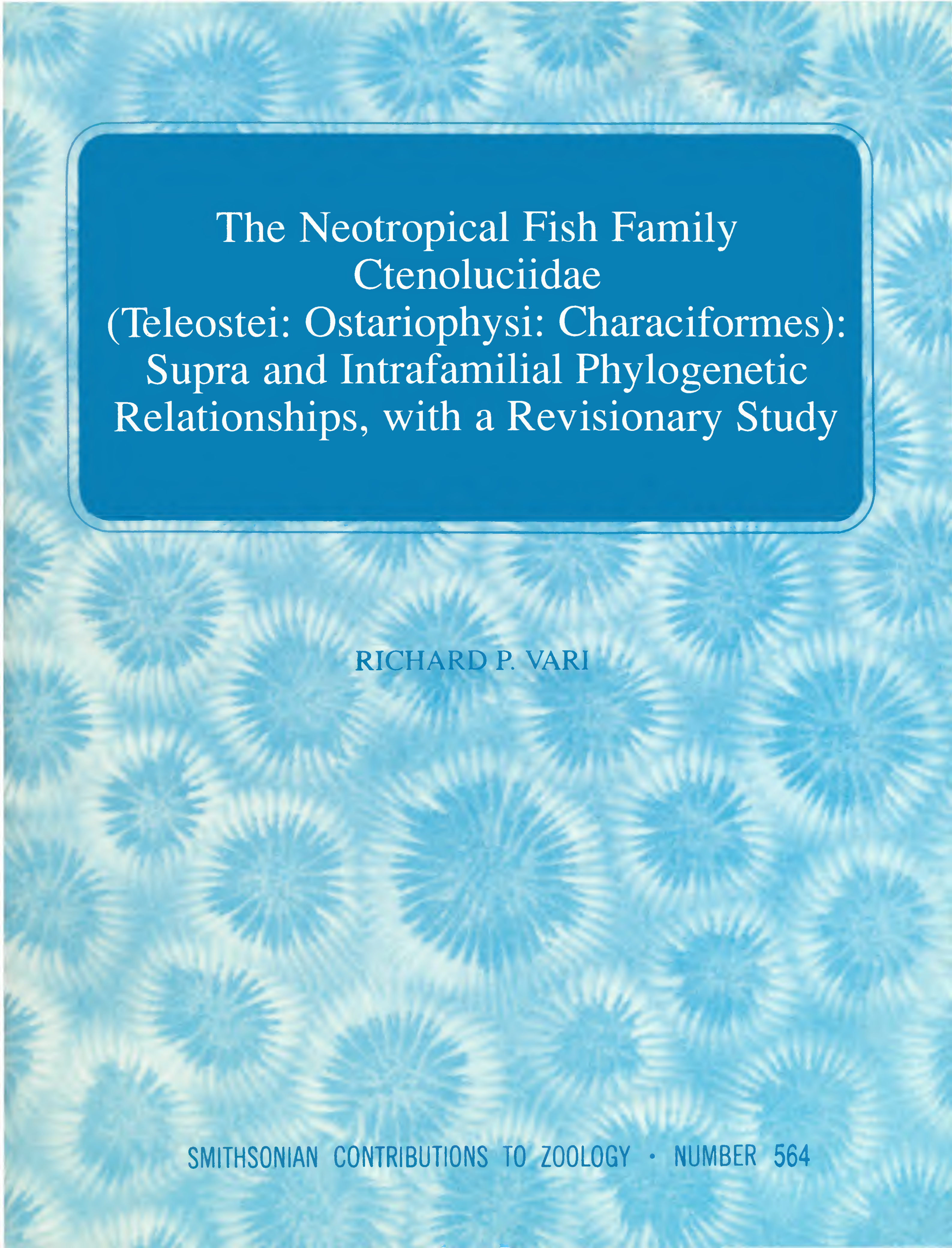

The Neotropical Fish Family Ctenoluciidae (Teleostei: Ostariophysi: Characiformes): Supra and Intrafamilial Phylogenetic Relationships, with a Revisionary Study

RICHARD P. VARI

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 564

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SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 564

The Neotropical Fish Family Ctenoluciidae (Teleostei: Ostariophysi: Characiformes): Supra and Intrafamilial Phylogenetic Relationships, with a Revisionary Study

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ABSTRACT

Vari, Richard P. The Neotropical Fish Family Ctenoluciidae (Teleostei: Ostariophysi: Characiformes): Supra and Intrafamilial Phylogenetic Relationships, with a Revisionary Study. *Smithsonian Contributions to Zoology,* number 564, 97 pages, 51 figures, 12 tables, 1995.—Osteological and soft anatomical features of the species of the Neotropical characiform family Ctenoluciidae and other characiforms were studied to examine the hypothesis that the family was monophyletic, and to advance an hypothesis of phylogenetic relationships within the family and of the Ctenoluciidae to proximate outgroups. A series of derived features corroborate the hypothesis of monophyly of the Ctenoluciidae and are congruent with the hypothesis that the Ctenoluciidae and Erythrinidae are sister groups. A less-extensive series of derived features indicate that the African family Hepsetidae is the sister group of the clade formed by the Ctenoluciidae and Erythrinidae, with the Neotropical family Lebiasinidae the sister group to the clade formed by those three families. Shared derived features of a variety of body systems define phylogenetic subunits of the Ctenoluciidae and characterize the majority of its species. The ctenoluciid genera *Ctenolucius* Gill (1861a) and *Boulengerella* Eigenmann (1903) are defined as monophyletic units.

Luciocharax Steindachner (1878) and *Belonocharax* Fowler (1907) are considered synonyms of *Ctenolucius,* with *Spixostoma* Whitley (1951) placed as a synonym of *Boulengerella.*

Two species are recognized in *Ctenolucius. Ctenolucius hujeta* (Valenciennes in Cuvier and Valenciennes, 1849) ranges from the Lago Maracaibo basin of northwestern Venezuela through the Río Magdalena system to the Río Sinú of northwestern Colombia. *Ctenolucius beani* (Fowler, 1907) occurs in the Río Atrato and Río San Juan basins of northwestern Colombia and the rivers of the Pacific slopes of Panama as far west as Veraguas Province. *Luciocharax insculptus* Steindachner (1878) is a synonym of *C. hujeta,* and *Luciocharax striatus* Boulenger (1911) is a synonym of *C. beani.*

Five species are recognized in *Boulengerella. Boulengerella lateristriga* (Boulenger, 1895) occurs in the Río Negro drainage of the Amazon basin in Brazil and Venezuela and uppermost portions of the Río Orinoco in southern Venezuela. *Boulengerella maculata* (Valenciennes in Cuvier and Valenciennes, 1849) is widely distributed through the Rio Amazonas, Rio Tocantins, and Río Orinoco basins. *Boulengerella lucius* (Cuvier, 1819) occurs in the Rio Amazonas and Río Orinoco systems. *Boulengerella cuvieri* (Agassiz in Spix and Agassiz, 1829) is widespread through the Río Orinoco, Rio Amazonas, and Rio Tocantins basins, the Essequibo River of Guyana, the Oyapock River along the boundary between French Guiana and Brazil, and the coastal rivers of Amapá and Pará states in Brazil. *Boulengerella xyrekes,* new species, a relatively rare form, inhabits the Río Orinoco and Rio Amazonas basins. *Xiphostoma taedo* Cope (1872) is a synonym of *B. maculata. Xiphostoma oseryi* Castelnau (1855) and *Xiphostoma ocellatum* Schomburgk (1841) are considered synonyms of *B. cuvieri. Xiphostoma longipinne* Steindachner (1876), based on a juvenile from the mouth of the Rio Negro in Brazil, tentatively is considered a synonym of *B. cuvieri.* Reports of *Boulengerella* from the Rio Parnaíba of northeastern Brazil and in the Río de La Plata system in Argentina either are based on specimens with questionable locality data or are probable misidentifications.

Keys are provided to distinguish *Ctenolucius* and *Boulengerella* and for the species in each genus. Lectotypes are designated for *Xiphostoma hujeta* Valenciennes, *Luciocharax insculptus* Steindachner, *Xiphostoma ocellatum* Valenciennes, and *Luciocharax striatus* Boulenger.

The phylogenetic biogeography of the group indicates a vicariance event between the Hepsetidae and the lineage consisting of the Ctenoluciidae and Erythrinidae associated with, or predating, the final separation of Africa and South America about 85 mya. Fossil and distributional data indicate that major cladogenesis within the Ctenoluciidae and Erythrinidae predates the late Miocene.

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Contents

The Neotropical Fish Family Ctenoluciidae (Teleostei: Ostariophysi: Characiformes): Supra and Intrafamilial Phylogenetic Relationships, with a Revisionary Study

Richard P. Vari

Introduction

Fishes of the family Ctenoluciidae, with their elongate tapering heads and bodies, large gapes, numerous relatively small jaw teeth, and posteriorly positioned dorsal fins, are among the most distinctive of Neotropical characiforms. Ctenoluciids also are among the larger New World characiforms, with *Boulengerella cuvieri* reaching at least 675 mm SL in the Amazon basin. In addition to their importance in the aquatic ecosystem as high-level predators (Smith, 1981:22), various ctenoluciids are exploited for food by both artesanal fishermen and commercial fisheries (Mendes dos Santos et al., 1984) and for export in the aquarium fish trade (Castro, 1986:3).

Ctenoluciids have a broad geographic distribution in the streams, rivers, and lentic water bodies of the lowlands and lower elevation highlands on both sides of the Andean Cordilleras. *Ctenolucius* Gill ranges from the Pacific versant rivers of western Panama, through the rivers of northwestern and northern Colombia, to the Lago Maracaibo basin of northwestern Venezuela. Complementing this distribution is the occurrence of *Boulengerella* Eigenmann in the massive Orinoco, Amazon, and Tocantins basins and the shorter coastal rivers of Guyana, French Guiana, and the states of Amapá and Pará in Brazil.

The first ctenoluciid species (*lucius*) was described by Cuvier (1816) in *Hydrocynus* Cuvier. *Hydrocynus,* as defined by that author, consisted of six species from South America and Africa, now assigned to a variety of different characiform families (sensu Greenwood et al., 1966). The first author to propose a distinct taxon to encompass what now are considered ctenoluciids was Agassiz in Spix and Agassiz (1829), who placed *lucius* in the newly proposed *Xiphostoma* and who described a second species, *cuvieri,* in the genus. *Xiphostoma,* however, already was occupied in Hemiptera.

During the next 83 years, five nominal genera and 10 nominal species of ctenoluciids were proposed by authors commencing with Valenciennes in Cuvier and Valenciennes (1849), and ending with Boulenger (1911). Subsequent taxonomic treatments have differed on which of the nominal genera and species should be recognized and as to the exact distributional ranges of the recognized species.

These problems were largely a consequence of the limitations inherent to many of the studies dealing with ctenoluciids. Most discussions focused on the representatives of the family in a particular river basin or political unit (e.g., Dahl, 1971). Only Schultz' (1950) relatively brief treatment of the family attempted to deal with the spectrum of generic and specific problems among ctenoluciids. However, with the exception of the *Ctenolucius* populations from Lago Maracaibo, Schultz examined only a handful of specimens from scattered localities across the family range. Those limited samples were insufficient to permit a critical evaluation of the validity of various nominally recognizable species or the estimation of the actual distribution of the various ctenoluciid taxa.

The relationships of the Ctenoluciidae to other characiforms has not been critically examined based on shared derived features. Regan (1911) compared what we now consider ctenoluciids to taxa presently assigned to the Characidae. Whether that comparison was intended as a hypothesis of close

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Richard P. Vari, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Review Chairman: Stanley H. Weitzman, National Museum of Natural History, Smithsonian Institution.

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relationship of the Ctenoluciidae (his Xiphostomidae) with the Characidae is unclear. Gregory and Conrad (1938:321) proposed the subfamily Sarcodacinae for taxa assigned by Greenwood et al. (1966) and many subsequent authors to the New World families Ctenoluciidae (*Luciocharax*) and Characidae (*Acestrorhynchus*) and the African family Hepsetidae (*Sarcodaces*). Roberts (1969) expanded on that hypothesis by highlighting various features shared by the Ctenoluciidae and the African characiform family Hepsetidae. Fink and Fink (1981), in turn, proposed that the Ctenoluciidae, Erythrinidae, and Hepsetidae form a monophyletic group on the basis of dentition characters. That intriguing hypothesis of trans-Atlantic relationships has not, however, been critically examined within the framework of a more encompassing rigorous phylogenetic study.

This paper has five primary aims: (1) to further examine the hypothesis of the monophyly of the Ctenoluciidae and its relationships within the Characiformes; (2) to define *Boulengerella* and *Ctenolucius* as monophyletic units; (3) to resolve the intrafamilial phylogenetic relationships; (4) to determine the recognizable species of *Ctenolucius* and *Boulengerella* and estimate their geographic distributions; (5) to determine what the information about the phylogeny and distribution of ctenoluciids might tell us about the biogeographic history of the family.

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METHODS AND MATERIALS

Measurements were made with dial calipers and data recorded to tenths of a millimeter for distances under 100 mm and to a millimeter for larger distances. Counts and measurements were made on the left side of specimens when possible. Standard length (SL) measurements were made from the bony tip of the snout, not including the fleshy appendage at the end of the snout present in many ctenoluciids (particularly species of *Boulengerella*). Measurements of snout length, orbital diameter, and postorbital length were made from the bony margin of the orbit. Interorbital width was taken at the joint between the supraorbital and sixth infraorbital on each side of the head. Length of the lower jaw was measured from the posteroventral corner of the retroarticular to the tip of the dentary, not including the fleshy anterior projection on that portion of the jaw in various ctenoluciids. In tables and the text, subunits of the head are presented as proportions of head length (HL). Head length and measurements of body parts are given as proportions of standard length (SL).

Counts of lateral-line scales include all scales, pored and unpored, in that midlateral series. Counts of middorsal scales include all rows between the posterior margin of the supraoccipital and the dorsal fin and between the dorsal fin and adipose fin. Middorsal scales anterior to the dorsal fin are somewhat irregularly arranged, introducing some uncertainty into that count. Counts of scales in a transverse series are made from the lateral-line series to the origin of the dorsal or anal fins in *Ctenolucius* and the species of *Boulengerella* with complete lateral lines (*lucius, cuvieri, xyrekes*) and from the origin of the dorsal fin to the midventral line in the species of *Boulengerella* with truncate lateral lines (*lateristriga, maculata*). Vertebral counts were taken from radiographs, with the fused $PU_1 + U_1$ considered a single bone and the vertebrae incorporated into the Weberian apparatus counted as four elements. Numbers in parentheses following a particular vertebral count are the numbers of radiographed specimens with that count. In counts of fin rays, the unbranched fin rays are indicated by lower case roman numerals, and the branched fin rays as arabic numerals. Counts of the outer series of maxillary and dentary include teeth in the process of replacement, as indicated by a gap in an otherwise continuous series of teeth. The inner tooth row on the upper jaw referred to by Schultz (1950:50) as "vomerine teeth" can be seen to be premaxillary teeth when examined in cleared and stained specimens.

The first entry under the "Material Examined" section for each species summarizes the number of specimens examined (with the number in parentheses being the specimens forming the basis for meristic and morphometric data for both head and body parts, and the range of standard lengths for those specimens). A number of the specimens were damaged to varying degrees making it impossible to take all data in every instance. Because of the elongate bodies of ctenoluciids, many specimens were twisted during preservation making the measurement of their standard length impossible. Proportional data on subunits of the head, along with meristic data, were taken from those specimens whenever possible, and the number of specimens from which such partial data were taken is noted in the summary entry.

The summary entry is followed by the listing of material, including collection locality, institutional abbreviation, catalog number, and number of specimens in the lot (in parentheses, the number of specimens in the lot from which counts and measurements were taken if that is less than the total number of specimens, and the range of standard lengths (in mm) of the individuals for which standard length could be determined). Collector and date of collection are provided only for new species.

Geographic descriptors are in the sequence of country (capitalized), state, province, department or district (italicized), followed by specific locality data. The common names are those reported in the literature. In the synonymies for each species, localities are presented as originally cited, followed by modern or corrected equivalents, in parentheses, if that differs. Genders of generic names follow Eschmeyer and Bailey in Eschmeyer (1990). Authorship of genera and species in Spix and Agassiz (1829) follows Kottelat (1988).

Osteological preparations were cleared and counterstained for cartilage and bone using a modification of the method outlined by Taylor and Van Dyke (1985). Previously cleared specimens stained solely with alizarin Red-S, dry skeletons, and dissected alcohol-preserved specimens were used as supplemental sources of osteological data.

The following specimens are the basis of text illustrations or specific observations noted in the text. Number of specimens and the standard length of specimens in each lot follow museum catalog numbers. Head length is listed for some skeletal preparations. Specimens are cleared and counterstained and stored in glycerin unless indicated as being dry skeletons (S), whole specimens examined via radiographs (R) or external examination (E), or specimens dissected to examine osteological (D) or myological (M) features.

Characidae

Acestrorhynchus falcatus. Surinam, Nickerie District, Corantijn River basin, tributary to Sisa Creek; USNM 225614, 2, 81.0–85.1 mm. Venezuela, Amazonas, Río Mavaca; AMNH 93098, head only, 70.0 mm HL (S).

Acestrorhynchus guianensis. Venezuela, Guarico, Guariquito River; USNM 258162, 1, 116 mm (M).

Acestrorhynchus heterolepis. Venezuela, Amazonas, Río Mavaca; AMNH 93095, head only, 98.0 mm HL (S).

Acestrorhynchus macrolepis. Surinam, Nickerie District, Corantijn River basin; USNM 278988, 1, 128 mm.

Agoniates species. Brazil, Amazonas, mouth of Rio Iça; USNM 243222, 1, 106 mm.

Alestes dentex. Mali, Mopti, Niger River; USNM 224869, 1, 138 mm (R).

Alestes lateralis. Botswana, Xuguna; USNM 285664, 1, 75.0 mm.

Brycinus longipinnis. Togo, Togble-Kope; USNM 285665, 3, 45.8–54.0 mm. Ghana, Half Assini, Millers Wharf, USNM 310061, 4, 74.8–85.6 mm (R).

Brycinus macrolepidotus. Togo, Togble-Kope; USNM 310067, 1, 120 mm.

Brycinus nurse. Atbara River; USNM 52088 and 52089, 2, 112–133 mm (R); USNM 310088, 4, 43.6–89.7 mm.

Brycon argenteus. Panama, Comaraca Kuna Yala, Quebrada Sigdi at Pingandi; USNM 293136, 1, 100 mm.

Brycon falcatus. Surinam, Corantijn River; USNM 226161, 2, 71.3–78.3 mm.

Bryconaethiops species. Zaire, Stanleyville; USNM 176365, 2, 81.4–84.6 mm (R).

Crenuchus spilurus. Surinam, Nickerie District, Lana Creek; USNM 225630, 4, 21.7–28.2 mm. Venezuela, Amazonas, Caño Loro, where crossed by road from San Carlos de Rio Negro to Solano; USNM 270132, 4, 37.5–39.0 mm.

Hydrocynus species. Volta [Ghana], Black Volta River; USNM 231342, 3, 38.5–59.2 mm.

Hydrolycus pectoralis. Peru, Río Ucayali; USNM 231549, 1, 167 mm.

Lepidarchus adonis. Ghana, Aluku; USNM 267290, 5, 14.6–18.1 mm.

Micralestes acutidens. Cameroon, Cross River system; USNM 304033, 4, 50.9–59.3 mm (R).

Moojenichthys myersi. Brazil, Bahia, Rio do Braço, 2 km SW of town of Rio do Braço (~14°38′S, 39°16′W); USNM 304497, 1, 84.8 mm.

Oligosarcus hepsetus. Brazil, Santa Catarina, município de Tubarão, Rio Correia; USNM 278988, 1, 110 mm.

Petersius intermedius. Ghana, Dayi River, Gbefi; USNM 310844, 9, 34.8-49.7 mm (R); Ghana, Dayi River; USNM 326309, 2, 32.5-36.5 mm.

Phenacogrammus interruptus. Zaire; USNM 163405, 2, 55.7-57.8 mm (R).

Phenacogrammus pabrensis. Ghana, Dayi River; USNM 326209, 2, 32.3-35.4 mm.

Rhaphiodon vulpinus. Brazil, Amazonas, Rio Solimões, 15 km W of Coari; USNM 231549, 4, 42.1-48.0 mm.

Salminus species. Peru, Madre de Dios, Parque Nacional Manu, Pakitza, Río Manu; USNM 319315, 1, 110 mm.

Triportheus angulatus. Venezuela, Bolivar, small caño connecting with Río Orinoco, immediately S of El Burro; USNM 270343, 2, 67.0-74.1 mm.

Citharinidae

Citharinus citharus. Egypt, Nile River; USNM 52146, 1, 218.7 mm (only gill-arches cleared and stained).

Ctenoluciidae

Boulengerella cuvieri. Brazil, Pará, Rio Capim and tributary streams; USNM 319784, 1, 147 mm (head myology examined before clearing and staining). Venezuela, Amazonas, Río Mavaca; AMNH 93100, head only, 101.5 mm HL (S). Venezuela, Barinas, Río Apure basin, USNM 326304, 1, 25.5 mm SL.

Boulengerella lateristriga. Venezuela, Amazonas, small caño off Caño Urami, just upriver of Santa Lucia; USNM 270331, 1, 145 mm and 1, 139 (M).

Boulengerella lucius. Brazil, Pará, Rio Trombetas, Oriximiná; USNM 319782, 1, 145 mm. Aquarium specimen without locality data; USNM 326202, 1, 99.0 mm.

Boulengerella maculata. Venezuela, Guarico, quebrada draining into Río Orinoco, near Paramana; USNM 391780, 1, 156 mm. Brazil, Rondonia, Rio Machado; USNM 319781, 1, 127 mm. Brazil, Amazonas, Rio Urubu, 25 km from Itacoatiara; USNM 179506, 1, 150 mm (M). Venezuela, Amazonas, Río Mavaca; AMNH 93099, head only, 94.5 mm HL (S).

Boulengerella xyrekes. Brazil, Amazonas, Rio Negro basin, Rio Marauiá; USNM 319783, 1, 167 mm (head myology examined before clearing and staining).

Ctenolucius beani. Panama, Darien, Río Tuira, 1/2 km above Boca de Cupe; USNM 293169, 1, 143 mm. Panama, Río Pirre; USNM 310488, 1, incomplete (M). Panama, coastal stream south of Chepo, USNM 226435, 1, 161 mm (M).

Ctenolucius hujeta. Venezuela, Zulia, Río Motatán system, Río San Pedro, at bridge; USNM 121334, 1, 140 mm and 1, 138 (M).

Cyprinidae

Opsariichthys bidens. China, Anhwe, Ningkwo; AMNH 10955, 1, 80.2 mm.

Distichodontidae

Congocharax olbrechtsi. Zaire, Zaire River, stream flowing into Lac Tumba, near Bikoro; USNM 227394, 2, 21.7-23.5 mm.

Distichodus species. Zaire, Zaire River basin, Stanley Pool; USNM 175436, 66.7 mm.

Eugnatichthys species. No locality data; USNM 326204, 1, 96.0 mm.

Hemistichodus species. No locality data; USNM 326203, 1, 35.5 mm.

Mesoborus species. No locality data; USNM 285674, 1, 74.5 mm.

Nannocharax intermedius. West Africa; USNM 231555, 2, 50.7-63.4 mm.

Paradistichodus dimidiatus. Ghana, Dayi River; USNM 213556, 2, 45.6-47.3 mm.

Xenocharax spilurus. Gabon, Lac Ezanga; USNM 227693, 1, 89.3 mm.

Erythrinidae

Erythrinus erythrinus. Trinidad and Tobago, Trinidad, N flowing stream at mile 71 [= km 113.6] of Southern Main Road, close to Banasse; USNM 260223, 1, 102 mm. Brazil, near Pará [= Pará, Belém]; USNM 163759, 1, incomplete (D). Brazil, Mato Grosso, upper Rio Juruena; USNM 199203, 1, 109 mm (M).

Hoplerythrinus unitaeniatus. Bolivia, Beni, small pond S of El Porvenir Biological Station, 41 airkm E of San Borja; USNM 305370, 1, 108 mm. Surinam, Nickerie, small stream entering east side of Corantijn River about 300 m N of Amotopo boat landing; USNM 225313, 1, 36.2 mm. Peru, Madre de Dios, small stream draining into Río Tambopata, Reserva National de Tambopata; USNM 264020, 2, 79.3-84.0 mm and 1, 97.2 mm (M).

Hoplias cf. *malabaricus*. Bolivia, Beni, canal by El Porvenir Biological Station, 41 airkm E of San Borja; USNM 303853, 1, 95.5 mm. Brazil, Amazonas, Lago Terra Preta, Januari; USNM 308914, 1, 19.0 mm. Brazil, Amazonas, Ilha de Marchantaria; USNM 308910, 1, 94.0 mm (M). Brazil, Ceará, Reservoir at Pentecoste; USNM 310671, 1, 119 mm (M). Venezuela, Monagas, Río Orinoco, Barrancas; USNM 226265, 2, 22.8-26.5 mm.

Hepsetidae

Hepsetus odoe. Liberia, St. Johns River, 0.5 mi [0.8 km] downstream of bridge at Sanniquellie District border; USNM 179331, 1, 107 mm. Cameroon, Cross River system, Akwen Gorge, stream draining into Munaya River; USNM 304047, 1, 121 mm. Cameroon, Manyu, Cross River system; USNM 303782, 3, 18.7–41.0 mm. Cameroon, upper Cross River system, tributaries of Marube River; USNM 304096, 1, 119 mm (M).

Lebiasinidae

Copella eigenmanni. Brazil, Marapanim; MZUSP uncat, 2, 29.0–36.2 mm.

Copella species. Surinam, von Blummenstein Reservoir (Brokopondo); ZMA 106.131, 1, 39.0 mm.

Lebiasina bimaculata. Ecuador, Esmeraldas Province; USNM 326205, 1, 102 mm; USNM 326206, 1, 97.3 mm (M). Peru, Río Moche, Salavery; USNM 88692, 1, 117 mm (M).

Lebiasina species. Venezuela, rivers to the west of the Llanos; USNM 326208, 1, 56.0 mm.

Nannostomus beckfordi. Guyana; USNM uncat., 2, 28.5–29.5 mm.

Nannostomus eques. Venezuela, Amazonas, Caño Manu, tributary of Río Casiquiare, near Solano; USNM 272329, 2, 33.4–37.0 mm (D).

Piabucina panamensis. Panama, Río Cardenas; USNM 304211, 5, 41.0–105 mm. Panama, Culebra; USNM 78658, 1, 100 mm (M).

Pyrrhulina semifasciata. Brazil; MZUSP uncat., 1, 57.5 mm.

Pyrrhulina species. Surinam, Nickerie District, Corantijn River system; USNM 326207, 1, 68.0 mm.

Parodontidae

Apareidon affinis. Argentina, upper Río Parana, Yabebyry; USNM uncat.; 2, 73.0–84.0 mm (E).

Apareidon piracicaba. Brazil; MZUSP 20467, 1, 56.7 mm.

Parodon suborbitalis. Colombia, Río Salado; USNM 231552, 2, 56.0–56.7 mm. Paraguay, Cordillera, Salto de Pirareta; UMMZ 205671, 1, 121 mm (E).

Saccodon dariensis. Panama, Río Sabalo, tributary to upper Río Bayano; USNM 208503, 3, 52.1–74.5 mm. Panama, Río Morti at Hydro Station; USNM 208505, 1, 73.5; 1, 91.3 mm (M). Colombia, Río Salado; USNM uncat., 1, 76.5 mm.

Saccodon wagneri. Ecuador, Los Ríos, Río Cristal, 16 km E of Babahoyo; MCZ 49956, 2 (disarticulated).

Additional observations on osteological characters in outgroups to *Ctenolucius* and *Boulengerella* in other taxa in the Characiformes are based on specimens cited in Vari (1989b: 10–11).

TERMINOLOGY

Osteological terminology is that used by Weitzman (1962) with a few modifications. Vomer is substituted for prevomer, and intercalar for opisthotic as in most recent papers dealing with characiforms. The use of epioccipital rather than epiotic follows Patterson (1975). The substitution of angulo-articular for articular and retroarticular for angular by Nelson (1973) best reflects the homologies of these bones across teleosts. The ossification traditionally termed the epihyal is referred to as the posterior ceratohyal, and the ceratohyal of many previous authors as the anterior ceratohyal, following Nelson (1969). Use of mesethmoid rather than ethmoid follows Fink and Fink (1981).

Unless otherwise noted, the concepts of characiform families in this paper are those of Greenwood et al. (1966), with three modifications. The Ichthyboridae of Greenwood et al. (1966) is placed within the Distichodontidae, following Vari (1979). *Anodus* Spix and *Eigenmannina* Fowler, assigned to the Curimatidae by Greenwood et al. (1966), are considered hemiodontids, as demonstrated by Roberts (1974). The Cynodontidae of Greenwood et al. (1966) is recognized as a tribe within the Characidae, in keeping with the results of Howes (1976). The nomenclature for African characids is that proposed by Paugy (1984:140–183; 1990b:195–236) and that for subunits of the Lebiasinidae is as proposed by Weitzman and Cobb (1975:2).

Menezes and Géry (1983:588) proposed that the subfamily Acestrorhynchinae (sensu Menezes, 1969:80) may not be monophyletic, an hypothesis further detailed by Menezes (1988:296) and supported by the outgroup analyses in this study. Descriptions of features found in either of the two nominal genera within the Acestrorhynchinae (*Acestrorhynchus* and *Oligosarcus*) should not be considered to be general for that nominal subfamily. Myological terminology follows Winterbottom (1974) and that for scales follows Roberts (1993).

ABBREVIATIONS

INSTITUTIONAL ABBREVIATIONS.—Abbreviations for institution names follow Leviton et al. (1985) and Leviton and Gibbs (1988) with the addition of the following:

MHNLS	Museo de Historia Natural La Salle, Caracas
MUSM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima
SU	Stanford University (fish collections now at CAS)

TEXT AND FIGURE ABBREVIATIONS.—The following abbreviations are used in the text figures and text:

AC	anterior ceratohyal
ADO	anterior portion of dilatator operculi muscle
AVPP	anteroventral process of palatine
BR	branchiostegal rays (1–4)
CART	cartilage
CMO	coronomeckelian ossification
DEN	dentary
DH	dorsal hypohyal
DO	dilatator operculi muscle

DPSO	dorsal process of supraoccipital
ECT	ectopterygoid
FFDEN	fleshy flap of lateral surface of dentary
FR	frontal
HYO	hyomandibula
IH	interhyal
IO	infraorbital (1–6)
LAP	levator arcus palatini muscle
LCS-IO$_5$	laterosensory canal segment along dorsal margin of fifth infraorbital
LE	lateral ethmoid
LPF	lateral process of frontal contacting anterior portion of sphenotic spine
MC	Meckel's cartilage
MES	mesopterygoid
MEST	mesopterygoid teeth
METH	mesethmoid
MAX	maxilla
NA	nasal
OP	opercle
PA	parietal
PAL	palatine
PC	posterior ceratohyal
PMAX	premaxilla
PMLIG	palatine-mesethmoid ligament
POP	preopercle
PPAC	posterolateral process of anterior ceratohyal
PPLO	posterior portion of passage for levator operculi muscle
PT	pterotic
SOS	supraoccipital spine
SPH	sphenotic
SPHS	sphenotic spine
SUO	supraorbital
SUOC	supraorbital canal of laterosensory canal system
VH	ventral hypohyal
VMP-DEN	ventromedial process of dentary

Character Description and Analysis

Derived features informative about the hypothesis of proximate sister groups to the Ctenoluciidae and that diagnose that family and its hypothesized monophyletic subunits are analyzed. Features pertinent to the question of the monophyly of the Erythrinidae, Lebiasinidae, and Hepsetidae are discussed. The latter characters are those that have been proposed by previous authors or discovered in this study incidental to outgroup comparisons focused on intrafamilial character variation in the Ctenoluciidae and are thus not the result of detailed comparisons to identify synapomorphies for the Erythrinidae, Lebiasinidae, and Hepsetidae. Outgroup comparisons are made to a diversity of other characiforms including *Xenocharax*, the hypothesized primitive characiform (Fink and Fink, 1981). General statements about characters in characiform outgroups include *Xenocharax* and the other members of the basal clade formed by the Citharinidae and Distichodontidae.

The number in parentheses beginning the vast majority of character discussions corresponds to that of Table 1. Hypothesized synapomorphies at suprafamilial through intrageneric levels (unique unreversed features and unambiguously opti-

TABLE 1.—Character Summary

1. Antorbital. 0, present; 1, absent.
2. First infraorbital. 0. anterior portion not elaborated; 1, anterior portion with medial and anterior processes.
3. First infraorbital and supraorbital. 0, separate; 1, in contact.
4. Margins of first infraorbital and supraorbital. 0, not interdigitating; 1, interdigitating.
5. Dorsal ramus of first infraorbital. 0, small; 1, well developed.
6. Lateral surface of first infraorbital. 0, no dorsal ridge; 1, with dorsal ridge.
7. Anterior portion of first infraorbital. 0, not anteriorly expanded and not close to nasal; 1, anteriorly expanded and nearly reaching nasal.
8. Medial surface of first infraorbital. 0, without horizontal shelf; 1, with horizontal shelf.
9. Supraorbital. 0, present; 1, absent.
10. Supraorbital. 0, without deep-lying canal system; 1, with deep-lying canal system.
11. Medial surface of supraorbital. 0, without vertically aligned process; 1, with vertically aligned process.
12. Fourth infraorbital. 0, well developed; 1, reduced or absent.
13. Fifth infraorbital. 0, forming portion of orbital rim; 1, excluded from orbital rim.
14. Fifth infraorbital. 0, without laterosensory canal segment along dorsal margin; 1, with laterosensory canal segment along dorsal margin.
15. Posterodorsal portion of laterosensory canal system in sixth infraorbital. 0, present; 1, absent.
16. Anterodorsal portion of laterosensory canal system in sixth infraorbital. 0, present; 1, reduced or absent.
17. Nasal. 0, tubular; 1, with dorsal and ventral lamellae.
18. Nasal. 0, length less than width of orbit; 1, slightly longer than orbit; 2, distinctly longer than orbit.
19. Nasal. 0, situated anterior to frontal; 1, situated at least partially anterior to supraorbital.
20. Mesethmoid and vomer. 0, abutting each other ventrally or with vomer overlapping ventral surface of mesethmoid; 1, medial process of vomer inserting into matching depression on posteroventral surface mesethmoid.
21. Lateral ethmoid. 0, with well-developed blade-like process laterally, and no process or small process for articulation with palatine; 1, with relatively small blade-like process laterally, and prominent transversely elongate process articulating with palatine.
22. Frontal. 0, not distinctly expanded anteriorly along margin of nasal; 1, distinctly expanded anteriorly along margin of nasal.
23. Sphenotic spine. 0, spine approximately vertical, with dorsal portion proximate to main portion of bone and continuous with ventral surface of frontal; 1, spine more horizontal, with dorsal portion proximate to main portion of bone and not continuous with ventral surface of frontal.
24. Frontal. 0, without lateral process extending to contact lateral process of sphenotic; 1, with lateral process extending to contact lateral process of sphenotic.
25. Sphenotic spine. 0, extending anteriorly to transverse plane through joint between sphenotic and pterosphenoid; 1, extending anteriorly to transverse plane through joint between pterosphenoid and orbitosphenoid; 2, extending anteriorly distinctly anterior to transverse plane through joint between pterosphenoid and orbitosphenoid.
26. Epiphyseal bar. 0, epiphyseal bar either a distinct transverse bar within fronto-parietal fontanel, or a ridge across ventral surface of frontal; 1, no indication of epiphyseal bar.
27. Parietal branch of laterosensory canal in frontal and parietal. 0, present; 1, absent.
28. Posterior portion of supraorbital canal that contacts pterotic canal. 0, present; 1, absent.

