front of hyoid arch, its sides meeting at a severely acute angle near mandibular symphysis. Gill membranes free, variously overlapping or not, then diverging below or behind level of eyes, supported by 12-14 branchiostegal rays, 6 on posterior ceratohyal + 1 on cartilage between ceratohyals + 6-7 on anterior ceratohyal. Gill rakers well-ossified, long, slender and densely arranged on all five arches; total rakers on 1st branchial arch 130-227 (12-30 upper, 117-197 lower; N=10) increasing with size above 160 mm SL at approximately 1.1 rakers per mm of growth in SL.

Anterior nostril located dorsally on snout behind snout margin by about its own diameter, medial to base of maxillary barbel; anterior nostril aperture dorsally directed, with a pale, elevated fleshy rim. Posterior nostril much closer to anterior nostril than to eye (ca. 12-14 times its own diameter in front of eye); medially offset from a line between midpoint of anterior border of eye and anterior nostril; posterior nostril rim bordered anteriorly and posteriorly by thin, hyaline membranes, incomplete laterally and medially.

Eye circular, ventrolaterally placed, its dorsal margin on or below a straight line between pectoral spine insertion and anterior nostril, centered on a vertical at about 55% of HL. Orbital margin free, eye without a covering fleshy "eyelid". Eye (horizontal orbital diameter) 5.9-10.1 times in HL, 2.8-5.4 in times snout; its growth negatively allometric.

Cephalic lateralis sensory canals thin, with finely branched, anastomosing networks of side canals extending onto nuchal area, top, sides and mandibular areas of head. Lateral line canal complete, extending onto caudal-fin where abruptly upturned along base of upper lobe. Main canal straight, with superficial tubular ossicles plus dorsal and ventral side branches in line with myosepta. With increasing body size the dorsal and ventral side canal branches lengthen and develop complex dendritic patterns and some cross-branch commissures especially posteriorly above anal fin and along caudal peduncle. Upturned caudal section of lateralis canal with long branches extending posteriorly over principal caudal-fin rays.

Dorsal-fin origin near 40% of SL, posterior to anal-fin origin and anterior to tip of adpressed pectoral fin. Dorsal-fin base contained 7-10 times in predorsal length. Dorsal-fin with a delicate leading, spinelet, long, fin spine plus 6 (7 in one) soft, branched fin rays; bases of last two rays separate, respectively articulating with sixth and seventh (last) pterygiophores. Dorsal spine straight, slender, pungent, nearly as long as first branched ray, with a segmented, flexible tip. Dorsal-fin spine without dentations or distal serrae. First dorsal-fin soft ray longest, last ray less than half length of first ray; margin of dorsal fin nearly straight.

Table 1. Morphometric data for *Hypophthalmus oremaculatus* samples by drainage basin and expressed in % of standard length (SL) or head length (HL). Additional abbreviations; M=mean, N = number of specimens, R=range, H=holotype, SOC=supraoccipital.

