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Morphological variation in *Acestrorhynchus microlepis* and *A. falcatus* (Characiformes: Acestrorhynchidae), reassessment of *A. apurensis* and distribution of *Acestrorhynchus* in Venezuela

Hernán López-Fernández* and Kirk O. Winemiller*

We report findings from an analysis of morphological variation in *Acestrorhynchus microlepis* over most of its distribution in South America and *A. falcatus* from northern drainages of the continent. *Acestrorhynchus apurensis* and *A. microlepis* could not be distinguished on the basis of diagnostic characters accompanying species descriptions, and no other character, morphometric or meristic, clearly distinguished these species; we consider *A. apurensis* a junior synonym of *A. microlepis*. Morphometric and meristic analyses of populations of *A. microlepis* from throughout South America revealed broad variation, yet overlapping values among characters prevented us from identifying additional species among major drainage basins. A similar analysis of *A. falcatus* from the major drainages of Venezuela and the Guianas failed to reveal characters useful for diagnosis of additional taxa. Nevertheless, subtle differences in pigmentation and body shape suggest one or more cryptic taxa under the names *A. microlepis* and *A. falcatus*. We identified seven species of *Acestrorhynchus* occurring in Venezuela: *A. microlepis*, *A. falcatus*, *A. falcirostris*, *A. grandoculis*, *A. heterolepis*, *A. minimus*, and *A. nasutus*. *Acestrorhynchus microlepis* is broadly distributed in a variety of habitats throughout the Orinoco basin. Other species occur in rivers of the Guiana Shield and Amazon regions of Venezuela, as well as in a few clear-water and black-water rivers of the llanos.

Analizamos la variación morfológica en *Acestrorhynchus microlepis* de la mayor parte de su área de distribución en Sur América y en *A. falcatus* de las cuencas del norte del continente. *Acestrorhyncus apurensis* no pudo ser distinguido de *A. microlepis* sobre la base de los caracteres diagnósticos que acompañan la descripción de la especie, y ningún otro atributo, morfométrico o merístico, distingue claramente a las dos especies; consideramos a *A. apurensis* como un sinónimo menor de *A. microlepis.* Análisis morfométricos y merísticos de poblaciones de *A. microlepis* de varias localidades en Sur América revelaron amplia variación, pero la sobreposición de los valores de los caracteres examinados nos impidió identificar especies adicionales entre las principales cuencas. Un análisis similar de *A. falcatus* de las principales cuencas de Venezuela y las Guayanas no reveló ningún rasgo morfológico útil en el diagnóstico de taxa adicionales. Sin embargo, diferencias sutiles en la pigmentación y la forma del cuerpo sugieren uno o más taxa crípticos bajo los nombres *A. microlepis* y *A. falcatus.* Identificamos siete especies de *Acestrorhynchus* presentes en Venezuela: *A. microlepis, A. falcatus, A. grandoculis, A. minimus, A. falcirostris, A. heterolepis*, y *A. nasutus*. *Acestrorhynchus microlepis* se distribuye ampliamente en una variedad de hábitats en la cuenca del Orinoco. Otras especies se encuentran en ríos del Escudo Guayanés y la región Amazónica de Venezuela, y en unos pocos ríos de aguas claras y negras en los llanos.

* Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA. E-mail: hlopez@tamu.edu, k-winemiller@tamu.edu

Introduction

Acestrorhynchus Eigenmann & Kennedy is a genus of piscivorous characiform fishes previously included in the family Characidae, but recently classified in its own family, Acestrorhynchidae (Buckup, 1998). Although relationships within the Characiformes are not well resolved, the Acestrorhynchidae appears to be part of a clade including the piscivorous Cynodontidae (Vari, 1995; Buckup, 1998; Lucena & Menezes, 1998). A detailed description of the genus, as well as anatomical illustrations can be found in (Menezes, 1969).

Acestrorhynchus is widespread in tropical and subtropical South America, from the Río Paraná and Paraguay drainages (Menezes, 1969), the Orinoco basin in Venezuela and Colombia (Taphorn et al., 1997), to the Rio São Francisco in eastern Brazil (Campos, 1945; Menezes, 1969) and the Guianas (Menezes, 1969; Géry, 1977). Highest species richness in the genus is found in the Amazon and Orinoco basins, from where over a dozen species have been described (e.g. Menezes, 1969; Menezes & Géry, 1983; Toledo-Piza & Menezes, 1996).

Recent ichthyological surveys in Venezuela have yielded new specimens as well as distributional and ecological information. *Acestrorhynchus falcatus* and *A. microlepis* both appear to be highly variable species with wide continental distribution. We analyzed morphological variation of extensive samples of *A. falcatus* (northern continental drainages) and *A. microlepis* (continent-wide) to determine whether additional taxa could be diagnosed. We also reassessed the taxonomic status of *A. apurensis* Toledo-Piza & Menezes, a species described solely from juveniles from a restricted area of the Venezuelan llanos. We examined representative samples of *Acestrorhynchus* from Venezuela and recognized seven species present in the country, and provide distribution maps and a species identification key.

Material and methods

All measurements were taken using dial and/or digital calipers to the nearest 0.1 mm when linear distance was less than 130.0 mm and with a tape measure to the nearest mm when more than 130.0 mm. Counts of fin rays and scales were made under a dissecting microscope. Measures and counts procedures follow those described in Menezes (1969), with the following exceptions: head length: distance from the tip of the snout to the posterior edge of the opercle, without including the opercular membrane; dorsal to anal distance: straight line between the base of the first ray of the dorsal fin to the base of the first ray of the anal fin; middle caudal lobe: distance from the insertion of the caudal fin into the caudal peduncle to the tip of the principal caudal rays in the midline of the body; and pectoral fin rays: count of all rays, including the first (contra Menezes, 1969).

Diagnostic morphometric characters of *A. microlepis* and *A. apurensis* were selected from Toledo-Piza & Menezes (1996) and analyzed using Principal Component Analysis as a means of clustering. Measurements were log-transformed to achieve normality of data distributions. All other analyses were performed on untransformed data.

Museum abbreviations: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia; CAS, California Academy of Sciences, San Francisco; INHS, Illinois Natural History Survey, Champaign; MBUCV, Museo de Biología de la Universidad Central de Venezuela, Caracas; MCNG, Museo de Ciencias Naturales de Guanare, Guanare; TCWC, Texas Cooperative Wildlife Collection, College Station.

Key to the species of *Acestrorhynchus* from Venezuela

1. - Large humeral spot, generally shaped as an inverted teardrop, spanning from a third to almost the entire body height. ..... *A. falcatus*
   - Humeral spot small or completely absent. 2

2. - Lateral line scales with bifurcated canals. ..... *A. heterolepis*
   - Lateral line scales with simple canals. 3

3. - Small dark spot behind the operculum. 4
   - No spot behind the operculum. 5

4. - 77-87 lateral line scales; eye 31.1-36.6 % HL; snout 26.3-33.3 % HL.
..... *A. grandoculis*
- 91-131 lateral line scales; eye 17.9-34.1 % HL; snout 32.5-50.0 % HL.
..... *A. microlepis*

5. - Dark, longitudinal band extending from the tip of the snout through base of caudal fin.
..... *A. nasutus*
- No longitudinal band.
..... 6

6. - Black pigmentation on edge of operculum, especially on dorsal half; 140-175 lateral line scales.
..... *A. falcirostris*
- Operculum unmarked; 74-85 lateral line scales.
..... *A. minimus*

Acestrorhynchus microlepis (Schomburgk)
(Fig. 1a-b)

Hydrocyon microlepis Schomburgk, 1841: 247 (Rio Negro, Rio Branco, Essequibo River, South America).

Xiphorhynchus falcatus Valenciennes, 1849: 337 9 (in part, Mana).

Acestrorhynchus cachorro Fowler, 1939: 274, fig. 61 (Boca Chica, Ucayali River basin, Peru).

Acestrorhynchus guianensis Menezes, 1969: 70, fig. 54 (Botanic Garden, trenches in Georgetown with water from the Demerara River, [British] Guyana).

Acestrorhynchus apurensis Toledo-Piza and Menezes, 1996: 18, fig. 10 (Venezuela, Apure, Módulo de la UNELLEZ [72°05'50"N 69°35' 30"W]).