TABLE 1.—Character matrix for species of the Ctenoluciidae and genera of proximate families (0, primitive state; 1-3 derived states).

Taxon	1-5	5-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-85	86-88
Family LEBIASINIDAE																		
Lebiasina	00000	00010	00000	01000	01000	01000	00000	00000	00000	00000	00001	01000	00000	00010	01010	10000	10000	000
Piabucina	00000	00010	00000	01000	01000	01000	00000	00000	00000	00000	00001	01000	00000	00010	01010	00000	00000	000
Pyrrhulina	00000	00010	00000	01000	00000	01000	00000	00000	00000	00000	00001	00000	00000	00010	01010	00000	00000	000
Nannostomus	00000	00010	00000	00000	00000	01000	00000	00000	00000	00000	00001	00000	00000	00010	01010	00000	10000	000
Copella	00000	00010	00000	01000	00000	01000	00000	00000	00000	00000	00001	00000	00000	00010	01010	00000	00000	000
Family HEPSETIDAE																		
Hepsetus	00100	00000	00000	01010	00000	01000	01000	00000	00001	10000	00000	00000	00011	00011	00010	00000	00000	000
Family ERYTHRINIDAE																		
Erythrinus	11000	00010	00000	01000	01011	10100	01000	00000	00100	10000	00000	11100	10000	00021	00010	00000	10112	000
Hoplerythrinus	11000	00010	00000	01000	01011	10100	01000	00000	00100	10000	00010	11100	10000	00021	00010	00000	10112	000
Hoplias	11000	00010	00000	01000	01011	10100	01000	00000	00100	10000	00000	11200	10000	00021	00010	00000	10112	110
Family CTENOLUCIIDAE																		
Ctenolucius beani	10111	00000	01000	01111	11112	11101	00110	10100	11111	11101	10000	01201	00011	10131	10111	11101	01111	110
Ctenolucius hujeta	10111	00000	01000	01111	11112	11101	00110	10100	11111	11101	10000	01201	00011	10131	10111	11101	01111	110
Boulengerella lateristriga	10110	10001	11101	01211	11111	11110	10101	11111	11010	11010	11110	01210	02111	10131	21011	00001	01111	110
Boulengerella maculata	10110	10001	11101	01211	11111	11110	10101	11111	11010	11010	11110	01210	02111	10131	21011	00001	01111	110
Boulengerella cuvieri	10110	11101	11010	11111	11111	11100	00101	11111	11010	11010	11100	01210	01110	11131	10011	00010	01111	111
Boulengerella lucius	10110	11101	11010	11111	11111	11100	00101	11111	11010	11010	10100	01210	01110	11131	10011	00010	01111	111
Boulengerella xyrekes	10110	11101	11010	11111	11111	11100	00101	11111	11010	11010	11100	01210	01110	11131	10011	00010	01111	111

29. Supratemporal laterosensory canal segment in parietal. 0, complete; 1, reduced.
30. Pterotic. 0, not extending anterior to sphenotic spine; 1, extending anteriorly to sphenotic spine.
31. Supraoccipital. 0, not extending dorsally to surface of head anteromedially; 1, extending dorsally to surface of head anteromedially.
32. Plate-like suprapreopercle. 0, absent; 1, present.
33. Premaxilla. 0, not distinctly elongate; 1, elongate.
34. Premaxilla. 0, margin not distinctly convex anteriorly; 1, margin distinctly convex anteriorly.
35. Premaxilla. 0, medial margin anterior to tip of mesethmoid straight; 1, medial margin anterior to tip of mesethmoid concave.
36. Maxilla. 0, with distinct anterodorsal process and movably articulated with premaxilla; 1, lacking distinct anterodorsal process and immovably attached to rear of premaxilla.
37. Posteroventral margin of maxilla. 0, smoothly rounded; 1, distinct notched.
38. Ligamentum primordiale. 0, relatively flat and attaching to anterodorsal portion of maxilla; 1, distinctly thickened and attaching to central portion of maxilla.
39. Area of attachment of ligamentum primordiale in maxilla. 0, without distinct process; 1, with distinct process.
40. Snout. 0, without elongate fleshy process at tip in mid-size specimens; 1, with elongate fleshy process at tip in mid-size specimens.
41. Dentary and Meckel's cartilage. 0, not distinctly elongate; 1, elongate.
42. Median mandibular fossa. 0, largely open medially; 1, largely enclosed by broad plate extending ventrally from dorsomedial margin of main portion of dentary.
43. Coronomeckelian bone. 0, situated dorsal of Meckel's cartilage; 1, located within Meckel's cartilage.
44. Area of attachment of ligamentum primordiale on lower jaw. 0, broad attachment onto fascia of adductor mandibulae muscle and rear of lower jaw; 1, restricted attachment onto distinct process and adjoining region of posteroventral portion of angulo-articular.
45. Dorsoventrally flattened flap of tissue extending horizontally along lower jaw. 0, absent; 1, present.
46. Teeth. 0, not as in 1; 1, large and compressed distally.
47. Crown of teeth. 0, not recurved; 1, recurved.
48. Relative size of teeth along premaxilla. 0, not as in 1; 1, smallest teeth in jaw in a series anteriorly, bracketed anteriorly and posteriorly by distinctly larger teeth.
49. Teeth at anterior of premaxillae. 0, forming arch anteriorly; 1, meeting at acute angle anteriorly.
50. Portion of palatine articulating with lateral ethmoid. 0, cartilaginous laterally; 1, ossified laterally.
51. Attachment of anterior portion of suspensorium to neurocranium. 0, not as in 1; 1, via a thick ligament extending from palatine to mesethmoid.
52. Palatine. 0, without distinct anterior process in region of attachment of ligament to mesethmoid; 1, with distinct anterior process in region of attachment of ligament to mesethmoid.
53. Ectopterygoid teeth. 0, not as in 1; 1, in two or three irregular rows, with teeth approximately one-half size of jaw teeth.
54. Mesopterygoid teeth. 0, absent; 1, present.
55. Metapterygoid-quadrate fenestra. 0, distinct rotund or ovate opening; 1, absent.
56. Basihyal cartilage. 0, single cartilage at anterior of basihyal; 1, pair of cartilages at anterior of basihyal.
57. Lateral surface of anterior and posterior ceratohyals. 0, without interdigitations; 1, with interdigitations.
58. Medial surface of anterior and posterior ceratohyals. 0, without interdigitations; 1, with interdigitations; 2 with interdigitations highly developed.
59. Anterior portion of branchiostegal rays. 0, rounded; 1, with distinct anteriorly directed attenuate process.
60. Posterior ceratohyal. 0, with one attached branchiostegal ray; 1, with two attached branchiostegal rays.
61. Branchiostegal rays. 0, three of four rays; 1, five rays.
62. Interhyal. 0, cylindrical or slightly flattened; 1, with distinct plate-like process posteriorly; 3, with very large plate-like process posteriorly.
63. Gill rakers on trailing edge of second through fourth ceratobranchials. 0, present; 1, lacking on second and greatly reduced or missing on third and fourth.
64. Postcleithrum 3. 0, present; 1, absent.
65. Postcleithrum 2. 0, present; 1, absent.
66. Form of tripus. 0, distinctly triangular anteriorly; 1, elongate.
67. Medial margin of tripus. 0, without median process; 1, with distinct medially directed process.
68. Fourth pleural rib. 0, ventral portions situated under fourth centrum; 1, angled posteriorly, with ventral portions extending distinctly under fifth centrum.
69. Tripus and fourth pleural rib. 0, joined by loose connective tissue; 1, joined by variably developed ligament; 2, joined by discrete ligament; 3, joined by thick ligament.
70. Transverse process of the third neural arch. 0, narrow; 1, wide.
71. Transverse process of the third neural arch. 0, extending anteriorly to laterally overlap the ascending process of intercalarium; 1, falling short of ascending process of intercalarium; 2, greatly reduced.
72. Laterosensory canal system on body. 0, complete; 1, limited to anterior of body.
73. Scales. 0, not as in 1; 1, scales with numerous closely approximated ridges terminating as series of strong teeth along scale margin.
74. Scales at rear of head. 0, not extending over supraoccipital spine to medial portions of parietal; 1, extending over supraoccipital spine to medial portions of parietal.
75. Scales at rear of parietal. 0, not inserting into groove along rear of parietal; 1, scales inserting into such a groove.
76. Anal-fin rays. 0, not sexually dimorphic; 1, sexually dimorphic, with rays expanded.
77. Anterior margins of anal-fin rays in males. 0, symmetrically developed; 1, asymmetrically developed, with asymmetry alternating on subsequent rays.
78. Basal portions of third to eight anal-fin rays in males. 0, unmodified; 1, with distinct lateral flanges.
79. Posterior anal-fin rays. 0, approximately of same relative size in juveniles and adults; 1, relatively much larger in juveniles.
80. Dorsal-fin position. 0, base of dorsal fin situated anterior to vertical through anterior of base of anal fin; 1, base of dorsal fin situated, at least in part, posterior to vertical through anterior of base of anal fin.
81. Adipose fin. 0, present; 1, absent (see comments in text concerning coding for *Nannostomus*).
82. Caudal fin bony stays. 0, present; 1, absent.
83. Dilatator operculi muscle. 0, origin limited to lateral surface of frontal and posterior surface of sphenotic spine, muscle fan-shape; 1, origin not from lateral surface of frontal, but at least in part from within orbit, muscle pinnate.
84. Central portion of dilatator operculi muscle. 0, neither constricted nor with central ligamentous band; 1, constricted, with central ligamentous band.
85. Anterior portion of dilatator operculi muscle. 0, not broadly expanded into orbit; 1, expanded and reaching at least one-half distance across orbit; 2, greatly expanded and reaching to lateral ethmoid.
86. Adductor mandibulae muscle. 0, not arising from sphenotic spine; 1, arising in part from sphenotic spine.
87. Levator arcus palatini muscle. 0, arising only from ventral portion of sphenotic spine; 1, arising from entire ventral margin of sphenotic spine.
88. Anal-fin pigmentation. 0, anal fin of juveniles not particularly dark; 1, anal fin of juveniles black.

mized characters) and autapomorphies are numbered sequentially on the cladogram of Figure 15 to simplify the visualization of their distribution within the proposed phylogenetic scheme. Synapomorphy numbers in the character description and analysis and in the "Synapomorphy List and Phylogenetic Reconstruction" correspond to that numbering system. For purposes of uniformity and clarity, both synapomorphies for supraspecific clades and the autapomorphies for the species of *Boulengerella* and *Ctenolucius* are highlighted by "SYNAPOMORPHY" in the text. Autapomorphic characters are not included in Table 1, nor utilized for in the Paup and Hennig 86 analysis, and such sections of the discussion are not preceded by a number in parentheses. For some characters, two or rarely three equally parsimonious hypotheses can explain the distribution of the character within the overall most-parsimonious phylogeny. The alternative explanations of the evolutionary history of those ambiguous characters are discussed in the text and are numbered sequentially for each node in the cladogram of Figure 15. All ambiguous characters for various levels of inclusiveness are identified by sequential letters (A to K), with individual ambiguous characters at each node numbered by sequential subscripts.

ANTORBITAL

(1) The anterior margin of the orbit in characiformes typically is delimited by three elements; in ventral to dorsal order, the first infraorbital, antorbital, and supraorbital (e.g., *Brycon meeki*, Weitzman, 1962, fig. 8). Ctenoluciids (Figure 1A-C) and erythrinids lack a separate antorbital. Although the anterior process of the first infraorbital in erythrinids occupies the position generally filled by the antorbital, there is no indication of a separate antorbital in any of the examined cleared and stained young juvenile erythrinids (22.8–36.2 mm

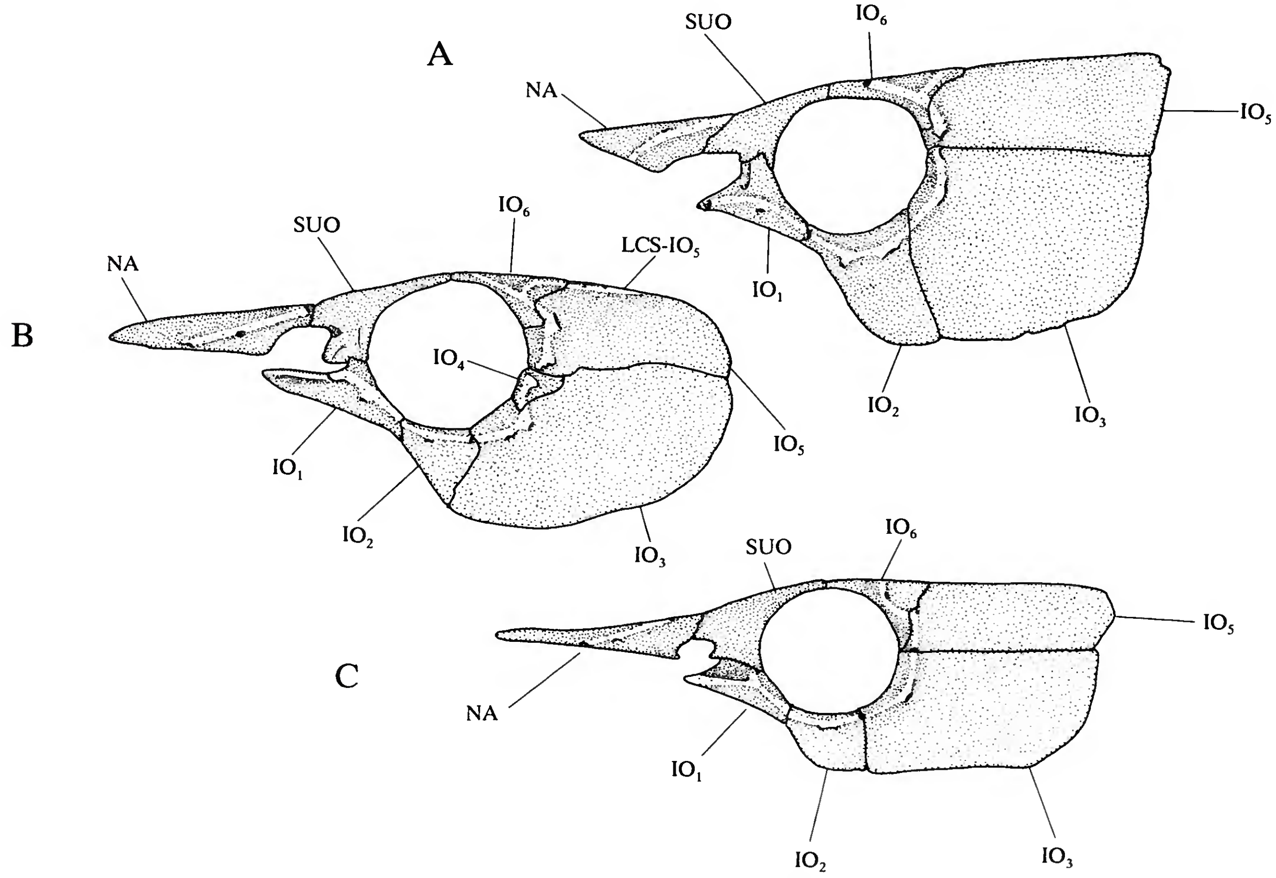

FIGURE 1.—Infraorbital series, supraorbital, and nasal of (A) *Ctenolucius hujeta*, USNM 121334; (B) *Boulengerella xyrekes*, USNM 319783; and (C) *Boulengerella lateristriga*, USNM 270331. Detailed surface sculpturing of bones not shown; left side, lateral view, anterior to left.

SL). Neither is there an indication of a discrete antorbital in the ontogeny of ctenoluciids. Because the antorbital (the adnasal of Gregory, 1933; Daget, 1958 to 1968) is present in the vast majority of characiforms, including the basal characiform families Citharinidae (e.g., *Citharinus*, Daget, 1962a, fig. 7) and Distichodontidae (e.g., *Xenocharax*, Daget, 1960, fig. 7; *Distichodus*, Daget, 1959, fig. 9), the absence of the bone is hypothesized to be a synapomorphy for the Ctenoluciidae and Erythrinidae (SYNAPOMORPHY 15).

An absent antorbital is not, however, unique to these families among characiforms. Discrete antorbitals are absent in some curimatids (*Curimatopsis*, Vari, 1982:8) and the diminutive African characid *Lepidarchus adonis* (Roberts, 1966:212). *Curimatopsis*, a basal lineage of curimatids, shares numerous synapomorphies with members of the Curimatidae (Vari, 1989b:52–53), with that family being, in turn, the sister lineage to the Prochilodontidae, and those families together constituting the sister group to the Anostomidae and Chilodontidae (Vari, 1983:46–47). All of the cited outgroups to *Curimatopsis* retain antorbitals, and it is most parsimonious to hypothesize that the absence of the antorbital in *Curimatopsis* is homoplastic relative to the lack of the ossification in the Ctenoluciidae and Erythrinidae. *Lepidarchus adonis* shares various derived features with African characids, all of which retain the antorbital, and is thus also judged to have lost the antorbital independently of ctenoluciids and erythrinids.

FIRST INFRAORBITAL AND SUPRAORBITAL

(2) The expanded first infraorbital of erythrinids has an anterior process extending ventral of the posterior nares and a broad medial process that extends along the anterior surface of the ventral wing of the lateral ethmoid. Together these two processes encompass the ventral and posterior portions of the nasal capsule. The form of the first infraorbital in the Erythrinidae is unknown elsewhere among characiforms and is diagnostic for the family (SYNAPOMORPHY 27).

(3) The first infraorbital (IO_1) and supraorbital (SUO) in ctenoluciids (Figure 1A–C) and hepsetids (Roberts, 1969, fig. 1) are in direct contact anterior to the orbit. Such direct contact contrasts with the distinct separation of these bones in most characiforms (the supraorbital is absent in various groups; see also below). Distinctly separated first infraorbitals and supraorbitals occur even in the curimatid *Curimatopsis* in which the antorbital is absent (Vari, 1982:8, 1989b:37). Contact between these bones in ctenoluciids and hepsetids, although derived, can be explained by two alternative scenarios under the overall most-parsimonious phylogeny, gain of such contact in the ancestor of the Hepsetidae, Ctenoluciidae, and Erythrinidae (A_1), with secondary loss in the latter family (D_1), or the independent acquisition of contact in the two former families (B_1 and E_1).

(4) Although both ctenoluciids and hepsetids have contact of the first infraorbital and supraorbital, in hepsetids this is a consequence of the lateral overlap of the dorsal portion of the first infraorbital with the ventral process of the supraorbital. In the Ctenoluciidae these two ossifications interdigitate, a form of contact unique for the family among characiforms (SYNAPOMORPHY 34).

(5) *Ctenolucius* species (Figure 1A) have the interdigitations between the dorsal ramus of the first infraorbital and the ventral process of the supraorbital more pronounced than in *Boulengerella*. Similarly, the dorsal ramus is proportionally larger in *Ctenolucius* than *Boulengerella* (Figure 1B,C). Given the absence of contact between the these elements in characiform outgroups and the small or absent dorsal ramus of IO_1 with weaker interdigitations in *Boulengerella*, the morphology of the first infraorbital in *Ctenolucius* is hypothesized to be derived (SYNAPOMORPHY 56).

(6) The species of *Boulengerella* have a distinct lateral ridge situated along the dorsal margin of the anterior portion of the laterosensory canal segment in the first infraorbital (Figure 1B,C). This ridge and the medial depression on the anterior portion of the dorsal ramus of the infraorbital jointly form a distinct shelf ventral of the nares, a condition not encountered in other examined characiforms (SYNAPOMORPHY 68).

(7) Characiforms typically have a broad gap between the first infraorbital and nasal ventral of the nares. Both *Ctenolucius* and the clade in *Boulengerella* consisting of *B. lateristriga* and *B. maculata* have moderately developed anterior portions of the first infraorbital that extend approximately to the vertical through the joint between the supraorbital and nasal (Figure 1A,C). The second major clade of *Boulengerella* (*xyrekes*, *lucius*, and *cuvieri*) have the anterior portion of the first infraorbital nearly reaching the ventral margin of the nasal (Figure 1B). As a consequence, the nares in these three species are nearly encircled by a ring of bones, a derived condition (SYNAPOMORPHY 96).

(8) The medial surface of the first infraorbital typically lacks distinct medial processes in characiforms, with that generalized condition found in the species of *Ctenolucius* and two species of *Boulengerella* (*lateristriga* and *maculata*). The three remaining species of *Boulengerella* (*cuvieri*, *lucius*, and *xyrekes*) have a distinct horizontal shelf on the medial surface of the first infraorbital. This shelf overlies a portion of the dorsal surface of the maxilla and forms a part of the floor of the nasal cavity. In light of its unique nature, this feature is hypothesized to be synapomorphic for these three species (SYNAPOMORPHY 97).

(9) The supraorbital is present in the basal characiform families Distichodontidae and Citharinidae (see figures in Daget, 1958 to 1968) and, among Ostariophysan outgroups to characiforms, in primitive cypriniforms and gonorhynchiforms. This ossification is lacking among various characiforms including all erythrinids and lebiasinids and some members of the Characidae, most notably all "tetragonopterin" characids (Weitzman and Fink, 1983). The absence of the ossification is considered to be derived, and within the overall

phylogeny of groups of immediate interest, the supraorbital is hypothesized as having been lost independently in the Lebiasinidae (SYNAPOMORPHY 5) and Erythrinidae (SYNAPOMORPHY 28).

(10) The supraorbital has two derived modifications in *Boulengerella.* The first is a complex of deep-lying canals extending vertically through the portion of the supraorbital anterior of the orbit. This complex, which consists of a single deep-lying canal with smaller secondary canals penetrating to the lateral surface of the bone, is not apparent externally but is readily visible in cleared Alizarin-red stained supraorbitals examined in transmitted light, particularly those of smaller individuals (Figure 2). The function of the canal system is uncertain, but apparently it communicates ventrally with a deep-lying dorsal branch of the laterosensory canal segment situated in the dorsal region of the first infraorbital. The supraorbital canal system thus is tentatively identified as a laterosensory canal segment. Such a supraorbital canal system, whether or not a segment of the laterosensory system, is unknown in other characiforms and thus is hypothesized to be derived (SYNAPOMORPHY 69).

(11) Another derived modification of the supraorbital involves the medial surface of the bone immediately anterior to the orbital margin. The supraorbital typically lacks pronounced medial processes in characiform outgroups, a condition also found in *Ctenolucius.* Species of *Boulengerella,* in contrast, have a distinct, nearly vertically aligned process extending medially to varying degrees from the main body of the supraorbital. Given the unique nature of this process among examined characiforms, it is hypothesized to be derived (SYNAPOMORPHY 70).

FOURTH INFRAORBITAL

(12) Characiforms usually have six canal-bearing bones along the anteroventral, ventral, and posterior margins of the orbit. This pattern occurs in *Xenocharax* (Vari, 1979, fig 20), the hypothesized primitive characiform (Fink and Fink, 1981), and diverse other groups in the order (e.g., Anostomidae (Winterbottom, 1980), Lebiasinidae and Erythrinidae (Weitzman, 1964), Curimatidae (Vari, 1989b), and Hemiodontidae and Parodontidae (Roberts, 1974)). Roberts (1969:419) noted that *Ctenolucius* has only five infraorbitals and hypothesized that its relatively large third infraorbital might represent fused third and fourth infraorbitals. Gregory and Conrad (1938, fig. 24c) also identified the large infraorbital posteroventral of the orbit as fused third and fourth infraorbitals. Five infraorbitals occur not only in *Ctenolucius* (Figure 1A) but also in *Boulengerella maculata* and *B. lateristriga* (Figure 1C). The three other *Boulengerella* species (*cuvieri, lucius,* and *xyrekes*) have six canal-bearing bones around the orbital margin, with the sixth element a small ossification at the rear of the orbital rim (Figure 1B). Based on its position, this posterior ossification is identified as a greatly reduced fourth infraorbital, with the bones ventral and dorsal to it identified as the third and fifth infraorbitals, respectively.

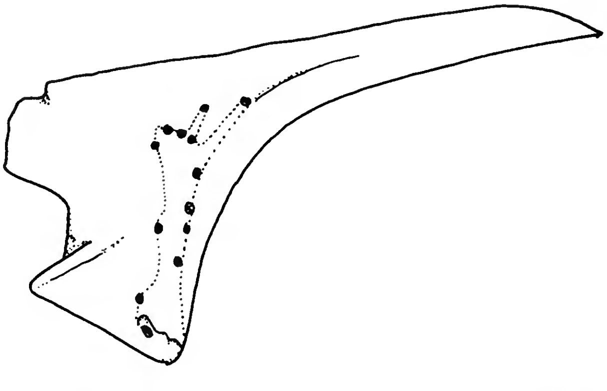

FIGURE 2.—Supraorbital of *Boulengerella lucius,* USNM 319782, showing extent of deep-lying canal system apparent in transmitted light; left side, lateral view, anterior to left.

The presence of a reduced fourth infraorbital in the majority of *Boulengerella* species invalidates the hypothesis that the presence of only five infraorbitals defines the Ctenoluciidae. Rather, the pronounced reduction or loss of the fourth infraorbital is hypothesized to be synapomorphic for the family (SYNAPOMORPHY 35). Within the overall most-parsimonious hypothesis of relationships among ctenoluciids proposed herein, two alternative, equally parsimonious hypotheses account for the distribution of the fourth infraorbital. The first involves the independent loss of the bone in the ancestor of *Ctenolucius* (F_1), on the one hand, and basally in the lineage formed by *Boulengerella lateristriga* and *B. maculata,* on the other (H_1). It is equally parsimonious to hypothesize the absence of the fourth infraorbital in the ancestor of all ctenoluciids (E_2) and the secondary reacquisition of the bone in the ancestor of the clade consisting of *Boulengerella xyrekes, B. lucius,* and *B. cuvieri* (I_1).

FIFTH INFRAORBITAL

(13) The generalized characiform fifth infraorbital (IO_5) is a plate-like ossification that occupies a relatively wide portion of the posterior margin of the orbit (e.g., *Brycon;* Weitzman, 1962, fig. 8), with a laterosensory canal segment only at or near the orbital rim. Two modifications of this plan occur among ctenoluciids. *Ctenolucius* and the clade consisting of *Boulengerella cuvieri, B. lucius,* and *B. xyrekes* retain contact of the fifth infraorbital, albeit somewhat reduced, with the orbital margin (Figure 1A,B). *Boulengerella maculata* and *B. lateristriga* have the fifth infraorbital excluded from the orbital margin by the ventral process of the expanded sixth infraorbital, which contacts the anterodorsal corner of the third infraorbital (Figure 1C; see comments under "Fourth Infraorbi-

tal" concerning identification of infraorbitals at rear of orbit). Although derived based on outgroup comparisons, an exclusion of an infraorbital from the orbital rim is not unique to these species among characiforms. Roberts (1969:419) noted that the erythrinid *Hoplias* has one or two infraorbitals excluded from the orbital rim. These are, however, the fourth and sometimes third infraorbitals rather than the fifth. Neither *Hoplerythrinus* nor *Erythrinus*, the other erythrinid genera, have excluded infraorbitals. *Ichthyborus*, an African distichodontid, also has an excluded infraorbital, but in that genus it is the sixth infraorbital (Vari, 1979:303). Given that the exclusion of the fifth infraorbital from the orbital rim is unique to *Boulengerella maculata* and *B. lateristriga* among examined characiforms, that feature is hypothesized to be derived for the two species (SYNAPOMORPHY 81).

(14) Laterosensory canal segments in the fifth infraorbital of characiforms are nearly universally limited to the anterior portion of the bone. That arrangement occurs in *Ctenolucius*, *Boulengerella lateristriga* and *B. maculata*. The other *Boulengerella* species (*cuvieri*, *lucius*, and *xyrekes*) have an additional laterosensory canal segment on the dorsal margin of the fifth infraorbital (Figure 1B; LCS-IO_5). This canal communicates anteriorly with the posterior branch of the laterosensory canal system of the sixth infraorbital and posteriorly with the pterotic laterosensory canal. The only other characiforms with a shift of a portion of the pterotic laterosensory canal to the infraorbital series are some genera in the Old World family Distichodontidae (Vari, 1979:300, figs. 22–25). Those distichodontids have, however, the additional canal segment in the sixth rather than the fifth infraorbital. The condition in *Boulengerella cuvieri*, *B. lucius*, and *B. xyrekes* apparently is unique in characiforms and is hypothesized to be derived (SYNAPOMORPHY 98).

SIXTH INFRAORBITAL

The laterosensory canal system in the sixth infraorbital (IO_6, the dermosphenotic of some authors), an independent ossification overlying the dilatator fossa on the lateral surface of the neurocranium, is variously developed in characiforms. The generalized condition consists of a tripartite arrangement with the ventral arm contacting the laterosensory canal segment in the fifth infraorbital, the posterodorsal branch proximate to the anterior opening of the pterotic sensory canal, and the anterior branch approximating the medial border of the infraorbital proximate to the lateral of the frontal. Such a tripartite arrangement occurs in *Xenocharax* (Daget, 1960, fig. 7), the hypothesized most-generalized characiform, a variety of other characiform taxa (see also summary in Vari (1989b:39)), and in the ctenoluciid *Ctenolucius* (Figure 1A).

(15) *Boulengerella lateristriga* and *B. maculata* have the anterior branch of the laterosensory canal system in IO_6 terminating in the middle rather than anterior end of the ossification. More noteworthy is the lack in those species of the posterodorsal branch of the laterosensory canal in the sixth infraorbital (Figure 1C), and the lack of contact between the sixth infraorbital and the pterotic, with the sixth infraorbital instead being bordered posteriorly by the fifth infraorbital. In light of the condition in the outgroups, the absence of the posterodorsal canal in the sixth infraorbital and the lack of contact of that ossification with the pterotic are hypothesized to be derived (SYNAPOMORPHY 82).

(16) *Boulengerella cuvieri*, *B. lucius*, and *B. xyrekes* have a pronounced reduction of the anterodorsal branch of the laterosensory canal in the sixth infraorbital. In these species of *Boulengerella*, that canal segment either has the form of a very narrow irregular tube (*lucius*, *xyrekes*) (Figure 1B) or is completely absent (*cuvieri*). The reduction or complete loss of the canal is hypothesized to be a synapomorphy for that three-species clade (SYNAPOMORPHY 99), and the absence of the canal is hypothesized to be autapomorphic for *B. cuvieri* (SYNAPOMORPHY 106).

NASAL

(17) The nasal, the anteriormost of the laterosensory canal-bearing bones of the lateral surface of the head, demonstrates several modifications among ctenoluciids. The typical characiform nasal is tubular (e.g., *Acestrorhynchus*; Roberts, 1969, fig. 5) with at most limited dorsal and ventral laminar processes (e.g., *Brycon*; Weitzman, 1962, fig. 8) even in groups with heavily ossified facial bones (e.g., *Salminus*; Roberts, 1969, fig. 4). Among outgroups, the nasal is shorter than the orbital diameter, even in taxa that have elongate jaws such as *Acestrorhynchus* (Roberts, 1969, fig. 3) and the distichodontid *Ichthyborus* (Daget, 1967, fig. 8). Ctenoluciids, in contrast, have well-developed nasals with extensive heavily ossified laminar processes dorsal and ventral to the laterosensory canal segment. Nasals with distinct laminar processes bordering the laterosensory canal segment also occur in *Hepsetus* (Roberts, 1969, fig. 1) and in erythrinids, particularly *Hoplerythrinus* and *Erythrinus*, in which they are broad plate-like bones. The nasal in the Lebiasinidae demonstrates several conditions. Most of the members of the Pyrrhulininae have relatively wide nasals with distinct lamellae bordering the laterosensory canal segment in *Pyrrhulina* and a wide nasal without any canal in *Copella*. *Nannostomus*, in contrast, lacks the lamellae but retains the canal. Lebiasinins, the other lebiasinid subfamily, have relatively wide nasals, although somewhat reduced in relative size. The expanded laminar portions of the nasals are hypothesized to be a synapomorphy for the clade consisting of lebiasinids, erythrinids, hepsetids, and ctenoluciids (SYNAPOMORPHY 1), albeit with a secondary reversal in *Nannostomus*.

(18) The relative length of the nasals of ctenoluciids is unique within characiforms, being at least as long as (*Ctenolucius*; Figure 1A) or longer than (*Boulengerella*; Figure 1B,C) the orbital diameter. Three degrees of development of the

nasals are obvious in the family. The elongation of the bone to a length at least equal to that of the orbit is a derived feature common to all ctenoluciids (SYNAPOMORPHY 36). The further lengthening of the nasal to a length longer than the orbital width in *Boulengerella* is considered to be a further derived state (SYNAPOMORPHY 71), with the particularly elongate form of the bone in the clade consisting of *B. lateristriga* and *B. maculata* (Figure 1B) hypothesized to be a third, less-inclusive, derived feature (SYNAPOMORPHY 83).

(19) The nasal in characiforms typically lies lateral to the mesethmoid and anterior to the frontal. The Hepsetidae and Ctenoluciidae, in contrast, have the nasal more laterally situated, lying partially (*Hepsetus;* Roberts, 1969, fig. 6) to nearly completely (Ctenoluciidae; Roberts, 1969, fig. 7) anterior to the supraorbital, an arrangement commented on previously by Gregory and Conrad (1938:338; note: those authors identified the supraorbital as the "prefrontal," a term they applied in most cases to the lateral ethmoid). Within the overall most-parsimonious phylogeny, the lateral shift of the nasal can be explained by two alternative, equally parsimonious hypotheses: an independent lateral shift in the Hepsetidae (B_2) and Ctenoluciidae (E_3); or a shift of the ossification laterally in the ancestor of those two families plus the Erythrinidae (A_2), with the secondary return to a more medial position in the latter family (D_2). The pronounced lateral shift of the nasal in ctenoluciids, not found elsewhere in characiforms, is diagnostic of the family (SYNAPOMORPHY 37).