	Orinoco						Amazon						Paraná		
	M	N	R	M	N	R	M	N	R	H	M	N	R		
	SL (mm)	231.3	43	107-355	255.0	20	120-387	335	272.3	15	180-335				
Gape length (HL)	29.3	14	26.5-33.9	27.5	20	23.0-32.7	30.2	28.7	15	23.0-43.8					
Snout length (HL)	50.6	14	47.4-53.3	50.2	20	46.5-54.8	54.7	50.6	15	46.5-54.8					
Orbital diameter (bony orbit) (HL)	13.7	14	11.5-16.8	12.2	20	10.3-15.8	11.8	12.6	15	09.9-16.8					
Head length	25.3	14	22.9-27.6	24.6	20	22.3-27.4	22.5	24.4	15	22.5-25.8					
Snout to pectoral-fin origin	25.2	10	23.0-26.7	24.7	20	22.2-2.74	21.0	23.9	15	21.0-26.8					
Snout to end of SOC process	26.9	14	25.4-28.6	26.3	20	24.3-28.3	19.3	21.1	15	15.4-28.3					
Snout to dorsal-fin origin	42.0	14	39.2-44.2	41.6	20	38.7-44.3	40.8	41.3	15	39.8-42.8					
Body width at pectoral-fin origins	13.0	14	11.7-14.0	12.7	20	11.4-14.3	13.5	12.4	15	11.1-13.5					
Pectoral-fin origin to dorsal-fin origin	24.7	14	23.1-26.3	24.2	20	22.7-26.4	27.3	23.6	15	21.1-27.3					
Dorsal-fin base length	05.3	14	04.6-06.4	04.9	20	04.2-05.7	05.2	05.0	15	04.4-05.7					
Pectoral-fin origin to anal-fin origin	15.6	14	14.6-17.2	17.0	20	14.7-18.9	20.8	17.5	15	12.6-20.8					
Dorsal-fin origin to anal-fin origin	23.0	14	17.9-26.7	22.1	20	19.5-25.2	20.8	20.6	15	16.8-22.8					
Anal-fin base length	49.9	14	45.8-62.8	47.0	20	44.0-50.5	49.5	46.6	15	43.5-50.4					
Dorsal-fin insertion to adipose-fin origin	32.4	14	30.0-35.9	32.8	20	28.8-38.8	36.1	32.8	15	29.8-36.1					
Adipose-fin base length	05.2	14	04.0-06.6	04.4	20	03.7-05.4	xxx	04.5	15	03.6-05.3					
Adipose-fin origin to anal-fin insertion	14.7	14	12.7-16.0	14.2	20	12.7-16.3	14.4	13.8	15	12.9-14.7					
Dorsal-fin insertion to anal-fin insertion	43.1	14	40.9-45.2	42.9	20	39.8-49.0	45.3	42.5	15	39.9-45.3					
Adipose-fin insertion to center of C-fin base	20.3	14	18.4-22.0	21.5	20	19.2-23.6	20.9	21.0	15	19.8-22.5					
Anal-fin insertion to center of C-fin base	14.1	14	12.6-15.2	16.0	20	13.1-22.2	14.3	15.8	15	14.3-22.2					
Anal-fin origin to adipose-fin origin	43.3	14	41.5-45.7	41.8	20	37.8-45.9	47.7	41.9	15	39.3-47.7					
Dorsal-spine length	10.7	3	10.4-10.9	09.9	5	07.5-11.5	10.7	08.2	10	05.5-11.0					
Pectoral-spine length	21.3	6	12.7-36.2	21.1	6	12.0-33.2	xxx	14.9	1	14.9-14.9					

Adipose fin (damaged in holotype) narrowly based, expanded distally with a free lobe posteriorly, its anterior and posterior margins convex, apex abruptly rounded, inserted near 75% of SL, above posterior fifth of anal fin, remote from dorsal fin (separated by a distance about 30% of SL). Adipose-fin length about equal to length of dorsal fin base, 3-6 times in caudal peduncle length; adipose-fin height about equal to its attached base.

Caudal fin emarginate or shallowly forked, and lower lobe may be broadly rounded, uppermost rays normally produced but often damaged; principal caudal-fin rays strongly modal 1,7-8,1 (rarely 1,6;-9,1 or -10,1 or 11,1),18-24 upper, and 14-24 lower procurrent caudal-fin rays.

Anal fin long, contained 1.6-2.3 times in SL, its origin at about 35% of SL, its insertion near 85% of SL; fin margin slightly convex, without an anterior lobe. Anal-fin rays 58-71. Last two anal-fin rays separately articulating with their pterygiophores; 58-71 anal-fin pterygiophores.

Pectoral fin expansive, with a slender spine and 14-16 branched rays, its posterior margin obliquely sigmoid, the spine and first soft ray longest, 3-4 times longer than innermost fin ray, longest rays reaching beyond pelvic fins and anal-fin origin. Pectoral-fin spine slender comprising a proximal coossified part and long distal section (ca. 20% of spine-shaft length) of ossified but flexibly-jointed segments. Spine-shaft surface with fine ridges, anterior margin of smaller specimens have small dentations along proximal third of spine; posterior margin without dentations. Pectoral-spine base lacking dorsal and anterior articulating processes; spine articulation socket of cleithrum shallow, partially open laterally. Posterior cleithral process obsolete. Axillary pore absent.