Material examined. VENEZUELA: MCNG 956, 2, 81.1-84.0 mm SL; Bolívar: pool 20 km from Anacoco, on the way to Tumeremo, 6°55'N 61°15'W. – MCNG 11323, 11, 36.9-57.8 mm SL; Apure: UNELLEZ module, E-W dike, 7°28'25"N 69°35'20"W. MCNG 4339, 2, 66.3-68.2 mm SL; Apure: UNELLEZ module, E dike, 7°29'30"N 69°31'W. – MCNG 11516, 2, 132.0-132.2 mm SL; Apure: Caño Maporal, at bridge by UNELLEZ module, 7°25'20"N 69°35'40"W. – MCNG 3620, 4, 76.0-130.0 mm SL; Apure: UNELLEZ module, adjacent to S dike and Caño Caicara, 7°4250 N 69°5389 W. – MCNG 4160, 46, 66.8-116.5 mm SL (9 measured); Apure: UNELLEZ module on E dike, 7°44N 69°58W. MCNG 4425, 17, 62.7-107.2 mm SL (7 measured); Apure: UNELLEZ module. MCNG 15740, 2, 70.9-78.1 mm SL; Caño Maporal at bridge by UNELLEZ module, 7°4667 N 69°75 W. MCNG 16101, 5, 73.5-115.7 mm SL; Apure: Caño Caicara, near bridge between Bruzual and Mantecal, 7°5833 N 69°1667 W. MCNG 36224. 2, 58.7-65.3 mm SL; Apure: Caño Las Palmeras, UNELLEZ module. – MCNG 16372, 2, 101.7-105.3 mm SL; Bolívar: Morichal near Puerto Ayacucho. – MCNG 16436, 2, 97.6-136.0 mm SL; Bolívar: Quebrada Clara, under bridge near Anacoco island, 6°42'N 61°9'W. – MCNG 16503, 1, 58.0 mm SL; Bolívar: Río Venamo near confluence with Río Cuyuní, 6°41'N 61°10'W. – MCNG 16558, 1, 98.3 mm SL; Bolívar: lagoon in front of Anacoco hydrology station, 6°45'N 61°8'W. – MCNG 18125, 2, 82.6-83.6 mm SL; Bolívar: Río Tocomita, near María Luisa. – MCNG 18159, 2, 117.3-170.1 mm SL; Bolívar: Guri lake, Las Banderas sector. – MCNG 18187, 1, 120.2 mm SL; Bolívar: Río Caroní at the mouth of the Río Claro, 7°54'45"N 63°2'35"W. – MCNG 18201, 1, 126.0 mm SL; Bolívar: Río Caroní, at Paso Caruachi, 8°6'35"N 62°49'10"W. – MCNG 18228, 7, 46.6-60.3 mm SL; Bolívar: Río Tocoma E from San Juan de Tocoma, 7°43'45"N 63°9'30"W. MCNG 18246, 3, 59.3-89.9 mm SL; Bolívar: Río Claro at bridge on main road to Guri, 7°55'N 63°5'20"W. – MCNG 18580, 1, 93.5 mm SL; Quebrada El Muerto near Hato Mata Linda, 7°47'40"N 63°17'10"W. – MCNG 23351, 1, 131.0 mm SL; Amazonas: Caño Cuchakén 10 km from confluence with Río Atabapo, 3°0'31"N 67°23'W. – MCNG 26383, 1, 116.9 mm SL; Amazonas: Río Atabapo at San Fernando de Atabapo, 4°2'N 67°42'W. – MCNG 27011, 1, 133.4 mm SL; Amazonas: creek 61 km E from Puerto Ayacucho, on the road to Caicara, 5°35'47"N 67°12'38"W. – MCNG 27187, 1, 123.7 mm SL; Amazonas: isolated lagoon from Río Mavaca, 2°24'N 65°6'W. – MCNG 27255, 7, 107.9-161.4 mm SL (1 measured); Amazonas: Río Atabapo at San Fernando de Atabapo, 5°37'6"N 67°36'36"W. – MCNG 28852, 1, 101.3 mm SL; Amazonas: creek flowing into a lagoon of Río Mavaca, 2°17'22"N 65°6'28"W. – MCNG 29022, 1, 144.9 mm SL; Monagas: Río Morichal Largo at bridge, 9°8'N 62°47'50"W. – MCNG 30056, 1, 101.8 mm SL; Bolívar: Guri dam at Los Arrendajos. – MCNG 30076, 4, 108.6-113.3 mm SL; Bolívar: Guri camp. – MCNG 30732, 12, 100.9-191.0 mm SL (1 measured); Bolívar: Laguna Madera, beside Río Orinoco, 7°33'40"N 65°0'50"W. – MCNG 31012, 15, 86.2-166 mm SL; Bolívar: Laguna Madera, 7°33'40"N 65°0'50"W. MCNG 31446 – 32814 – 34390 – MCNG 35146, 1, 215.0 mm SL; Amazonas: Río Casiquiare, Cadamuhedeyedi (Diablo) lagoon, 2°22.25N 66°30.65W. – MBUCV-20457, 1, 172.5 mm SL; Bolívar: Río Carapo. – MBUCV-25405, 4, 108.7-226.98 mm SL (1 measured); Amazonas: Río Ventuari. – MBUCV-26739, 4, 127.9-223.8 mm SL (1 measured); Bolívar: Río Tabaro 1 km upstream from ECONATURA camp. – MBUCV-27168, 1, 97.6 mm SL; Amazonas: Caño Guaya Guayare, Río Orinoco system. – MBUCV-27183, 1, 174.5 mm SL; Amazonas: Río Cataniapo, 1 km upstream from Las Pavas. – MBUCV-7880, 4, 170.6-208.42 mm SL

(1 measured, 2 identified as *A. minimus*); Amazonas: Río Atabapo. – ANSP 159394, 1, 104.7 mm SL; Bolívar: Morichal Los Pavones, affluent of Río Sipao, behind Hacienda Fundo Malama, 7°35'N 65°25'W. – ANSP 161447, 4, 114.1-222.2 mm SL; Amazonas: Río Pamoni lagoon ca. 0.5 km from confluence of Río Casiquiare, 2°50'N 65°53'W. – ANSP 161448, 2, 227.1-238.3 mm SL; Amazonas: Río Pamoni ca. 0.5 km from confluence of Río Casiquiare, 2°50'N 65°54'W. – ANSP 161451, 2, 115.8-154.2 mm SL; Amazonas: Caño Caripo, 1st caño ca. 5 min. from confluence of Casiquiare and Orinoco, left side, 3°06'N 65°50'W. BOLIVIA: AMNH 39726, 8, 52.4-104.3 mm SL; Beni: Río Itenez 2 km SE of Costa Marques. – AMNH 77446, 2, 72.5-81.6 mm SL; Beni: Río Mamoré, Puerto Siles. SURINAM: AMNH 54885, 10, 133.4-153.6 mm SL; Nickerie: Toeboeroe creek, km 220, 300-900 m from mouth. Guyana: AMNH 72032, 3, 28.2-36.2 mm SL; Essequibo: Cebo creek, north bank Mazaruni river, few hundred yards E of St. Edwards church, Kartabo. – AMNH 72105, 1, 73.7 mm SL; Essequibo: abandoned flooded stone quarry behind Gideon's store, north bank Mazaruni river, near Kartabo. – AMNH 73009, 1, 111.5 mm SL; Mazaruni-Potaro: Sandbar, north bank Cuyuni River, just upstream of Caowry creek. – AMNH 215019, 1, 62.3 mm SL; Demerara: Demerara river, Wismar. – ANSP 175502, 15, 106.8-160.0 mm SL (2 measured, 13 identified as *A. falcatus*); Siparuni: Flooded roadside pool / creek along Kurupukari-Surama River road, 4°15'25"N 58°54'07"W. BRAZIL: INHS 37658, 116.5 mm SL; Amazonas: Sao Jose, Lake do Castanho, Janauaca, about 42 km SW Manaus. – INHS 62320, 1, 44.5 mm SL; Amazonas: Sao Jose, Lake do Castanho, Janauaca, about 42 km SW Manaus. – INHS 71007, 9, 50.0-106.7 mm SL (3 measured); Amazonas: Lake Canta Galos off Lake Janauari, about 8 km SW Manaus. – INHS 71454, 5, 47.6-125.2 mm SL; Amazonas: Lake Canta Galos off Lake Janauari, about 8 km SW Manaus. – INHS 71740, 7, 47.1-50.4 mm SL; Amazonas: Lake Janauaca, near Paraíso, behind Lake do Castanho, Janauaca, about 42 km SW Manaus. – INHS 72396, 1, 110.7 mm SL; Amazonas: Lake Janauaca, Sao Jose farm, Lake do Castanho, Janauaca, about 42 km SW Manaus. PERU: INHS 40352, 1, 102.5 mm SL; Loreto: Río Nanay, Pampa Chica , N edge of Iquitos, 3°45'07"S 73°16'59"W. – INHS 40438, 2, 88.5-150.9 mm SL; Loreto: Río Nanay, Miz Playa, about one hour by canoe upstream from Santa Clara, 0°46.63S 73°22.21W. – INHS 43925, 2, 95-133.4 mm SL; INHS 43998, 4, 112.5-136.5 mm SL; Loreto: Río Nanay, Pampa Chica, 4.54 km W of center of Iquitos bearing 269°, 3°45'08.8"S 73°17'00.1"W. – ANSP 136799, 6, 95.3-118.0 mm SL; Loreto: Vicinity Iquitos, Río Nanay opposite naval base, backwater pools off Coche, 4 miles above Amazon. ECUADOR: ANSP 168888, 1, 97.0 mm SL; Napo: Río Lagartococha, an affluent of Río Aguarico, 0°40'00"S 75°15'00"W.