VOMER

(20) The vomer in ctenoluciids abuts against and articulates anteriorly with the ventral surface of the mesethmoid via an interdigitating joint formed by an anterior extension of the middle of the vomer that extends anteriorly into a matching depression on the posteroventral surface of the mesethmoid. Some variability in the degree of development of this suturing is apparent in the cleared and stained specimens examined, and at least the single available large dry skeleton of *Boulengerella cuvieri* (AMNH 93100) has a more complex suturing pattern. Outgroup comparisons have revealed that the typical situation is a synchondral, straight to variably wavy, transverse articulation between these elements. Although at least some *Acestrorhynchus* species have the anterior portion of the vomer extending over the ventral surface of the mesethmoid, the arrangement in those taxa does not demonstrate the interdigitation characteristic of ctenoluciids and apparently is nonhomologous. Roberts (1969:405) noted that in *Hepsetus* and large specimens of *Acestrorhynchus* the suture between the mesethmoid and vomer is "strongly interdigitating" and illustrated (1969, fig. 16) such a suture for the former species. A vomer separate from the mesethmoid has not been detected in any of the specimens of *Hepsetus* examined during this study (18.7–121 mm SL). Even in the 18.7 mm SL cleared and counterstained individual, the region typically occupied by these two bones is a single ossification. Thus, the ontogenetic evidence does not indicate that the complex interdigitations between the mesethmoid and vomer comparable to those of the Ctenoluciidae are a precursor to the fusion of those elements in *Hepsetus*. Consequently, the data does not support a hypothesis of homology between the fused mesethmoid-vomer of that genus and the suturing between those elements found in ctenoluciids.

The situation in *Acestrorhynchus* differs from that in the Ctenoluciidae in several respects. In juvenile and most adult ctenoluciids the nearly straight transverse margin of the vomer abuts against a comparable discrete margin on the ventral surface of the mesethmoid, with an anterior process of the vomer inserting into a matching median groove in the mesethmoid. In *Acestrorhynchus,* as noted above, there is an overlap of the posteroventral median portion of the mesethmoid by an anterior projection of the vomer, a very different and evidently nonhomologous condition. The unique interdigitating articulation between the mesethmoid and vomer in ctenoluciids consequently is hypothesized to be synapomorphic for the family (SYNAPOMORPHY 38).

LATERAL ETHMOID

(21) The lateral ethmoid of most characiforms bears a blade-like ventral process that forms the anterior wall of the orbit. Various groups in the order have the medial portion of the ventral blade expanded into a flattened process, typically capped with cartilage, that contacts a comparable cartilaginous process of the palatine. When present, such articular surfaces on the lateral ethmoid in characiform outgroups are round or only slightly transversely elongate and small relative to the main body of the ventral wing. In contrast, ctenoluciids have the articular surfaces on the lateral ethmoid significantly larger than the reduced blade-like portion of the bone, and the articular surfaces are expanded into a distinctly transversely elongate surface, a restructuring not encountered elsewhere in characiforms (SYNAPOMORPHY 39).

FRONTAL

(22) Among ctenoluciids, the frontal extends distinctly more anteriorly along the medial margin of the nasal than in most other examined characiforms (SYNAPOMORPHY 40). The only examined characiform outgroup with a pronounced extension of the frontals anterior of the posterior limit of the nasals involves the subunit of the Distichodontidae with elongate jaws. In those taxa, however, the anterior expansion occurs along the midline rather than laterally in the region proximate to the nasals (e.g., *Ichthyborus;* Daget, 1967, fig. 8).

DILATATOR GROOVE

(23) Sagemehl (1885:61–62), Weitzman (1964:139), and Roberts (1969:408) all commented on the form of the dilatator

groove of characiforms, which serves as the area of attachment for the dilatator operculi muscle. The groove among characiforms is a variously developed fossa extending from the sphenotic spine onto the skull roof. This occurs not only in *Xenocharax*, the hypothesized most-generalized characiform, but also in *Opsariichthys bidens*, a morphologically primitive cypriniform (Fink and Fink, 1981:305) and is thus hypothesized to be plesiomorphic. Sagemehl (1885:61-62), Weitzman (1964:139), and Alexander (1964:184) noted that in erythrinids the lateral margin of the frontal extends laterally to contact the dorsal process of the sphenotic, thus encompassing the dilatator groove. Sagemehl further noted that the resultant tubular canal allows the dilatator operculi muscle to extend forward into the orbit and that the muscle thus has a much different origin than typical for characiforms. Roberts (1969:409) proposed that the similar tubular dilatator groove in *Ctenolucius* and *Boulengerella* presumably has the "same significance as in the Erythrinidae." Weitzman (1964:139) noted that in lebiasinids "the dilator groove is covered but not encircled by the frontal."

A reduction of the dorsal portion of the sphenotic spine proximal to the main body of the neurocranium such that it no longer contacts the ventrolateral margin of the frontal is common to ctenoluciids, erythrinids, and the subfamily Lebiasininae in the Lebiasinidae (*Lebiasina bimaculata, Piabucina panamensis*). No such reduction is found in the lebiasinid subfamily Pyrrhulininae (*Pyrrhulina* sp., *Nannostomus eques, Copella* sp.). All the taxa with dorsally reduced sphenotic spines have a longitudinal expansion of the remainder of the spine that is reoriented to a more horizontal alignment. Therefore, this restructured spine is considered to be derived. Under the overall most-parsimonious scheme of relationships the reduction of the dorsal portion of the sphenotic spine and its horizontal reorientation is considered to be independently acquired in the clade formed by the Erythrinidae and Ctenoluciidae (SYNAPOMORPHY 16) and in the Lebiasininae (SYNAPOMORPHY 8). A reoriented sphenotic spine with a near horizontal alignment also occurs in the subunit of the Distichodontidae formed by *Ichthyborus, Microstomatichthyoborus, Mesoborus, Eugnatichthys, Paraphago, Phago*, and *Belonophago* (Vari, 1979:285, figs. 12-14), but it differs significantly in its overall structure from that just described for the Neotropical taxa. Contrary to the situation in lebiasinins, erythrinids, and ctenoluciids, these distichodontid genera have the sphenotic spine proportionally reduced in overall size. Furthermore, the seven distichodontid genera retain continuity between the dorsal margin of the sphenotic spine and the ventral surface of the frontal. As such, the conditions in the New and Old World taxa are considered to be nonhomologous.

(24) The restructured sphenotic spine and dorsally adjoining region of the frontal are distinctly separated in the lebiasinid family Lebiasininae (Figure 3), whereas the laterally expanded frontal contacts the lateral margin of the sphenotic spine in both the Erythrinidae and Ctenoluciidae (Figure 4). As a consequence, the central portion of the dilatator operculi muscle is completely surrounded by a tubular canal formed by the frontal and sphenotic. Such a lateral contact of the sphenotic and frontal is unique to ctenoluciids and erythrinids among examined characiforms and is hypothesized to be synapomorphic for those families (SYNAPOMORPHY 17).

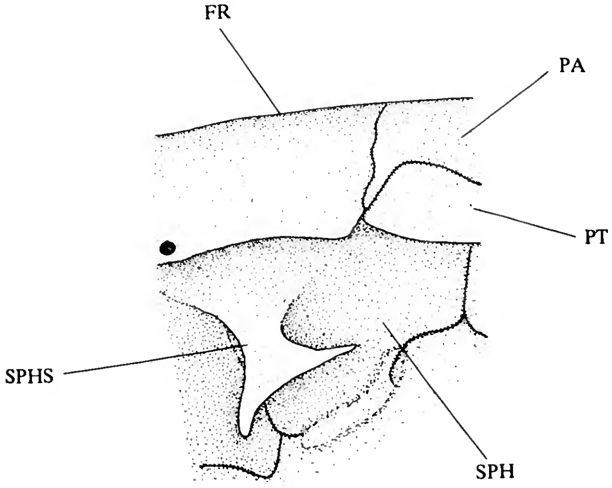

FIGURE 3.—Sphenotic and adjoining bones of *Piabucina panamensis*, USNM 304211, showing dorsally reduced and horizontally realigned sphenotic spine; left side, lateral view, anterior to left.

(25) The sphenotic spine in the Lebiasininae, although more extensive horizontally than in the hypothesized plesiomorphic condition, nonetheless has its anterior margin approximately at the transverse plane through the joint between the sphenotic and pterosphenoid, the condition found in many characiforms including primitive lineages (e.g., *Xenocharax spilurus;* Daget, 1960, fig. 8). In the Erythrinidae and Ctenoluciidae, in contrast, the sphenotic spine is much more elongate horizontally and extends anteriorly to at least the level of the transverse plane through the joint between the orbitosphenoid and pterosphenoid (SYNAPOMORPHY 18). Within the Ctenoluciidae this elongation is particularly pronounced in *Ctenolucius* where the sphenotic spine extends distinctly anterior of the latter joint (SYNAPOMORPHY 57).

As discussed under "Myology," the modifications of the frontal and sphenotic are correlated with the origin of the dilatator operculi muscle in the orbit. Roberts (1969:410) noted that *Acestrorhynchus* has a "large passageway between the sphenotic and the frontal" and suggested that it might serve the same function as the "sphenotic-frontal canals" in erythrinids and ctenoluciids. Although the passage in *Acestrorhynchus* also encompasses an anterior extension of the dilatator operculi muscle, the opening in that genus is not bordered by the sphenotic. Rather, the passage for the dilatator operculi muscle in *Acestrorhynchus* is located entirely within a lateral process of the frontal. This aperture has at least two very different forms

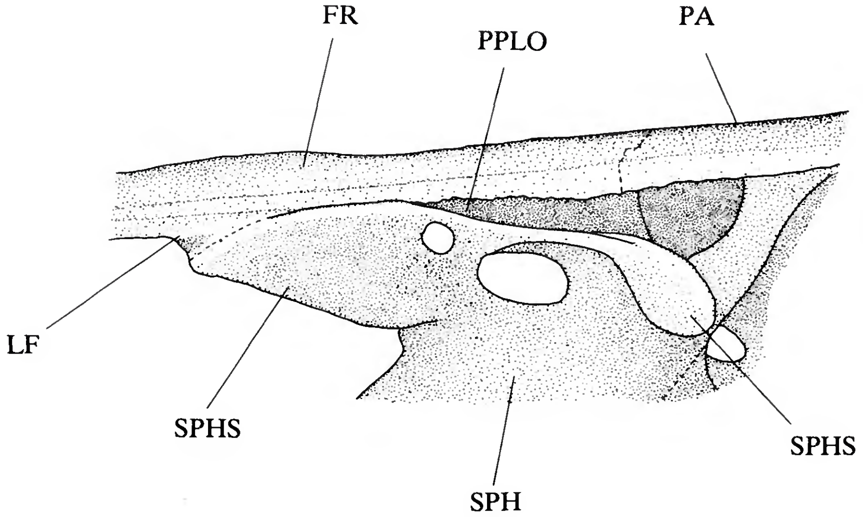

FIGURE 4.—Dorsal portion of sphenotic and immediately adjoining bones of *Boulengerella cuvieri*, AMNH 93100, dry skeleton, showing horizontally aligned sphenotic spine and lateral process of frontal, which together encircle a portion of dilatator operculi muscle; left side, lateral view, anterior to left.

in the genus. In *A. falcatus* the opening for the muscle is bordered ventrally by a very narrow, ventrally concave process of the frontal. *Acestrorhynchus heterolepis*, in contrast, has a distinct bridge of bone separated posteriorly from the sphenotic spine by a distinct foramen ventral to the aperture. Both of the conditions in *Acestrorhynchus* differ completely from that in erythrinids and ctenoluciids and are considered to be nonhomologous.

A passage for the dilatator operculi muscle similar to that in *Acestrorhynchus* also occurs in the parodontid genus *Saccodon* (*dariensis*, *wagneri*), albeit with the process of the frontal situated ventral and lateral to the opening being proportionally thicker than that in *Acestrorhynchus*. This aperture, previously reported by Roberts (1974:425), does not occur in *Apareidon* and *Parodon*, the other parodontid genera. Given the numerous derived features that characterize the Parodontidae (Roberts, 1974), it is most parsimonious to hypothesize that this aperture in *Saccodon* is homoplastic to that in *Acestrorhynchus* and the Ctenoluciidae, with the differences between the elements contributing to the opening in *Saccodon* versus ctenoluciids and erythrinids further indicative of the nonhomology of the apertures in those taxa.

EPIPHYSEAL BAR

(26) The majority of characiforms have the parietals and to varying degrees the frontals separated by the median frontoparietal fontanel. Each frontal contacts its contralateral partner through the ossified epiphyseal bar. Such apertures occur in *Xenocharax* (Daget, 1960, fig. 7) and noncharaciform ostariophysans. The absence of fontanels in ctenoluciids consequently is hypothesized to be derived. Such an absence, however, is of wider occurrence, also occurring in adult erythrinids, hepsetids, lebiasinids (Weitzman, 1964, fig. 2), and parodontids (Roberts, 1974, fig. 56) in the New World. The African characid *Alestes* (sensu lato) has notable variation in the degree of development of the opening. Some species have openings extending anterior of the epiphyseal bar (e.g., *A. baremoze*, *A. leuciscus* (Monod, 1950, figs. 90, 92) and *A. liebrechstii* (Myers, 1929, fig. 1)), whereas others completely lack the opening (e.g., *A. grandisquamis*, Myers, 1929, fig. 2; *A. macrolepidotus*, Monod, 1950, fig. 99) and have been assigned by most recent authors (e.g., Géry and Mahnert, 1977; Paugy, 1990b) to the genus *Brycinus*. The fontanel in the Distichodontidae ranges from an extensive opening extending from the mesethmoid to the supraoccipital to a small aperture between the parietals (Vari, 1979:290). The common possession of a drastically reduced or absent frontoparietal fontanel is a homoplastic feature in characiforms. Indeed, there is notable variation in the development of the opening in closely related species (Vari and Vari, 1989, fig. 1; Vari, 1991, fig. 10).

Although I conservatively prefer not to utilize the absence of the fontanel as an additional hypothesized synapomorphy for a more-extensive assemblage including ctenoluciids and related taxa, one feature associated with the dorsally uninterrupted neurocranium in the Ctenoluciidae and Erythrinidae appears unique to those families. Most characiform taxa with the frontals in contact along their entire medial margins retain a well-developed epiphyseal bar along the ventral surfaces of the frontals. Roberts (1969:408) commented that "in a large specimen of *Hepsetus* in which the cranial fontanels are completely roofed over ... the epiphyseal bar is represented by a narrow, bony, transverse ridge on the ventral surface of the frontal bones" and that "in *Hoplias* ... the ventral intracranial surface is smooth ... in a relatively small specimen in which the fontanels have become closed."

The epiphyseal bar is a distinct ridge on the ventral surface of the frontals in juvenile and adult lebiasinids and parodontids, families characterized by the total elimination of the fontanel in adults by the expansion of the frontals and parietals. Examination of cleared and stained specimens of *Hepsetus* of a range of sizes (18.7–121 mm SL) confirms the presence of the bar, albeit less developed in the larger specimens. Very small specimens of *Hoplias* (USNM 226265, 22.8–26.5 mm SL) and *Boulengerella cuvieri* (USNM 326304, 25.5 mm SL) have a distinct epiphyseal bar, the median portions of this bar apparently are progressively reduced in erythrinids with a 36 mm SL specimen of *Hoplerythrinus* lacking the bar medially. Similar reductions of the bar occur in *Boulengerella lucius* by 99 mm SL (USNM 306202). The medial portions of the ventral surface of the frontal are smooth in adults of all erythrinid and ctenoluciid genera. Given the presence of the epiphyseal bar in outgroup taxa, its ontogenetic reduction and the resultant medially smooth ventral surface of the frontals in both the Ctenoluciidae and Erythrinidae is hypothesized to be synapomorphic for these families (SYNAPOMORPHY 19).

LATEROSENSORY CANALS IN FRONTAL AND PARIETAL

(27) In most characiforms including *Xenocharax* (Daget, 1960, fig. 7) the supraorbital portion of the laterosensory canal system in the frontal has a posterior side branch (the parietal branch of the supraorbital canal), which continues from the main canal posteriorly into the parietal and sometimes extending over the laterosensory canal in the extrascapular to the posterior border of the parietal. The posterior portion of this canal in the frontal and the entire segment in the parietal are lacking in ctenoluciids (Figure 5). Broader outgroup comparisons have demonstrated that comparable reductions of this canal segment also characterize the Lebiasinidae and Hepsetidae, but that the canals are present in the Erythrinidae. Under the overall most-parsimonious hypothesis of suprafamilial phylogenetic relationships, the canal segments were lost in the ancestor of the clade consisting of the Lebiasinidae, Hepsetidae, Erythrinidae, and Ctenoluciidae (SYNAPOMORPHY 2), and secondarily reacquired in the Erythrinidae (SYNAPOMORPHY 31).

(28) The posterior portion of the supraorbital canal, which primitively contacts the pterotic canal, also is modified in the groups of interest. In the Ctenoluciidae there is no contact between the supraorbital and the pterotic canals, and indeed there is no posterolaterally angled portion of the supraorbital canal complex that can be readily homologized with the portion of the system that primitively contacts the pterotic. Rather, there is short canal segment that extends directly laterally, which may represent a dramatically shortened and reoriented portion of that system. A comparable arrangement of these canals also occurs in the Erythrinidae (Weitzman, 1964:154), and this condition is considered to be a synapomorphy for the two families (SYNAPOMORPHY 20).

The lack of contact of the supraorbital and pterotic laterosensory canals also occurs in the Pyrrhulininae, Chi-

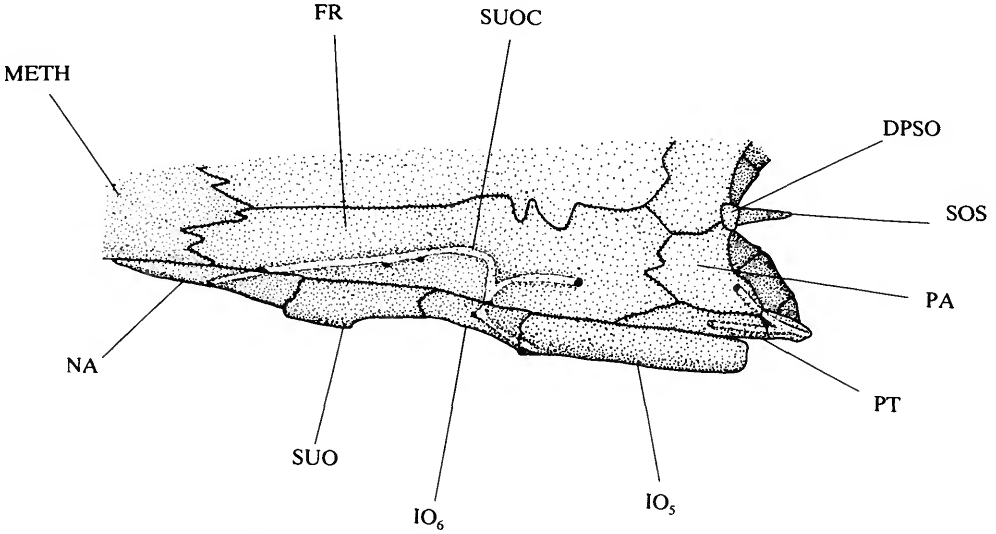

FIGURE 5.—Dorsal surface of neurocranium and associated bones, middle and posterior sections, left side of *Boulengerella lateristriga*, USNM 270331; anterior to left.

lodontidae, Distichodontidae, and Hepsetidae in outgroup characiforms. The lack of contact between the supraorbital and pterotic laterosensory canals in the Pyrrhulininae results from the lack of a canal segment in the pterotic (Weitzman, 1964:150) rather than a reduction of the canal within the frontal as in ctenoluciids and erythrinids.

Vari et al. (in press) noted that the chilodontid *Chilodus* has the posterior portion of the supraorbital canal reduced and falling short of the pterotic, but that in *Caenotropus,* the other chilodontid genus, the reduction is less pronounced. Both genera, nonetheless, retain at least a portion of the canal posterior to the point where the parietal branch exits the supraorbital, a condition different than that of erythrinids and ctenoluciids. Chilodontids also share a long series of synapomorphies with the Anostomidae, in which the canals are continuous, further supporting the hypothesis of the nonhomology of the condition in that family with the lack of contact between these canals in erythrinids and ctenoluciids.

Vari (1979:298) noted that in most distichodontids the supraorbital canal does not directly communicate with that of the pterotic, having instead the sixth infraorbital located between the canals in those two bones (see Daget, 1960, fig. 7; Vari, 1979, fig. 20), a condition different than that in erythrinids and distichodontids. Furthermore, the Citharinidae, the sister group to the Distichodontidae, have the supraorbital and pterotic canals in direct contact. *Opsariichthys,* a hypothesized generalized cypriniform, has these canals aligned, albeit with the proximate apertures somewhat separated. The citharinid condition, widespread in a number of characiform groups and approximating the condition in *Opsariichthys,* thus is hypothesized to be primitive for characiforms, with the condition in distichodontids derived, which is an additional synapomorphy for the family and a condition nonhomologous with that of ctenoluciids and erythrinids.

The final taxon discovered during this study without continuity between the supraorbital and pterotic laterosensory canals is *Hepsetus.* In contrast to erythrinids and ctenoluciids, *Hepsetus* retains a well-developed posterior portion of the supraorbital laterosensory canal posterior of the point of exit of the parietal branch of that system. In all but smaller individuals of *Hepsetus,* this branch extends posteriorly nearly to the lateral margin of the frontal medial to the anterior section of the pterotic. The pterotic and its associated canal, in turn, also are well developed anteriorly, but with the anterior portion of the canal paralleling the posterior section of the supraorbital canal in the frontal rather than being aligned with it. Thus, the lack of contact between the pterotic and frontal canals is a consequence of the lateral shift and anterior extension of the pterotic canal rather than a truncation of the supraorbital canal, as in erythrinids and ctenoluciids, and therefore a nonhomologous condition.

(29) The species of *Ctenolucius* and three *Boulengerella* species (*cuvieri, lucius, xyrekes*) have a continuous supratemporal laterosensory canal segment running along the posterodorsal margin of the parietals. A well-developed canal in that region occurs both in the proximate outgroups to the Ctenoluciidae lacking frontoparietal fontanels and in taxa with that aperture (e.g., *Brycon;* Weitzman, 1962, fig. 9). *Boulengerella maculata* and *B. lateristriga,* in contrast, have the supratemporal canal reduced to a small lateral section proximate to the anterodorsal portion of the extrascapular (Figure 5), a condition hypothesized to be derived (SYNAPOMORPHY 84).

PTEROTIC

(30) The pterotic in ctenoluciids is elongate, a shape reflecting the overall elongation of the neurocranium rather than a proportional increase in the length of the bone relative to the rest of the skull. Anteriorly the pterotic extends as a process along the lateral margin of the frontal and overlies the dilatator operculi muscle. In *Boulengerella* species this anterior process of the pterotic falls short of the modified sphenotic spine, the condition in examined characiform outgroups. *Ctenolucius* species, in contrast, have the anterior process of the pterotic extending anteriorly to contact the lateral process of the frontal, with the lateral margin of the process contacting the dorsal margin of the sphenotic spine. This contact of the pterotic in *Ctenolucius* with the proximate portions of the frontal and sphenotic results in a posterior expansion of the tubular portion of the dilatator groove formed by the sphenotic spine and lateral process of the frontal.

Hoplias has an anteriorly lengthened anterior projection of the pterotic that does not, however, contact the sphenotic spine. Furthermore, the pterotic in *Erythrinus* and *Hoplerythrinus,* the other erythrinid genera, does not extend anteriorly to the region of contact between the lateral process of the frontal and the dorsolateral process of the sphenotic spine. Thus, the conditions in *Hoplias* and *Ctenolucius* are considered to be nonhomologous. *Hepsetus* also has a somewhat elongate anterior process of the pterotic that, however, falls distinctly short of the sphenotic spine and thus is not comparable to that of *Ctenolucius.* The form of the pronounced extension of the pterotic in *Ctenolucius* evidently is unique to the genus (SYNAPOMORPHY 58).

The characiform pterotic typically includes a branch of the laterosensory canal system that extends forward to the canal system in the sixth infraorbital. The condition is found in all ctenoluciids other than *Boulengerella lateristriga* (Figure 5), in which the canal is reduced to a short segment in the posterior half of the bone (SYNAPOMORPHY 92).

SUPRAOCCIPITAL

(31) The portion of the supraoccipital anterior to the supraoccipital spine typically does not reach the body surface medially in characiforms; rather, the region is occupied by the

parietal portion of the fronto-parietal fontanel. Among those taxa in which the parietals are in contact medially, thereby eliminating the fontanel, these bones exclude the supraoccipital from contact with the surface medially, although the supraoccipital spine may be visible externally posterior to the parietal. Ctenoluciids and proximate sister groups typically lack a frontoparietal fontanel and the supraoccipital spine is covered dorsally by scales, thereby completely covering the supraoccipital in nearly all taxa (see "Squamation at the Posterodorsal Margin of the Head" below). *Boulengerella maculata* and *B. lateristriga*, in contrast, have a small medial process of the supraoccipital that forms a very small component of the dorsal surface of the neurocranium medially (Figure 5), a unique condition (SYNAPOMORPHY 85).

SUPRAPREOPERCLE

(32) Roberts (1969:421) noted that both the Hepsetidae and Erythrinidae had a distinct lamellar ossification above the opercle. He challenged the equivalence of the ossification, which he termed the supraopercle, with what had been termed the suprapreopercles in other characiforms. In those outgroups, the suprapreopercle has the form of tubular ossifications proximate to the dorsal surface of the laterosensory canal in the dorsal portion of the preopercle. Fink and Fink (1981, fig. 10) identified the series of independent ossifications carrying the laterosensory canal system between the preopercle and neurocranium as all suprapreopercles. At least in *Hepsetus* the lamellar ossification dorsal to the opercle carries a segment of the laterosensory canal system (Roberts, 1969, fig. 1), and the ossification in *Hoplias*, although lacking such a canal segment, occupies the same position (Roberts, 1969, fig. 3). These bones in the Hepsetidae and Erythrinidae thus are identified herein as suprapreopercles, recognizing that a definitive statement on their identity requires further study.

A lamellar suprapreopercle occurs not only in hepsetids and erythrinids but also in the anostomid genus *Abramites*. Given the numerous synapomorphies for the Anostomidae and the series of synapomorphies common to that family and the Chilodontidae (Vari, 1983), the ossification in *Abramites* is most parsimoniously hypothesized to have been acquired independently of that in the Hepsetidae and Erythrinidae. The possession of a lamellar supraperopercle in the two latter families is hypothesized to be derived given the lack of such an ossification in most characiforms. Under the overall most-parsimonious phylogeny, the distribution of this form of suprapreopercle can represent equally parsimoniously either independent gains in the Hepsetidae (B_3) and Erythrinidae (D_3), or the gain of such a form of the ossification in the ancestor of those two families and the Ctenoluciidae (A_3) with their secondary loss in the latter family (E_4).

JAWS AND ASSOCIATED SOFT TISSUES

The remarkably elongate upper and lower jaws of ctenoluciids readily distinguish them from the vast majority of characiforms, being approximated only in some members of the African family Distichodontidae. The complex morphological restructuring associated with this elongation involve not only the changes in the jaws discussed herein, but also modifications in other body systems that are discussed under the appropriate functional complex.

(33) UPPER JAW.—The pronounced development of the upper jaw largely reflects the lengthening of the premaxilla (Figure 6A), with a comparable elongation encountered elsewhere among characiforms only in the African distichodontids *Ichthyborus monodi* (see Thys van den Audenaerde, 1975, figs. 1–2) and *Belonophago tinanti* (see Poll, 1957, fig. 142). Those species are united by a series of synapomorphies to distichodontid and citharinid taxa with moderately elongate jaws or jaws whose lengths do not differ from the generalized characiform condition (Vari, 1979:324–339). The elongate premaxilla of ctenoluciids thus are hypothesized to be synapomorphic for the members of the family (SYNAPOMORPHY 41) albeit homoplastically present within the Distichodontidae. It is also noteworthy that the elongate forms of upper jaws of ctenoluciids and the distichodontid genera with moderately to notably elongate jaws (*Belonophago, Eugnatichthys, Hemistichodus, Ichthyborus, Microstomatichthyoborus, Mesoborus, Paraphago*, and *Phago*) differ in the association of the premaxilla with the neurocranium. The eight cited distichodontid genera have pronounced vertical movement of the premaxilla with respect to the mesethmoid, which contrasts with the inflexible attachment of the upper jaw to the mesethmoid in ctenoluciids. Although Regan (1911:20), followed by Gregory and Conrad (1938:340), commented that the upper jaw is "somewhat moveable" in ctenoluciids, the premaxilla in the family is actually tightly joined to the anterior portions of the neurocranium, with minimal movement apparent even when the jaw is forced fully open in cleared and stained specimens and no such movement when the jaws are opened in preserved specimens.

Several features of the premaxilla, in addition to its marked elongation, are of phylogenetic interest. The modifications of the upper jaw and associated restructuring of the ethmoid region of the neurocranium result in a dramatically altered association of the upper jaw with the neurocranium. The lateral ethmoid wing of the mesethmoid (sensu Weitzman, 1962:19) of many characiforms serves as an anterior place of attachment for ligamentous tissues joining that process to the overlying posteromedial ramus of the premaxilla. No such pronounced degree of overlap of a process on the dentary onto the lateral ethmoid wing of the mesethmoid occurs in ctenoluciids, which instead have a relatively elongate, narrow shelf on the lateral margin of the mesethmoid that underlies the medial portion of the overlying premaxilla. It is difficult to determine whether this narrow shelf along the margin of the mesethmoid corresponds to the lateral ethmoid wing of many other characiforms. If it does, the pronounced horizontal elongation of the process would be another synapomorphy for the

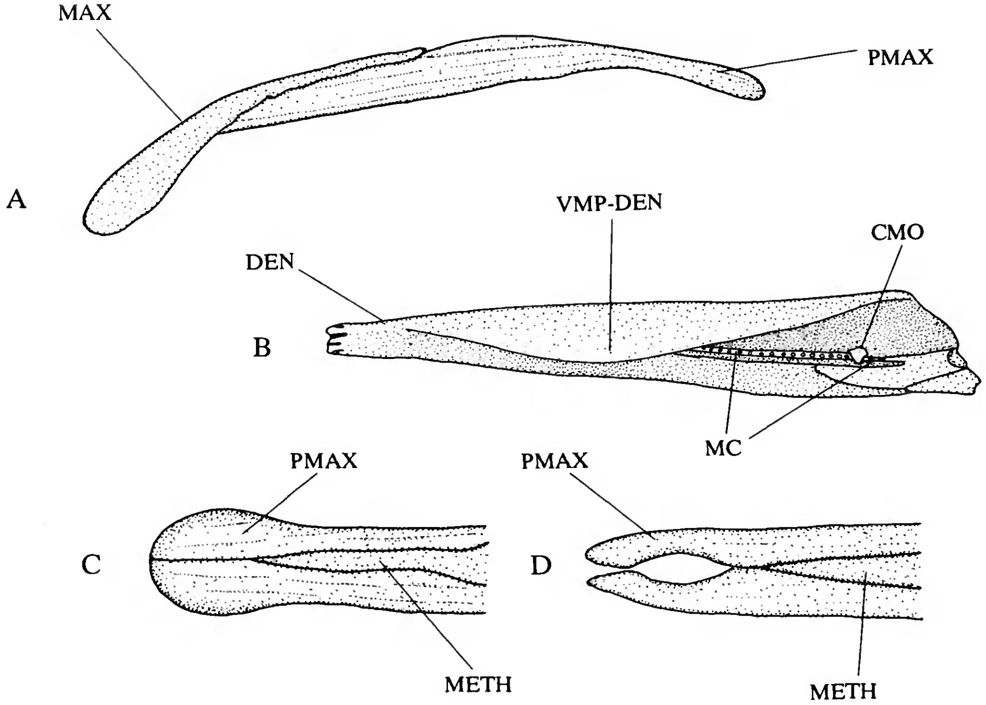

FIGURE 6.—(A) upper jaw of *Ctenolucius beani*, USNM 293169, lateral view, anterior to right, numerous teeth on premaxillary and maxillary not shown; (B) lower jaw of *Ctenolucius beani*, USNM 293169, medial view, anterior to left, numerous teeth on dentary not shown, small circles indicate cartilage; (C) anterior portions of premaxillae and mesethmoid of *Ctenolucius beani*, USNM 293169, dorsal view, anterior to left, showing spatulate anterior portion of snout; and (D) anterior portions of premaxillae and mesethmoid of *Boulengerella maculata* USNM 319781, dorsal view, anterior to left, showing median gap between premaxillae anterior to tip of mesethmoid.

Ctenoluciidae, but this is not utilized as such herein in light of the uncertainty as to its homology.

(34) In *Ctenolucius* species, the anterior portion of the premaxilla is well developed, with the margin bowed laterally (Figure 6C). In dorsal view this gives the anterior portion of the snout a distinctly spatulate appearance unique to these species among characiforms (SYNAPOMORPHY 59).

(35) *Boulengerella* species have the snout tapering laterally, with the ventromedial margins of the premaxillae in contact or nearly in contact proximate to the anterior tip of the mesethmoid. Anterior to that area, the medial margins of the premaxillae diverge laterally before coming again into contact anteriorly. As a consequence, there is a distinct medial gap between the premaxillae slightly anterior of the tip of the mesethmoid (Figure 6D). Such a gap has not been encountered elsewhere among characiforms and is hypothesized to be derived (SYNAPOMORPHY 72).

(36) The pronounced elongation of the upper jaw in all ctenoluciids has an unusual association of the premaxilla and maxilla and of those elements to the ethmoid region. In the typical characiform condition the maxilla is a proportionally moderately to markedly elongate element movably articulated with the posterodorsal portion of the premaxilla and terminating anterodorsally in a medial process that attaches via a ligament to the palatine or to cartilage bodies associated with that bone. The ligamentum primordiale, in turn, attaches to the medial surface of the maxilla, most typically at the basal portion of the medially directed anterodorsal process of that ossification.

The maxilla of ctenoluciids, in contrast, lacks a distinct, medially directed, anterodorsal process, although *Ctenolucius* does have a small process on the medial surface of the maxilla proximate to the enlarged palatine, which may represent a greatly reduced anteromedial process of the maxilla. The anterior portion of the maxilla of ctenoluciids is, rather, a lengthy tapering process applied tightly to the posterodorsal surface of the premaxilla (Figure 6A) and extending forward of the anterior limit of the enlarged palatine. These modifications of the maxilla in association with the tight joint between the main portion of the maxilla and the posterior margin of the premaxilla (Figure 6A) eliminate movement between the two bones of the upper jaw. This arrangement, previously noted by Regan (1911:20) and Gregory and Conrad (1938:340), undoubtedly is derived, given that mobility between the upper jaw bones is nearly universal among characiforms. The only other characiforms sharing a comparable association of the premaxilla and maxilla and the lack of the anterodorsal process of the maxilla are a subunit of the Distichodontidae (*Belonophago, Eugnatichthys, Hemistichodus* (Daget, 1968, fig. 2), *Ichthyborus* (Vari, 1979, fig. 4), *Microstomatichthyoborus, Mesoborus, Paraphago,* and *Phago*), which have the reduced, toothless maxilla immovably attached, but not fused, to the rear of the premaxilla. Although the contact between the upper-jaw bones in these distichodontids are comparable to those of ctenoluciids, the African genera are hypothesized, on the basis of a number of derived features, to be most closely related to other distichodontids with mobile premaxillary-maxillary joints (Vari, 1979) and maxilla morphology comparable to that typical for characiforms (e.g., *Paradistichodus,* see Daget, 1958, fig. 9; *Nannocharax,* see Daget, 1961, fig. 7). As a consequence, the derived morphology of the maxilla and its association with the premaxilla in the Ctenoluciidae is hypothesized to be nonhomologous with that in the cited subunit of the Distichodontidae but, rather, to be synapomorphic for ctenoluciids (SYNAPOMORPHY 42).