Pelvic fin inserted before anal-fin origin at about 32% of SL; its base oriented obliquely posteromedially. Pelvic fin containing 6 rays, the first simple, about as long as second ray, both reaching anal-fin origin; middle and inner pelvic rays diminishing in length, medial edge of short inner pelvic ray tied by a thin membrane to side of analurogenital area.

Total vertebrae 56-59, strongly bimodal at 57 and 58; 1st-6th vertebrae forming Weberian complex; precaudal including Weberian vertebrae 11-14, modally 12; caudal vertebrae 43-47, modally 45; 3-6, modally 4, vertebrae (7th - 11th) with expanded neural spines behind the Weberian complex and before the first vertebra with a neural spine contacting supraneural of dorsal fin.

Urogenital papilla short, blunt, located in a pit immediately behind anus between pelvic fins midway along their inner fin rays.

Coloration. Specimens in life and fresh (Fig. 3A) strongly and abruptly countershaded; dorsally black to dark gray often with metallic blue and purplish reflections;

sides silvery, venter white. Top and sides of head heavily pigmented as above downward to margin of snout, along rictal fold, below eye, along ventral and posterior margins of interopercle and opercle. Underside of head mostly white. Barbels vary from entirely black to lighter gray or white proximally, then blackish distally. Back and upper sides of body heavily pigmented downward half way to main lateralis canal, anteriorly dark pigment extends below lateral line onto tympanic area or pectoral fin insertion. Sides silvery and white ventrad onto base of anal fin and lower parts of caudal peduncle. Ground color of fins hyaline to dusky gray, with black or dark gray margins; generally the fin membranes pigmented but not the fin rays. Pectoral spine darkly pigmented dorsally and anteriorly, base of upper lobe of caudal fin dark.

In preservative (Fig. 1-3) darkly pigmented areas fade to variable dark to light shades of gray or brown. Dark pigmentation of barbels and fin margins often persisting in preservative. In juveniles the pigmentation is more intense; the dorsal fin has a large dark blotch that persists in some adults. Summarizing the original description, in the holotype, the head and dorsum are an intense violet bluish that decreases ventrally; at the level of lateral line the sides are light violet-pink and then pale yellowish over the rest of the body. The margins of the fins strongly pigmented with black and the barbels also are tinted with black.

Distribution and habitat.—Rivers and open-water lakes of the Paraná, Amazon and Orinoco basins (Fig. 5). Like other *Hypophthalmus*, *H. oreamaculatus* is a lowland species that, across its range, occurs below 200 m asl. Often in schools, in mid- and surface waters. Primarily zooplanktivorous (Abujanra and Agostinho, 2002). Larvae and juveniles commonly caught in fine mesh nets in river channels of the Amazon and Orinoco (JGL, pers. obs); and in the Itaipú Reservoir (Nakatani et al., 1998).

Etymology.—Not indicated in original description by Nani and Fuster (1947); *oreamaculatus* is possibly a reference to the reported presence of dark spots on the palatal surface of the mouth.

DISCUSSION

Comments on the holotype specimen and original description of Hypophthalmus oreamaculatus.—The holotype *H. oreamaculatus* MACN 3496 has a good state of preservation of body form, including the fins except the damaged adipose fin, barbels, and calcification of the bony skeleton. Our measurements are close to those reported in the original description, and the radiographs clearly show all of the vertebrae and other parts of the skeleton

including fin rays. The obvious points of damage are to the margins of the median fins, base of the pectoral fins and the abdomen is cut open from behind the pectoral girdle to the ano-urogenital region. Although the adipose fin is illustrated as a small tab-like fin in Nani and Fuster (1947, Fig. 2) it is now missing and the midline of the back is damaged where the fin once was. Nani and Fuster note that the base of the adipose fin is smaller than the diameter of the eye in *H. oremaculatus*, but that *H. edentatus* has the inverse proportion, the base of the adipose fin is larger than the diameter of the eye. (We do not attempt to reconcile these features). Figures 2 and 3 in the original description show perfect fin margins and a shallowly forked caudal fin with short but prominent filamentous outer caudal-fin rays. There is no trace of the filamentous fin rays in the specimen today, but we find one well preserved specimen from the Orinoco with a well developed filament on the uppermost principal caudal-fin ray (Fig. 2F).