Diagnosis. Distinguished from all other species of *Acestrorhynchus* except *A. grandoculis* by the possession of a minute spot behind the opercle, versus a large humeral spot *(A. falcatus)* or no spot (all other species). Distinguished from *A. grandoculis* by the following combination of features: higher lateral line scale counts (91-131 vs. 77-87), smaller eye (17.9-34.1 % HL vs. 31.1-38.6), and longer snout (32.5-50.0 % HL vs. 26.3-33.3). Maximum size in Venezuela is 215.0 mm SL.

Remarks. Although Toledo-Piza & Menezes (1996) reported that they could not find any adult specimens of *A. apurensis*, they described the species based on juveniles (smaller than 80.0 mm SL). Distinction of *A. apurensis* was justified based on two criteria (Toledo-Piza & Menezes, 1996: 20): (1) in specimens of comparable size (i.e., smaller than 80.0 mm SL), there is no overlap in orbital diameter with *A. microlepis*; (2) juveniles of the species can be readily distinguished from small species of *Acestrorhynchus* based on snout length and pigmentation. The second criterion seems to hold for Venezuelan *Acestrorhynchus*, as *A. apurensis* can be clearly distinguished from the small species *A. nasutus* and *A. minimus* (see below). Our analyses, however, revealed no consistent character, morphometric or meristic, that clearly distinguished *A. apurensis* from *A. microlepis* of any size.

Toledo-Piza and Menezes (1996: fig. 11) plotted orbital diameter against snout length and identified two groups among specimens below 80 mm SL. We repeated that analysis with a larger sample (176 individuals) from a broader geographic area that encompassed a wider size distribution. The plot shows clear overlap between juvenile *A. apurensis* and *A. microlepis* (Fig. 2). Although the paratypes of *A. apurensis* (MCNG 11323) showed a tendency to have smaller orbital diameters, these and 34 additional specimens from the type locality (Módulo de la UNELLEZ) showed no clear distinction from *A. microlepis* from other drainages within the Orinoco basin or other major basins in South America. PCA of orbital diameter, snout length, and head length yielded an ordination scatter-plot (PCA axis 1 vs. PCA axis 2) lacking group separation (Fig. 3). A second PCA including all morphometric features in Table 1 also failed to distinguish two groups (not shown). Overall, neither analysis revealed consistent differences between specimens from the type locality of *A. apurensis* and other drainages in the Orinoco, Guianas or Amazon basins. Meristic characters associated with scales and fins showed no consistent pattern distin-

Fig. 1. a, *Acestrorhynchus microlepis*, TCWC 7500.35, 124.4 mm SL; Venezuela. **b,** *A. microlepis*, MCNG 11323, 54.7 mm SL, paratype of *A. apurensis*; Venezuela. **c,** *A. falcatus*, AMNH 54766, 145.0 mm SL; Surinam.

guishing *A. apurensis* from *A. microlepis* from any geographic origin (Table 2).

The diagnosis of *A. apurensis* is problematic even for specimens within the "correct" size range (below 80.0 mm SL). Furthermore, characters used for the description of juvenile *A. apurensis* appear to be of no aid in identifying adults of this form. Figures 2 and 3 indicate high levels of intraspecific variation in morphology associated with *A. microlepis* and *A. apurensis* of all body sizes, and our analyses show considerable overlap of morphological features among geographically distant populations. Differences between our results and those of Toledo-Piza & Menezes (1996) are probably due to the smaller sample size used for the latter study. Analyses of additional morphometric and meristic features (Tables 1 and 2) revealed no other characters supporting the distinction of the two species. Because our findings show that *A. apurensis* is not distinguishable from *A. microlepis* from the type locality, or any other locality examined, we consider it a junior synonym of the latter.

At least two other reasons can be pointed out to support this view. First, the entire region of the lower llanos of the Río Apure undergoes extensive annual flooding that creates conditions favorable for dispersal. Consequently, there are few areas of local endemism, and species tend to be widely distributed throughout the Apure Basin

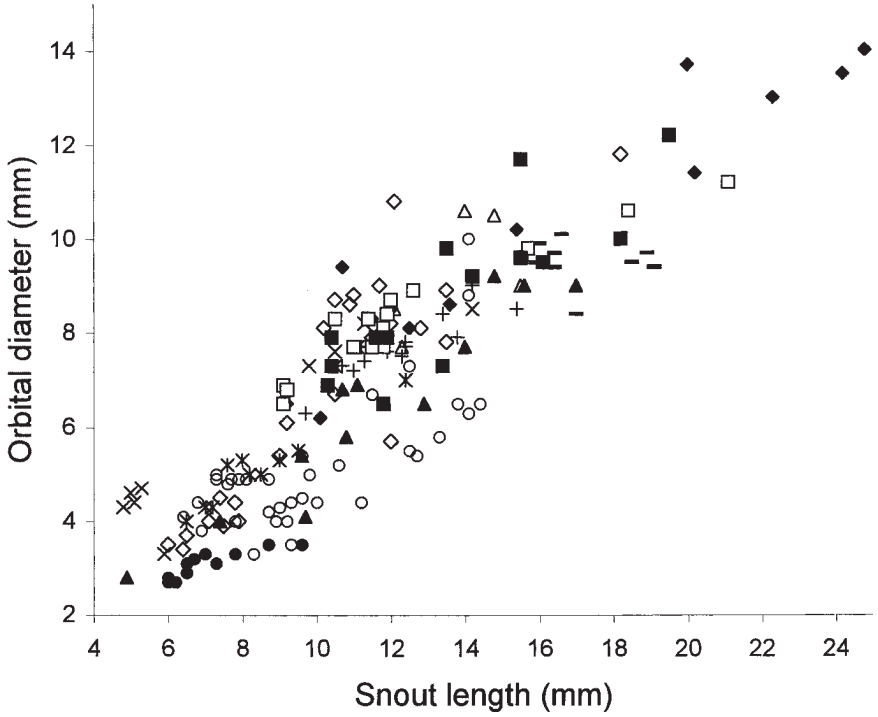

Fig. 2. Plot of orbital diameter against snout length for 176 specimens of *Acestrorhynchus microlepis*. The analysis included 11 paratypes (MCNG 11323) and 34 non-type specimens from Módulo de la UNELLEZ, type locality of *A. apurensis* (Toledo-Piza & Menezes, 1996). ●: *A. apurensis* paratypes; ○: non-type material from Módulo de la UNELLEZ; ◆: higher Orinoco drainage; ■: middle Orinoco drainage; □: lower Orinoco drainage; △: Caura river; ◇: Caroní river; ▲: Essequibo drainage, including rivers Cuyuní, Mazaruni and Siparuni; ▬: Nickerie river; ×: Amazonas river; +: Nanay river; ✳: Beni / Mamoré drainage. To improve clarity, single specimens from rivers Napo and Morichal Largo removed from plot, and specimens from Cuyuní river lumped with remaining specimens from Essequibo drainage.

(Taphorn, 1992). Since the Orinoco llanos are believed to have formed approximately 8 MYA (Lundberg et al., 1998), similar conditions probably have existed for at least that long. Under this circumstance, allopatric speciation appears unlikely as a mechanism that accounts for a restricted distribution of *A. apurensis* within the lower Apure floodplains. Second, the region of the Apure Basin from where *A. apurensis* was described is one of the best-surveyed areas in Venezuela (e.g., Taphorn & Lilyestrom, 1984; Taphorn, 1992, and references therein), making it unlikely that no adult specimens of *A. apurensis* have been captured and preserved.