(37) *Ctenolucius* species have smooth posterior and posteroventral margins to the maxilla, which terminates posteriorly in an obtuse point. The generally smooth profile of that portion of the maxilla is typical of characiforms and thus is judged to be primitive. The species of *Boulengerella,* in contrast, have irregular posterior and posteroventral margins of the maxilla, typically with a distinct notch in the region where the margin of the bone overlies the enlarged ligamentum primordiale (see below), a uniquely derived condition (SYNAPOMORPHY 73).

(38) Associated with the lack of a discrete anterodorsal process of the maxilla is a restructuring of the ligamentum primordiale and a shift of its attachment to the upper jaw. In ctenoluciids the ligamentum primordiale is considerably thicker than in other characiforms and arises from the medial surface of the central portion of the maxilla rather than the anterodorsal portion of the bone as in other characiforms. This form of the ligament and area of attachment thus is hypothesized to be derived within characiforms (SYNAPOMORPHY 43).

(39) The area of attachment of the ligamentum primordiale on the maxilla is relatively flat in *Ctenolucius,* a morphology comparable to that in most characiforms. *Boulengerella* species, in contrast, have a distinct process on the medial surface of the maxilla that serves, in part, as an area of attachment for the ligamentum primordiale. Such an elaboration of the maxilla is hypothesized to be derived (SYNAPOMORPHY 74).

(40) One of the distinctive features *Boulengerella* species, particularly in intermediate-size specimens, is the presence of an elongate, somewhat stiff, fleshy process at the tip of the snout (e.g., *B. lateristriga,* Figure 32). Although comparable-size specimens of *Ctenolucius* have a slightly anteriorly elongated fleshy pad at the tip of the snout, the relative development and form of the process in that genus is not as well developed as the attenuate process of intermediate-size individuals of all *Boulengerella* species. No other characiform is known to have such a well-developed snout process, which is hypothesized to be synapomorphic for the species of the genus (SYNAPOMORPHY 75).

Many juvenile specimens of *Boulengerella xyrekes* from across the geographic range of that species have the fleshy anterior portion of the snout expanded into a variably developed, dorsoventrally flattened pad. Although not universally expressed in the species, this modification does not occur elsewhere in the family, or indeed in any other examined characiform, and thus is hypothesized to be derived (SYNAPOMORPHY 107).

(41) LOWER JAW.—Associated with the elongation of the upper jaw in ctenoluciids is a pronounced development of the lower jaw. This results primarily from an elongation of the dentary (Figure 6B), with the remaining bones of the lower jaw (angulo-articular and retroarticular) not notably modified. As in the case of the premaxilla, the degree of development of the dentary is approximated among characiforms only in the African family Distichodontidae. The two distichodontids with elongate dentaries (*Ichthyborus monodi,* see Thys van den Audenaerde, 1975, figs. 1, 2) and *Belonophago tinanti* (see Poll, 1957, fig. 142) are, however, most closely related to different lineages in the Distichodontidae, each otherwise consisting of species without remarkably lengthened dentaries. The elongate lower jaws of those distichodontid genera consequently are considered to be homoplastic relative to the apparently comparable condition in ctenoluciids. Thus, the elongate dentary of the Ctenoluciidae is another synapomorphy for the family (SYNAPOMORPHY 44).

(42) In most characiforms the median mandibular fossa (sensu Weitzman, 1962:33) is broadly open medially and largely occupied by the A_w portion of the adductor mandibulae muscle. The dorsal portion of the dentary, particularly in groups with well-developed dentition (e.g., cynodontins), is sometimes relatively thick in cross section both to anchor the enlarged teeth and in order to accommodate replacement dentition, but that thickened region does not enclose the mandibular fossa medially. *Boulengerella* and *Ctenolucius,* in contrast, have a broad plate extending from the ventral margin of the dentigerous surface of the dentary over the medial surface of the horizontally elongate A_w portion of the adductor mandibulae (Figure 6B). This horizontally elongate, plate-like process begins at a point approximately one-fifth of the length of the dentary from the anterior tip of the bone, gradually expands vertically as it continues posteriorly until to a point slightly beyond the mid-length of the bone, and then gradually tapers posteriorly to terminate at the posterodorsal corner of the

bone. Given the unique nature of the partial enclosure of the median mandibular fossa and the A_w portion of the adductor mandibulae among characiforms, the condition in ctenoluciids is hypothesized to be a synapomorphy for the family (SYNAPOMORPHY 45).

(43) Characiforms typically have an uninterrupted Meckel's cartilage extending from a process on the medial surface of the angulo-articular anteriorly along the medial surface of that ossification and the dentary. The coronomeckelian bone, the area of attachment for a portion of the adductor mandibulae, in that arrangement is situated somewhat dorsal of the posterior portion of Meckel's cartilage or contacts its dorsal surface. *Boulengerella* species retain this generalized arrangement whereas both *Ctenolucius beani* and *C. hujeta* have the coronomeckelian bone shifted ventrally to lie within the cartilage, dividing it into a short posterior segment and a lengthy anterior portion (Figure 6B). Such a shift of the ossification has been found only in the Erythrinidae among the examined characiform outgroups. Under the most-parsimonious hypothesis of relationships of ctenoluciids and proximate groups, there are two possible explanations for the phylogenetic distribution of this feature. The shift of the coronomeckelian ossifications into Meckel's cartilage may have arisen in the ancestor of the Erythrinidae and Ctenoluciidae (C_1) and secondarily shifted dorsally to its primitive position in the ancestor of *Boulengerella* (G_1). Alternatively, the ossification may have independently shifted ventrally in the ancestors of the Erythrinidae (D_4) and *Ctenolucius* (F_2).

(44) The ventral portion of the ligamentum primordiale in characiforms typically attaches to the sheet of fascia associated with the anterior portion of the adductor mandibulae muscle and the rear of the lower jaw. In ctenoluciids, the thick ligamentum primordiale instead attaches onto a distinct lateral process and the adjoining region of the posteroventral portion of the angulo-articular. The correlated modification of the area of attachment of the ligamentum primordiale and restructuring of the primitively nonelaborated lateral surface of angulo-articular are considered derived (SYNAPOMORPHY 46).

(45) *Ctenolucius* species have a horizontal, dorsoventrally flattened flap of tissue on the lateral surface of the dentary slightly ventral of the line of emergence of the dentition from the jaw (Figure 7). This fleshy flap extends approximately from the vertical through the first dentary tooth to the area where the maxilla overlaps the dentary laterally. Anteriorly the fleshy flap forms a distinct, dorsoventrally flattened, acutely triangular lateral appendage (Figure 7) that is proportionally larger in specimens under 30 mm SL. The portion of the horizontal flap posterior to this highly developed lateral process is narrower and gradually decreases in width posteriorly. Roberts (1969:216) noted comparable flaps, albeit of somewhat different shape, in the Hepsetidae. The function of these flaps in *Ctenolucius* and *Hepsetus* is unknown, although given the habitats from which *Ctenolucius* has been reported (flowing streams and other apparently well-oxygenated waters) it seems unlikely that the flaps are an adaptation to low dissolved-oxygen levels as are the lip modifications in various characids and gasteropelecids (Braum and Junk, 1982; Winemiller, 1989; Casciotta, 1993). Whether the flaps in *Hepsetus*, which commonly lives in swamps (Budgett, 1901:130; Svensson, 1933:48–50), are modifications associated with low dissolved-oxygen levels is unknown. Nonetheless, the form of the flaps in *Ctenolucius* is unique to that genus and consequently is hypothesized to be synapomorphic for its species (SYNAPOMORPHY 60), with the distinct form of flaps in *Hepsetus* most parsimoniously considered a synapomorphy for that genus (SYNAPOMORPHY 13).

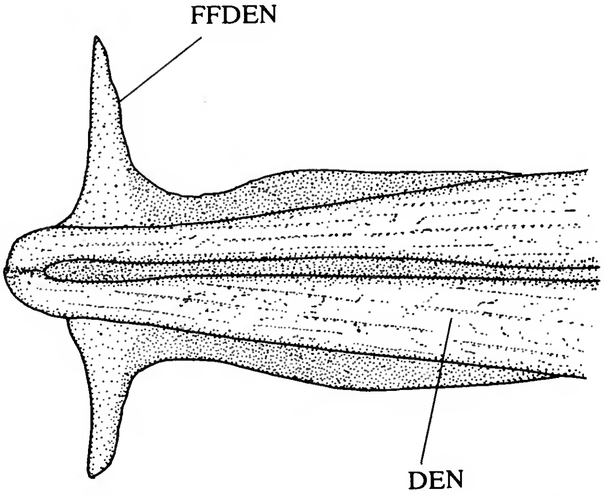

FIGURE 7.—Anterior portion of lower jaw and lateral fleshy flaps of *Ctenolucius beani*, USNM 293169; ventral view, anterior to left.

DENTITION

(46) Fink and Fink (1981:306) noted that "the teeth in *Hepsetus*, erythrinids and ctenoluciids are large and compressed distally rather than small and conical as is common in gymnotoids, siluroids and in teleosts generally" and proposed that the tooth form in these groups was a synapomorphy for the assemblage, a hypothesis in keeping with the results of this study (SYNAPOMORPHY 11).

(47) Roberts (1969:431) pointed out that "in *Boulengerella* all of the teeth and in *Ctenolucius* most of the teeth have recurved crowns ... unlike the teeth in any other characoids" (see also Roberts, 1967, fig. 1). Outgroup comparisons have shown that recurved tooth crowns are not unique to the Ctenoluciidae, as they also occur on at least some teeth in various other characiforms (e.g., young *Salminus*). Nonetheless, such teeth are universal or nearly so in the jaws of ctenoluciids, a condition not encountered elsewhere among

characiforms. The presence of recurved crowns on all or nearly all of the numerous teeth in ctenoluciids is considered to be a synapomorphy for the family (SYNAPOMORPHY 47).

(48) Premaxillary dentition in characiforms demonstrates a broad range of tooth types and arrangements. As a general rule, however, there is a graded series of teeth in the jaw, with the largest teeth at the symphysis and a progressive, albeit sometimes abrupt, decrease in tooth size posteriorly. Various predatory characiforms (e.g., *Acestrorhynchus*, see Menezes 1969, fig. 61; cynodontins, see Howes, 1976, figs. 1, 5) have a pattern of variably developed canines along the jaws. The premaxillary dentition in *Ctenolucius* has larger teeth anteriorly, followed by the smallest teeth in the series at the posterior of the spatulate portion of the jaw, with the remaining extensive series of teeth larger and all of approximately the same size but not as large as those in the anterior of the jaw. This pattern of a series of small jaw teeth bracketed by larger teeth both anteriorly and posteriorly has not been encountered in other characiforms and thus is hypothesized to be derived (SYNAPOMORPHY 61).

(49) The teeth on the anterior portion of each premaxilla in *Boulengerella* do not arch medially toward the symphysis as in most characiforms, but, rather, they approximate each other anteriorly, with a resultant acute angle at the symphysis between the tooth row of each premaxilla. This pattern has not been encountered elsewhere in the order and is hypothesized to be a synapomorphy for the genus (SYNAPOMORPHY 76).

PALATINE

The palatine of ctenoluciids is a complex bone with a series of articulations and attachments to the neurocranium. Posterodorsally the ctenoluciid palatine has a synchondral articulation with an extensive articular facet on the ventral surface of the lateral wing of the relatively reduced lateral ethmoid. As noted by Vari (1983:26), the presence of an articular surface between the lateral ethmoid and the cartilage along the posterior margin of the palatine also occurs among characiforms in the Curimatidae (Vari, 1983, fig. 25), *Hepsetus, Salminus, Acestrorhynchus, Rhaphiodon, Hydrolycus,* and *Crenuchus*. Outgroup comparisons in this study also have revealed such articulations in the Erythrinidae (*Hoplias, Hoplerythrinus,* and *Erythrinus*) and most examined lebiasinids (*Lebiasina, Piabucina,* and *Pyrrhulina;* but not *Nannostomus beckfordi*).

Given the series of derived features uniting the Curimatidae to the Prochilodontidae, Anostomidae, and Chilodontidae, the latter three of which lack such palatine-lateral ethmoid articulations, it is most parsimonious to hypothesize that curimatids and ctenoluciids independently acquired this contact. Similarly, the cynodontines *Rhaphiodon* and *Hydrolycus* are apparently members of the Characinae (Howes, 1976), again a group otherwise lacking this contact. The situation with respect to the other taxa is equivocal, with *Acestrorhynchus*, the Erythrinidae, Hepsetidae, and Lebiasinidae sharing other derived features at various levels of inclusiveness with the Ctenoluciidae. The utilization of the common possession of an articulation between the lateral ethmoid and the palatine as an additional synapomorphy for the proposed clade consisting of those four families is complicated by the lack of that articulation in at least some lebiasinids and the absence of a phylogenetic hypothesis of relationships within that family. As a consequence, the palatine-lateral ethmoid articulation conservatively is not proposed as an additional synapomorphy for the clade at this time.

(50) The variation in the degree of ossification of the posterior portion of the palatine adjoining the lateral ethmoid in ctenoluciids is phylogenetically informative. Those characiforms with palatine-lateral ethmoid articulations typically have a broad cartilaginous pad at the rear of the palatine, a condition approximated in *Boulengerella* species. *Ctenolucius* species instead have a heavily ossified lateral process posteriorly that occupies the primitively cartilaginous region in other groups. As a consequence, the cartilage on the posterodorsal portion of the palatine is limited to a small, transversely elongate cartilage cap that articulates with a comparable cartilaginous region on the ventral margin of the lateral process of the lateral ethmoid. The development of this pronounced ossified process of the palatine and the restructuring of the associated cartilage is hypothesized to be derived and is synapomorphic for the species of *Ctenolucius* (SYNAPOMORPHY 62).

(51) The anterior portion of the palatine has a cartilaginous articular surface that abuts a matching articular facet of the vomer. Contact between these elements is relatively common among characiforms and therefore is not diagnostic for the Ctenoluciidae. What is distinctive is the manner in which the proximity of the palatine to the neurocranium is maintained in the family. In all ctenoluciids a thick ligament extends from the anteroventral portion of the palatine, ventral of the anterior articular facet on the bone (Figure 8), to the mesethmoid some distance anterior of the articular facet on the vomer. Thickening of the broad connective-tissue sheet that joins the suspensorium to the neurocranium also occurs in various groups of characiforms. Such suspensory ligaments in outgroups involve, however, more posterior portions of the palatine arch and/or neurocranium (ectopteryoid and lateral ethmoid in the Chilodontidae and Anostomidae (see Vari, 1983, fig. 26 for condition in *Anostomus*); mesopterygoid and vomer in the Curimatidae (Vari, 1989b:45) and Lebiasinidae). Ligamentous attachments of the anterior portion of the palatine arch and the neurocranium also occur in *Hepsetus, Acestrorhynchus, Oligosarcus,* and the Lebiasinidae. These have the form of a discrete ligament in *Hepsetus* and more diffuse bands in *Acestrorhynchus, Oligosarcus,* and the Lebiasinidae. None of these outgroups has a connective-tissue band as thick or as long as that in ctenoluciids. More significantly, the connective tissue band in the outgroups attaches onto the anteriorly lengthened ectopterygoid rather than onto the palatine as in the Ctenoluciidae. The ligament in ctenoluciids, unique both in terms of its

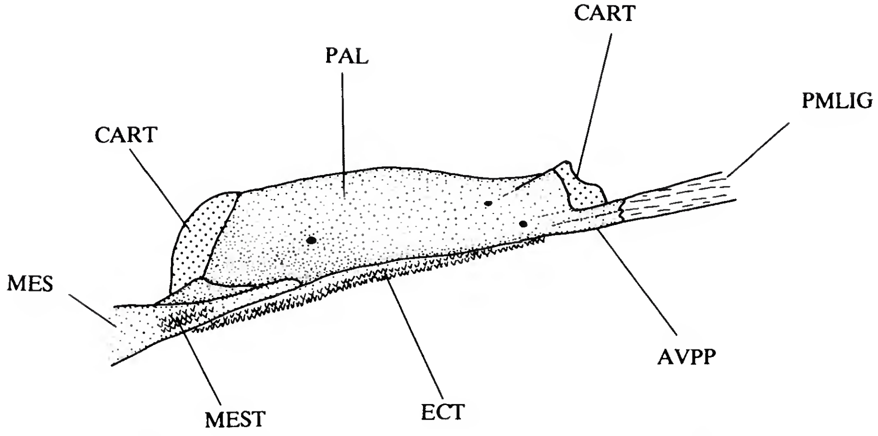

FIGURE 8.—Left palatine and anterior portions of suspensorium showing distribution of dentition and posterior portion of palatine-mesethmoid ligament in *Boulengerella maculata*, USNM 319781; medial view, anterior to right.

degree of development and area of attachment on the suspensorium, consequently is considered to be derived (SYNAPOMORPHY 48).

(52) The region of the palatine onto which the ligament attaches demonstrates two conditions in the Ctenoluciidae. This section of the bone does not extend anteriorly beyond the main body of the palatine in *Ctenolucius* species or *Boulengerella lucius*, but it has a distinct anterior extension ventrally in other *Boulengerella* species (*cuvieri, lateristriga, maculata,* and *xyrekes*) (Figure 8). Such an anterior extension of the palatine has not been encountered in other characiforms, and its possession is hypothesized to be derived. The distribution of the anterior process within *Boulengerella* does not, however, match the scheme of relationships derived from all examined characters, a situation further complicated by the unresolved trichotomy between *Boulengerella cuvieri, B. lucius,* and *B. xyrekes*. Two alternative, equally parsimonious, hypothesis are possible. The first is the acquisition of the process in the ancestor of the *Boulengerella* clade (G_2), with its autapomorphic secondary loss in *B. lucius* (J_1). Alternatively, the process may have arisen independently in the clade formed by *B. lateristriga* and *B. maculata* (H_2) and a lineage consisting of *B. xyrekes* and *B. cuvieri* (K_1). The latter sister-species relationship, however, is not supported by any unequivocal synapomorphies within what is otherwise a trichotomy between those two species and *B. lucius*.

ECTOPTERYGOID TEETH

(53) Both *Ctenolucius* and *Boulengerella* have longitudinally elongate ectopterygoids with large numbers of teeth along their ventral surfaces (Figure 8). Ectopterygoid teeth occur in diverse characiforms including the generalized genus *Xenocharax*, various lebiasinids, all erythrinid genera (Weitzman, 1964:144–145), *Oligosarcus* (Menezes, 1969:12, 15; see also Menezes and Géry (1983:588) concerning status of *Paroligosarcus*), *Acestrorhynchus* (Menezes, 1969:35), and *Serrasalmus* (Roberts, 1969:418). Fink and Fink (1981:316) noted that the tooth-bearing element termed the accessory ectopterygoid in *Hepsetus* by Roberts (1969, figs. 16, 29; see also discussion on p. 418 of that paper) was fused to the premaxilla in the specimen they examined, contrary to Roberts' observations that it was autogenous in his material. All examined *Hepsetus* specimens (18.7–121 mm SL) have the element identified as a tooth plate by Roberts (1969) and Fink and Fink (1981) solidly joined to the posteromedial margin of the main body of the premaxilla. This posterior tooth-bearing extension of the premaxilla lacks a separate tooth plate, even in a 18.7 mm SL specimen, and becomes progressively relatively longer and larger ontogenetically. Such a posterior process of the premaxilla is unique to the genus (SYNAPOMORPHY 14).

Ectopterygoid teeth are not proposed as a synapomorphy for the Ctenoluciidae, given their occurrence in other characiforms, including some proximate outgroups. The differences in ectopterygoid teeth in *Ctenolucius* and *Boulengerella* are, however, noteworthy. The ectopterygoid teeth of *Ctenolucius* are in two or three irregular rows, with the individual teeth approximately one-half the size of the teeth of the jaws. *Boulengerella*, in contrast, has a broad band of very small teeth covering much of the ventral surface of the ectopterygoid. Ectopterygoid teeth, when present in nonctenoluciid characiforms, are typically of moderate to large size; therefore, the unusual, very small ectopterygoid dentition of *Boulengerella* is hypothesized to be derived (SYNAPOMORPHY 77).

Mesopterygoid Teeth

(54) Mesopterygoid teeth apparently are rare in characiforms, being found in *Hoplerythrinus unitaeniatus* (Weitzman, 1964:145) and various *Acestrorhynchus* species, some of which have a broad patch of minute teeth and others having just a scattering of very small teeth. Among ctenoluciids, mesopterygoid teeth are limited to *Boulengerella maculata* and *B. lateristriga,* which have a small patch of very small teeth on the attenuate anterior portion of the mesopterygoid proximate to the medial margin of the posterior portion of the ectopterygoid (Figure 8). In light of the rarity of such dentition in characiforms, the presence of these teeth is considered to be derived (SYNAPOMORPHY 86).

Metapterygoid-Quadrate Fenestra

(55) The metapterygoid and quadrate in most characiforms jointly delimit a relatively large, rotund, or horizontally oblong opening, the metapterygoid-quadrate fenestra. This aperture, present in the Hepsetidae, Erythrinidae, and Ctenoluciidae, is absent in the Lebiasinidae (Weitzman, 1964:148), various distichodontids, and the curimatid genus *Curimatopsis.* As discussed by Vari (1989b:46–47), the distichodontids and curimatids lacking the aperture are most closely related to taxa with that opening. Thus, the lack of the fenestra in lebiasinids is hypothesized to be a synapomorphy for the family (SYNAPOMORPHY 6).

Basihyal

(56) The basihyal typically terminates anteriorly in a cartilage that may or may not be overlain by a basihyal tooth plate (e.g., curimatids, see Vari, 1989b, fig. 23). Such a condition is common to all examined characiforms with the exception of the Erythrinidae. In that family there are two distinct, somewhat horizontally elongate cartilages at the anterior margin of the basihyal, a condition evidently unique to the family (SYNAPOMORPHY 32).

Anterior and Posterior Ceratohyals

(57) The relationship of the anterior and posterior ceratohyals in ctenoluciids differs from that in most characiforms. The most common condition of those elements in characiforms, including *Xenocharax,* is for the two bones to articulate along a vertically elongate synchondral joint without interdigitating processes between the ceratohyals (see condition in *Brycon;* Weitzman, 1962, fig. 11c). Among New World characiforms, the anterior ceratohyal has a strong posteriorly directed process laterally that extends over the anterior portion of the posterior ceratohyal in all ctenoluciids (Figure 9A), erythrinids, *Aces-*

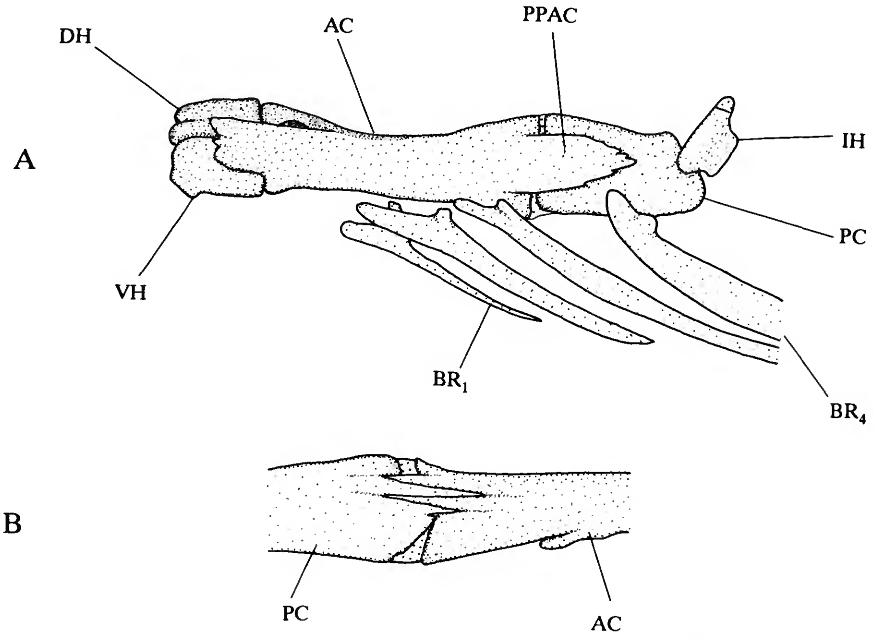

FIGURE 9.—*Boulengerella maculata,* USNM 319781: (A) lateral view of hyoid arch and branchiostegal rays (last two only basally), anterior to left; and (B) medial view of posterior portion of anterior ceratohyal and anterior portion of posterior ceratohyal, anterior to right.

trorhynchus, Oligosarcus, and within the Lebiasininae (but not Pyrrhulininae, the other lebiasinid subfamily). Among Old World characiforms such interdigitations are lacking in *Hepsetus,* the African Characidae (*Alestes, Hydrocynus* (see Brewster, 1986, fig. 12), *Phenacogrammus, Lepidarchus*), citharinids, and representatives of the more basal distichodontid clades (*Congocharax olbrechtsi, Nannocharax intermedius, Paradistichodus dimidiatus*). *Eugnatichthys, Hemistichodus,* and *Mesoborus,* all members of a distichodontid lineage with a series of pronounced jaw modifications, have a posterior process of the anterior ceratohyal that sutures laterally with the posterior ceratohyal.

Given the closer phylogenetic relationships of *Eugnatichthys, Hemistichodus,* and *Mesoborus* with numerous genera lacking such sutures (Vari, 1979), the condition in these three taxa is most parsimoniously hypothesized to have been acquired independently of that in various Neotropical characiforms. As noted in the introductory comments, the relationships of *Oligosarcus* apparently lie with various tetragonopterin characids. The phylogenetic placement of *Acestrorhynchus* has not been critically examined, but the data in this study does not support an hypothesis of a close relationship of the genus with either of the clades having such interdigitations (Lebiasininae and Erythrinidae plus Ctenoluciidae). The occurrence of distinct interdigitations between the lateral surfaces of the anterior and posterior ceratohyals is, within the overall most-parsimonious phylogeny, hypothesized to be a synapomorphy for the Erythrinidae and Ctenoluciidae (SYNAPOMORPHY 21) and independently acquired in the subfamily Lebiasininae (SYNAPOMORPHY 9).

(58) Among the four families of primary interest in this study, only two, the Erythrinidae and Ctenoluciidae (Figure 9B), have sutures joining the medial surfaces of the anterior and posterior ceratohyals, a derived condition given the absence of interdigitations on either face of the ceratohyals in outgroups (see above). Such interdigitations are absent in *Acestrorhynchus* (see Roberts, 1969, fig. 37) and *Oligosarcus,* and although these taxa are outside the four families of primary interest, nonetheless they have the lateral suturing of the anterior and posterior ceratohyals. The possession of such interdigitations on the medial surface of the anterior and posterior ceratohyals consequently is considered a shared derived feature for the Erythrinidae and Ctenoluciidae (SYNAPOMORPHY 22).

The characid genus *Salminus* has a different form of suture between the anterior and posterior ceratohyals consisting of a much less developed posterior process of the anterior ceratohyal without anterior extensions of the posterior ceratohyal (see Roberts, 1969, fig. 36). Given these differences, the sutures of *Salminus* do not appear to be homologous with the interdigitating sutures of erythrinids and ctenoluciids. Furthermore, no other characters indicate a close phylogenetic relationship of *Salminus* with those families.

The interdigitations on the medial surfaces of the anterior and posterior ceratohyals are particularly well developed and complex in the Ctenoluciidae and *Hoplias,* one of the three erythrinid genera. The highly developed anterior and posterior ceratohyal interdigitations of *Hoplias* on the one hand and the Ctenoluciidae (SYNAPOMORPHY 49) on the other are hypothesized to be independent acquisitions within the overall most-parsimonious phylogeny.

BRANCHIOSTEGAL RAYS

(59) The branchiostegal rays in *Boulengerella* have distinct anterior projections anterior to where the individual rays articulate with the hyoid arch (Figure 9A). These projections are particularly attenuate and proportionally elongate in *B. lateristriga.* The presence of such pronounced anterior projections contrasts with the lack of such processes or the slightly rounded anterior margins to the branchiostegals in other characiforms. These projections thus are hypothesized to be synapomorphic for *Boulengerella* species (SYNAPOMORPHY 78), with the particularly attenuate processes in *B. lateristriga* autapomorphic for that species (SYNAPOMORPHY 93).

(60) The distribution of the four branchiostegal rays along the anterior and posterior ceratohyals varies in the Ctenoluciidae. *Boulengerella* has a single ray on the posterior and three rays on the anterior ceratohyal (Figure 9A), whereas *Ctenolucius* has two rays on the anterior and two on the posterior ceratohyal. The majority of characiforms have only a single ray on the posterior ceratohyal, even in many of the taxa with five branchiostegal rays (e.g., *Hoplias, Hoplerythrinus, Erythrinus,* and *Crenuchus spilurus*). Two branchiostegal rays on the posterior ceratohyal is also the condition found in *Acestrorhynchus* (total of 4 rays) and the three cynodontin genera (*Rhaphiodon, Cynodon,* and *Hydrolycus,* all with a total of 5 branchiostegal rays). Given the lack of a second ray on the posterior ceratohyal in taxa hypothesized as closely related to cynodontins by Howes (1976), the occurrence of two rays on that element is hypothesized to have occurred independently in cynodontins and ctenoluciids. In light of the lack of a second ray in the species of *Boulengerella* and in proximate outgroups to the Ctenoluciidae, the presence of two rays on the posterior ceratohyal in *Ctenolucius* is most parsimoniously hypothesized to be a synapomorphy (SYNAPOMORPHY 63) homoplastically present among outgroups in *Acestrorhynchus* and the clade consisting of *Rhaphiodon, Cynodon,* and *Hydrolycus.*

(61) Erythrinids have five branchiostegal rays (Weitzman, 1964:152). Four rays are common to most characiforms (see Roberts, 1969:422), albeit with some variation in number of rays in lineages typically having four rays (e.g., in the Anostominae, see Winterbottom, 1980:39). Among proximate outgroups to erythrinids, four rays are found in ctenoluciids, hepsetids, and lebiasinins (Weitzman, 1964:149), with three rays present in pyrrhulinins (Weitzman, 1964:149). The higher number of rays in the Erythrinidae was found only in *Crenuchus, Rhaphiodon, Cynodon,* and *Hydrolycus* among examined characiform outgroups. Cynodotins evidently are

most closely related to taxa with four rays (Howes, 1976), and, although the phylogenetic position of *Crenuchus* has not been critically examined, it does not possess the series of higher-level synapomorphies common to erythrinids and proximate outgroups. The higher number of rays in those outgroups apparently is acquired independently from that in erythrinids, and the five rays of the Erythrinidae is hypothesized to be synapomorphic for its members (SYNAPOMORPHY 29).

INTERHYAL

(62) The relatively cylindrical or slightly laterally flattened interhyal typical of characiforms occurs in *Ctenolucius*. *Boulengerella* species have a transversely flattened interhyal with a distinct plate-like process posteriorly (Figure 9A). This derived flattened condition (SYNAPOMORPHY 79) is particularly pronounced in *B. lateristriga* and *B. maculata* in which the posterior plate-like process of the interhyal is greatly developed, which evidently is a further derived condition (SYNAPOMORPHY 87).

GILL-RAKERS

(63) Gill-rakers usually extend along both the leading and trailing margins of the ceratobranchials in a variety of examined characiforms, including *Xenocharax*. All ctenoluciids lack rakers on the trailing margin of the first ceratobranchial but vary in the presence of rakers along the trailing margin of the second through fourth ceratobranchials. Such ossifications are well developed in *Ctenolucius* but are absent on the trailing edge of the second ceratobranchial in *Boulengerella*. Rakers are, in turn, either greatly reduced or absent on the third and fourth ceratobranchials in *Boulengerella*. The reduction or loss of these elements in *Boulengerella* is hypothesized to be derived given the condition in outgroups (SYNAPOMORPHY 80).

Gill-raker form is rather variable across the spectrum of characiforms and is phylogenetically informative at various levels (e.g., acestrorhynchins, see Menezes, 1969). Roberts (1969:423) noted that in "*Hepsetus* and *Ctenolucius* ... some of the anterior rakers are elongate and toothless; the absence of teeth is probably a specialized condition." The rakers in question presumably are those toward the anterior end of the first ceratobranchial but not including the most anterior elements, which are not elongate. Elongate rakers along the length of the first branchial arch occur in diverse characiforms (e.g., *Xenocharax, Brycon, Triportheus, Agoniates, Moojenichthys, Piabucina*), in addition to *Hepsetus* and *Ctenolucius*, and that feature, therefore, is uninformative about a potential sister-group relationship of the latter two taxa. In addition to characterizing *Hepsetus, Ctenolucius*, and *Boulengerella*, absence of teeth on the elongate rakers also occurs in many of the cited taxa and are not uniquely derived for the Ctenoluciidae and *Hepsetus*.

POSTCLEITHRA

Roberts (1969:426) noted that only a single postcleithrum (postcleithrum 1) overlaps the medial surface of the junction of the cleithrum and supracleithrum in *Ctenolucius*, and in the same paper (p. 431) Roberts recognized "a pectoral girdle with a single postcleithrum" as "characteristic" of the Ctenoluciidae. The three postcleithra primitively present among characiforms are lost in various combinations in the order (see Vari, 1979:311, 1983:36; Winterbottom, 1980:46), and the condition in *Ctenolucius* is more explicitly stated as the loss of postcleithra 2 and 3 that lie medial to the posterior portion of the cleithrum. Examination shows that the splint-like postcleithrum 3, the ventral element in the series, is indeed absent in both *Ctenolucius* and *Boulengerella*. Postcleithrum 2, the middle element in the series, although lacking in *Ctenolucius* species, *Boulengerella lateristriga*, and *B. maculata*, is present in *B. cuvieri, B. lucius*, and *B. xyrekes*. Those latter three species have a rounded thin ossification attached to the inner surface of the posterior margin of the cleithrum. Although of approximately the same size and form as the overlying scales, this ossification is firmly attached to the posteromedial surface of the cleithrum and lacks the distinct pattern of radii of the scales in that region of the body and thus is identified as postcleithrum 2.

(64) A lack of postcleithrum 3, although common for ctenoluciids, is not unique to that family among characiforms. Roberts (1969:426) noted that there was only a single postcleithrum (postcleithra 1) in *Hepsetus*, and Vari (1983:36) commented on the absence of this ossification in the Neotropical chilodontid *Chilodus*. Weitzman (1954:226) cited the lack of all postcleithra in the genera of the Gasteropelecidae (*Carnegiella, Gasteropelecus, Thoracocharax*).