No doubt the most curious characterization of the holotype of *H. oremaculatus* made by Nani and Fuster refers to two large and irregular black spots on the palate on which there appear brilliant reflections of microscopic denticles although these are imperceptible when touched. We suspect that Nani and Fuster were describing not palatal teeth but reflections of moist preservative on small epithelial papillae. We observe that the holotype has numerous papillae on the palate but there is no trace of pigmentation or chromatophores on the palate. Oliveira (1981) also



Fig. 5. Distribution map of *Hypophthalmus oremaculatus* based on specimens documented with appropriately detailed collection locality data.

noted that he had not observed darkly pigmented patches or tooth-like structures on the palate in the many hundreds of specimens of *Hypophthalmus* examined.

Geographic range and variation.—The rio Paraná was originally subdivided into lower and upper basins by the Sete Quedas waterfalls between Paraguay and southern Brazil. The falls served as a barrier to the upstream movement of many fish species native to the lower Paraná and absent from the upper Paraná (Ringuelet, 1975; Bonetto, 1986). Following completion of the Itaipú dam and impoundment in 1982, the barrier falls were inundated and the free upstream movement of many fishes began. Júlio Jr. et al. (2009) have documented the spread into the upper rio Paraná basin of 33 fish species that were native to the lower basin. Essentially all of the literature to date on upper Paraná fishes that mentions *Hypophthalmus* refers to the species as *H. edentatus*. We have identified specimens from this region as *H. oremaculatus* based on diagnostic characters determined from radiographs and photographs provided by Drs. Carla Pavaneli, Flávio Bockmann and Francisco Langeani. We have not found in the Paraná Basin any specimens referable to *H. edentatus* as we now understand this species based on its two syntype specimens.

We compared our samples of *H. oremaculatus* from the Paraná, Amazon and Orinoco for variable morphological features that might suggest interbasin divergence. Coloration, body proportions and fin ray counts do not show any indications of geographic variation. There is minor interbasin variation in the frequency distributions of total vertebral counts (Table 2) in which the Paraná sample has a higher modal count of 58 total vertebrae, compared to the Amazon sample with a bimodal count of 56-57, and a modal count of 57 for the Orinoco sample. The vertebral frequency distributions are otherwise broadly overlapping, and alone vertebral number variation is insufficient evidence for taxonomic subdivision of *H. oremaculatus*. Of course, larger sample sizes and additional character data, including molecular sequences, can be brought to bear on the question of interbasin or other geographic variation.

Hypophthalmus oremaculatus is thus confirmed with specimens to occur in Paraná, Amazon and Orinoco drainage basins (Fig. 5) which makes this species the most wide ranging in its genus. *Hypophthalmus oremaculatus* is not alone among species of Pimelodidae in having such an extensive cis-Andean range with others being *Hemisorubim platyrhynchos*, *Pinirampus pinirampu* and *Sorubim lima*. *Pimelodus ornatus* also could be listed based on current taxonomy but this nominal species is more likely a species complex (Lundberg et al., 2011).

An exceptional specimen.—In addition to the 49 specimens in our sample from the Paraná Basin that we confidently identified as *H. oremaculatus*, we encountered

one exceptional fish in a sample of two (NUP 1730) from a tributary of the main river in Paraná State, BR in the county of Porto Rico. One specimen is typical *H. oremaculatus* (273 mm SL). The exceptional specimen is a relatively elongate fish of 297 mm SL. Both specimens have short, broad heads and the shallowly concave caudal-fin shape that clearly indicate their membership in the *Hypophthalmus oremaculatus* species group. The exceptional specimen, however, has a high count of 61 total vertebrae (12 precaudals; 49 caudals), seven post-Weberian vertebrae with slender neural spines before the anterior dorsal-fin pterygiophore, mental barbels (possibly damaged) not reaching the pectoral fins, and the dorsal-fin origin is posterior to the anal-fin origin. This combination of features identifies the specimen as the undescribed species *Hypophthalmus* n. sp. 1. This species is otherwise known from the Orinoco and Amazon basins. All other specimens in our Paraná sample are *H. oremaculatus*. The exceptional specimen needs our direct examination to confirm its identification but presently it is not within our reach. We list this specimen as *Hypophthalmus* cf. n. sp. 1. We can only speculate that the exceptional specimen

is either a phenotypic outlier of *H. oremaculatus*, or a geographic outlier of *Hypophthalmus* n. sp. 1 indicating the presence of that species in the Paraná Basin. These alternatives are testable in principle with additional diagnostic morphological characters, or discovery specimens with intermediate phenotypes, and/or genetic data obtained from specimens representing appropriate populations and phenotypes.