Morphometric and meristic analyses of populations throughout South America revealed broad variation (Table 2), yet overlapping values among all characters examined prevented us from identifying multiple species among major drainage basins. For example, the number of anal fin rays had a multimodal pattern in the distribution. Although overlapping, three groups can be distinguished based on anal fin counts. The first group, with a mode of III27 anal rays, included specimens mostly from the Amazon River drainage of Perú, Bolivia, Ecuador, and Brazil, but also included a few specimens from Guyana, Surinam and Venezuela. The second group, with a mode of V26-27 rays, included specimens from throughout the Orinoco Basin. The third group, with a mode of IV27-28 rays, was dominated by specimens of the lower Río Orinoco, but also included specimens from other areas. We could not identify any additional characters to support an unambiguous diagnosis of these groups. Variation in coloration pattern and body shape was observed, and appeared associated with environmental conditions more than geographic lo-

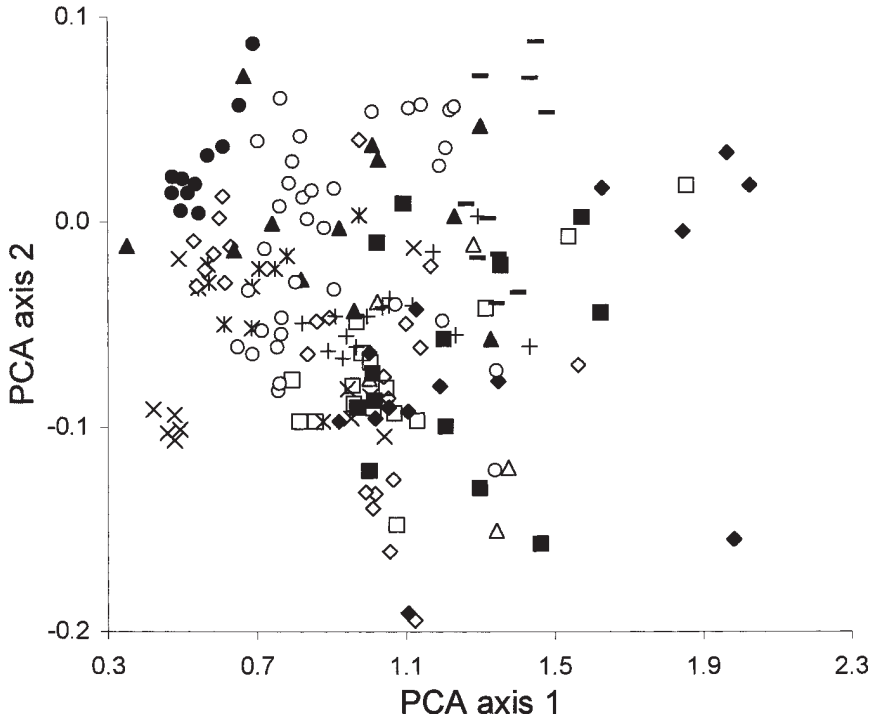

Fig. 3. Plot of PCA loadings of axes 1 and 2 for log-transformed head length, orbital diameter and snout length of 176 specimens of *Acestrorhynchus microlepis* from Venezuela and South American river drainages. Includes 11 paratypes (MCNG 11323) and 34 non-type specimens from Módulo de la UNELLEZ, type locality of *A. apurensis* (Toledo-Piza & Menezes, 1996). Populations and symbols as for Figure 2.

cation. Specimens from black waters usually were slender and shallow bodied, and frequently had larger caudal spots and darker background body pigmentation. Specimens from white or clear waters were more robust with deeper bodies, smaller caudal spots, and less body pigmentation. These patterns do not seem to have any geographic correlation, as specimens from distant drainage basins sometimes appear more similar than specimens from the same region but different habitats. Although our analysis did not allow diagnosis of different groups based on external morphological characters, high levels of variation in the group suggest further analysis of *A. microlepis* may reveal a complex of taxa in need of additional revision.

Distribution. *Acestrorhynchus microlepis* has been collected in virtually every sub-basin of the Rio Negro, Orinoco, and Cuyuní (Essequibo) in Venezuela (Fig. 4). The species is common in black and clear-water streams and rivers, as well as lagoons and other off-channel habitats associated with whitewater rivers. Relatively high water transparency may be a requirement for this visually orienting, diurnal piscivore. *Acestrorhynchus microlepis* is the only member of the genus found in rivers draining the Andean piedmont of Venezuela. Its distribution extends eastward through the llanos into the Río Morichal Largo and Río Cuyuní. To the south, the species is common in the Río Casiquiare region and the headwaters of the Río Orinoco. Records show a gap in the distribution in the middle Orinoco-Río Atabapo region, but this may reflect a paucity of collecting in this area.

Acestrorhynchus falcatus (Bloch)

(Fig. 1c)

Salmo falcatus Bloch, 1794: 120 (Surinam).

Material examined. VENEZUELA: AMNH 93025, 1, 230.0 mm SL; Amazonas: Río Mavaca at Tapirapecó, base camp near boat dock. – AMNH 93026, 1, 219.0 mm SL; Amazonas: Río Mavaca, at base camp. – AMNH

74572, 1, 109.2 mm SL; Amazonas: Río Mawarinuma, at Cerro de Neblina base camp, 0°55'N 66°10'W. – AMNH 74570, 2, 44.9-116.0 mm SL (1 measured); Amazonas: Río Mawarinuma, tributary mouth, 3 km downstream from Cerro de Neblina base camp on left bank, 0°55'N 66°10'W. – AMNH 74571, 1, 143.0 mm SL; Amazonas: Large creek at Cerro de Neblina base camp, from 0.5 km above mouth to mouth series of riffles and pools, 0°55'N 66°10'W. – ANSP 135652, 7, 131.0-191.0 mm SL; Bolívar: Caño Puerto Cabello at Puerto Cabello, 7°10'N 65°01'W. – ANSP 139888, 10, 122.0-189.0 mm SL; Bolívar: Small tributary of Río Mato (left bank), 7°08'N 65°10'W. – ANSP 159404, 1, 110.0 mm SL; Amazonas: Caño entering Río Sipapo at Raudal del Caldero, ca. 3 km above confluence with Río Orinoco, 5°04'N 67°46'W. – ANSP 161456, 1, 195.0 mm SL; Amazonas: Caño of Río Casiquiare ca. 22 km downstream from mouth of Río Pamoni (E side), 2°47'N 66°03'W. – ANSP 167841, 1, 261.0 mm SL; Bolívar: Río Botanamo, just beyond Vivero Forestal Intecmaca on road from Tumeremo to Bochinche, 7°23'N 61°13'W. – ANSP 167842, 1, 109.4 mm SL; Bolívar: Caño Curumito (tributary of Río Botanamo) on road from Tumeremo to Bochinche, 7°20'N 61°20'W. – MCNG 1076, 2, 81.9-88.1 mm SL; Bolívar: creek of Río Botanamo, 2.5 km upstream from confluence of the Botanamo with Río Cuyuní, 6°58'N 61°12'W.

Table 1. Comparison of morphometrics of *Acestrorhynchus microlepis* from different drainages in South America. Specimens from the type locality of *A. apurensis* are compared with paratypes of this species (MCNG 11323).

	A. apurensis paratypes					*A. microlepis* – Modulo UNELLEZ					Orinoco basin				
	n	mean	SD	min.	max.	n	mean	SD	min.	max.	n	mean	SD	min.	max.
SL	11	45.6	6.8	36.9	57.8	34	86.0	21.8	58.7	132.2	74	121.5	41.7	46.6	238.3
Percentages of SL															
Head length	11	33.8	0.8	32.7	35.5	34	29.8	1.3	26.2	32.7	74	27.5	3.3	2.8	32.0
Body depth	11	14.7	1.4	13.0	16.7	34	18.4	1.3	15.8	20.9	74	18.6	2.4	11.2	22.4
D-A	11	16.3	1.3	13.9	17.6	30	19.9	1.4	17.5	22.3	42	20.5	2.5	15.0	23.6
Pectoral length	7	10.6	0.4	10.0	11.1	31	14.4	1.4	11.9	16.9	64	14.2	1.2	11.2	16.0
Pelvic length	6	9.8	0.5	9.2	10.4	32	11.9	1.7	9.2	19.5	65	12.4	1.5	8.8	18.8
Predorsal distance	11	63.2	0.6	62.1	64.2	34	61.7	1.1	59.6	64.7	74	60.3	1.4	57.6	65.0
Postdorsal distance	11	37.0	1.1	34.5	38.1	34	37.9	3.3	27.9	41.8	74	34.7	4.8	28.4	42.3
Preanal distance	11	71.1	0.7	70.3	72.4	34	71.8	4.8	69.3	98.7	74	70.4	1.1	68.2	73.5
Caudal peduncle depth	11	5.5	0.2	4.9	5.7	34	5.6	0.4	4.9	6.4	74	5.8	0.5	4.6	6.5
Percentages of HL															
Snout length	11	46.3	1.6	43.3	49.2	34	39.0	2.6	34.4	44.3	74	42.5	35.7	32.5	344.4
Eye diameter	11	20.3	1.2	17.9	22.1	34	20.3	2.4	15.9	25.3	74	27.7	22.0	20.4	213.3
Interorbital	11	17.8	2.1	14.4	21.0	34	21.2	1.9	17.2	25.8	74	24.6	20.6	16.0	197.8