Chilodus shares numerous derived features with *Caenotropus*, the other chilodontid genus, which, in turn, retains postcleithrum 3 (Vari, 1983:36, 51–52). Chilodontids also share numerous unusual derived modifications with the Anostomidae (Vari, 1983:50), which retain postcleithrum 3. The lack of postcleithrum 3 in *Chilodus* thus is most parsimoniously hypothesized to be independent of that in ctenoluciids. Information concerning the phylogenetic relationships of the Gasteropelecidae is somewhat equivocal. The three genera of that family together form a highly specialized clade probably derived from a component of what Greenwood et al. (1966) recognized as the Characidae (Weitzman 1954:243). As noted by Castro and Vari (1990:529), gasteropelecids also lack the supraorbital (see Weitzman, 1954:7), an ossification that also is lacking in "tetragonopterine" characids (Weitzman and Fink, 1983:391). This provides some additional evidence that the relationships of gasteropelecids lie with the Characidae rather than Ctenoluciidae. Under the overall most-parsimonious scheme of relationships postulated herein the absence of postcleithrum 3 in *Hepsetus* (B_4) and the Ctenoluciidae (E_5) is equally parsimoniously hypothesized to have occurred independently in those taxa or to have taken place in the common ancestor of those taxa and the Erythrinidae (A_4), with a secondary reacquisition of the bone in the latter family (D_5).

(65) Postcleithrum 2 is absent in *Ctenolucius, Boulengerella maculata,* and *B. lateristriga* (but not the other species of *Boulengerella*) and also is missing in *Hepsetus* (Roberts, 1969) and gasteropelecids (Weitzman, 1954). As just discussed above, the relationships of gasteropelecids apparently lie with characids rather than ctenoluciids, and the lack of the bone in gasteropelecids and ctenoluciids consequently is hypothesized to be independent losses. The lack of the second postcleithrum in the Hepsetidae, *Ctenolucius,* and the clade consisting of *Boulengerella lateristriga* and *B. maculata* can be explained by three alternative scenarios under the overall most-parsimonious scheme of relationships in the family. These are: 1, the independent loss of the ossification in the ancestor of hepsetids, ctenoluciids, and erythrinids (A_5), with secondary independent reacquisition of the bone in erythrinids (D_6) and the clade consisting of *B. cuvieri, B. lucius,* and *B. xyrekes* (I_2); 2, the independent loss of the bone in *Hepsetus* (B_5) and the ancestral ctenoluciid (E_6), with secondary reacquisition in the clade consisting of *B. cuvieri, B. lucius,* and *B. xyrekes* (I_2); and 3, the independent loss of the bone in the Hepsetidae (A_5), *Ctenolucius* (F_3), and the clade consisting of *Boulengerella lateristriga* and *B. maculata* (H_3).

WEBERIAN APPARATUS

(66) TRIPUS.—The form of the tripus, the largest of the Weberian ossicles, typically observed in characiforms has a distinct anterior portion continuous posteriorly with a less robust process that extends medial to the lateral portion of the fused fourth pleural rib plus parapophysis to terminate in the medially curved transformator process (e.g., *Brycon,* see Weitzman, 1964, fig. 12; *Xenocharax,* see Fink and Fink, 1981, fig. 15). The tripus in *Ctenolucius* and *Boulengerella* is much more elongate anteroposteriorly than in other characiforms, with no obvious distinction between the main anterior portion of the ossification and the posterior section that terminates in the transformator process. This form of the tripus is considered synapomorphic for the family (SYNAPOMORPHY 50).

(67) The medial margin of the tripus is unelaborated in examined characiform outgroups, *Ctenolucius, Boulengerella lateristriga,* and *B. maculata. Boulengerella cuvieri, B. lucius,* and *B. xyrekes* have a distinct, medially directed, finger-like projection on the medial margin of the tripus. This process is moderately developed in *B. cuvieri* and *B. xyrekes* and particularly elongate in *B. lucius.* The possession of this unique process is considered to be synapomorphic for the three species (SYNAPOMORPHY 100), with the elongate process in *B. lucius* an hypothesized autapomorphy for the species (SYNAPOMORPHY 103).

(68) FOURTH PLEURAL RIB.—The fused fourth pleural rib and parapophysis of characiforms bears ventromedially a variably developed os suspensorium that extends anteriorly from the main body of the ventral shaft of the vertically shortened rib. The os suspensorium in this arrangement typically lies completely or mostly under the fourth centrum. The fourth pleural rib complex in ctenoluciids differs notably from this generalized condition. The entire complex angles much more posteriorly from its area of attachment to the fourth centrum and, as a consequence, the posterior portion of the bone, including the os suspensorium, extends distally distinctly under the fifth centrum, a unique arrangement that is hypothesized to be derived (SYNAPOMORPHY 51).

(69) LIGAMENT BETWEEN TRIPUS AND FOURTH PLEURAL RIB.—The medial surface of the tripus and proximal portion of the ventral process on the fourth pleural rib are joined by connective tissue in characiforms. This connection, however, typically is poorly developed, without any consolidation of the tissue into a discrete band. The Ctenoluciidae, Erythrinidae, Lebiasinidae, and Hepsetidae, in contrast, have a discrete ligament between the medial margin of the tripus and the basal portions of the fourth pleural rib. This ligament is moderately developed in hepsetids and lebiasinids and much more pronounced in erythrinids and particularly ctenoluciids. The various conditions of the discrete ligament are considered to be derived at various levels with the common possession of the ligament in Ctenoluciidae, Erythrinidae, Lebiasinidae, and Hepsetidae a synapomorphy for those families (SYNAPOMORPHY 3), the further developed form of the connection a synapomorphy for the Erythrinidae and Ctenoluciidae (SYNAPOMORPHY 23), and the particularly stout ligament in the Ctenoluciidae diagnostic for the family (SYNAPOMORPHY 52).

(70) TRANSVERSE PROCESS OF THE THIRD NEURAL ARCH.—Fink and Fink (1981:329) noted that "in characiforms the third neural arch has an elongate anterodorsal process, usually termed the transverse process of the third neural arch, which projects lateral to the ascending process of the intercalarium" and proposed this feature as a synapomorphy for Characiformes. Although a relatively lengthy process on the third neural arch does occur in most examined characiforms, the condition described by Fink and Fink is not universal in the order. In *Acestrorhynchus,* for example, the transverse process extends directly laterally rather than anterodorsally across the ascending process of the intercalarium. In the Hepsetidae, Erythrinidae, and Ctenoluciidae the process is proportionally much broader relative to its length than in other examined characiforms; this is considered to be a derived condition (SYNAPOMORPHY 12).

(71) The transverse process of the third neural arch in the Hepsetidae and Erythrinidae, although wider than in outgroups, nonetheless extends anteriorly to slightly overlap the ascending process of the intercalarium, the generalized characiform condition. In ctenoluciids, in contrast, the vertically expanded

process is notably reduced in *Ctenolucius* and *Boulengerella,* thus falling distinctly short of the intercalarium. In *Boulengerella lateristriga* and *B. maculata* the reduction is most pronounced, with the process represented only by a vertically elongate ridge on the lateral margin of the third neural arch. The secondary reduction in all ctenoluciids of the transverse process is a synapomorphy for the family (SYNAPOMORPHY 53), with the pronounced reduction of the process in *Boulengerella lateristriga* and *B. maculata* hypothesized to be synapomorphic for those species (SYNAPOMORPHY 88).

Laterosensory Canal System on Body

(72) The majority of characiforms have a completely developed laterosensory canal system on the body with all, or nearly all, of the lateral-line scales having minimally a pore opening to the surface. *Ctenolucius* and three species of *Boulengerella* (*cuvieri, lucius,* and *xyrekes*) retain a completely pored lateral-line system. The other two *Boulengerella* species (*lateristriga* and *maculata*), however, have pores developed at a maximum only on the anterior 25 of the 45 to 50 lateral-line scales. A reduction of the pored portion of the lateral line occurs in diverse characiforms in the New and Old Worlds, with such a truncation usually associated with a reduced body size, particularly with relative miniaturization (Weitzman and Vari, 1988). That correlation does not apply in this instance. Although *Boulengerella lateristriga* and *B. maculata* achieve the shortest maximum known standard lengths in the genus (258 and 319 mm SL, respectively) these lengths are comparable to, or greater than those of the species of *Ctenolucius* (*hujeta:* 228 mm SL; *beani:* 286 mm SL), which have complete lateral lines. Furthermore, even the two *Boulengerella* species with incompletely pored lateral lines are significantly larger than any other group of characiforms with comparable reductions of that system and many times the size of miniature species in which such reduction is common (Weitzman and Vari, 1988). Regardless of the underlying cause, the condition in *Boulengerella lateristriga* and *B. maculata* is hypothesized to be derived, given the prevalence of completely pored lateral lines among characiforms in general and their occurrence in the Erythrinidae and Hepsetidae, which are the hypothesized sequential sister groups to the Ctenoluciidae (SYNAPOMORPHY 89). The reduction of the system in all lebiasinids is most parsimoniously hypothesized under the overall phylogeny to be an independent acquisition (SYNAPOMORPHY 7).

Scales

(73) In his description of *Ctenolucius,* Gill (1861a:8) noted that its scales were "covered with numerous closely approximated ridges abruptly commencing at the bases of their exposed surfaces, and terminating in as many strong teeth on the posterior margin" (Figure 10). *Boulengerella* species, although having somewhat irregular posterior scale margins, lack both distinct ridges on the scale surface and the pointed teeth of *Ctenolucius* scales. Although the presence of pronounced teeth along the posterior margin of the scales in *Ctenolucius* distinguishes it from *Boulengerella,* the presence of noncycloid scales is not unique to *Ctenolucius* among characiforms.

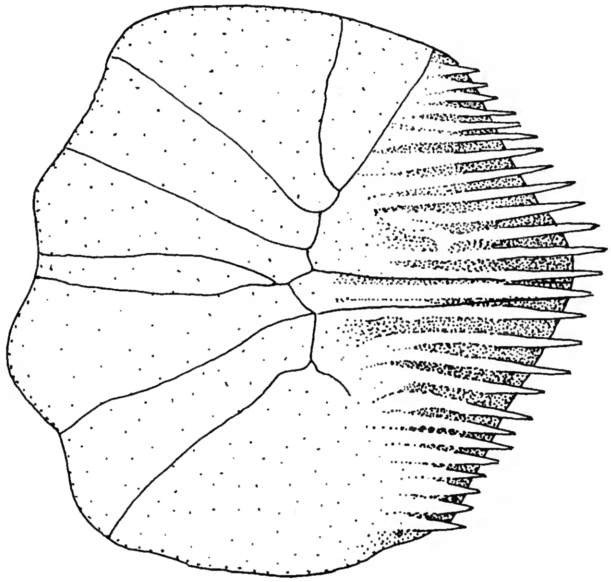

FIGURE 10.—Scale from anterior portion of midlateral surface of body of *Ctenolucius beani,* USNM 226435, showing pronounced ridges and posterior teeth, only major features of scales illustrated; lateral view, anterior to left.

Roberts (1993) emphasized that the term ctenoid subsumes a variety of types of noncycloid scales and restricted the term ctenoid to scales in which the spines along the margin of the scale are formed as separate ossifications. True ctenoid scales among characiforms are limited to the Distichodontidae, in which the spines are a series of independent ossifications on the posterior scale margin (e.g., *Xenocharax spilurus* and *Belonophago tinanti,* see Vari, 1979, fig. 38B,C; *Distichodus rostratus, Eugnatichthys eetveldtii,* and *Phago loricatus,* see Roberts, 1993, fig. 7), a totally different structure than that in *Ctenolucius.*

All other characiforms traditionally characterized as having ctenoid scales have what Roberts (1993) terms spinoid scales. One species in the African family Citharinidae, *Citharidium ansorgei,* has spines along the posterior margin of the scale (Daget, 1962b, fig. 1). The form of the scale in *C. ansorgei* differs from that of *Ctenolucius.* Furthermore, *Citharidium* is most closely related to *Citharinus* (Vari, 1979:326–327), the species of which have nonctenoid scales (Daget, 1962a, fig. 4). In *Cynopotamus* and allied Neotropical characid genera, the

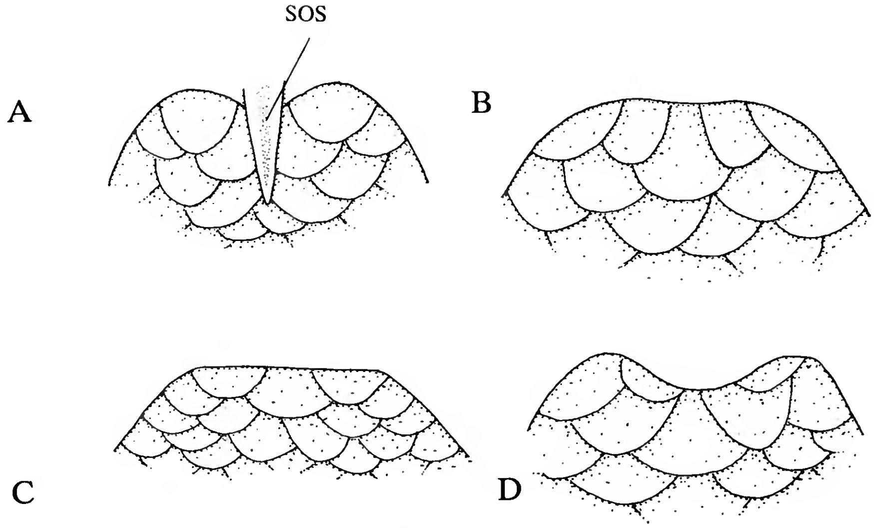

FIGURE 11.—Arrangement of body scales at posterodorsal margin of head: (A) *Brycon argenteus*, USNM 293136; (B) *Ctenolucius beani*, USNM 226435; (C) *Hepsetus odoe*, USNM 304096; and (D) *Parodon gesteri*, USNM 247312; dorsal views, anterior to top, details of surfaces of scales not shown.

irregular nature of the exposed portion of the scales is a consequence of a series of spicules along the posterior margin and the exposed surface of the scale (see Menezes, 1976, figs. 21, 29, 35; Roberts, 1993, fig. 7g,h), again different than the ctenoluciid condition. The scales of the tetragonopterin characid *Ctenobrycon* and some species of two curimatid genera (*Potamorhina* and *Psectrogaster;* Vari, 1989a:8) have irregular posterior margins to the scales but lack the distinctive ridges and regular posterior serrations of *Ctenolucius*. Moreover, curimatid species with ctenoid scales are most closely related to congenerics with cycloid scales (Vari, 1984 and 1989a). Scales with serrate margins also characterize the prochilodontid *Prochilodus* (Mago-Leccia, 1972, fig. 5A; Castro, 1990:106; Roberts, 1993, fig. 7e,f). The serrations in *Prochilodus* differ in overall form and distribution from those in *Ctenolucius* and lack the strong ridges characteristic of the latter genus. Furthermore, *Prochilodus* forms a monophyletic assemblage with *Ichthyoelephas* and *Semaprochilodus* (Vari, 1983:49), both of which have cycloid scales (Mago-Leccia, 1972; Castro, 1990). In light of the unique form of the scale in ctenoluciids and the data supporting the placement of other characiform taxa with scales with distinct spines along their margin as the closest relatives of species lacking such serrations, the spinoid scales of *Ctenolucius* are considered to be synapomorphic for the genus (SYNAPOMORPHY 64).

SQUAMATION AT POSTERODORSAL MARGIN OF HEAD

(74) In characiforms the scales on the dorsal surface of the body at the rear of the head usually are arranged along the margin of the supraoccipital spine, which extends posteriorly middorsally. As a consequence, the scale field in this region on each side of the middorsal line has a rounded or parabolic anterior margin (Figure 11A). Roberts (1969:412) noted that in "*Hepsetus, Ctenolucius,* and in *Hoplias* and other members of the Erythrinidae, the anteriormost scales of the dorsal scale rows are inserted in a groove along the posterior edge of the parietal bones." Broader surveys have shown that such an overlap of the supraoccipital spine by scales and the anterior expansion of the scale field medially to the rear of the parietals also occurs in *Boulengerella* and all examined lebiasinids. Such an overlap of the supraoccipital spine by scales also occurs in a component of the African characid genus *Alestes* that lack a fronto-parietal fontanel (e.g., *A. macrolepidotus*). The *Alestes* species with a covered supraoccipital spine are evidently most closely related to taxa with the spine exposed, and the expansion of the scale field anteriorly in some *Alestes* species thus is hypothesized to be homoplastic to that in the Neotropical taxa. Scales extending over the supraoccipital spine to the posterior margin of the parietals and arranged in a relatively straight or anteriorly convex pattern are hypothesized to be derived for lebiasinids, hepsetids (Figure 11C), erythrinids, and ctenoluciids (Figure 11B) (SYNAPOMORPHY 4).

Superficially, it appears that the Neotropical family Parodontidae also has scales extending over the supraoccipital spine to the posterior margins of the parietals. As discussed by Roberts (1974:425), parodontids have, however, the "supraoccipital crest absent." Thus, in parodontids the medial expansion of the scale field to the rear of the parietals does not involve expansion over the spine, thereby casting doubt on the

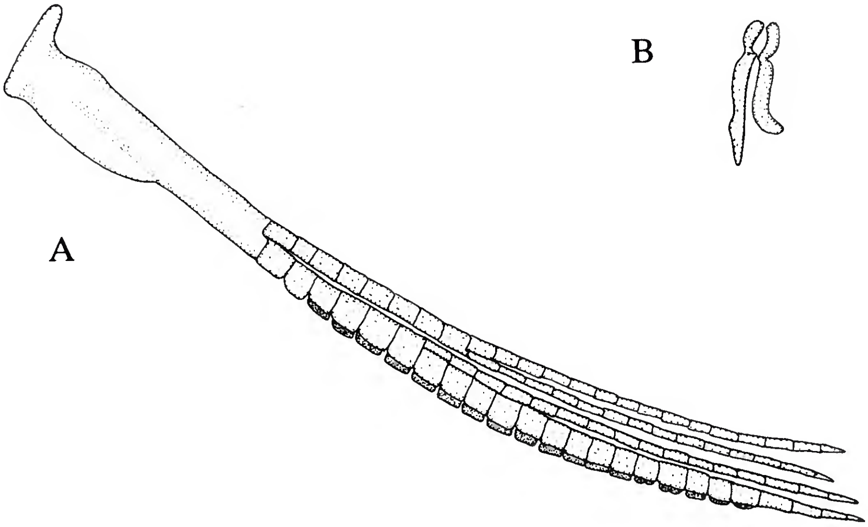

FIGURE 12.—Fourth branched anal-fin ray of male *Ctenolucius hujeta*, USNM 121334: (A) entire ray showing enlarged ray segments of anterior ray and asymmetrical development of those segments; lateral view, anterior to left; and (B) dorsal cross-section view of contralateral segments along middle of ray, showing lateral development on one side; anterior toward bottom.

equivalence of the parodontid condition with that in the Ctenoluciidae, Erythrinidae, Lebiasinidae, and Hepsetidae. Furthermore, in parodontids the margins of the scale fields have an anteriorly concave pattern to each side of the middorsal line (Figure 11D), an arrangement comparable to the hypothesized primitive condition for characiforms. This contrasts with the transversely straight or middorsally anteriorly concave pattern in the Ctenoluciidae, Erythrinidae, Lebiasinidae, and Hepsetidae. As a consequence, the parodontid condition is not equivalent to that in the latter four families.

(75) The anterior margins of the anterior scales of the dorsal surface of the body abut against a ridge along the posterior margin of the supratemporal canal on the posterodorsal margin of the parietal in the Hepsetidae, Lebiasinidae, and Erythrinidae. Ctenoluciids, in contrast, have the anterior margins of those scales inserting, at least in part, under an overhanging shelf extending posteriorly from that ridge, a uniquely derived condition among examined characiforms (SYNAPOMORPHY 54).

ANAL FIN

(76) SEXUAL DIMORPHISM.—In the generalized morphology of the anal fin among characiforms, the individual segments of the branched portions of the ray are of approximately the same anteroposterior width, with the ray gradually expanding in the sagittal plane distally as a consequence of the sequential branching of the ray. Both sexes of *Boulengerella* and females of *Ctenolucius* retain this morphology but the majority of the branched anal-fin rays of males of *Ctenolucius* differ notably from that generalized plan. The segments of the anterior branch of the second through seventh branched anal-fin rays in males are anteroposteriorly distinctly wider than adjoining segments on the posterior component of the first major branch of that ray or any segment of the second major branch in that ray (Figure 12A). As a consequence, the individual fin-rays in sexually mature *Ctenolucius* males are anteroposteriorly proportionally notably wider than in comparable-size females. This expansion results in a closer proximity of the individual fin-rays and a much stiffer fin than in females of *Ctenolucius* or either sex in outgroup characiforms.

Several other modifications are associated with the expansion of the anterior branch of most of the branched anal-fin rays. The longest anal-fin rays in *Ctenolucius* females are typically the last unbranched and first branched rays, with the distal margin of the fin distinctly convex. Males of the genus have the third and fourth anal-fin branched rays longest, with the posterior rays proportionally longer relative to the first branched rays than in females (approximately 60%–70% length of first ray versus 45%–50% in females). As a consequence, the anal fin in males of *Ctenolucius* are larger overall and have a rounded margin rather than the concave margin of females (see differences in photograph of male (upper) and female (lower) specimens of *Ctenolucius hujeta* in Axelrod et al. (1987:281). Outgroup studies have found expanded anal-fin rays in males of the lebiasinid genera *Lebiasina* and *Nannostomus*, but with the differences being the result of dissimilar, evidently nonhomologous modifications (see next section). The modifications in *Ctenolucius* thus are hypothesized to be a uniquely derived condition (SYNAPOMORPHY 65).

(77) Associated with the expansion of the majority of branched anal-fin rays in *Ctenolucius* males are several less obvious, but distinctive, modifications. The expanded anterior branches of the branched anal-fin rays have a highly developed channel along their anterior margins. This contrasts with the shallower channel of *Ctenolucius* females and both sexes in most other characiforms. Above and beyond the pronounced expansion of the channel in *Ctenolucius* males is the asymmetrical development of each contralateral ray segment. One side of the segment is expanded anteriorly with the other side expanded laterally (Figure 12B). All segments along the anterior margin of a ray demonstrate this pattern, with the resultant wide channel distinctly oriented laterally rather than anteriorly. Such an asymmetrical furrow on the anterior margin of the anal-fin rays apparently is unique to *Ctenolucius* among characiforms. Equally striking is the sequential alternation of the asymmetry between successive rays. The furrow alternates on successive fin rays between left and right orientations, with higher degrees of asymmetry on the third to seventh ray. These features are unique to *Ctenolucius* (SYNAPOMORPHY 66).

Weitzman (1966:24, fig. 6) described highly modified branched anal-fin rays in *Nannostomus* males, particularly *N. digrammus*. The enlarged rays in *Nannostomus* are equally expanded both anteriorly and posteriorly, contrary to *Ctenolucius* where the expansion is limited to the anterior portions of the ray segment. The asymmetrical expansion of the anterior segments of the ray characteristic of *Ctenolucius* have not been reported for *Nannostomus*. *Nannostomus* species also have a sequential asymmetrical overlap of the anteriorly and posteriorly enlarged fin rays, contrary to the partial enclosure of the unenlarged posterior margin of a ray by the assymetrically enlarged anterior portion of the following ray in *Ctenolucius*, a much different and apparently nonhomologous condition.

(78) *Ctenolucius* males have the basal portions of the third through eighth branched anal-fin rays more highly developed than in outgroups, congeneric females, or the remaining rays on the fin (Figure 12A). The pronounced anterolateral ridges present on the third ray and successively smaller processes on the posterior rays serve as attachment areas for muscles associated with the anal-fin ray movement. These modifications are unique to *Ctenolucius* males (SYNAPOMORPHY 67).

(79) ONTOGENETIC VARIATION.—The overall anal-fin form in juveniles of *Ctenolucius* (e.g., *C. hujeta*, Figures 20, 27) and two of the species of *Boulengerella* (*lateristriga* and *maculata*, Figure 35) does not differ notably from that of adults. Dramatic ontogenetic differences in the form of the anal fin characterize the three remaining species of *Boulengerella* (*cuvieri*, *lucius*, and *xyrekes*). Juveniles of those three species have the anal-fin rays notably elongate, with the posterior rays of the fin extending nearly to the tip of the ventral lobe of the caudal fin (Figures 42, 43, 46, 47). These *Boulengerella* species undergo a proportional ontogenetic shortening of the posterior rays of the anal fin (compare condition in *B. cuvieri*, Figures 92, 93 versus 94 and *B. xyrekes*, Figures 96 and 97 versus 98) resulting in an anal-fin form in adults comparable to that in the remainder of the family. The pronounced development of the anal-fin rays in juveniles in these *Boulengerella* species (*cuvieri*, *lucius*, and *xyrekes*) is unknown in the rest of the family or indeed other characiforms and thus is hypothesized to be derived (SYNAPOMORPHY 101).

DORSAL-FIN POSITION

(80) In *Ctenolucius* and two species of *Boulengerella* (*lateristriga* and *maculata*) the base of the dorsal fin extends, at least in part, posterior of the vertical through the anal-fin origin, with the first basal pterygiophore of the dorsal fin inserting behind the neural spine of the 26th to 30th vertebrae. The three other *Boulengerella* species (*cuvieri*, *lucius*, and *xyrekes*) have the dorsal fin more anteriorly positioned, with the anterior of the base nearly at the vertical through the pelvic-fin origin and the first basal pterygiophore of the dorsal fin inserting behind the neural spine of the 21st to 24th vertebrae. The majority of characiforms have the dorsal fin positioned approximately dorsal of the pelvic-fin insertion and anterior to the vertical line through the insertion of the first anal-fin ray. Such a pattern occurs in *Xenocharax* (Daget, 1960, fig. 2), the most generalized characiform, and other distichodontids, including elongate predators such as *Ichthyborus* (Daget, 1967, fig. 1). Most Neotropical characiforms also have the dorsal fin positioned approximately at the vertical through the pelvic-fin origin (e.g., Curimatidae, Prochilodontidae, Anostomidae, Chilodontidae, Erythrinidae), but the situation in the Characidae is somewhat equivocal. Various deeper bodied characid species, particularly those with elongate anal fins (e.g, *Gymnocorymbus*), have the dorsal fin positioned proximate to the vertical through the anal-fin origin. The relative position of the fins in those taxa are, in part, a function of the elongate anal fin. Various characid groups, including a number of predatory taxa with elongate bodies (e.g, *Rhaphiodon*, *Agoniates*), have their dorsal fins posteriorly positioned, a situation comparable to that in most ctenoluciids and perhaps a function of the mechanical advantages inherent in a posteriorly positioned dorsal fin in lurking predators that seize their prey with a rush. Looking at proximate outgroups to the Ctenoluciidae we find that *Hepsetus* and the Erythrinidae have anteriorly positioned dorsal fins. The dorsal fin in various lebiasinids has a somewhat intermediate position but is not situated dorsal of the anal fin. Given the anteriorly positioned dorsal fins in the majority of characiforms and proximate outgroups to the Ctenoluciidae, the posteriorly positioned fin of *Ctenolucius*, *Boulengerella lateristriga*, and *B. maculata* is considered to be derived. Two equally parsimonious alternative hypotheses explain the distribution of the feature among ctenoluciids. These are the

independent shift of the dorsal fin posteriorly in the ancestors of the clades comprising *Ctenolucius* (F_4) and the two *Boulengerella* species (H_4), or a posterior shift of the fin in the ancestral ctenoluciid (E_7), with a secondary shift anteriorly in the clade consisting of three *Boulengerella* species (*cuvieri, lucius,* and *xyrekes*, I_3).

ADIPOSE FIN

(81) Fink and Fink (1981:343) hypothesized that the presence of an adipose fin is primitive for characiforms within the context of their overall phylogeny, noting that the fin is missing in erythrinids, some *Nannostomus* species (Weitzman and Cobb, 1975), *Grundulus,* and *Nematobryon.* The fin also is absent in *Lebiasina* (Weitzman, 1964:149). The loss of the adipose fin is hypothesized to be derived, evidently having been lost independently in the Erythrinidae (SYNAPOMORPHY 30) and twice within the Lebiasinidae (*Lebiasina* and some *Nannostomus* species; note: conservatively coded in the analysis as missing in all members of the latter genus).

CAUDAL FIN BONY STAYS

(82) Roberts (1969:429, fig. 57) noted that the caudal-fin skeleton of ctenoluciids had vertical, plate-like bones anterior to the bases of both the dorsal and ventral procurrent fin rays. That author identified perhaps homologous, albeit much smaller, ossifications in the African characid genus *Hydrocynus* (Roberts, 1969, fig. 60; Brewster, 1986, fig. 20). Comparative studies have shown that bony stays are widely distributed among African characids, being present in *Brycinus longipinnis, Alestes lateralis, A. nurse, Bryconaethiops, Micralestes acutidens, Phenacogrammus pabrensis, P. interruptus,* and *Petersius intermedius,* but not *Lepidarchus adonis* (see also Roberts, 1966, fig. 9) or apparently *Brycinus macrolepidotus.* The possession of these plates may define a major subunit of the African Characidae, a group that has not been critically reviewed phylogenetically. Bony stays are unknown in other characiforms and their possession is hypothesized to be derived. Such processes are absent in the Lebiasinidae, Hepsetidae, and Erythrinidae, and the proportionally large bony stays in *Ctenolucius* and *Boulengerella* are unique among characiforms and synapomorphic for the family (SYNAPOMORPHY 55), with the less-developed ossifications in some African characiforms considered a homoplasy.

The homology of the bony stays is uncertain. Roberts (1969:429) suggested that in ctenoluciids the bones apparently are of dermal origin, given there was no indication of cartilage along their margins in the specimens he examined and that they may have "originated from fusion of anterior procurrent rays." Observations of this study confirm that no cartilage is apparent on the bony stays in larger specimens and that each bony stay lies anterior of the cartilage masses that typically occur at the anterodorsal and anteroventral limits of the caudal-fin fan. The smallest available cleared and counterstained ctenoluciid specimen (*Boulengerella cuvieri,* 25.5 mm SL) has, however, splint-like, unpaired blue-stained structures lying in the areas occupied by the stays in adults. These are separated from the anterior procurrent rays and are not readily homologized with those elements.

MYOLOGY

(83) DILATATOR OPERCULI MUSCLE.—The modifications of the portions of the frontal and sphenotic forming the dilatator groove in the lebiasinid genera *Lebiasina* and *Piabucina* (but not members of the subfamily Pyrrhulininae of the Lebiasinidae), erythrinids, and ctenoluciids are reflected in the dilatator operculi muscle. In characiforms this muscle typically arises from the dorsolateral surface of the sphenotic spine and the adjoining lateral portion of the frontal situated posterodorsal to the spine. The muscle in *Lebiasina, Piabucina,* the Erythrinidae, and Ctenoluciidae, in contrast, does not arise to any significant degree from the lateral surface of the frontal, but, rather, it extends anteriorly into the space between the dorsally reduced sphenotic spine and the ventral surface of the lateral margin of the frontal and then continues to varying degrees into the orbit (Figures 13, 14).

That reorientation and extension of the dilatator operculi into the orbit is hypothesized to be derived, but it has a broader distribution within characiforms beyond the groups of immediate interest. As discussed relative to the dilatator groove, there is an aperture within a lateral process of the frontal in *Acestrorhynchus.* Although this opening differs in being situated entirely in the frontal rather than being bordered by the frontal and sphenotic as in erythrinids and ctenoluciids, it does serve for passage of the dilatator operculi anteriorly into the orbit. The form of the muscle in *Acestrorhynchus* differs, however, from that in the Lebiasininae, Erythrinidae, and Ctenoluciidae. In *Acestrorhynchus* the muscle fibers radiate anteriorly from the region of insertion on the opercle, whereas in the Lebiasininae, Erythrinidae, and Ctenoluciidae the arrangement of the fibers is more pinnate, with a strong central ligamentous band attaching the main muscle mass onto the opercle. This difference raises questions about the homology of the two forms of the expanded dilatator operculi muscles.

The parodontid genus *Saccodon* also has an opening in the lateral process of the frontal, which is situated above the sphenotic spine. This opening also serves for the passage of a portion of the dilatator operculi muscle into the orbit. The overall form of the muscle in *Saccodon* differs significantly from that in the Ctenoluciidae and Erythrinidae, with most of the mass of the muscle located posterior of the sphenotic spine rather than anterior to it as in those families. Furthermore, an anterior expanded dilatator operculi does not occur in the two other parodontid genera (*Parodon, Apareidon*) that share numerous derived features with *Saccodon* (Roberts, 1974). Thus, it is most parsimonious to hypothesize that the anterior

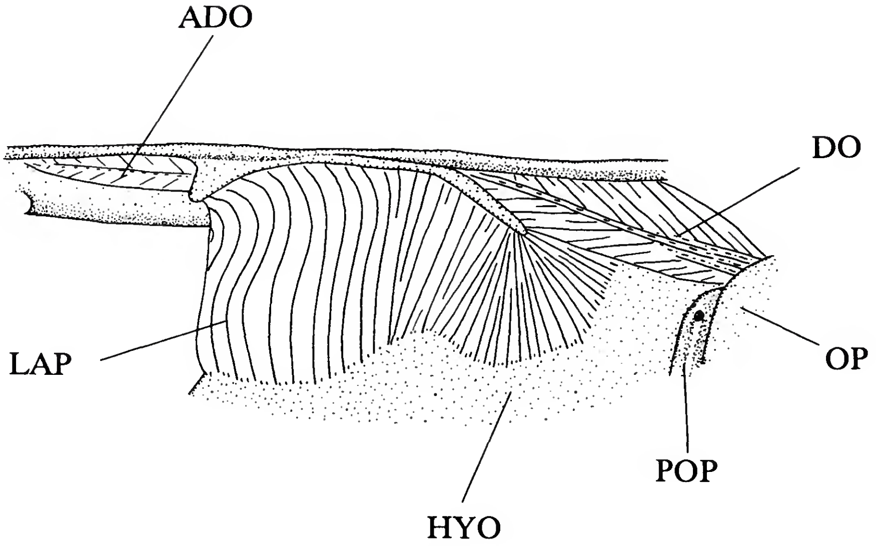

FIGURE 13.—Levator arcus palatini and dilatator operculi muscles of *Ctenolucius beani*, USNM 226435, slightly ventrolateral view, anterior to left.

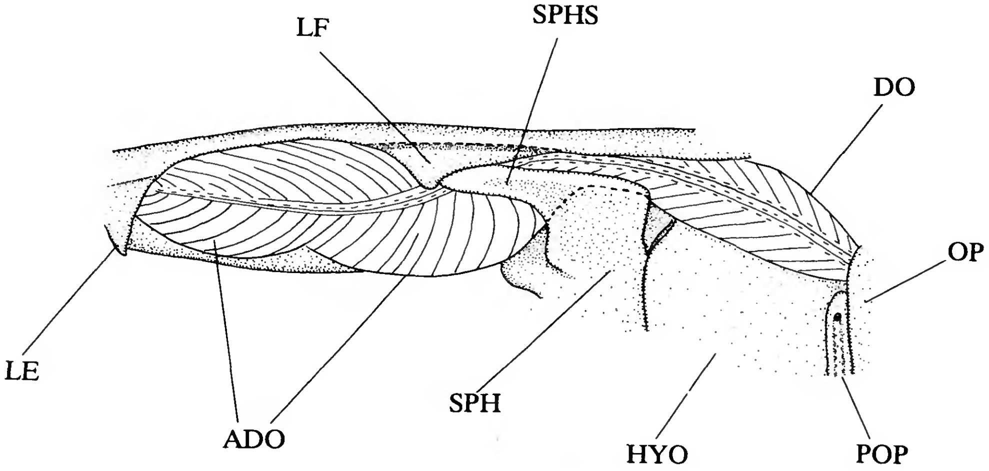

FIGURE 14.—Lateral view of middle portion of neurocranium showing dilatator operculi muscle of *Hoplias* cf. *malabaricus*, USNM 316071; ventrolateral view, anterior to left, dashed lines through sphenotic spine and lateral process of frontal indicate channel through which the muscle extends anteriorly into the orbit.

extension of the dilatator operculi in the *Saccodon* and the Lebiasininae, Ctenoluciidae, and Erythrinidae are acquired independently.