Comparative Material Examined.—We cite the primary type specimens examined and representative non-type specimens.

Hypophthalmus edentatus Spix and Agassiz, 1829.

Type specimens. Brazil, MHNN 706 (Syntypes, 2:193-209 mm SL) *Hypophthalmus edentatus* Spix and Agassiz, 1829; Peru, USNM 132589 (Holotype, 435 mm SL) *Hypophthalmus perporosus* Cope, 1878.

Non-type specimens, Brazil, NRM 16133 (236 mm SL), Amazonas, Manaus area, Nov 1954, N. Färnström; USNM 316619 (269 mm SL), Amazonas, muddy Igarape

Table 2. Meristic data for *Hypophthalmus oremaculatus*, ALL = combined data, OR = Orinoco Basin specimens, AM = Amazon Basin specimens, PA = Paraná Basin specimens. Free Neural spines are those on vertebrae between the Weberian complex and the last vertebra lacking contact with a dorsal-fin pterygiophore.

Total Vertebrae					
Species	55	56	57	58	59
<i>H. oremaculatus</i> ALL	1	16	32	23	6
<i>H. oremaculatus</i> OR	1	10	22	9	
<i>H. oremaculatus</i> AM		6	7	3	1
<i>H. oremaculatus</i> PAR			3	11	5

Species	Precaudal Vertebrae				Caudal Vertebrae					Free Neural Spines			
	11	12	13	14	43	44	45	46	47	3	4	5	6
<i>H. oremaculatus</i> ALL	1	57	19	1	2	23	33	18	1	5	51	21	1
<i>H. oremaculatus</i> OR	1	35	6		1	14	19	7		4	26	11	1
<i>H. oremaculatus</i> AM		14	4		1	7	6	2	1	1	13	3	
<i>H. oremaculatus</i> PAR		8	9	1		2	8	9			12	7	

Anal-fin Rays														
Species	58	59	60	61	62	63	64	65	66	67	68	69	70	71
<i>H. oremaculatus</i> ALL	2	2		4	7	6	7	10	5	3	7	3	1	1
<i>H. oremaculatus</i> OR	1	1		3	6	5	2	4	4	1	5	3	1	
<i>H. oremaculatus</i> AM				1	1	1	2	3	1	1				
<i>H. oremaculatus</i> PAR	1	1					3	3		1	2			1

connecting rio Solimões and blackwater Lago approx. 15 mi W of Coari, 7 Mar 1974, R.H. Axelrod and M.R. Brittan; ANSP 197652, (8, 58-76 mm SL), Pará, Xingu, Nov 2014, M.S. Sabaj-Pérez et al.; Peru: INHS 42286 (3, 205-234 mm SL), Loreto, Maynas, Belém fish market, Iquitos, Jul-Aug 1999, M.H. Sabaj et al.; Venezuela: ANSP 165780 (352 mm SL), Apure, río Capanaparo, backwater lagoon (mouth of Caño Las Varitas), near S. Fernando de Apure-Pto. Paez Hwy, 7 Nov 1989, S. Schaefer et al.; ANSP 162386 (442 mm SL), Amazonas, market at Pto. Ayacucho, 15 Nov 1985, no collector info.

Hypophthalmus fimbriatus Kner, 1857.

Type specimen. Brazil, NMW 50519 (Photograph of Syntype, 1, 232 mm SL) *Hypophthalmus fimbriatus* Kner, 1857.