Table 2. Meristics for *Acestrorhynchus microlepis* from selected drainages in Venezuela and South America, and comparison to paratypes of *A. apurensis*. Numbers in parenthesis indicate sample size; dashes indicate damaged specimens or individuals too small for reliable counting.

drainage	n	SL	lateral line scales	scales from lateral line to dorsal base	scales from lateral line to anal base
A. apurensis paratypes (UNELLEZ)	11	36.9-57.8	104-125	–	–
Non-type material (UNELLEZ)	34	58.7-132.2	93-118	21-29	12-21
Higher Orinoco	14	97.6-238.3	103-119	18-23	14-17
Middle Orinoco	14	101.7-174.5	100-116	17-23	13-17
Lower Orinoco	16	86.2-191.0	105-120	21-24	15-18
Caura	5	104.7-151.4	104-114	19-22	14-18
Caroní	24	46.6-170.1	101-131	16-18	10-16
Morichal Largo	1	144.9	106	21	15
Essequibo (including Cuyuni)	12	36.2-136.0	97-113	17-22	13-15
Nickerie	10	133.4-153.6	103-114	19-24	13-16
Amazonas	12	44.5-125.2	103-115	17-21	12-16
Nanay	15	88.5-150.9	91-111	18-21	13-17
Napo	1	97	109	–	13
Beni / Mamoré	10	52.4-104.3	92-102	–	–

– MCNG 7848, 8 ex, 135.0-166.0 mm SL; Amazonas: Caño Yutaje, at the end of the runway. – MCNG 11076, 1, 90.8 mm SL; Monagas: Caño Agua Clarita near Río Yabo and El Pelón, 8°53'N 62°52'W. – MCNG 20990, 3, 100.1-131.0 mm SL; Bolívar: Caño Yumucukena, within 4 km from mouth, 6°5'N 64°54'57"W. – MCNG 21477, 1, 160.0 mm SL; Bolívar: Puerto Cabello del Caura, at creek in Puerto Cabello, 7°12'N 65°0'W. – MCNG 23027, 1, 263.0 mm SL; Amazonas: Río Asisa, 40 km from confluence with Río Paru, 4°30'N 65°48'W. – MCNG 23953, 1, 135.1 mm SL; Amazonas: Caño Jayuvapuei, tributary of Río Ocamo, 3°03'N 64°38'30"W. – MCNG 25775, 5, 48.6-114.2 mm SL (4 measured); Amazonas: pool Pozo ca. 100 m from right bank of Río Mavaca, 2°03'N 65°6'W. MCNG 26023, 2, 179.0-199.0 mm SL; Amazonas: Río Siapa ca. 18 km upstream from site ABD91-17, 1°40'N 65°44'W. – MCNG 27873, 2, 173.0-213.0 mm SL; Amazonas: isolated oxbow lake of Río Mavaca, 2°02'N 65°06' 15"W. – MCNG 28937, 2, 110.2-124.5 mm SL; Anzoátegui: Río Aisme, tributary of Río Tigre NW from El Tigre, at bridge, 9°4'N 64°6'W. – MCNG 37722, 3, 160.0-171.0 mm SL; Amazonas: 2°5'47"N 66°10'78W. – MCNG 16463, 1, 84.2 mm SL; Bolívar: Río Botanamo at bridge on the way to Bochinche, 7°4167N 6°1833W. – MCNG 18124, 1, 108.0 mm SL; Bolívar: Río Tocomita near María Luisa. – MCNG 18512, 3, 71.6-143.9 mm SL; Bolívar: Río Tocoma, near Mereycito, 7°4708N 63°2417W – MCNG 17229, 1, 79.6 mm SL; Bolívar: Río Tocomita, 5 km NE from Guri dam, 7°8028N 63°0944W – MCNG 18287, 6, 54.8-91.6 mm SL; Bolívar: Río Tocomita 5 km NW from crossing to Guri airport, 7°48'25"N 63°5'55"W. – MCNG 18371, 3, 53.3-93.7 mm SL; Bolívar: Río Tocoma at bridge ca. 22 km S of Guri, 7°36'30"N 63°5'30"W. – AMNH 91148, 1, 132.0 mm SL; Bolívar: Río Lima, tributary of Río Carapo, along South face of Cerro Guaiquinima, approx. 5°30.4N 63°30.4W. – AMNH 91149, 1, 148.0 mm SL; Bolívar: Río Carapo tributary, just below first rapids of River, on left bank, ca. 5°40.1N 63°30.25W. SURINAM: AMNH 54766, 3, 144.0-165.0 mm SL; Nickerie: Kapoeri creek, ca. 7 km in from junction of Corintijn (Corantijn) River. – AMNH 54978, 4, 146.0-161.0 mm SL; Nickerie: Small stream S of Tiger Falls on Corintijn (Corantijn) River, km 405. – AMNH 54869, 1, 108.5 mm SL; Nickerie: Toeboeroe creek, km 220, 300-900 m from mouth. – AMNH 54846, 4, 125.0-176.0 mm SL; Nickerie: Stream near Avanavero, ca. 3 miles downstream Devis (Devils?) Falls. Guyana: AMNH 14362, 1, 80.8 mm SL; Essequibo: Essequibo River, Rockstone. – AMNH 17624, 1, 125.6 mm SL; Essequibo: blackwater creek, Essequibo River headwaters, 1°30'N 58°35'W. – ANSP 175501, 4, 118.9-141.0 mm SL; Siparuni: Forest stream at Burro Burro camp site, 4°43'54"N 58°51'01"W. – ANSP 175502, 15, 106.8-160.0 mm SL (13 measured, 2 identified as *A. microlepis*); Siparuni: flooded roadside pool/creek along Kurupukari-Surama River road, 4°15'25"N 58°54' 07"W. – CAS 68248, 1, 91.4 mm SL; below Packeoo Falls. – CAS 68249, 3, 74.0-86.2 mm SL; Mahaica drainage, Maduni Creek.- CAS 68211, 1, 98.2 mm SL; Demerara River at Christianburg. – CAS 68242, 3, 76.4-90.0 mm SL; Mahaica creek, Lama stop off. – CAS 68244, 2, 74.8-895 mm SL; R. Potaro at Amatuk. Colombia: ANSP 120329, 1, 104.8 mm SL; Lomalinda: near Río Ariari, SE of Villavicencio. – ANSP 134731, 1, 133.0 mm SL; Meta: Tributary of caño El Cocho, ca. 5 km N of La Siberia, 4°07'N 73°05'W.

Amazonas basin					Guyanas drainages				
n	mean	SD	min.	max.	n	mean	SD	min.	max.
38	91.1	28.6	44.5	150.9	22	115.9	35.7	36.2	153.6
38	27.7	1.1	26.0	31.0	21	28.9	1.3	27.2	31.5
38	17.3	2.2	13.7	22.6	21	17.6	2.4	12.2	20.6
38	20.0	2.4	16.2	30.6	18	22.2	10.5	14.4	63.4
37	14.9	1.4	11.2	17.6	15	15.4	0.9	13.9	16.9
38	13.1	1.6	11.2	20.6	14	12.9	0.8	11.3	14.3
38	61.8	1.2	59.0	64.3	21	61.8	1.9	59.5	67.0
38	37.9	4.5	29.3	42.8	21	32.1	3.7	27.5	40.6
38	69.9	1.6	66.0	72.6	21	69.5	1.3	65.9	71.1
38	5.9	0.4	5.1	6.7	21	5.6	0.3	5.0	6.0
38	39.5	2.2	35.4	43.4	22	42.7	2.8	37.9	50.0
38	26.5	2.9	22.4	34.1	22	23.7	1.7	21.1	27.7
38	22.1	3.3	15.5	27.9	22	21.1	2.7	14.4	24.4

dorsal rays	anal rays	pectoral rays	pelvic rays
II 9	IV 24-V 27	I 12-I 15 (4)	I 7
II 9-II 10	III 24-V 27	I 12 -I 16 (32)	I 7
II 9	III 25-V 29	I 14-I 18 (14)	I 7-I 8
II 9	IV 26-V 28	I 13-I 16 (14)	I 7-I 8
II 9-II 10	IV 25-V 28	I 13-II 16 (16)	I 7-I 8
II 9	III 25-V 26	I 14-I 18 (5)	I 7-I 8
II 9	III 27, V 22-V 29	I 13-I 16 (14)	I 6-I 8, II 6
II 9	V 28	I 16 (1)	I 8
II 9	III 27-IV 28	I 13-I 18 (7)	I 7-I 8
II 9	III 26-III 30	I 15-I 16 (10)	I 7
II 8-II 9	III 23-III 29	I 11-I 16 (12)	I 6-I 8
II 9	III 26-III 28	I 14-I 18 (14)	I 7-I 8
II 9	III 26	I 14 (1)	I 7
II 9	III 27-III 29	I 12-I 14 (10)	I 7