Although dilatator operculi muscle form in the Lebiasininae, Erythrinidae, and Ctenoluciidae apparently is homologous, within the overall most-parsimonious phylogeny proposed herein the anterior extension of the dilatator operculi into the space between the dorsally reduced sphenotic spine and lateral margin of the frontal in the Lebiasininae (SYNAPOMORPHY 10) is hypothesized to be convergent with that in the Erythrinidae and Ctenoluciidae (SYNAPOMORPHY 24).

(84) Erythrinids and ctenoluciids have the dilatator operculi muscle dramatically narrowed where it passes through the tunnel formed by the frontal and sphenotic. This constricted

region of the muscle, in turn, has a very well-developed central ligamentous band that continues anteriorly to the main body of the muscle within the orbit (Figure 13). Such a form of the dilatator operculi muscle, unique to these two families, is considered to be derived (SYNAPOMORPHY 25).

(85) *Piabucina,* ctenoluciids, and erythrinids have particularly well-developed adductor mandibulae muscles. This expansion has occurred in regions primitively occupied, at least in part, by the dilatator operculi. The reduction of the portion of the dilatator operculi proximate to the opercle in the Ctenoluciidae and Erythrinidae is compensated for by the expansion of the anterior portion of the muscle within the orbital cavity (Figure 14, see also Gijsen and Chardon, 1976, fig. 2). In ctenoluciids, approximately two-thirds of the mass of the muscle lies anterior to the tunnel formed by the frontal and sphenotic. The disproportionate anterior development of the muscle is most pronounced in erythrinids, in which the dilatator operculi extends anteriorly to the posterior margin of the lateral ethmoid. The extensive development of the dilatator operculi muscle in the orbit, a feature not encountered elsewhere in the order, is hypothesized to be derived for the Ctenoluciidae and Erythrinidae (SYNAPOMORPHY 26), albeit independently acquired in *Piabucina,* with the particularly pronounced anterior extension of the muscle in the Erythrinidae (Figure 14) a distinguishing feature for that family (SYNAPOMORPHY 33).

(86) ADDUCTOR MANDIBULAE MUSCLE.—The massive development of the adductor mandibulae muscles in erythrinids and ctenoluciids is commented on above. In characiform outgroups these muscles arise from various portions of the opercular series and to varying degrees on the pterotic, but not from the sphenotic. In all ctenoluciids the anterior portion of the adductor mandibulae also arises from the posterior two-thirds of the lateral margin of the sphenotic spine. The origin of the muscle within the Erythrinidae is variable. No attachment of the adductor mandibulae muscle onto the sphenotic is found in *Erythrinus* or *Hoplerythrinus.* The species of *Hoplias,* in contrast, have the adductor mandibulae attaching to at least the posterior half of the spine, or in some instances along the entire margin. Further study is necessary to determine whether the degree of attachment is an ontogenetic function or reflects variation between species. Given the two different conditions in the Erythrinidae, there are two equally parsimonious explanations for the distribution of this character. We can, on the one hand, assume that the presence of the attachment is a synapomorphy for *Boulengerella* and *Ctenolucius* (E_8) that independently arose in *Hoplias,* or we can hypothesize that such an attachment was ancestral for the Erythrinidae and Ctenoluciidae (C_2) and then lost in a lineage consisting of *Erythrinus* and *Hoplerythrinus,* a clade defined by various apparently derived features (e.g., the presence of an additional plate-like ossification between the sixth infraorbital and suprapreopercle).

(87) LEVATOR ARCUS PALATINI MUSCLE.—The levator arcus palatini (LAP) muscle of characiforms typically attaches to the ventral portion of the sphenotic spine, fanning out from that origin to insert on the lateral surface of the hyomandibula. Ctenoluciids have a notable horizontally elongate LAP that arises from the entire ventral margin of the sphenotic spine (Figure 13) and has much more of a sheet-like than fan-like overall form. The form of the muscle in ctenoluciids, hypothesized to be derived given the morphology of the LAP in other characiforms, is, however, approximated in *Hoplias,* albeit not the two other erythrinid genera (*Erythrinus* and *Hoplerythrinus*). The presence of two conditions of the LAP in the Erythrinidae results in two equally parsimonious explanations for the distribution of this character within the context of the overall most-parsimonious phylogeny. One alternative is that the presence of the attachment is a synapomorphy for *Boulengerella* and *Ctenolucius* (E_9) that independently arose in *Hoplias,* and the second is that such an attachment was ancestral for the Erythrinidae and Ctenoluciidae (C_3) and then lost in a lineage consisting of *Erythrinus* and *Hoplerythrinus.*

PIGMENTATION

BODY AND HEAD PIGMENTATION.—The pattern of relatively large dark spots on at least the dorsal, and often dorsolateral, surfaces of the body in *Boulengerella maculata* (Figures 35, 36) is not duplicated elsewhere among ctenoluciids and thus is hypothesized to be derived (SYNAPOMORPHY 90). The pattern of dark body spots in *B. lucius* are concentrated, in contrast, on the ventrolateral region of the body, an area otherwise lacking such pigmentation in the rest of the family, and the condition consequently is hypothesized to be derived (SYNAPOMORPHY 104). *Boulengerella lateristriga* has a striking dark midlateral stripe on the postorbital portion of the head and midlateral surface of the body that is delimited, at least dorsally, by a thin, particularly dark line, a pigmentation pattern unique not only to the species among ctenoluciids, but also rare among characiforms; thus it is hypothesized to be autapomorphic for the species (SYNAPOMORPHY 94).

One feature of head pigmentation in *Boulengerella xyrekes* is of note. Various members of the genus have a band of dark pigmentation across the posteroventral portion of the opercle in juveniles. This pigmentation typically disappears before the species reaches 150 mm SL. Only in *B. xyrekes* is the pigmentation retained to larger sizes, an evidently derived condition that is autapomorphic for the species (SYNAPOMORPHY 108).

FIN PIGMENTATION.—*Boulengerella maculata* has both a marmorated pattern of dark and light pigmentation on the lobes of the caudal fin (Figures 35–37) that is unique to that species in the family (SYNAPOMORPHY 91). The pattern of distinct dark crossbars on the lobes of the caudal fin in *B. lateristriga* (Figures 32, 33) also is not duplicated within the family or other taxa possibly closely related to the Ctenoluciidae and thus is hypothesized to be another autapomorphy of the species (SYNAPOMORPHY 95).

(88) As noted above under "Ontogenetic Variation in Anal Fin," juveniles of the clade consisting of *Boulengerella cuvieri, B. lucius,* and *B. xyrekes* have notably elongate posterior anal-fin rays. Associated with this elongation is a change from the typically lightly pigmented anal-fin rays of the juveniles of other ctenoluciids and the adults of all members of the family to a very dark pigmentation of the anal fin in the juveniles of *Boulengerella cuvieri, B. lucius,* and *B. xyrekes.* This juvenile pigmentation of the anal fin in these three species consequently is hypothesized to be derived (SYNAPOMORPHY 102).

The form of the dark pigmentation at the base of middle rays of the caudal fin is universal in the Ctenoluciidae, perhaps being an additional synapomorphy for the family. This pigmentation takes the form of either an ocellated spot in the adults of *Ctenolucius* (Figures 21-23, 28-30), a discrete spot lacking an ocellus in *B. cuvieri* (Figure 44) and *B. xyrekes* (Figure 48), or a variably discrete spot in *B. maculata* (Figure 37) and *B. lateristriga* (Figure 32). *Boulengerella lucius,* in contrast, lacks the definitive basal spot, but instead it has a series of dark horizontal stripes between the basal portions of the central rays of the caudal fin. This pigmentation pattern is unusual among characiforms and is unique to the species within the Ctenoluciidae, and thus it is hypothesized to be autapomorphic (SYNAPOMORPHY 105).

Phylogenetic Reconstruction

The preceding sections detail the series of shared derived characters congruent with an hypothesis of the suprafamilial relationships of the Ctenoluciidae and diagnostic for the species of the Ctenoluciidae or subunits of differing levels of inclusiveness within the family. The synapomorphies and autapomorphies are numbered sequentially in the following text, with the numbering in this section and the immediately preceding "Character Description and Analysis" corresponding to that in Figure 15. Of the 88 characters discussed in the previous text and detailed in Table 1, 66 are unique and unreversed. Eleven of the 22 remaining characters (characters 9, 17, 23, 27, 45, 54, 57, 58, 72, 81 and 83) have a single most-parsimonious optimization on the final cladogram. The 108 character states for those 77 characters are assigned numbers in Figure 15. The remaining 11 characters (characters 3, 12, 19, 32, 43, 52, 64, 65, 80, 86, 87) are ambiguous, having two (10 characters) or three (character 65) equally parsimonious explanations for their distribution within the final most-parsimonious scheme of relationships proposed herein. For purposes of completeness, the various permutations of these ambiguous characters are plotted on the cladogram. They are grouped at appropriate levels within the final phylogeny (assemblages A to K), with individual characters identified by subscripts. These 11 ambiguous characters represent 43 potential additional synapomorphies, some of which are mutually exclusive in their different combinations.

To supplement the brief descriptions of the characters in the following enumeration, consult the table of contents for the location of more complete discussions of the characters, their phylogenetic distributions, and associated polarity assumptions in "Character Description and Analysis."

MONOPHYLY OF THE LEBIASINIDAE, HEPSETIDAE, ERYTHRINIDAE, AND CTENOLUCIIDAE CLADE

The following synapomorphies for the clade consisting of the Lebiasinidae, Hepsetidae, Erythrinidae, and Ctenoluciidae have been identified during this study:

1. The possession of lamellar extensions on the dorsal and ventral margins of the ossified laterosensory canal segment in the nasal (secondarily reversed in the lebiasinid *Nannostomus*).
2. The loss of the portion of the supraorbital laterosensory canal system in the parietal and the posterior portion of the frontal (secondarily reversed in the Erythrinidae).
3. The presence of a discrete ligament between the tripus and basal portion of the fourth pleural rib.
4. The extension anteriorly of the middorsal scales of the body over the supraoccipital spine.

COMMENTS ON MONOPHYLY OF LEBIASINIDAE AND SUBUNITS

Weitzman (1964:148-149) listed defining features for the Lebiasinidae (his Lebiasininae). Although that definition differentially diagnoses the family, it was proposed prior to the application of rigorous methods of phylogenetic reconstruction within fishes and thus is not appropriately interpreted as a series of proposed synapomorphies for the family. Some of these features, although derived within characiforms, have broader distributions than the Lebiasinidae, whereas others may be plesiomorphic. Although a critical analysis of the question of the monophyly of the family lies outside the scope of this study, at least three of the characters discussed by Weitzman (1964) are synapomorphies for the two subfamilies of the Lebiasinidae, the Lebiasininae and Pyrrhulininae:

5. The absence of the supraorbital (independently lost in the Erythrinidae).
6. The lack of the metapterygoid-quadrate fenestra.
7. The reduction of the laterosensory canal system on the body (independently acquired in the clade consisting of *Boulengerella lateristriga* and *B. maculata*).

The modifications of the anal-fin rays in males of various lebiasinid genera may represent another potential synapomorphy for the family.

Weitzman (1964) defined two major components of the Lebiasinidae, now recognized as the subfamilies Lebiasininae and Pyrrhulininae. Questions of intrafamilial relationships

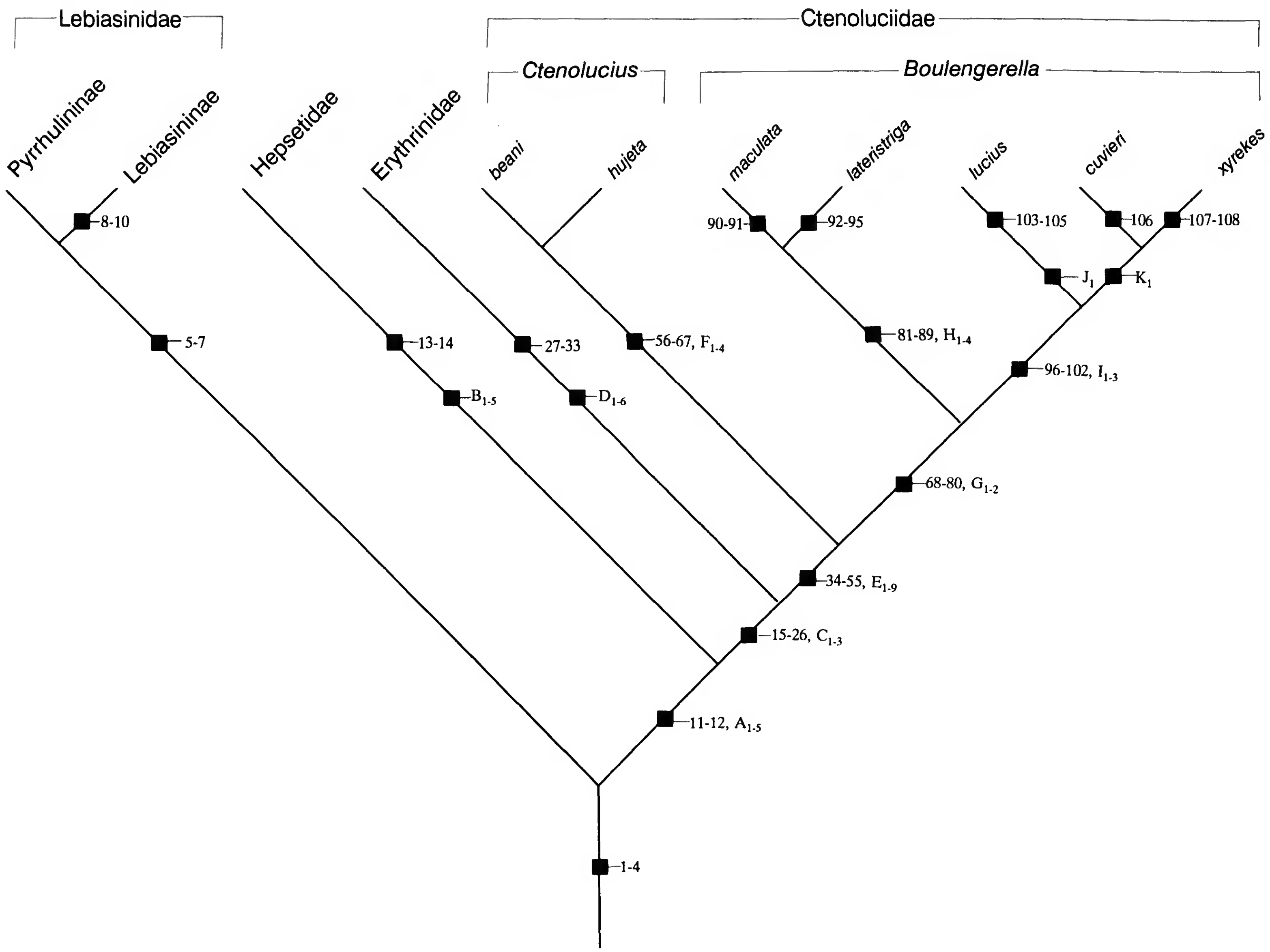
Lebiasinidae
Ctenoluciidae
Ctenolucius
Boulengerella
Pyrrhulininae
Lebiasininae
Hepsetidae
Erythrinidae
beani
hujeta
maculata
lateristriga
lucius
cuvieri
xyrekes
8-10
5-7
13-14
B_{1-5}
27-33
D_{1-6}
56-67, F_{1-4}
90-91
92-95
81-89, H_{1-4}
103-105
106
107-108
J_1
K_1
96-102, I_{1-3}
68-80, G_{1-2}
34-55, E_{1-9}
15-26, C_{1-3}
11-12, A_{1-5}
1-4

FIGURE 15 (opposite page).—Cladogram of the most-parsimonious hypothesis of relationships of the families Lebiasinidae, Hepsetidae, Erythrinidae, and Ctenoluciidae and genera and species within the Ctenoluciidae (numbered characters correspond to those of the text; CI = 0.871). Unique and unreversed character states and unambiguously optimized character states indicated by roman numbers. The various permutations of 11 characters whose distributions could be explained by two or more equally parsimonious hypotheses indicated by letters and subscript numbers.

within the family are outside the scope of this study, but three derived features, homoplastically present in other clades among the groups under consideration, are hypothesized to be synapomorphies for the Lebiasininae:

8. The reduction of the dorsal portion of the sphenotic spine and the reorientation of the spine into a more horizontal alignment (independently acquired in the clade consisting of the Erythrinidae and Ctenoluciidae).
9. The interdigitations medially between the anterior and posterior ceratohyals (independently acquired in the clade consisting of the Erythrinidae and Ctenoluciidae).
10. The extension of the dilatator operculi muscle to at least the rear of the orbit (independently acquired in the clade consisting of the Erythrinidae and Ctenoluciidae).

MONOPHYLY OF THE HEPSETIDAE, ERYTHRINIDAE, AND CTENOLUCIIDAE CLADE

The clade consisting of the Hepsetidae, Erythrinidae, and Ctenoluciidae is diagnosed by two uniquely derived features and several characters whose distribution can be explained by two or more equally parsimonious hypotheses. The two uniquely derived features are as follows:

11. The relatively large, distally compressed teeth.
12. The vertical expansion of the transverse process of the third neural arch.

Ambiguous features for this clade are as follows:

A_1. The contact of the first infraorbital and supraorbital (with secondary loss in the Erythrinidae).

A_2. The lateral shift of the nasal (secondarily lost in the Erythrinidae).

A_3. The plate-like suprapreopercle (secondarily lost in the Ctenoluciidae).

A_4. The loss of the third postcleithrum (secondarily reacquired in the Erythrinidae).

A_5. The loss of the second postcleithrum (ossification secondarily reacquired at less-inclusive levels; derived under two of three alternatives).

COMMENTS ON MONOPHYLY OF HEPSETIDAE

The Hepsetidae contains a single species, *Hepsetus odoe*, which is widespread in subsaharan Africa (Paugy, 1990a:192). Roberts (1969) discussed a number of features diagnostic of the family. Of its evidently derived features, the following have been critically examined in this study:

13. The distinctive form of the dorsoventrally flattened fleshy flaps along the lateral margin of the lower jaw.
14. The well-developed tooth-bearing ramus of the premaxilla extending posteriorly medial to the anterior portion of the maxilla.

Ambiguous features for this clade are as follows:

B_1. The contact of the first infraorbital and supraorbital (independently acquired in the Ctenoluciidae).

B_2. The lateral shift of the nasal (independently acquired in the Ctenoluciidae).

B_3. The plate-like suprapreopercle (independently acquired in the Erythrinidae).

B_4. The absence of the third postcleithrum (independently lost in some ctenoluciids).

B_5. The absence of the second postcleithrum (independently lost within the Ctenoluciidae).

MONOPHYLY OF THE ERYTHRINIDAE AND CTENOLUCIIDAE CLADE

The Erythrinidae and Ctenoluciidae share the following 12 synapomorphies:

15. The lack of a discrete antorbital.
16. The reduction of the dorsal portion of the sphenotic spine and the reorientation of the spine into a more horizontal alignment (independently acquired in the Lebiasininae).
17. The lateral contact of the frontal and dorsolateral process of the sphenotic spine that together form an aperture for the dilatator operculi muscle.
18. The horizontal elongation and anterior extension of the sphenotic spine that extends forward to or anterior to the transverse plane through the joint between the orbitosphenoid and pterosphenoid.
19. The lack of an epiphyseal bar in all but the smallest juveniles either as a discrete structure subdividing the frontoparietal fontanel into two sections or as a ridge across the ventral surface of the frontals.
20. The absence of the portion of the supraorbital laterosensory canal posterior of the divergence of the parietal branch and the consequent lack of contact between the supraorbital and pterotic laterosensory canal systems.
21. The interdigitations between the lateral surfaces of the anterior and posterior ceratohyals (independently

acquired in the Lebiasininae).

22. The interdigitations between the medial surfaces of the anterior and posterior ceratohyals.
23. The thickening of the ligament between the tripus and the basal portion of the fourth pleural rib.
24. The anterior extension of the dilatator operculi muscle to at least the posterior portion of the orbit.
25. The pronounced restriction of the dilatator operculi muscle in the region of the tunnel formed by the lateral processes of the frontal and sphenotic and the development of a well-developed ligamentous band in that portion of the muscle.
26. The expansion of the dilatator operculi muscle distinctly anteriorly into the orbital cavity.

Ambiguous features for this clade are as follows:

C_1. The shift of the coronomeckelian bone into Meckel's cartilage (secondarily lost in *Boulengerella*).

C_2. The attachment of the adductor mandibulae muscles onto the sphenotic spine (secondarily lost in *Erythrinus* and *Hoplerythrinus*).

C_3. The broad origin of the levator arcus palatini muscles from the horizontally elongate sphenotic spine (secondarily lost in *Erythrinus* and *Hoplerythrinus*).

COMMENTS ON MONOPHYLY OF ERYTHRINIDAE

The Erythrinidae is hypothesized as the sister group of the Ctenoluciidae on the basis of twelve synapomorphies. Three other derived features (attachment of the adductor mandibulae muscle onto the horizontally elongate sphenotic spine, anterior extension of the pterotic that approaches the lateral process of the frontal, and the highly developed suturing between the medial surfaces of the anterior and posterior ceratohyals) are shared by the Ctenoluciidae and *Hoplias* within the Erythrinidae. This raises the question of whether *Hoplias* is more closely related to the Ctenoluciidae than to the other erythrinid genera (*Erythrinus* and *Hoplerythrinus*).

Weitzman (1964:151) listed a series of defining features for the Erythrinidae (his Erythrininae). This listing subsumed features that served both to distinguish the family from hypothesized close relatives and those recognized herein as synapomorphies for the family. A critical examination of all of these features lies outside the scope of the present study, nonetheless, a number of the characters cited by Weitzman are hypothesized to be derived on the basis of outgroup comparisons in this study. However, many of these evidently are derived for suprafamilial groupings more inclusive than the Erythrinidae. Hypothesized synapomorphies for the Erythrinidae noted by Weitzman and critically examined during this study are as follows:

27. The distinctive form of the first infraorbital.
28. The absence of a supraorbital (also absent in the Lebiasinidae among hypothesized proximate sister groups).
29. The presence of five branchiostegal rays.
30. The absence of the adipose fin (also absent in *Lebiasina* and some *Nannostomus* species among hypothesized proximate sister groups).

Synapomorphies for the Erythrinidae identified during this study are as follows:

31. The secondary reacquisition of the posterior portion of the supraorbital laterosensory canal (loss hypothesized as a synapomorphy for the Lebiasinidae, Hepsetidae, Erythrinidae, and Ctenoluciidae clade).
32. The presence of a pair of cartilages at the anterior margin of the basihyal instead of a single cartilage body in that region.
33. The extension of the dilatator operculi muscle within the orbit across the ventral surface of the frontal to the region of the lateral ethmoid.

Ambiguous features for this clade are as follows:

D_1. The secondary absence of contact between the first infraorbital and supraorbital.

D_2. The position of the nasal (secondarily shifted to plesiomorphic position).

D_3. The plate-like suprapreopercles (independently acquired in the Hepsetidae).

D_4. The ventral shift of the coronomeckelian ossification into Meckel's cartilage (independently shifted in *Ctenolucius*).

D_5. The presence of the third postcleithrum (secondary reacquisition of ossification lost at higher level; see A_4).

D_6. The presence of the second postcleithrum.

MONOPHYLY OF THE CTENOLUCIIDAE

The hypothesis of the monophyly of the family Ctenoluciidae is supported by a series of 22 synapomorphies, discussed above, as follows:

34. The interdigitations joining the first infraorbital and the supraorbital.
35. The pronounced reduction and loss of the fourth infraorbital (IO_4).
36. The elongation of the nasal.
37. The pronounced shift of the nasal, which lies entirely anterior of the supraorbital.
38. The form of the interdigitating articulation between the mesethmoid and vomer.
39. The relatively large, transversely elongate articular surface on the ventral wing of the lateral ethmoid.
40. The anterior extension of the frontal along the medial

margin of the nasal.

41. The pronounced elongation of the premaxilla.
42. The loss of the anteromedial process of the maxilla and the immobile articulation of the maxilla with the rear of the premaxilla.
43. The expansion of the ligamentum primordiale with a shift of its dorsal attachment to the medial surface of the maxilla rather than the anterodorsal portion of the bone.
44. The pronounced elongation of the dentary and Meckel's cartilage.
45. The partial enclosure of the median mandibular fossa by a bony plate extending ventrally from the ventral margin of the dentigerus surface.
46. The shift of the area of attachment of the ligamentum primordiale to the posteroventral portion of the angulo-articular and the development of a distinct lateral process for the attachment of the ligament on that ossification.
47. The posteriorly recurved crowns on the numerous teeth in each jaw.
48. The well-developed ligament extending from the anteroventral portion of the palatine to the ventral surface of the mesethmoid.
49. The highly developed interdigitating suture joining the anterior and posterior ceratohyals on the medial surface of those bones (independently acquired in *Hoplias*).
50. The anteroposteriorly elongate tripus.
51. The posteroventrally angled fourth pleural rib with the os suspensorium situated ventral of the fifth centrum.
52. The very well-developed ligament between the tripus and basal portion of the fourth pleural rib.
53. The pronounced horizontal shortening of the transverse process on the third neural arch.
54. The posteriorly developed shelf along the posterior margin of the ridge at the rear of the supratemporal laterosensory canal, which overlies the anterior margin of the first series of scales on the dorsal surface of the body.
55. The large bony stays anterior to the dorsal and ventral procurrent fin rays of the caudal fin.

Ambiguous features for this clade are as follows:

E_1. The contact of the first infraorbital and supraorbital (also present in the Hepsetidae).

E_2. The absence of the fourth infraorbital (secondarily reacquired within family).

E_3. The lateral shift of the nasal (also present in the Hepsetidae).

E_4. The absence of the plate-like suprapreopercle (a secondary loss of a feature acquired in a more inclusive group; see A_3).

E_5. The absence of the third postcleithrum (also absent in Hepsetidae).

E_6. The absence of the second postcleithrum (secondarily reacquired within family).

E_7. The posterior position of the dorsal fin (secondarily shifted posteriorly within family).

E_8. The origin of the adductor mandibulae muscle, in part, from the horizontally elongate sphenotic spine (also present in *Hoplias*).

E_9. The horizontally elongate origin of the levator arcus palatini muscle from the sphenotic spine (also present in *Hoplias*).

The family Ctenoluciidae, defined by the derived features enumerated above, consists of two primary monophyletic lineages herein recognized as the genera *Ctenolucius* and *Boulengerella* in keeping with recent taxonomic practice.

MONOPHYLY OF *Ctenolucius*

The two species of *Ctenolucius* share 12 synapomorphies:

56. The enlarged dorsal ramus of the first infraorbital articulating with the supraorbital via well-developed interdigitations.
57. The pronounced horizontal elongation and anterior extension of the sphenotic spine, which extends anterior to the transverse plane through the joint between the orbitosphenoid and pterosphenoid.
58. The anterior extension of the pterotic that contacts the lateral process of the frontal and dorsal margin of the sphenotic spine.
59. The lateral expansion of the premaxilla, which gives the snout a spatulate profile in dorsal view.
60. The horizontally elongate fleshy flap on the lateral surface of the dentary.
61. The relatively small teeth at the posterior of the spatulate portion of the jaw bracketed anteriorly and posteriorly by larger teeth.
62. The ossification of the vertically aligned lateral process on the posterior portion of the palatine, which supports the articular surface abutting the lateral ethmoid.
63. The shift of the articulation of the penultimate branchiostegal ray from the posterior section of the anterior ceratohyal onto the anterior portion of the posterior ceratohyal.
64. The distinctive form of the ctenoid scales.
65. The sexually dimorphic fins with the expansion of the anterior portion of the second through seventh branched fin-rays in males (independently acquired in *Lebiasina* and *Nannostomus*).
66. The asymmetrical development of broad canals along

the anterior surface of the expanded anal-fin rays in males.

67. The elaboration of the basal processes on the third through eighth anal-fin rays in males.

Ambiguous features for this clade are as follows:

F_1. The absence of the fourth infraorbital (also absent in a clade within *Boulengerella*).

F_2. The ventral shift of the coronomeckelian ossification into Meckel's cartilage (condition also present in the Erythrinidae).

F_3. The absence of the second postcleithrum (also absent in *Hepsetus* and a clade within *Boulengerella*).

F_4. The anterior position of dorsal fin.

No unique autapomorphies were discovered for either of the species of *Ctenolucius* in the course of this study. The pattern of discrete body striping typical of *C. beani*, which extremely rarely occurs in one population of *C. hujeta*, may be autapomorphic for the species.

MONOPHYLY OF *Boulengerella*

The five species of *Boulengerella* share the following 13 synapomorphies:

68. The distinct shelf on the lateral surface of the first infraorbital ventral of the nares.
69. The system of deep-lying, vertically aligned canals within the supraorbital.
70. The vertically aligned process on the medial surface of the supraorbital.
71. The elongation of the nasal to a length longer than the orbital width.
72. The gap between the medial surfaces of the premaxillae anterior to the mesethmoid.
73. The distinct notch in the posteroventral portion of the maxilla.
74. The medial process on the main body of the maxilla that serves as the area of attachment for the ligamentum primordiale.
75. The fleshy, elongate process at the tip of the snout in intermediate-size specimens.
76. The acute angle at which the rows of teeth of the contralateral premaxilla meet anteriorly.
77. The band of small, very numerous ectopterygoid teeth.
78. The well-developed anterior processes of the branchiostegal rays proximate to the region of articulation of the rays with the hyoid arch.
79. The transversely flattened interhyal with a distinct plate-like process posteriorly.
80. The absence of gill-rakers along the trailing margin of the second ceratobranchial and the reduction in the number of or absence of rakers along the trailing margin of the third and fourth ceratobranchials.

Ambiguous features for this clade are as follows:

G_1. The location of the coronomeckelian ossification dorsal of Meckel's cartilage (secondary shift to plesiomorphic position).

G_2. The well-developed anteriorly directed process extending from the anteroventral margin of the palatine (secondarily lost in family).

INTRAGENERIC RELATIONSHIPS IN *Boulengerella*

Two major clades are defined within *Boulengerella* on the basis of a series of derived features. The first consists of two species, *B. lateristriga* and *B. maculata.* These species share the following nine synapomorphies:

81. The exclusion of the fifth infraorbital from the orbital rim.
82. The absence of the posterodorsal laterosensory canal segment in the sixth infraorbital and the lack of contact of the sixth infraorbital and pterotic.
83. The pronounced elongation of the nasal, which is distinctly longer than the orbital width.
84. The pronounced reduction in the supratemporal laterosensory canal segment to a small section proximate to the anterodorsal portion of the extrascapular.
85. The expansion of the supraoccipital dorsally in the region immediately posterior of the median overlap of the parietals.
86. The presence of mesopterygoid dentition (independently acquired in *Hoplerythrinus*).
87. The greatly expanded plate-like process on the posterior margin of the interhyal.
88. The extreme reduction of the transverse process of the third neural arch.
89. The reduction of the laterosensory canal system on the body.

Ambiguous features for this clade are as follows:

H_1. The absence of the fourth infraorbital (also lacking in *Ctenolucius*).

H_2. The well-developed anteriorly directed process on the palatine.

H_3. The absence of the second postcleithrum (also lacking in *Ctenolucius* and the Hepsetidae).

H_4. The posterior position of the dorsal fin (also occurring in *Ctenolucius*).

Boulengerella maculata is distinguished by two autapomorphies:

90. The pattern of relatively large dark spots on at least the dorsal and often the dorsolateral surfaces of the body.
91. The pattern of dark and light marmoration on the lobes of the caudal fin.

Boulengerella lateristriga is characterized by four autapomorphies:

92. The reduction of the portion of the laterosensory canal system in the pterotic.
93. The extremely attenuate anterior processes of the branchiostegal rays in the region proximate to the attachment of the ray to the hyoid arch.
94. The striking dark midlateral stripe on the postorbital portion of the head and midlateral surface of the body delimited dorsally by a thin, particularly dark line.
95. The distinct dark crossbars on the lobes of the caudal fin.

The second major clade in *Boulengerella* consists of three species (*cuvieri, lucius,* and *xyrekes*) characterized by the following seven synapomorphies:

96. The pronounced horizontal elongation of the first infraorbital, which reaches nearly to the ventral margin of the nasal.
97. The horizontal shelf on the medial surface of the first infraorbital.
98. The presence of a laterosensory canal segment along the dorsal margin of the fifth infraorbital.
99. The reduction or loss of the anterodorsal portion of the laterosensory canal system in the sixth infraorbital.
100. The medially directed process on the medial margin of the tripus.
101. The pronounced development of the posterior rays of the anal fins in larval and juvenile individuals.
102. The very dark anal fin in larval and juvenile individuals.

Ambiguous features for this clade are as follows:

I_1. The presence of a fourth infraorbital.
I_2. The presence of the second postcleithrum (derived under two of three alternative hypotheses).
I_3. The anterior position of the dorsal fin.

Despite the numerous derived features defining the Ctenoluciidae and its subunits, no unambiguous synapomorphies have been found to resolve the relationships within the tritomy of *Boulengerella cuvieri, B. lucius,* and *B. xyrekes.*

Boulengerella lucius is defined by three autapomorphies:

103. The pronounced development of the medial process on the medial margin of the tripus.
104. The pattern of dark body spots on the ventrolateral region of the body.
105. The pattern of dark, horizontally elongate stripes between the basal portions of the central rays of the caudal fin.

One ambiguous autapomorphy has been identified for this species:

J_1. The absence of the well-developed, anteriorly directed process on the palatine.

No unique and unreversed or unambiguous characters were found for *Boulengerella cuvieri* and *B. xyrekes,* but one ambiguous feature common to the two species was found:

K_1. The well-developed, anteriorly directed process on the palatine.

Boulengerella cuvieri is characterized by a single autapomorphy:

106. The absence of the anterodorsal portion of the laterosensory canal system in the sixth infraorbital.

Boulengerella xyrekes is characterized by two autapomorphies:

107. The presence in a high percentage of the juveniles of a well-developed, dorsoventrally flattened pad at the anterior of the snout.
108. The retention of the dark band of pigmentation along the posteroventral angle of the opercle in mid-size individuals.