Non-type specimens, Brazil: FMNH 114017 (7, 155-200 mm SL), Amazonas, rio Jurua btw Lago Pauapixuna and rio Solimões, btw towns Pauapixuna and Vitoria, 02°41'09"S, 65°48'30"W, 9 Nov 1993, J.G. Lundberg et al.; INPA 24831 (11, 106-150 mm SL), Amazonas, Manaquiri, Lago Janauacá, 28 Jan 1978, F. Martinho; MZUSP 57335 (3, 48.1-60.5 mm SL), Amazonas, near Manaus, 03° 01'49" S, 60° 21'53" W, 18 Jul 1996, Zanata et al.; USNM 376307 (235 mm SL), Amazonas, 3.83486° S, 61.3996° W, 26 Jul 1996, M. Toledo-Piza et al.; Venezuela: MCNG 37236 (5, 299-355 mm SL), Río Casiquiare, Amazonas, below Curimacare, 22 Jan 1998, K. Winemiller et al.

Hypophthalmus marginatus Valenciennes, 1840.

Type specimens. French Guyana, MNHN A8961 (Syntype, 237 mm SL), MNHN A8961 (Syntype, 237 mm SL), MNHN A8963 (Syntype, 308 mm SL), RMNH D1932 (Syntype, 388 mm SL), RMNH 1933 (Syntype, 412 mm SL) of *Hypophthalmus marginatus* Valenciennes, 1840; Surinam, RMNH D1931 (Syntype, 107 mm SL), RMNH 2974 (Syntype, 143 mm SL), RMNH 2988 (Syntype, 143 mm SL) of *Hypophthalmus longifilis* Valenciennes, 1840.

Non-type specimens. Surinam: UF 16279 (3, 131-156 mm SL), Suriname River, near Paramaribo, 20 Jun 1968, W. Greenhood et al.; USNM 226141 (2 of 6, 103-126 mm SL), Nickerie Dist., Corantijn River, mi. 43 (start)-near Robertson Is., 5.888°N, 57.117°W, 5 Sep 1980, R. Vari et al.

Hypophthalmus n. sp. 1.

Venezuela: ANSP 166613 (4, 198-209 mm SL), río Orinoco, Anzoátegui, Lago Terecaya, Soledad, 23 Apr 1987, M. Rodriguez; USNM 270112 (2, 165-182 mm SL), Bolívar, sm caño connecting w río Orinoco, immed S of

El Burro, 06.18°N, 67.42°W, 25 Aug 2014, R.P. Vari et al.; ANSP 149888 (386 mm SL), Meta, río Metica, ca 1 km dnst of connection with Lake Mozambique, 24 May 1969, J.E. Bohlke; Peru: ANSP 21275 (3, 252-292 mm SL), río Amazonas, 1873, J. Orton and E.D. Cope; ANSP 178457 (175 mmSL), Loreto, Maynas, río Nanay at Pampa Chica, village 4.54 km W of Iquitos, 2 Aug 2001, M.W. Littmann et al.; INHS 52182 (2 of 6, 198-242 mm SL), Loreto, Maynas, Belém fish market, Iquitos, Jul-Aug 1999, M.H. Sabaj et al.

Hypophthalmus cf. n. sp. 1.

Brazil: NUP 1730 (297 mm SL), Est. Paraná, County Porto Rico, tributary of rio Paraná, 22°46'04"S, 053°16'06"W, 1990-1995, NUPELIA.

Hypophthalmus n. sp. 2

Venezuela: MCNG 32953 (277 mm SL), Río Orinoco, Guárico, río Guariquito, fast water approx. 4 km from Medanos de Gomez, 08°10'N, 67°07'W, 6 Sep 1995, C. Vispo; MZUSP 27888 (3, 60-63.1 mm SL), Guárico, Laguna Los Laureles, near Camaguán, 22 Apr 1980, O. Castillo; USNM 235065 (2:262-320 mm SL), Bolivar, Laguna on S side of Isla Isabela, btw Palua and Ciudad Bolivar, 201 Nm from sea bouy, 08.3119°N, 65.9478°W, 7 Nov 1979, J.G. Lundberg et al.; Peru: ANSP 120353 (241 mm SL), río Ucayali, Peculpa, 14 Jun 1969, E.J. Hughins; ANSP 178512 (1 of 8, 272 mm SL), Loreto, Maynas, Belem market, Iquitos, 1 Aug 2001, M.W. Littmann and M. H. Sabaj; INHS 52182 (2 of 6, 242-274 mm SL), Loreto, Maynas, Belém fish market, Iquitos, Jul-Aug 1999, M.H. Sabaj et al.

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