Diagnosis. *Acestrorhynchus falcatus* can be distinguished from all other *Acestrorhynchus* species in Venezuela by possessing a humeral spot shaped as an oval or inverted teardrop, occupying not less than a quarter of the height of the body. Additionally, the caudal peduncle has a black

spot covering between one third and almost the totality of its depth. Size up to 264.0 mm SL.

Remarks. We analyzed specimens of *A. falcatus* from the major drainages of Venezuela and the Guyanas region to the east, including the type locality (Surinam). Our findings indicate that *A. falcatus* is highly variable and presents a case similar to that described for *A. microlepis*. Morphometric and meristic attributes vary broadly (Tables 3 and 4, respectively), but no pattern clearly distinguished populations or geographic races. As for *A. microlepis*, the fact that we were unable to diagnose different populations of *A. falcatus* does not prove that all populations correspond to the same species. Meristic features, although overlapping, suggest some partitioning within the taxon. For instance, specimens from the Essequibo / Demerara area of Guyana and from the lower Orinoco tend to have higher scale counts in the lateral line (Table 4). Specimens from Surinam (type locality region) lack consistent meristic or morphometric features distinguishing them from individuals from Guyana, Venezuela, or Colombia (the latter based on relatively few specimens).

Variation in pigmentation is considerable in *A. falcatus* in Venezuela, and further suggests interdemic differentiation. The specimens from the Caroní and Aro rivers in eastern Venezuela have larger humeral and caudal spots (reaching almost the entire height of the body and the caudal peduncle, respectively) than populations from other areas, with the exception of some specimens from Surinam. These populations might constitute a different taxon, but we were unable to identify any external morphological feature that unambiguously distinguished them from *A. falcatus* of other regions. Specimens from the Casiquiare region, the Orinoco headwaters, the Caura and the Ventuari drainages frequently have a smaller, rounder humeral spot (covering only about a quarter of the body height vs. a third to almost the totality of body height in specimens from other regions), yet no character could diagnose any of these populations. Despite our inability to find external morphological characters useful in the diagnosis of additional taxa, subtle differences in pigmentation and body shape suggest that, currently, one or more cryptic taxa may be grouped under the name *A. falcatus*.

Distribution. *Acestrorhynchus falcatus* has a broad distribution in the Guiana shield region of Venezuela (Fig. 4), but is restricted to black or clear water drainages. The species is common in the Río Negro-Casiquiare drainages, including the

Table 3. Morphometrics of *Acestrorhynchus falcatus* from Venezuela and the Guyanas.

	n	mean	SD	min.	max.
SL (mm)	128	129.0	41.7	48.6	270.0
Percentages of SL					
Head length	128	29.1	1.5	20.6	33.6
Body depth	126	20.4	2.0	14.7	24.4
Dorsal to anal distance	128	21.8	1.9	15.8	25.9
Pectoral length	128	17.0	1.6	12.0	23.7
Pelvic length	127	14.0	1.4	10.0	17.0
Predorsal distance	128	61.1	2.2	42.4	64.2
Postdorsal distance	128	39.7	3.5	28.5	71.3
Preanal distance	128	69.5	2.3	49.1	73.5
Caudal peduncle depth	127	6.5	0.5	4.8	7.9
Percentages of HL					
Snout length	128	36.8	2.1	31.3	43.3
Eye diameter	128	25.2	2.6	18.1	32.7
Interorbital	128	27.3	2.2	20.8	32.3

Table 4. Meristics of *Acestrorhynchus falcatus* from selected drainages of Venezuela and the Guyanas.

drainage	n	SL	lateral line scales	scales from lateral line to dorsal base	scales from lateral line to anal base	dorsal rays	anal rays	pectoral rays	pelvic rays
Higher Orinoco	19	48.6-270.0	81-92	15-22	8-13	II 9	IV 22-V 27	I 15-I 17	I 7
Middle Orinoco	11	110.0-263.0	85-97	18-22	11-13	II 9	IV 22-IV 24	I 16-I 18	I 7
Lower Orinoco	26	67.3-191.0	84-105	17-23	8-14	II 9	IV 21-V 24	I 14-I 15	I 6-I 8
Caroni	16	53.3-148.0	84-92	18-20	8-12	II 9	IV 22-V 27	I 15-I 17	I 7
Morichal Largo	8	90.8-148.0	80-88	17-20	9-12	II 9	IV 23	I 15-I 16	I 7
Cuyuni	7	74.0-81.9	83-88	18-20	10-11	II 9	III 25-IV 23	I 14-I 15	I 7
Essequibo / Demerara	29	84.2-261.0	88-100	19-24	11-14	II 9	IV 23-V 24	I 15-I 17	I 7-I 8
Nickerie / Corantijn	12	108.5 -176.0	85-96	18-23	10-14	II 9	IV 23-IV 25	I 15-I 17	I 7

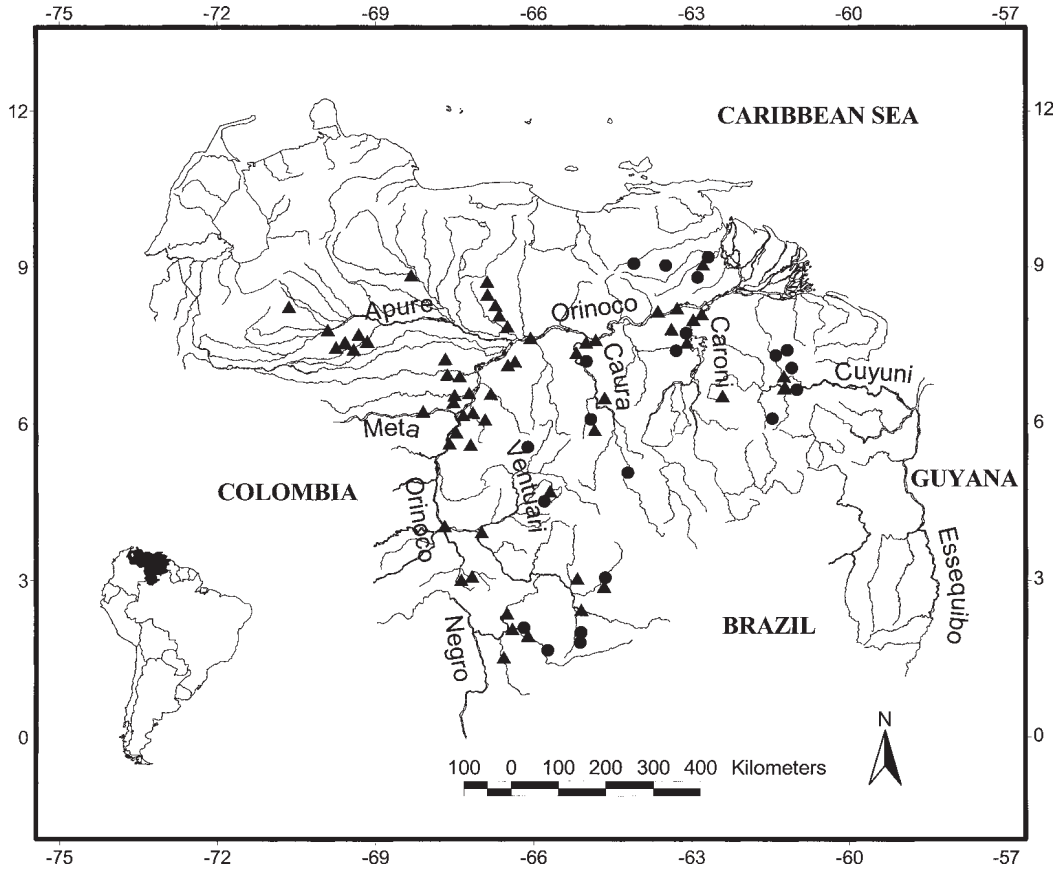

Fig. 4. Distribution of *Acestrorhynchus microlepis* (▲) and *A. falcatus* (●) in Venezuela. Each dot may indicate more than one collection or collecting sites.