Family CTENOLUCIIDAE Schultz, 1944

Ctenolucinae Schultz, 1944:258.
Ctenoluciidae Greenwood et al., 1966:345.

DIAGNOSIS.—The family Ctenoluciidae is distinguished within Characiforms by a series of derived features (see list of synapomorphies in "Monophyly of the Ctenoluciidae" under "Phylogenetic Reconstruction," above). Externally the family is most readily diagnosed by its attenuate body, elongate jaws, and by the numerous relatively small teeth with posteriorly recurved tips arranged in a single primary series in each jaw, a combination of features not encountered elsewhere among characiforms.

REMARKS.—Schultz' concept of the Ctenolucinae (1944) included *Sarcodaces* Günther (1864), which Hubbs (1939:168) demonstrated was antedated by *Hepsetus* Swainson (1838). Schultz (1950:50) consequently substituted Hepsetinae for his earlier Ctenolucinae. Although various authors have united *Hepsetus, Ctenolucius,* and *Boulengerella* in a single familial-level taxon, the results of this study indicate that these taxa do not constitute a monophyletic assemblage, and *Boulengerella* and *Ctenolucius* herein are recognized as the family Ctenoluciidae following Greenwood et al. (1966).

Key to *Ctenolucius* Gill and *Boulengerella* Eigenmann

Lateral margins of anterior portion of lower jaw with distinct, fleshy, dorsoventrally flattened, laterally tapering process on each side; snout spatulate anteriorly in dorsal view, either rounded anteriorly or with at most a short anterior fleshy appendage; premaxillary teeth forming rounded arch anteriorly, with anterior 4 or 5 teeth distinctly larger than other teeth in jaw; scales with distinct posterior cteni; 45–50 lateral-line scales to end of series . . . . ***Ctenolucius***
(rivers of Lago Maracaibo basin in Venezuela, Ríos Magdalena and Atrato of Caribbean slopes of Colombia, and Río San Juan of Pacific slope in Colombia, and rivers of Pacific versant of Panama)

Lateral margins of anterior portion of lower jaw without distinct, fleshy, dorsoventrally flattened, laterally tapering process on each side; snout pointed anteriorly in dorsal view, terminating anteriorly in elongate, tapering, fleshy appendage except in very large specimens; premaxillary tooth rows of each side meeting at acute angle anteriorly, all premaxillary teeth of approximately same size; scales with surface sculpturing and irregular posterior margins, but lacking distinct cteni; 87–124 lateral-line scales . . . . ***Boulengerella***
(Rio Amazonas and Río Orinoco basins, Essequibo River of Guyana, Oyapock River (Rio Oiapoque) along French Guiana-Brazilian frontier, coastal rivers of Amapá and Pará states in Brazil)

Genus *Ctenolucius* Gill, 1861

Ctenolucius Gill, 1861a:8 [type species *Xiphostoma hujeta* Valenciennes in Cuvier and Valenciennes, 1849, by subsequent monotypy; established by Bean 1908:701 who incorrectly identified his material as *Ctenolucius hujeta;* gender masculine].

Luciocharax Steindachner, 1878:91 [type species *Luciocharax insculptus* Steindachner, 1878:91 (= *Ctenolucius hujeta*), by monotypy; gender masculine].

Belonocharax Fowler, 1907:464 [type species *Belonocharax beani* Fowler, 1907:464, by original designation; gender masculine].

DIAGNOSIS.—*Ctenolucius* is characterized by a series of derived features listed above in "Monophyly of *Ctenolucius*" under "Phylogenetic Reconstruction" and is readily distinguished externally from *Boulengerella,* the other ctenoluciid genus, by the possession of 45–50 lateral-line scales, in contrast to the 87–124 scales in that series in *Boulengerella.* The scales of *Ctenolucius* have distinct posterior serrations whereas those of *Boulengerella,* although having surface sculpturing and irregular posterior borders, lack such serrations. *Ctenolucius* also has distinct, dorsoventrally flattened flaps along the anterior portion of the lower-jaw margin (Figure 7) that are absent in *Boulengerella. Boulengerella,* by comparison, has an elongate fleshy appendage at the tip of the snout (e.g., *B. lateristriga,* Figure 32) in all but the largest specimens. This contrasts with the poorly developed or absent snout appendage in *Ctenolucius.* The rounded arch of enlarged dentition anteriorly on the upper jaw of *Ctenolucius* contrasts with the more uniformly sized dentition that meets at an acute angle anteriorly in *Boulengerella.* The genera are allopatric, with *Ctenolucius* occurring to the west of and *Boulengerella* to the east of the Andean Cordilleras.

DISTRIBUTION.—Pacific versant rivers of Panama from Veraguas Province east, Río San Juan of the Pacific slope of Colombia, Río Atrato and Río Magdalena of the Caribbean versant of Colombia, and rivers draining into Lago Maracaibo of northwestern Venezuela. Reports of *Ctenolucius* from the western portions of the Río Orinoco basin (Cala, 1977:8; Castro, 1986:3) are evident misidentifications of *Boulengerella.*

REMARKS.—Four generic names have been applied to the lineage formed by the two *Ctenolucius* species recognized in this study. *Xiphostoma,* the generic name used by early researchers (Agassiz in Spix and Agassiz, 1829; Cuvier, 1829) for species now assigned to *Ctenolucius,* is, however, unavailable in fishes, being preoccupied in Hemiptera. Gill (1861a:8), in a lengthy footnote, proposed *Ctenolucius* on the basis of specimens from the Río Atrato, which he indicated were "closely allied" to *Xiphostoma* (= *Ctenolucius*) *hujeta* Valenciennes. Gill's description and his subsequent references to *Ctenolucius* (1861b:258; 1895:199) were overlooked by researchers until Bean (1908:701) redescribed the genus in detail based on two of the three specimens (USNM 1658) that were the basis of Gill's (1861a) note.

Steindachner (1878:91) proposed *Luciocharax* for *L. insculptus,* which he described at the same time. Apparently he was unaware of Gill's *Ctenolucius* and contrasted *Luciocharax* to *Xiphostoma,* the genus utilized by Valenciennes in Cuvier and Valenciennes (1849). The ctenoluciids in the Río Magdalena, the type locality of *Luciocharax insculptus,* which is the type species of *Luciocharax,* are conspecific with those in the

Lago Maracaibo basin, the type locality of *Xiphostoma hujeta,* which is the type species of *Ctenolucius* (see "Remarks" under *Ctenolucius hujeta*). *Luciocharax* consequently is considered a synonym of *Ctenolucius.*

In the interval between Gill's proposal of *Ctenolucius* (1861a:8) and its redescription by Bean (1908:701), one of the specimens examined by Gill (USNM 1658, in part) was exchanged with the Academy of Natural Sciences, Philadelphia. Fowler (1907:464) proposed a new genus and species, *Belonocharax beani,* based on this specimen (ANSP 16642). Fowler contrasted *Belonocharax* with *Boulengerella,* although he puzzlingly noted at the end of the account (1907:466) for *Belonocharax beani* that the species was very similar to *Xiphostoma* (= *Ctenolucius*) *hujeta.* He neither explained why he did not critically compare his new species with *Xiphostoma,* nor why he proposed a new genus rather than using *Luciocharax,* previously described by Steindachner (1878). Soon thereafter Eigenmann (1907:770) questioned Fowler's new genus, noting that "there is no excuse for passing over the *Luciocharax* (*insculptus*) of Steindachner ... which is undoubtedly the same genus to which *Belonocharax beani* belongs." Regardless of Fowler's reasoning, the ctenoluciids from the Río Atrato, the type locality of *Belonocharax beani,* and those from the Lago Maracaibo basin, the type locality for *Xiphostoma hujeta,* the type species of *Ctenolucius,* differ only in some pigmentary, meristic, and morphometric features (see "Key to Species of *Ctenolucius*" and "Diagnosis" for each species). The species also are hypothesized as sister-species based on 13 synapomorphies, nearly all of which are unique for the genus (see "Monophyly of *Ctenolucius*"). No advantage exists in recognizing two genera for a clade of two species. Thus, *Belonocharax* is considered a synonym of *Ctenolucius.*

Key to Species of *Ctenolucius* Gill, 1861

Body typically without horizontal lines, or with lines very faint; occasional individuals of approximately 100–140 mm SL from Río Magdalena (and possibly Río Sinú) with dark, thin, wavy horizontal lines on body (see "Variation in Pigmentation" under species account for *C. hujeta*); vertebrae 45-48 [Figure 16]; least depth of caudal peduncle 0.084–0.097 in SL [Figure 17]; articulation between supraorbital and sixth infraorbital typically angled posteromedially [Figure 18]; scales in lateral-line series 44–49 [Figure 19]; insertion of first basal pterygiophore of dorsal fin behind neural spine of 26th or 27th vertebrae . . . . **C. hujeta**

(rivers of Lago Maracaibo basin of northwestern Venezuela;
Río Magdalena and Río Sinú of northern Colombia)

Body with series of dark, thin, wavy horizontal lines in specimens greater than approximately 100 mm SL; vertebrae 42—46 [Figure 16]; least depth of caudal peduncle 0.072–0.085 in SL [Figure 17]; articulation between supraorbital and sixth infraorbital typically aligned transversely [Figure 18]; scales in lateral-line series 46–50 [Figure 19]; insertion of first basal pterygiophore of dorsal fin behind neural spine of 28th to 30th vertebrae . . . . **C. beani**

(rivers of Pacific versant of Panama, Río Atrato
and Río San Juan of northwestern Colombia)

Ctenolucius hujeta (Valenciennes in Cuvier and Valenciennes, 1849)

FIGURES 16–26; TABLE 2

Xiphostoma hujeta Valenciennes in Cuvier and Valenciennes, 1849:358 [type locality: (Venezuela) rivers of (Lago) Maracaibo].—Günther, 1864:358 [based on Valenciennes in Cuvier and Valenciennes, 1849].—Eigenmann and Eigenmann, 1891:59 [based on Valenciennes in Cuvier and Valenciennes, 1849].—Eigenmann, 1922:106 [footnote; based on Valenciennes in Cuvier and Valenciennes, 1849; species questionably equated with *Ctenolucius insculptus* (Steindachner)].—Bertin, 1948:31 [depository of syntypic series].

Luciocharax insculptus Steindachner, 1878:91 [type locality: Río Magdalena; brief description; type species of *Luciocharax* Steindachner, by monotypy]; 1879a:67, pl. 13, figs. 2, 2a,b [Colombia: Río Magdalena; more extensive description]; 1880:85 [Colombia: Río Cauca].—Eigenmann, 1910:446 [Río Magdalena basin; *Belonocharax beani* erroneously listed as a synonym].—[not Steindachner, 1879b; Jordan and Evermann, 1896; Regan, 1908; Cockerell, 1915].

Luciocharax hujeta.—Eigenmann, 1910:446 [Lago Maracaibo].

Hydrocynus hujeta.—Eigenmann, 1922:166 [footnote; based on *Xiphostoma hujeta* Valenciennes in Cuvier and Valenciennes, 1849; species questionably equated with *Ctenolucius insculptus* (Steindachner)].

Ctenolucius insculptus.—Eigenmann, 1922:167, pl. XXVI, fig. 5 [Colombia: Soplaviento, Calamar, Bernal Creek, Girardot, Apulo, marsh at Fundación].—Miles, 1941:65 [Colombia: Río Magdalena; general account of external anatomy and behavior]; 1947:175 [Colombia: Río Magdalena and Río Cauca; behavioral comments].—Fowler, 1975:124 [literature compilation].

Ctenolucius hujeta.—Myers, 1942:94 [Venezuela: Lago Maracaibo basin, Río

TABLE 2.—Morphometrics and meristics of (A) lectotype of *Xiphostoma hujeta*, MNHN 4231; (B) lectotype of *Luciocharax insculptus*, NMW 68252; and (C) all other specimens of *Ctenolucius hujeta* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 16 are proportions of standard length; 17 to 21 are proportions of head length. Dashes indicate values that could not be determined as a consequence of the condition of the specimen.

Character	A	B	C
		Morphometrics	
Standard Length	181	192	66.0–228
1. Body depth at dorsal-fin origin	-	0.176	0.147–0.192
2. Snout to dorsal-fin origin	0.818	0.802	0.786–0.830
3. Snout to anal-fin origin	0.845	0.870	0.830–0.880
4. Snout to pectoral-fin origin	0.365	0.345	0.321–0.372
5. Snout to pelvic-fin origin	0.619	0.623	0.576–0.628
6. Dorsal-fin origin to hypural joint	0.220	0.208	0.184–0.233
7. Dorsal-fin origin to anal-fin origin	0.159	0.177	0.153–0.189
8. Dorsal-fin origin to pelvic-fin insertion	-	0.260	0.250–0.301
9. Dorsal-fin origin to pectoral-fin insertion	-	0.496	0.467–0.542
10. Caudal peduncle depth	0.087	0.091	0.084–0.097
11. Pectoral-fin length	-	0.146	0.135–0.170
12. Pelvic-fin length	-	0.122	0.112–0.137
13. Length of longest dorsal-fin ray	-	0.142	0.133–0.165
14. Length of longest anal-fin ray	-	0.148	0.130–0.160
15. Anal-fin base	-	0.072	0.066–0.99
16. Head length	0.376	0.359	0.332–0.387
17. Snout length	0.465	0.442	0.410–0.471
18. Orbital diameter	0.108	0.109	0.104–0.170
19. Postorbital length	0.419	0.436	0.347–0.460
20. Lower-jaw length	0.603	0.597	0.534–0.607
21. Interorbital width	0.176	0.181	0.160–0.201
		Meristics	
Scales along lateral-line series	46*	46	45–49
Pored lateral-line scales	-	26	18–35
Scale rows between dorsal-fin origin and lateral-line series	–	5	4–6
Scale rows between anal-fin origin and lateral-line series	-	6	5–6
Predorsal median scales	-	-	30–36
Postdorsal median scales	-	-	5–7
Branched dorsal-fin rays	7	7	7–8
Branched anal-fin rays	8	8	8
Pectoral-fin rays	-	7	7–8
Branched pelvic-fin rays	-	14	11–16
Vertebrae	45	43	42–46

* Lectotype of *Xiphostoma hujeta* lacks scales; number of lateral-line scales estimated from scale pockets.

Limon basin, Quebrada Sargento, N of Maracaibo; *Luciocharax insculptus* Steindachner considered a synonym].—Schultz, 1950:52 [key to subspecies].—Lawson and Manly, 1973:383 [tooth replacement mechanism].—Fowler, 1975:124 [literature compilation].—Arefjev, 1990:293, fig. 1 [karyotype].—[not Gill, 1861a:8; Bean, 1908; Cala, 1977:8].

Ctenolucius hujeta hujeta.—Schultz, 1944:259 [Venezuela: Lago Maracaibo basin: caño W of Sinamaica, Río Machango, Río San Pedro, Río Socuy, Río Negro, Ciénega del Guanavana, Río Apon, Río Palmar, Río San Juan, Lago Tulé; distinguishing features]; 1950:52 [Lago Maracaibo basin].—Fernández-Yépez and Martin, 1953:228 [Venezuela: Lago Maracaibo basin, Río San Juan].—Mago-Leccia, 1970:74 [Venezuela, common name].—Rodríquez, 1973, fig. 106 [Venezuela: Lago Maracaibo].

Ctenolucius hujeta insculptus.—Schultz, 1944:259 [distinguishing features; Río Magdalena basin]; 1950:52 [Río Magdalena basin].—Dahl in Dahl et al., 1963:42 [Colombia: Rio San Jorge; common name].—Dahl, 1964:54 [Colombia: Río Sinú system]; 1971:106 [Colombia: lower reaches of Río Magdalena and Río Cauca, lower and middle portions of Río Sinú; common name].—Santos-Martínez and Acero P., 1991:253 [Colombia: Ciénega Grande de Santa Marta].

Ctenolucius hujeta beani.—Dahl, 1964:54 [Colombia: Río Sinú system; misidentification]; 1971:106 [Colombia: upper Río Sinú; misidentification].

DIAGNOSIS.—*Ctenolucius hujeta* can be distinguished from its only congener, *C. beani*, by differences in body pigmentation (a plain body in the vast majority of specimens over 70 mm

SL, in contrast to the presence of very dark, wavy stripes on the body in *C. beani;* see also comments under "Variation in Pigmentation" below); number of vertebrae (42–46 versus 45–48; Figure 16); relative least depth of the caudal peduncle (0.084–0.097 of SL versus 0.072–0.085; Figure 17); the alignment of the articulation between the sixth infraorbital and supraorbital (angled posteriorly versus transversely aligned; Figure 18), and number of lateral-line scales (44–49 versus 46–50; Figure 19).

DESCRIPTION.—A moderately sized ctenoluciid species,

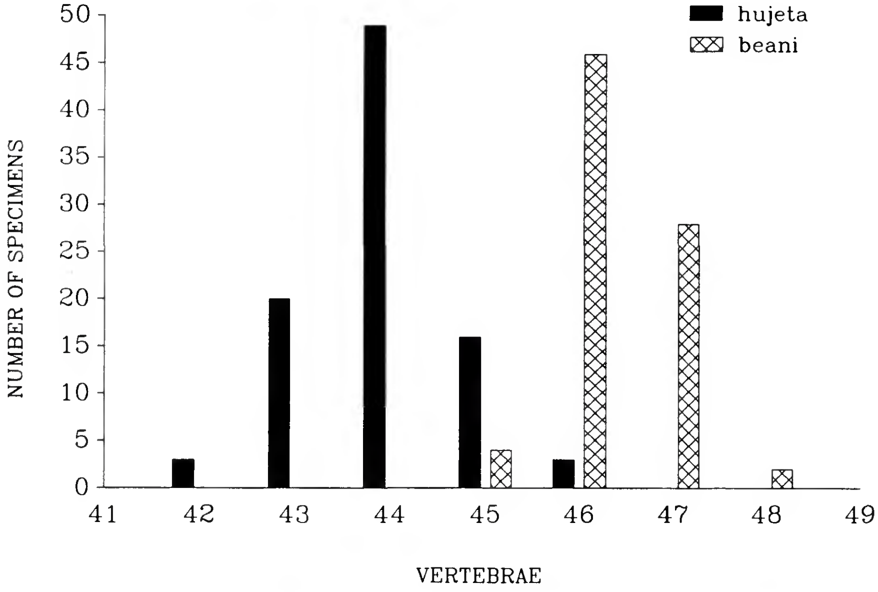

FIGURE 16.—Histogram of vertebral number for examined specimens of *Ctenolucius hujeta* and *C. beani.*

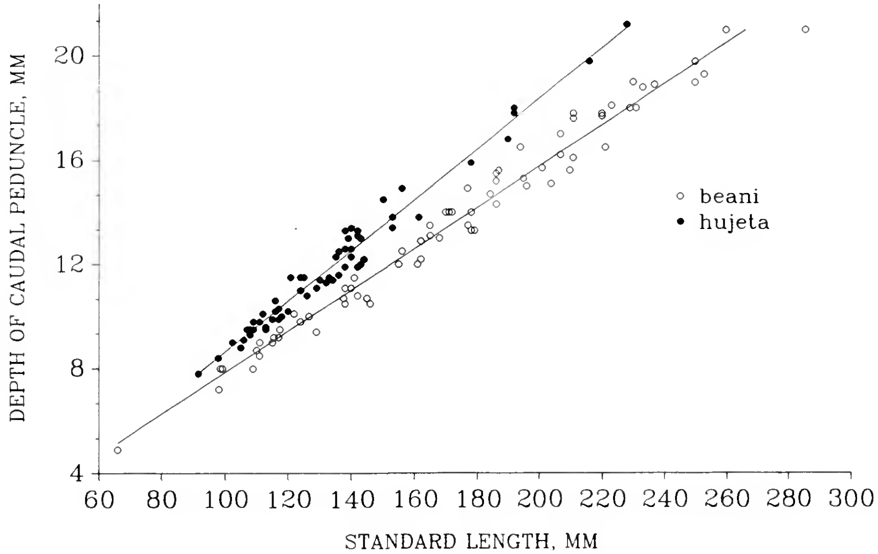

FIGURE 17.—Plot of least depth of caudal peduncle against standard length for *Ctenolucius hujeta* (n = 62) and *C. eani* (n = 70). Some symbols represent more than one specimen or data point.

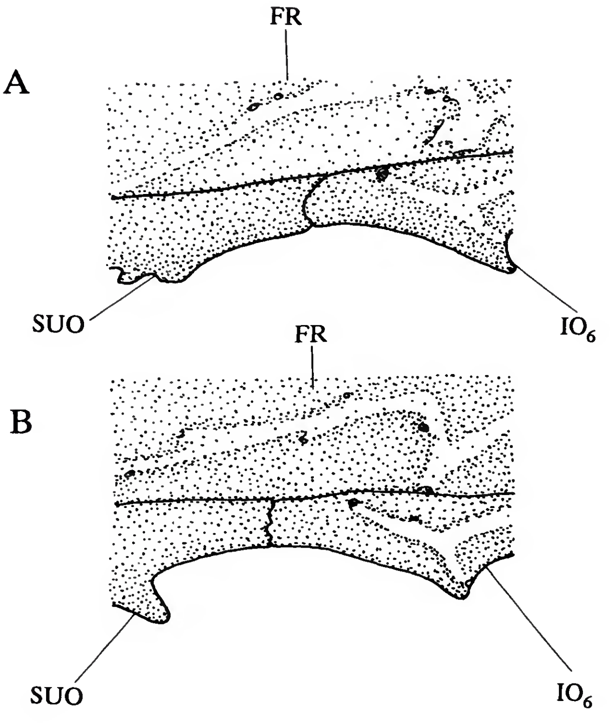

FIGURE 18.—Dorsal view of left lateral margin of the central portion of the head of (A) *Ctenolucius beani* and (B) *C. hujeta* showing contact of sixth infraorbital with supraorbital.

achieving 228 mm SL. Head and body markedly elongate (Figures 20–23). Greatest body depth at origin of dorsal fin in smaller individuals, progressively shifting anteriorly with increasing standard length, most obviously so in ripe females. Dorsal profile of head somewhat convex anteriorly from tip of snout to region of snout dorsal to fleshy processes on lower jaw; nearly straight from that region to rear of head. Dorsal profile of body slightly convex anteriorly, then straight to origin of dorsal fin; straight and slightly posteroventrally slanted at base of dorsal fin, straight or nearly so from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body smoothly rounded transversely anterior and posterior to dorsal fin. Ventral profile of head slightly concave ventral of fleshy lateral processes on anterior portion of lower jaw, gently convex from that region to under pectoral girdle. Ventral profile of body slightly convex in smaller individuals, increasingly curved to origin of anal fin in larger individuals; base of anal fin distinctly angled posterodorsally with ventral margin of caudal peduncle nearly straight.

Head distinctly pointed in profile, proportionally more so in specimens over 30 mm SL; upper jaw with dentigerous surface concave anteriorly dorsal to fleshy lateral processes of lower jaw, straight from that region to maxilla, gently convex along anterior margin of maxilla in specimens greater than 30 mm SL, convexity more pronounced in smaller individuals; upper jaw and anterior premaxillary dentition overlapping tip of lower jaw. Snout elongate, proportionally more so in individuals over 30 mm SL. Anterior portion of snout spatulate in dorsal

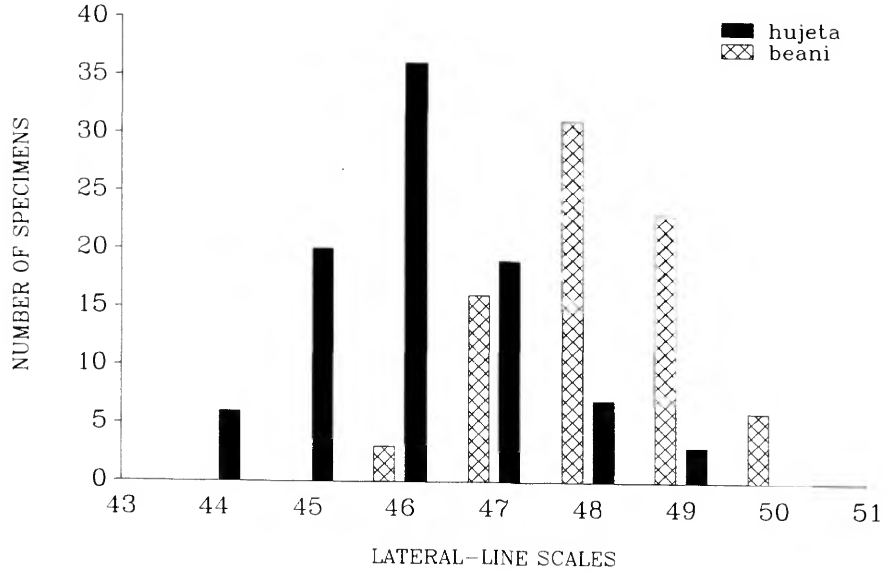

FIGURE 19.—Histogram of number of lateral-line scales in examined specimens of *Ctenolucius hujeta* and *C. beani*.

FIGURE 20.—*Ctenolucius hujeta*, UF 30706, juvenile, 28.5 mm SL; Venezuela, Zulia, flooded area 0.8 km NW of intersection of road to Tule and road to Cuatro Bocas (at Los Veras).

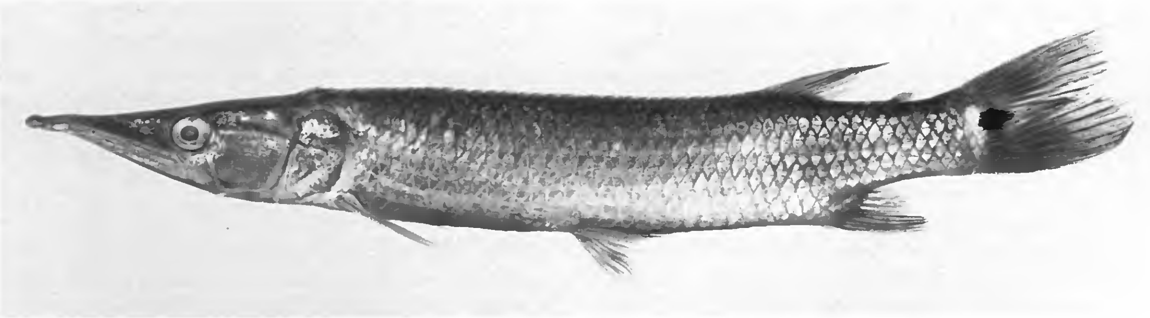

FIGURE 21.—*Ctenolucius hujeta*, USNM 121345, 168 mm SL; Venezuela, Zulia, Lago Maracaibo basin, caño 0.5 mi (0.8 km) E of Sinamaica.

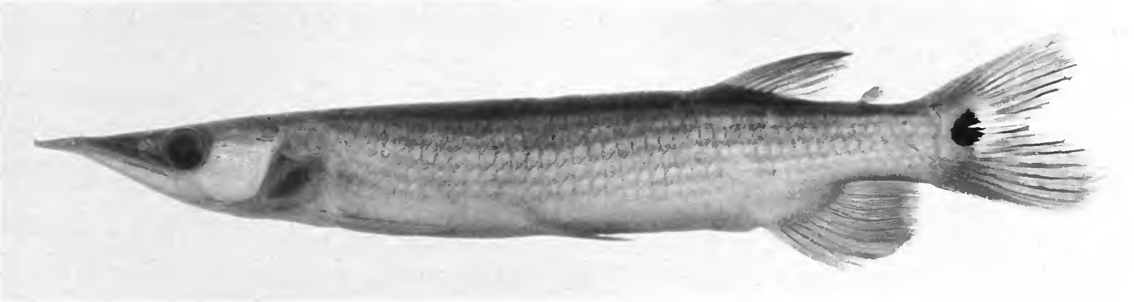

FIGURE 22.—*Ctenolucius hujeta*, UF 25443, 121 mm SL; Venezuela, Zulia, municipio Rosario, caño on Hacienda El Tigre.

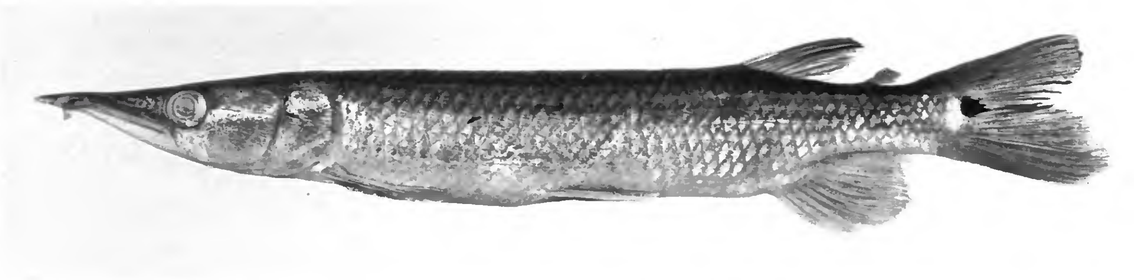

FIGURE 23.—*Ctenolucius hujeta*, ANSP 128279, 141 mm SL; Colombia, Caldas, small tributary of Río Miel, 6.8 km by road downstream from San Miguel (5°25'N, 75°00'W).

view. Tip of snout in some individuals with moderately developed fleshy process. Spatulate anterior portion of snout followed posteriorly by distinct transverse constriction. Lower jaw elongate, proportionally more so in individuals above 30 mm SL, rounded anteriorly, with tip inserting in space behind enlarged anterior teeth of upper jaw. Lateral surfaces of lower jaw with horizontally aligned flap of tissue slightly ventral of line of emergence of dentition. Flap extends from approximately vertical line through first dentary tooth to area where maxilla overlaps dentary laterally. Anterior portion of flap highly developed, forming distinct, dorsoventrally flattened lateral process (Figure 7) that is proportionally larger in specimens under 30 mm SL; portion of horizontal flap posterior to lateral process much less extensive, gradually decreasing in width posteriorly. Nostrils of each side proximate; anterior somewhat tubular, posterior distinctly larger and semicircular.

Teeth in jaws vary in both relative size and form. Premaxillary teeth in two rows, with outer row with numerous teeth and short inner row. Teeth in outer premaxillary row numbering 41-105 in specimens of 14.7-78.0 mm HL, with number somewhat variable at particular head length (Figure 24). Overall ontogenetic trend is an allometric increase in number of teeth; rate of increase decreasing at larger standard lengths. In many specimens, dentition of outer premaxillary row consisting of two sections, with short anterior section and much longer posterior portion. Anterior section of outer row of premaxillary dentition with 4-6 teeth distinctly larger than those on rest of jaw. Symphyseal and most posterior teeth in anterior series smallest. Anterior series of enlarged conical teeth usually separated by gap from lengthy posterior series of recurved premaxillary teeth, but with anterior and posterior series of premaxillary dentition continuous in some individuals. Anterior teeth of posterior series of premaxilla smaller than those in rest of jaw, gradually increasing in size posteriorly. Inner row of 3-5 well-developed teeth on each premaxilla in anterior expanded region. Maxilla with 15-27 teeth along its anterior margin, with general trend to increased number of teeth with increasing size, but with wide variation in number of teeth present across limited range of standard lengths. Dentary without teeth anteriorly in region proximate to symphysis, with 41-114 teeth in outer series in specimens of 14.7-78.0 mm HL. Number of dentary teeth somewhat variable at particular head length (Figure 25). Overall ontogenetic trend is an allometric increase in number of dentary teeth; rate of increase decreasing at larger standard lengths. Anterior teeth of dentary series somewhat enlarged, followed by series of small teeth that gradually increase in size with all of recurved teeth along posterior half of series of approximately same size. Dentary with inner series of much smaller teeth paralleling outer dentary row posteriorly. Teeth on pharyngeal tooth-plates small, conical.

Scales with longitudinal ridges and distinctly ctenoid posterior margin. Scales along pre- and postdorsal midlines arranged in somewhat irregular rows. Anterior 18-35 scales of lateral line perforated; number of perforated scales increasing up to approximately 100 mm SL. Number of scales along lateral-line series 45-49. Poring of lateral-line scales occasionally irregular posteriorly.

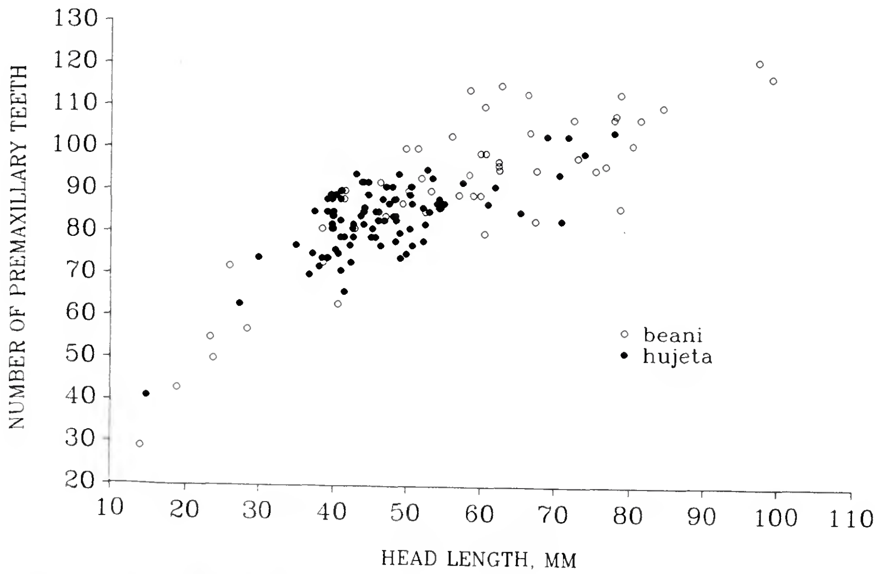

FIGURE 24.—Plot of head length against number of premaxillary teeth for *Ctenolucius hujeta* (n = 90) and *C. beani* (n = 59). Some symbols represent more than one specimen or data point.

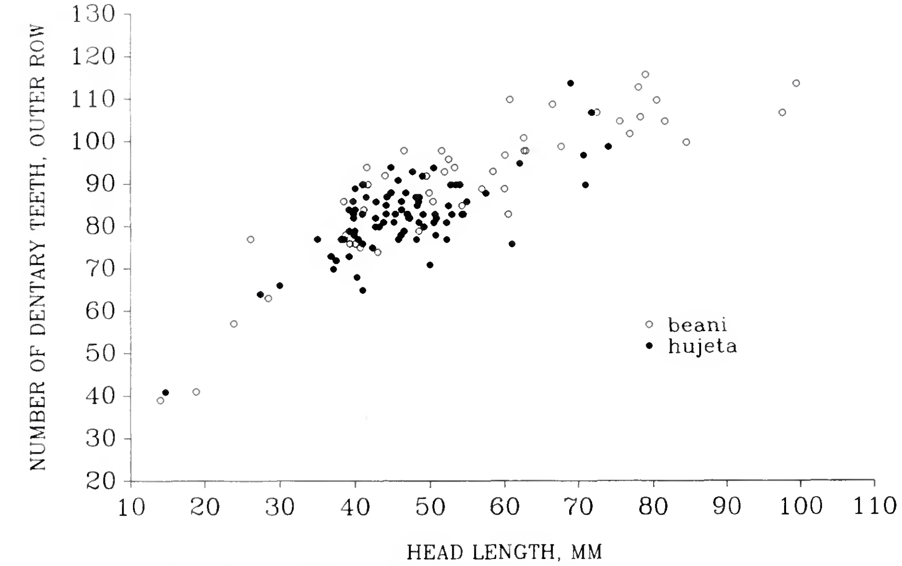

FIGURE 25.—Plot of head length against number of dentary teeth for *Ctenolucius hujeta* (n = 85) and *C. beani* (n = 57). Some symbols represent more than one specimen or data point.