Pasimoni, Siapa, and Emoni rivers, and black-water tributaries of the upper Orinoco. Further north, *A. falcatus* is present in the Ventuari drainage. A single specimen was collected in the middle Orinoco near the mouth of the black water Río Atabapo, and the species is widespread in the Rio Caura Basin. To the east, *A. falcatus* is common in the Río Cuyuní drainage, and the northern distribution limit is Río Morichal Largo, a relatively isolated, clear-water drainage that flows into the Orinoco delta. Although *A. falcatus* is sympatric with *A. microlepis* in southern Venezuela and the Guiana shield, it appears to be absent from the western and central llanos, presumably because of intolerance of prevalent white-water conditions. The species' absence from the Río Aguaro drainage (clear water) in the central llanos and the Río Cinaruco and Capanaparo drainages (black water) in southern Apure State in the western llanos is inconsistent with its occupation of similar habitats in upper and lower reaches of the Orinoco Basin.

Other species of *Acestrorhynchus* from Venezuela

Acestrorhynchus heterolepis (Cope)

Diagnosis. *Acestrorhynchus heterolepis* is distinguished from all other known species of *Acestrorhynchus* by the bifurcated canals of the lateral line scales (vs. simple canals). Additionally, scales are smaller than in any other species, with 52 rows (vs. 12-37) between the lateral line and the base of the dorsal fin and 31-35 (vs. 8-22) between the lateral line and the base of the anal fin. Maximum size reported in Venezuela is 306.0 mm SL.

Distribution. Records of *A. heterolepis* are restricted to clear and black-water rivers in the upper and middle sections of the Orinoco, such as the Río Mavaca, Río Padamo, and Río Ventuari (Fig. 5). The species is most abundant in the Rio Negro Basin of Venezuela, where it is found in the Río Casiquiare and its tributaries. To the east, the distribution is limited to a single record from the Río Caura. The northernmost record corresponds to the clear waters of the Río Aguaro, and the western limit is the Río Cinaruco.

Acestrorhynchus nasutus Eigenmann

Diagnosis. *Acestrorhynchus nasutus* can be distinguished by a dark, longitudinal band extending from the tip of the snout through the base of the caudal fin, which is not present in any other species of *Acestrorhynchus* recorded for Venezuela. It can also be distinguished from all its congeners except some juvenile specimens of *A. microlepis* and *A. falcatus* by its long snout (42.8-48.0 % HL vs. 35.3-46.3 % HL). Maximum reported size is 63.1 mm SL.

Distribution. The only record for Venezuela is two *A. nasutus* specimens collected in 1989 (MCNG 23437) from Caño Cuchakén, a tributary of the Río Atabapo (Fig. 5) and a single specimen collected in 2002 from a tributary of the Río Ventuari (MCNG 45023). These collections represent a significant expansion of the range of the species, which was originally described from the Essequibo River at Rockstone, Guyana (Eigenmann, 1912).

Acestrorhynchus minimus Menezes

Diagnosis. *Acestrorhynchus minimus* can be distinguished from *A. grandoculis* and *A. microlepis* for lacking a small, dark spot behind the opercle, which the latter two species present. *Acestrorhynchus minimus* has lower lateral line scale counts than *A. microlepis* (74-85 vs. 91-131), and lower counts of rows between the lateral line and the dorsal fin than *A. grandoculis* (12-14 vs. 16-17). *Acestrorhynchus minimus* can be distinguished from the remaining Venezuelan congeners, except *A. nasutus*, by its small size (up to 91.5 mm SL vs. >200.0 mm SL in all other species) and by the possession of a narrow, dark line that extends from behind the opercle to about two thirds of the body length that is absent in all other species. Maximum size is 91.5 mm SL.

Distribution. *Acestrorhynchus minimus* is restricted to clear and black waters in the major drainages of Venezuela (Fig. 5). Most records are from the Casiquiare region and the Capanaparo and Cinaruco rivers in the western llanos. Northernmost records are from the Río Aguaro in the central llanos. The species has also been collected in the Caura and Caroní basins; it seems to be restricted to the lower reaches of the latter.

Acestrorhynchus grandoculis Menezes & Géry

Diagnosis. *Acestrorhynchus grandoculis* is distinguishable from all other *Acestrorhynchus* except *A. microlepis* by the possession of a minute, dark spot behind the operculum, which is much larger and teardrop-shaped in *A. falcatus* or completely absent in all other species. *Acestrorhynchus grandoculis* has a lower count in lateral line scales (77-87 vs. 91-131), larger eye (31.1-38.6 % HL vs. 17.9-34.1), and shorter snout (26.3-33.3 % HL vs. 32.5-50.0) than *A. microlepis*. It can be distinguished from *A. minimus* by higher counts of scale rows between the lateral line and the base of the dorsal fin (16-17 vs. 12-14). Maximum size in Venezuela is 137.8 mm SL.

Distribution. *Acestrorhynchus grandoculis* occurs in black-water rivers, mostly within the Río Negro-Casiquiare drainages and the middle Orinoco near the Atabapo and Ventuari rivers. The species is also recorded from the Venezuelan Amazon, from Río Cinaruco in the western llanos and Río Caura in the Guyana Shield region.

Acestrorhynchus falcirostris (Cuvier)

Diagnosis. *Acestrorhynchus falcirostris* is a large species distinguishable by the possession of a black fringe on the posterior edge of the operculum, especially on the dorsal half, that creates the appearance of a dark “collar”, whereas in all other species the area behind the operculum has the same color as the rest of the body. It has the highest lateral line scale counts in the genus (140-175 vs. 74-131 in all species except *A. heterolepis*). Scale counts overlap only with exceptional spec-

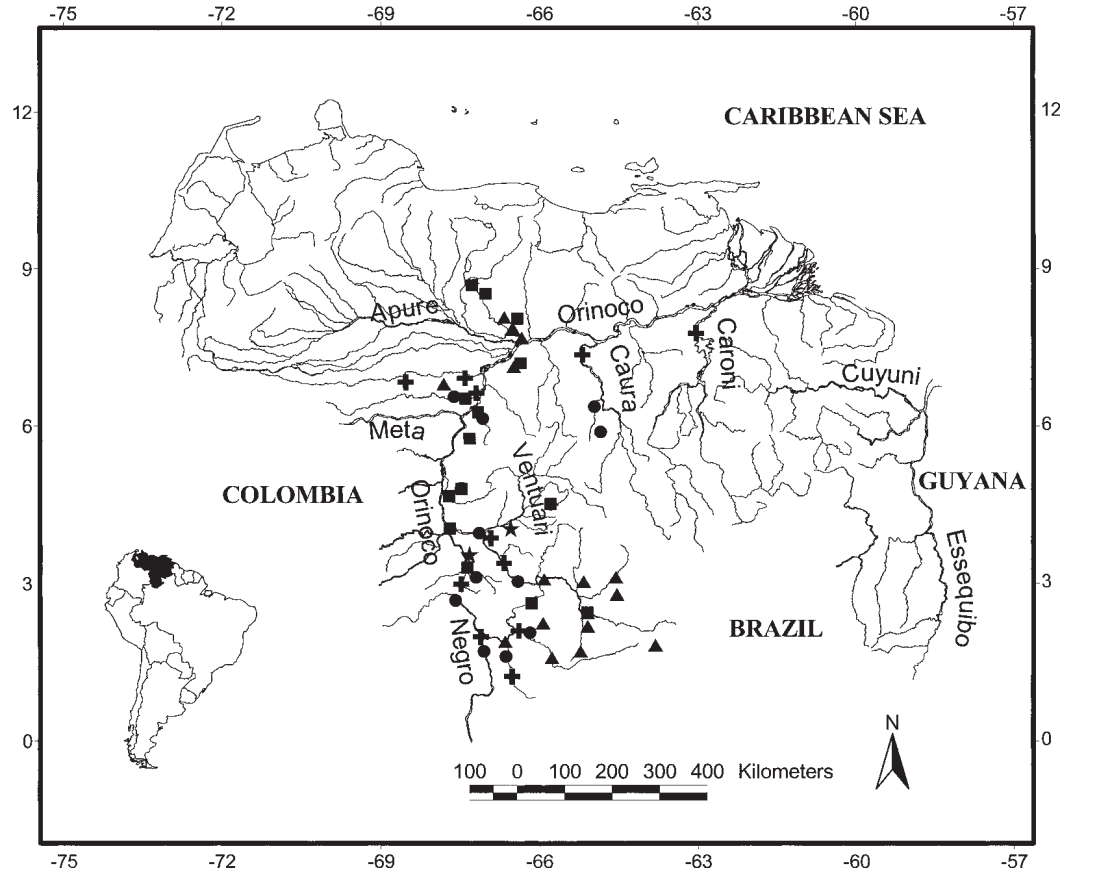

Fig. 5. Distribution of *Acestrorhynchus heterolepis* (▲), *A. nasutus* (★), *A. minimus* (+), *A. grandoculis* (●), and *A. falcirostris* (■) in Venezuela. Each dot may indicate more than one collection or collecting sites.

imens of *A. heterolepis* (130-143). The two species are easily separated by the presence of single branched lateral line canals in *A. falcirostris* (vs. bifurcated canals in *A. heterolepis*). Maximum size in Venezuela is 490.0 mm SL.

Distribution. *Acestrorhynchus falcirostris* is common in clear and black waters of the llanos and upper Orinoco-Rio Negro drainages (Fig. 5). The species is recorded from the main stem of the Orinoco in its upper and middle reaches, as well as the Río Casiquiare. *Acestrorhynchus falcirostris* also is recorded from small black or clear-water tributaries of the lower Orinoco near the Río Cuchivero. In the llanos, records exist from the Capanaparo and Cinaruco rivers and Río Aguaro and its tributaries.

Discussion

Despite extensive taxonomic study relative to most Neotropical fish taxa (e.g. Menezes, 1969; Menezes & Géry, 1983; Toledo-Piza & Menezes, 1996), the genus *Acestrorhynchus* remains poorly understood. Despite our inability to diagnose any new taxon, high levels of variability within *A. microlepis* and *A. falcatus* suggest that these broadly distributed species could actually be complexes of closely related taxa. Taxonomic and biogeographic studies of other fish taxa in South America indirectly suggest that the systematics of *Acestrorhynchus* may be more complex than our analysis of external morphology has revealed. For example, anatomical study at a broad geographic scale led Kullander (1983) to subdivide the genus *Cichlasoma* sensu stricto (Cichlidae) into a dozen species that were traditionally lumped

together, and to recognize a suite of species within the *Satanoperca jurupari* and *Geophagus surinamensis* groups (Kullander, 1986; Kullander & Nijssen, 1989). Similarly, using molecular analyses, Lovejoy & Araújo (2000) found the genus *Potamorrhaphis* (Belonidae) to be a complex of mitochondrial haplotypes hidden by a relatively uniform morphology, and suggested the existence of cryptic species. Although molecular structure of these populations was highly correlated with geography, genetic patterns were not reflected in morphology. In addition, the complicated biogeography of northern South America (Lundberg et al., 1998) may introduce further difficulty in the interpretation of patterns of variation in *Acestrorhynchus*. Biogeographic analyses have suggested complex evolutionary scenarios for several groups of fishes in the Orinoco-Guiana Shield region of Venezuela. For instance, Chernoff et al. (1991) proposed a historical connection between rivers of the Guiana Shield (upper Caura) and the upper Orinoco based on patterns of morphological variation in *Leporinus brunneus* (Anostomidae). Kullander et al. (1992) suggested a connection between the upper reaches of the Caroní and Caura rivers within the Guiana Shield to account for the apparent sistergroup relationship of two endemic species of *Geophagus* (Cichlidae). Lovejoy & Araújo (2000) found populations of *Potamorrhaphis* from the western llanos related to Amazonian populations, probably due to a historical connection between the lower Orinoco and Essequibo drainages to the Amazon through the Rupununi or Mapuera basins in southern Guyana; a pattern similar to that found by Rodríguez & Pereira (1992) for freshwater crabs of the genus *Fredius*. These examples from other taxa suggest that there probably are hidden patterns in the taxonomy and biogeography of *Acestrorhynchus* that we were unable to detect due to the limited resolution of the morphological and meristic characters used in this study. Since taxonomic resolution of *A. microlepis* and *A. falcatus* is apparently not possible based on external morphology, the result is an apparent lack of correlation between morphological variation and geographic distribution. However, molecular techniques or inclusion of additional anatomical characters may uncover complexes of species or intricate biogeographic patterns suggested but not corroborated by our analysis.

Acestrorhynchus microlepis is the most ecologically general and widespread member of the genus in Venezuela (Fig. 4), being the only *Acestrorhynchus* species associated with white-water ecosystems, and the only one that reaches the Andean piedmont in Venezuela. Until recently (Taphorn et al., 1997), *A. grandoculis* had been misidentified as *A. microlepis* in most collections, and for this reason its broad distribution was overlooked for several decades. With the exception of the Río Cinaruco (moderate black water) in southern Apure state, *A. grandoculis* in Venezuela is restricted to black water systems in Amazonas State in southern Venezuela (Fig. 5). Further collecting likely will extend the known distribution of *A. grandoculis* further north into the drainages of the Capanaparo and Cunaviche rivers. *Acestrorhynchus microlepis*, *A. grandoculis*, and *A. minimus* are broadly sympatric in black waters, and are abundant in shallow waters in the Río Cinaruco and the Casiquiare region (López-Fernández & Winemiller, pers. obs.). Although *A. minimus*, *A. falcirostris*, and *A. heterolepis* are common in the clear waters of the Río Aguaro Basin where *A. microlepis* is also abundant, *A. microlepis* and *A. falcatus* are the only species found in clear-water streams of the Río Morichal Largo drainage of the eastern llanos (Fig. 5). *Acestrorhynchus nasutus* has only been collected twice in a period of over a decade (1989 and 2002), from two localities in a restricted region of the middle Orinoco, Amazonas State (Fig. 5). *Acestrorhynchus nasutus* appears to be extremely rare in Venezuela, and could be a candidate for listing as a species vulnerable to regional extirpation. Little is known about its ecology other than it inhabits black waters.

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Appendix

Catalogue numbers from MCNG used to draw the distribution maps in Figures 4 and 5. For *A. microlepis* and *A. falcatus*, see Material examined above. Details on each locality are available at the Neodat project website (http: / / www.neodat.org).

A. falcirostris: MCNG 1754, MCNG 11133, MCNG 14326, MCNG 17144, MCNG 18039, MCNG 19438, MCNG 21908, MCNG 21913, MCNG 22332, MCNG 23350, MCNG 25346, MCNG 26518, MCNG 27000, MCNG 31923, MCNG 33887, MCNG 35277, MCNG 35494, MCNG 35841, MCNG 35843, MCNG 41621.

A. grandoculis: MCNG 12099, MCNG 12276, MCNG 17452, MCNG 22141, MCNG 22348, MCNG 22562, MCNG 22930, MCNG 23026, MCNG 23313, MCNG 23352, MCNG 23449, MCNG 25870, MCNG 27952, MCNG 34665, MCNG 35498, MCNG 35501, MCNG 35853, MCNG 39664, MCNG 39682, MCNG 39701, MCNG 39749, MCNG 42104, MCNG 42263.

A. heterolepis: MCNG 6808, MCNG 23704, MCNG 24315, MCNG 24349, MCNG 24381, MCNG 25347, MCNG 25938, MCNG 25977, MCNG 26052, MCNG 27871, MCNG 28423, MCNG 28757, MCNG 31817, MCNG 32023, MCNG 32067, MCNG 32410, MCNG 35310, MCNG 35324, MCNG 35493, MCNG 37218, MCNG 38180, MCNG 38215, MCNG 38294, MCNG 41971, MCNG 42082, MCNG 42170.

A. minimus: MCNG 6251, MCNG 6809, MCNG 6951, MCNG 12173, MCNG 12274, MCNG 12374, MCNG 17958, MCNG 20026, MCNG 20298, MCNG 20962, MCNG 21730, MCNG 22147, MCNG 23349, MCNG 23605, MCNG 25875, MCNG 26318, MCNG 26777, MCNG 29702, MCNG 33216, MCNG 34628, MCNG 35495, MCNG 35503, MCNG 35504, MCNG 37769, MCNG 38081, MCNG 39390, MCNG 39442, MCNG 39666, MCNG 39702, MCNG 39724, MCNG 39810, MCNG 40062, MCNG 40442, MCNG 40556, MCNG 40759, MCNG 42013, MCNG 42105, MCNG 42168, MCNG 42265, MCNG 42431.

A. nasutus: MCNG 23437, MCNG 45023.

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