Dorsal fin ii–iii,8 or ii–iii,7,i. First basal dorsal-fin pterygiophore inserting behind neural spine of 26th or 27th vertebrae. Posterior terminus of base of dorsal fin approximately at vertical line through origin of anal fin. Distal margin of dorsal fin straight or slightly convex. Anal fin ii–iii,8. First basal pterygiophore of anal fin inserting behind hemal spine of 29th to 31st vertebrae. Anal fin of females emarginate distally and without branched rays anteroposteriorly expanded (Figure 21), that of males distinctly rounded distally, with greatly expanded branched rays (Figure 22). Pectoral fin lobulate, without developed fin rays in specimens under 35 mm SL; larger individuals with i,11–16,iii–iv rays. Pectoral fin pointed in profile with first to third branched rays longest; tip extends posteriorly approximately one-half distance to pelvic fin. Pelvic fin i,7, rarely i,8; margin of fin pointed, with first unbranched ray longest; tip reaches approximately one-third distance to anal fin. Caudal fin forked, lobes somewhat rounded. Adipose fin proportionally relatively small.

VERTEBRAE.—42(3), 43(20), 44(49), 45(16), 46(3) [45].

KARYOTYPE.—2n = 36 = 26M, SM + 10ST, A (Arefjev, 1990:293).

LIFE COLORATION.—Photographs of live specimens apparently of *Ctenolucius hujeta* from unspecified localities (Géry, 1977:101; Axelrod et al., 1987:281) show that the species is bright silver on both the head and body. Silver coloration notably brighter immediately anterior to dark spot on basal portions of caudal peduncle. Caudal fin with yellow tint on middle rays, distinct dark spot basally, and white margins to dorsal and ventral fin-rays. Photograph in Axelrod et al. (1987:281) does not reveal any difference in life coloration between males (upper specimen in photograph) and females (lower specimen).

COLOR IN ALCOHOL.—Juveniles of approximately 20–35 mm SL from Lago Maracaibo basin (USNM 121335; UF 30706) with pigmentation pattern much different than in larger individuals. Stripe of dark pigmentation extending along upper and lower jaws to anteroventral margin of eye. Stripe continues across ventral margin of eye and lateral surface of infraorbitals to posterior margin of opercle. Body with distinct strip of dark pigmentation extending from above insertion of pectoral fin posteriorly to rear of caudal peduncle, contacting ventral margin of body in region of anal fin. Ventral portion of body lacking dark pigmentation. Juveniles of 20–35 mm SL lacking distinct spot of dark pigmentation on basal portions of middle caudal-fin rays characteristic of adults of species. Caudal fin dusky and anal fin with scattered dark chromatophores. Dorsal fin with rays outlined by small dark chromatophores.

Broad stripe on opercle and along body no longer apparent in specimens of 70 mm SL and larger. Specimens over 70 mm SL that retain guanine on scales silvery overall, somewhat darker dorsally. Nearly all larger specimens that lack guanine on scales with tan ground coloration on head and body that gradually becomes darker dorsally, but without any distinct pattern on lateral and dorsolateral surfaces of body. Occasional smaller individuals from Lago Maracaibo tributary rivers with faint longitudinal stripes on body. Small number of examined specimens from the lower Río Magdalena system with distinct dark stripes on body comparable to those of *Ctenolucius beani*. Both individuals with striped and plain bodies with distinct rotund or slightly horizontally elongate dark spot on basal portion of middle caudal-fin rays. Spot centered slightly above midline of fin. Dorsal, anal, pelvic, and caudal fins in larger individuals variably dusky, more so in larger individuals. Basal caudal spot surrounded by lightly pigmented region that is widest posteriorly. Specimens that retain guanine on scales with particularly intense silvery spot immediately anterior to caudal spot.

VARIATION IN PIGMENTATION.—Most specimens of *Ctenolucius hujeta* either have relatively uniformly pigmented dorsal and dorsolateral surfaces of the body, or only slightly discernable longitudinal striping in the region. Various authors (Eigenmann, 1922:167; Dahl and Medem, 1964:54; Dahl, 1971:106) have noted that the populations of *Ctenolucius* in the Ríos Magdalena and Sinú vary in the presence or absence of horizontal striping on the body. Dahl (1964, 1971) used such variation in body pigmentation to distinguish a uniformly pigmented form in the lower Ríos Magdalena and Cauca, and middle and lower Río Sinú, which he identified as *Ctenolucius hujeta insculptus*, from a striped form of the upper Sinú that he called *C. h. beani*.

None of the examined *Ctenolucius* specimens from the Río Sinú (SU 49492, USNM 175294) have body stripes nor do the vast majority of the extensive series of *Ctenolucius* specimens from throughout the Río Magdalena basin. Four smaller specimens (100–140 mm SL) in a sample of 16 specimens of *C. hujeta* from the lower Magdalena have body stripes. Those specimens (CAS 69849, formerly IU 12717, in part) have, however, 46 and 47 vertebrae, counts that are typical of the vast majority of radiographed specimens of *C. hujeta* but that are either outside the range for *C. beani* (47 vertebrae) or are very rare in that species (46 vertebrae) (Figure 16). The relative least depth of the caudal peduncle in these four individuals (0.084–0.089 of SL) also falls in the range for *C. hujeta*, but not of *C. beani*. All other features in the striped specimens agree with those of the plain bodied individuals captured with them and with other populations herein considered *C. hujeta*. The striped individuals thus are considered atypically pigmented individuals of *C. hujeta*.

COMMON NAME.—Colombia: “Aguja, Agujeta, Agujeto” (Dahl in Dahl et al., 1963:42; Dahl, 1971:166). Venezuela: “Hujeta” (Valenciennes in Cuvier and Valenciennes, 1849), “Agujeta” (Mago-Leccia, 1970:74).

ECOLOGY.—Miles (1941:65) noted that, at least in aquaria, *Ctenolucius insculptus* (= *hujeta*) would take only live fish. According to that author, in the wild, individuals of unspecified size “hunt alone, lying in wait in small inlets.” He also reported that the species has a sudden strike involving bending the body into a Z and capturing its prey cross-wise in its jaws. Dahl (1971:106) reported that this species, identified by him as *Ctenolucius hujeta insculptus*, is a carnivore not found in turbulent waters.

DISTRIBUTION.—Rivers draining into Lago Maracaibo of northwestern Venezuela, Río Magdalena and Río Sinú basins of northern Colombia (Figure 26).

REMARKS.—*Ctenolucius hujeta* of this study encompasses two of the four nominal species assigned to *Ctenolucius; Xiphostoma hujeta* Valenciennes in Cuvier and Valenciennes (1849) and *Luciocharax insculptus* Steindachner (1878). Considerable confusion has existed concerning these nominal species and their geographic ranges.

Valenciennes in Cuvier and Valenciennes (1849:358), described *Xiphostoma hujeta* from specimens originating in the Lago Maracaibo basin. Three decades later Steindachner (1878:91) described *Luciocharax insculptus* based on specimens from the Río Magdalena system of northern Colombia. Steindachner (1878, 1879a) did not mention *Xiphostoma hujeta* in his description of *Luciocharax insculptus*, and it is unclear whether he considered Valenciennes' description of *X. hujeta*. Instead, Steindachner compared his genus and species with nominal species assigned herein to *Boulengerella*. Soon thereafter, Steindachner (1879b) reported *Luciocharax insculptus* from Panama. The species name *insculptus* subsequently was applied to Panamanian ctenoluciid populations by various authors (Jordan and Evermann, 1896; Regan, 1908; and Cockerell, 1915). Under that concept, *Luciocharax insculptus* ranged from the Río Magdalena west to central Panama. Bean (1908), in contrast, recognized *Ctenolucius hujeta* as occurring in the Río Atrato of western Colombia, giving that nominal form a supposedly disjunct distribution in that basin and Lago Maracaibo, and a range that significantly overlapped the range reported at that time for *Luciocharax insculptus*.

Eigenmann (1910:446) restricted nomenclatural usage of *hujeta* to Lago Maracaibo and of *insculptus* to the Río Magdalena basin. Although listing *Belonocharax beani* as a synonym of *Luciocharax insculptus*, he did not include the Río Atrato, the type locality of *beani*, in the purported range of *insculptus*. He also did not include Panama in the range of *Luciocharax* (= *Ctenolucius*), apparently having overlooked citations of the genus in that country (Steindachner, 1879b; Jordan and Evermann, 1896; Regan, 1908). Subsequently, Eigenmann (1922:166–169) modified his concepts of the distribution of *Ctenolucius* species, recognizing *C. insculptus* from the Río Magdalena and *C. beani* in the Ríos Atrato and San Juan of northwestern Colombia and the Pacific versant rivers of Panama. In a footnote, Eigenmann (1922:166) noted that *Xiphostoma hujeta* had been described from Lago Maracaibo and questionably equated it with *Ctenolucius insculptus*. Thus Eigenmann (1922) tentatively recognized three *Ctenolucius* species, albeit with qualifications about the distinctiveness of two nominal forms.

Myers (1942:94) proposed that *Luciocharax insculptus* was a synonym of *Ctenolucius hujeta* and noted that Bean's (1908) Río Atrato citation of the latter was a misidentification of *C.*

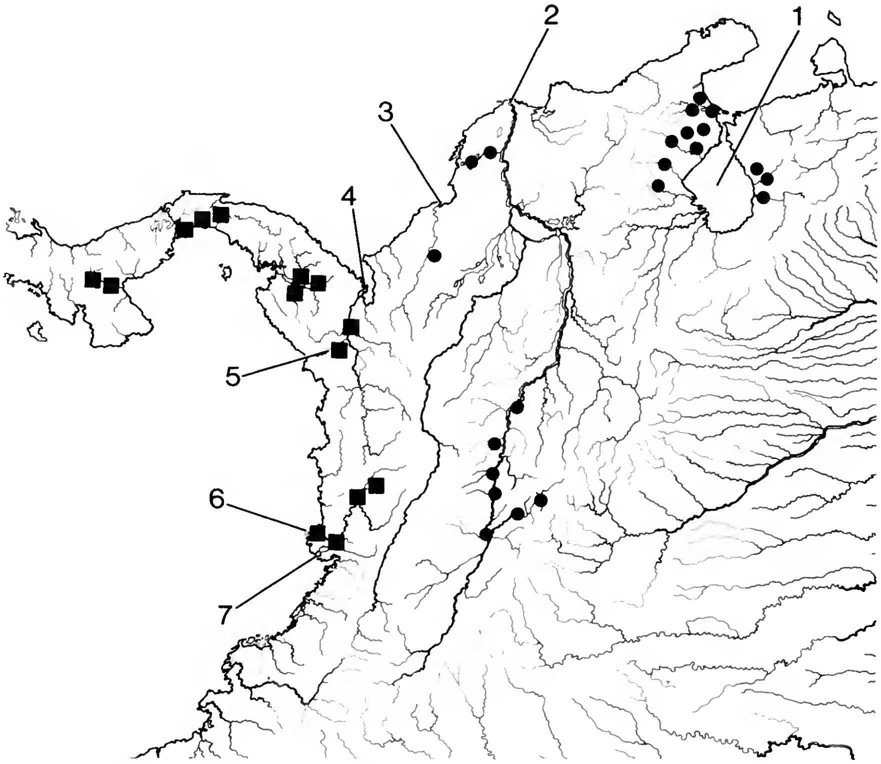

FIGURE 26.—Map of northern South America showing geographic distribution of *Ctenolucius hujeta* (filled in circles; 1 = Lago Maracaibo, inexact type locality of *Xiphostoma hujeta;* 2 = mouth of Río Magdalena, inexact type locality of *Luciocharax insculptus;* 3 = mouth of Río Sinú) and *Ctenolucius beani* (squares; 4 = mouth of Río Atrato; 5 = approximate type locality of *Belonocharax beani;* 6 = mouth of Río San Juan; 7 = type locality of *Luciocharax striatus*). Some symbols represent more than one lot of specimens or locality.

beani. These actions, in conjunction with those of Eigenmann (1922), resulted in two species of *Ctenolucius* being recognized, *hujeta* in Lago Maracaibo and the Río Magdalena basin and *beani* in western Colombia and the Pacific slope of Panama. Myers (1942) did not, however, detail the features that distinguished the nominal forms.

Soon thereafter, Schultz (1944:258–261), in a shift from Myers' (1942) taxonomic scheme, recognized a single species, *Ctenolucius hujeta. Ctenolucius hujeta* as defined by Schultz included three subspecies, *hujeta* of the Lago Maracaibo basin, *insculptus* from the Río Magdalena, and *beani* from the "Pacific slope of Panama and of Colombia." The latter distribution, however, excluded the type locality of *beani*, the Río Atrato, which drains into the Caribbean Sea. This lapse was repeated in Schultz (1950:52).

Schultz (1944:259) noted that "the forms of *Ctenolucius*... are very closely related, and it is difficult, if not impossible to separate them on one or two specimens." The meristic values of Schultz' "Key to the subspecies of *Ctenolucius hujeta*" either do not differ (transverse scale counts), or largely or completely overlap (various scale counts) between his nominal subspecies. Schultz did note that the pigmentation varied somewhat between the different population samples, although not dramatically.

Examination of an extensive series of *Ctenolucius* specimens from throughout its range for this study indicates the existence of two very similar species. These are differentiated based on a combination of vertebral counts (Figure 16), relative depth of the caudal peduncle (Figure 17), and to a lesser degree on lateral-line scale counts (Figure 19). The vast majority of *Ctenolucius* specimens are readily distinguished on the basis of body pigmentation, with *C. beani* having a series of dark body stripes that are absent in *C. hujeta* (see also comments below concerning variation in this feature in Río Magdalena populations).

Ctenolucius hujeta as defined herein includes two nominal species, *Xiphostoma hujeta* Valenciennes and *Luciocharax insculptus* Steindachner. As noted above, Steindachner's

(1878:91) description of *insculptus* did not contrast it with *hujeta* Valenciennes. Schultz recognized the two nominal forms as subspecies of *Ctenolucius hujeta*. The transverse scale-row counts for the subspecies cited by Schultz are identical and the number of circumpeduncular scales in his *C. h. insculptus* (Río Magdalena) are completely overlapped by those of *C. h. hujeta* (Lago Maracaibo). Although Schultz (1944:259-260) indicated different lateral-line scale counts for the nominal subspecies, the examined population samples from the Ríos Magdalena (and Sinú) and Lago Maracaibo have identical scale-count ranges (45–49), with very similar mean values (Maracaibo: 46.89, n = 39; Magdalena and Sinú: 46.26, n = 34). Schultz (1944:259) indicated that *C. h. hujeta* of Lago Maracaibo was characterized by "more or less evident brown wavy lines between rows of scales" contrary to "practically no trace of brown wavy lines along upper sides" in *C. h. insculptus* of the Río Magdalena system. A lack of such stripes is, however, typical for most individuals of *Ctenolucius* from both basins. Such body pigmentation, when present, is actually better developed in individuals from the Río Magdalena system (see "Variation in Pigmentation," above). No differences were found to distinguish the *Ctenolucius* populations from the Ríos Magdalena and Sinú (*insculptus*) from that in the tributaries to Lago Maracaibo (*hujeta*). *Luciocharax insculptus* consequently is considered a synonym of *Ctenolucius hujeta*.

Xiphostoma hujeta was described by Valenciennes in Cuvier and Valenciennes (1849), on the basis of three specimens from unspecified Lago Maracaibo localities. An 181 mm SL specimen (MNHN 4231), in the best overall condition, is designated as the lectotype with the other two syntypes (MNHN 1992-292) thus becoming paralectotypes.

Steindachner's (1878:91) description of *Luciocharax insculptus* evidently was based on five specimens (NMW 68252, 68253, 68254:1-3). An 192 mm SL specimen (NMW 68252), that apparently is also the individual illustrated by Steindachner (1879a, pl. 13: fig. 2), is here designated as the lectotype, with the other specimens (NMW 68253, 68254:1-3) thus becoming paralectotypes.

MATERIAL EXAMINED.—156 specimens (complete data taken on 88 specimens, ~66–228 mm SL; partial data taken on 12 additional specimens).

VENEZUELA. *Zulia:* "rivìeres de Maracaïbo" (= rivers of Lago Maracaibo basin), MNHN 4231, 1 (181; lectotype of *Xiphostoma hujeta*); MNHN 1991-292, 1 (specimen not measurable due to poor condition; paralectotype of *Xiphostoma hujeta;* second specimen in lot not examined). Río Motatán system, Río San Pedro, at bridge, USNM 121334, 9 (5, 116–135; 1 specimen cleared and counterstained). Río Machango, 20 km above bridge south of Lagunillas, USNM 121335, 4 (2, 106–190). Río Negro, below mouth of Río Yasa, USNM 121336, 7 (2, 124–140). Río Palmar, near Totuma, about 100 km SW of Maracaibo, USNM 121337, 1 (228). Lago Tulé, about 80 km W of Maracaibo, USNM 121338, 2. Río Apón, about 35 km S of Rosario, USNM 121339, 6 (3, 138–143). Río Palmar at bridge, 70 km SW of Maracaibo, USNM 121340, 1. Río Machango, at bridge S of Lagunillas, USNM 121341, 3 (2, 113–125). Ciénega del Guanavana, about 10 km N of Sinamaica, USNM 121342, 1 (109). Cienega Gran Eneal, NW of Sinamaica, MBUCV V-13959, 1. Río Motatán system, Río San Juan, near bridge, USNM 121343, 10 (6, 136–142). Rio Socuy, 3 km above mouth, USNM 121344, 10 (3, 91.5–125). Caño 0.75 km E of Sinamaica, USNM 121345, 8 (5, 102–192). Lago de Maracaibo, USNM 310446, 1 (161.5). Flooded area 0.8 km NW of intersection of road to Tule and road to Cuatro Bocas (at Los Veras), UF 30706, 3. Hacienda El Tigre, UF 25443, 5 (2, 121–138). Distrito Perija, Río Guaco, near Cienega de Lagunetas, MBUCV V-13957, 3; MBUCV V-13956, 5. Río Limon at Puerto Rosas, NW of Carrasquero, MBUCV V-13955, 2. Río Cachiri, at Hacienda La Abeja, NE of Maracaibo, MBUCV V-13958, 4. Río Cachiri, near Embalse de Cachiri Tule, MBUCV V-8263, 2. Carrasquero, Centro Agropecuiario "Don Bosco," laguna de cultivo, MBUCV V-13172, 1.

COLOMBIA. Magdalenen-Stromes (= Río Magdalena), NMW 68252, 1 (192, lectotype of *Luciocharax insculptus*); NMW 68253, 1 (216, paralectotype of *Luciocharax insculptus*); NMW 68254.3 1 (178, paralectotype of *Luciocharax insculptus*). Río Magdalena, BMNH 1947.7.1:126–127, 2 (1, 126). *Bolivar:* Soplaviento, along Canal del Dique between Cartagena and Calamar, CAS 69480, 16 (8, 74.0–169, formerly IU 12717, in part); USNM 79221, 4 (109–117, formerly IU 12717, in part); AMNH 7071, 3 (111–153, formerly IU 12717, in part). Calamar, CAS 69481, 4 (3, 107–132, formerly IU 12718, in part). *Tolima:* Bernal Creek, near Honda, CAS 69482, 3 (108–138, formerly IU 12719). Río Magdalena, Honda, MCZ 35803, 1 (115); ANSP 84405, 1 (~68); ANSP 84408, 1 (~66). *Cudinamarca:* Bogata, MCZ 32151, 1. Río Bogota, Juntas de Apulo, on railway between Girardot and Facatativa, CAS 69484, 4 (105–122, formerly IU 12721). Río Magdalena, Girardot, CAS 69583, 2 (120–126; formerly IU 12720, in part). *Caldas:* Río Purnio, above La Dorada, ANSP 84406, 1 (91.5). Small tributary of Río Miel, 6.8 km by road downstream from San Miguel (5°25'N, 75°00'W), ANSP 128279, 7 (113–153). At or near junction of Ríos Samana and La Miel, near La Dorada (5°29'N, 74°40'W), SU 50392, 4 (97.8–124). *Antioquia:* Río Magdalena, Estacion Grecia, near Puerto Berrío, LACM 32146-1, 2 (136–144). *Cordoba:* Quebrada Lorenzo, Río Sinú basin (not located), SU 49492, 2 (116–117). Río Sinú basin, Betancí, USNM 175294, 4 (109–124).

Ctenolucius beani (Fowler, 1907)

FIGURES 16–19, 24–30; TABLES 3, 4

Luciocharax insculptus.—Steindachner, 1879b:169 [Panama: Río Mamoni at Chepo; misidentification].—Jordan and Evermann, 1896:268 [Panama: Río Mamoni; presumably based on Steindachner, 1879b].—Regan, 1908:168 [in part, Panama: Río Mamoni; presumably based on Steindachner, 1879b].—

Cockerell, 1915:155 [Panama: Río Abaco; scale morphology].

Belonocharax beani Fowler, 1907:464, fig. 51 [type locality: Colombia: Truando, Río Atrato basin; type species of *Belonocharax* Fowler, by original designation].—Böhlke, 1984:66 [depository of holotype].

Ctenolucius hujeta.—Bean, 1908:701 [redescription of *Ctenolucius* Gill; specimens from Colombia: Río Truando, Río Atrato system; misidentification].

Luciocharax striatus Boulenger, 1911:212 [type locality: Colombia, Choco, Boca de [Río] Calima].—Regan, 1913:466 [Colombia: Pacific Slope, Río San Juan].—Eigenmann, 1922:168 [placed as a synonym of *Ctenolucius beani*].

Luciocharax beani.—Meek and Hildebrand, 1916:302 [Panama: Río Tuyra (= Tuira), Río Mamoni, Río Marte Arnade, and Río Juan Diaz].

Ctenolucius beani.—Eigenmann, 1920:11 [Colombia: Río San Juan and Río Atrato basins]; 1922:168 [Colombia: Río San Juan basin, Puerto Negria, Istmina; Río Atrato basin, Managru, Río Sucio, Truando. Panama, Río Calobre. *Luciocharax striatus* Boulenger considered a synonym of *Belonocharax beani* Fowler].—Breder, 1925:144 [Panama: Pacific slope, Río Tapia]; 1927:128 [Panama: Río Chucunaque system: below Yavisa, at Yavisa, above Río Sansan, above Río Chiati, below Río Sucubti].—Hildebrand, 1938:289 [Panama: Pacific slope, La Jagua Hunting Club].—Rendahl, 1941:12 [Colombia: Río San Juan, Cabaceras].—Gosse, 1966:9 [Panama: Panama, Río Bayano basin, Río Silugandi and Río Escobar].—Fowler, 1975:124 [literature compilation].—McPhail, 1977:1063 [predatory habits].

Ctenolucius hujeta beani.—Schultz, 1944:259 [distinguishing features; Pacific slope of Panama and Colombia]; 1950:52 [Pacific slopes of Panama and Colombia].—[not Dahl and Medem, 1964].

DIAGNOSIS.—*Ctenolucius beani* can be distinguished from its only congener, *C. hujeta*, by differences in body pigmentation (the possession of dark, wavy stripes on the body in all specimens greater than approximately 80 mm SL in contrast to the typical absence of such body pigmentation in *C. hujeta;* see also "Variation in Pigmentation" in species account of *C. hujeta*); number of vertebrae (45–48 versus 42–46; Figure 16); relative least depth of the caudal peduncle (0.072–0.085 versus 0.084–0.097 of SL; Figure 17); the alignment of the articulation between the sixth infraorbital and supraorbital (typically transversely aligned versus angled posteriorly; Figure 18); and number of lateral-line scales (46–50 versus 44–49; Figure 19).

DESCRIPTION.—Largest species of the genus, achieving at least 286 mm SL. Head and body markedly elongate at all sizes (Figures 27–30). Greatest body depth at origin of dorsal fin in individuals to about 150 mm SL, progressively shifting anteriorly with increasing standard length, especially in ripe females. Dorsal profile of head somewhat convex anteriorly to region above fleshy lateral process on lower jaw; nearly straight from that region to rear of head. Dorsal profile of body slightly convex anteriorly and then straight to slightly convex to origin of dorsal fin; straight and posteroventrally slanted at base of dorsal fin, nearly straight from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body transversely rounded anterior and posterior to dorsal fin. Ventral profile of head slightly concave anteriorly and then convex to under pectoral girdle. Ventral profile of body nearly straight to anal fin in specimens up to approximately 150 mm SL, increasingly convex in larger specimens.

Head distinctly pointed in profile. Form of upper jaw, snout, lower jaw, lateral fleshy flaps on lower jaw, and nostrils as described for *Ctenolucius hujeta*, above.

Teeth in jaws vary in both relative size and form. Premaxillary teeth in single row with 29–121 teeth in specimens of 14.0–102 mm HL, with number somewhat variable at particular standard length (Figure 24). Overall ontogenetic trend is an allometric increase in number of teeth; rate of increase decreasing at larger standard lengths. Form and variation in size of premaxillary teeth in *Ctenolucius beani* comparable to those described for *C. hujeta*, above. Maxilla with 14–26 teeth along its anterior margin, with general trend of increased number of teeth with increasing body length, but with wide variation in number of teeth present in discrete range of standard lengths. Inner row of 3–5 well-developed premaxillary teeth on each side. Dentary without teeth in region proximate to symphysis, with 39–116 teeth in outer series in specimens of 14.0–102 mm SL. Number of teeth somewhat variable at particular standard length (Figure 25). Overall ontogenetic trend is an allometric increase in number of teeth; rate of increase less pronounced at larger standard lengths. Dentary with inner series of much smaller teeth paralleling outer dentary row posteriorly. Teeth on upper and lower pharyngeal tooth-plates small and conical.

Anterior 14–34 scales of lateral line perforated; number of pored scales increasing up to approximately 110 mm SL. Poring of lateral-line scales occasionally irregular posteriorly. Scales with ridges on surface and distinctly ctenoid posterior margin. Scales along pre- and postdorsal midlines arranged in somewhat irregular rows.

Dorsal fin ii–iii,8 or ii–iii,7,i. First basal pterygiophore of dorsal fin inserting behind neural spine of 28th to 30th vertebrae. Posterior portion of base of dorsal fin anterior to vertical line through origin of anal fin. Distal margin of dorsal fin straight to slightly convex. Anal fin usually ii–iii,8,i, sometimes ii–iii,8. First basal pterygiophore of anal fin inserting behind hemal spine of 30th or 31st vertebra. Anal fin of males distinctly rounded distally with greatly expanded branched rays (Figures 28, 29) and that of females emarginate distally and without anteroposteriorly expanded branched rays (Figure 30). Pectoral fin i,12–16,iii–iv. Pectoral-fin profile pointed, with first to third branched rays longest; tip extends posteriorly approximately one-half distance to pelvic fin. Pelvic fin i,7, very rarely i,8. Margin of pelvic fin pointed, with first unbranched ray longest; tip reaches approximately one-third distance to anal fin. Caudal fin forked, lobes somewhat rounded. Adipose fin relatively small.

VERTEBRAE.—45(4), 46(46), 47(28), 48(2) [47].

LIFE COLORATION (description based on a color transparency provided by Sven O. Kullander and Anita Hogeborn-Kullander of a recently captured specimen from western Colombia).—Overall coloration of body bright silver, somewhat more olive colored dorsally. Head dark dorsally, with scattered regions of guanine. Lower jaw, opercle, and iris

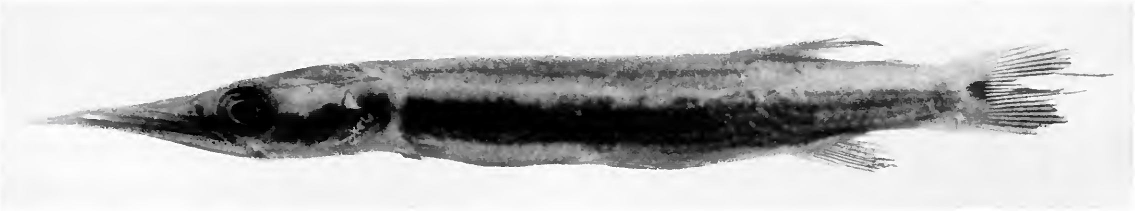

FIGURE 27.—*Ctenolucius beani*, CAS 18534 (formerly IU 13052), juvenile, 66.0 mm SL; Colombia, Chocó, Río Atrato basin, Managrú.

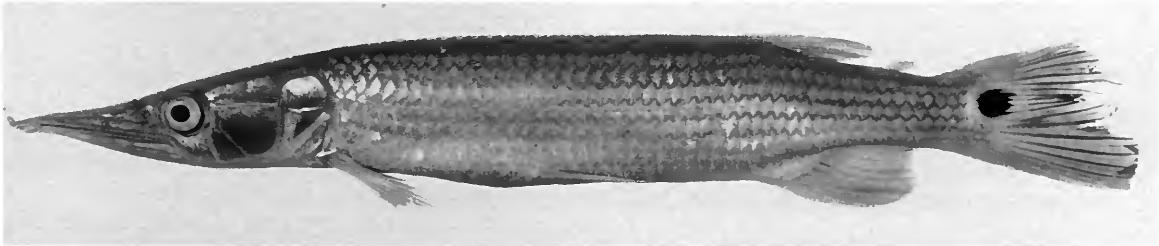

FIGURE 28.—*Ctenolucius beani*, CAS 18534 (formerly IU 13052), adult male, 170 mm SL; Colombia, Chocó, Río Atrato basin, Managrú.

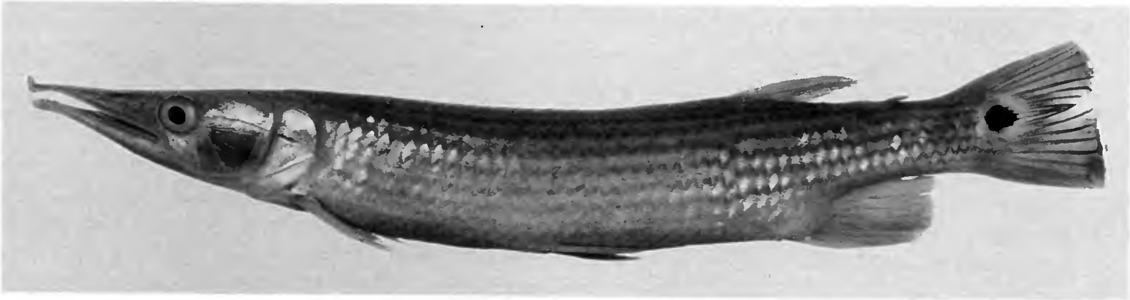

FIGURE 29.—*Ctenolucius beani*, CAS 13909 (formerly IU 13909), adult male, 186 mm SL; Colombia, Chocó, Istmina, Río San Juan basin.

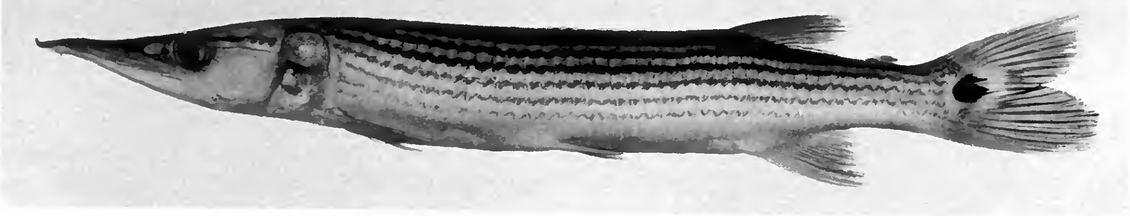

FIGURE 30.—*Ctenolucius beani*, USNM 323555, 177 mm SL; Panama, Panama, Río Mamoni at Pan American Highway, 5 km NE of Chepo, Río Bayano system.

silver. Distinct rotund dark spot on basal portions of middle caudal-fin rays. Anterior margin of anal fin and dorsal and ventral margins of caudal fin white.

COLOR IN ALCOHOL.—Juveniles up to at least 70 mm SL with dark pigmentation bordering mouth and continuing posteriorly to anteroventral margin of orbit (Figure 27). Pigmentation continuing posteriorly as narrow band ventral of orbit and from posteroventral margin of orbit as horizontal band to rear of opercle. Broad dark band extends along body from above insertion of pectoral fin to caudal peduncle, contacting ventral margin of body in region of anal fin. Broad body stripe separated from dusky dorsolateral band on body by light stripe. Smallest specimens examined (USNM 310498, 34.2-46.0 mm SL) lacking distinct dark spot on basal portion of middle rays of caudal fin. Individuals greater than approximately 58 mm SL (USNM 78635) with distinct dark spot present on basal portions of caudal-fin rays.

Larger specimens that retain guanine on scales and head silvery-golden with series of dark stripes apparent on lateral and dorsolateral surfaces of body. Distinct dark spot present on basal portions of caudal fin (Figures 28-30), with bright region of guanine immediately anterior to dark spot. Specimens lacking guanine on scales with ground coloration tan, darker dorsally. Head without pronounced pigmentation pattern, dusky dorsally. Body with series of dark, thin, somewhat wavy stripes extending posteriorly to basal portion of caudal fin; stripes becoming increasingly prominent dorsally until merging into overall darker dorsal pigmentation of body. Caudal fin with dark spot on basal portions of middle caudal-fin rays. Spot rotund to somewhat elongate horizontally and centered somewhat dorsal of middle of caudal fin. Caudal spot outlined by lightly pigmented region, more so anteriorly. Dorsal, anal, pelvic, and caudal fin with dusky rays.

ECOLOGY AND LIFE HISTORY.—Breder (1925:144, 1927:128) noted that *Ctenolucius beani* was abundant in rivers of the Pacific versant of Panama, with immature specimens gathering in schools and adults being solitary hunters, often hiding in the shade of overhanging vegetation. Breder (1927) surmised that the species is a rainy-season spawner, feeding largely on fishes and decapods. McPhail (1977:1064-1065) reported that in Panama mature specimens lie quietly just below the water surface in pools, with 2-5 similar-size individuals aggregated within an area of a few meters. Laboratory observations by McPhail indicate that *Ctenolucius beani* stalks its prey by sculling with the paired fins followed by a rapid strike. Prey items are captured crosswise in the elongate jaws and manipulated until they can be swallowed headfirst.

DISTRIBUTION.—Río Atrato and Río San Juan of northwestern Colombia, Pacific versant rivers of Panama as far west as the Río Santa Maria system of Veraguas Province, Panama (Figure 26). The distribution of *Ctenolucius beani* in Panama is disjunct, presumably as a consequence of uneven collecting efforts.

REMARKS.—*Ctenolucius beani* of this study encompasses two nominal species, *Belonocharax beani* Fowler and *Luciocharax striatus* Boulenger. Fowler (1907:464) proposed *Belonocharax beani* based on one specimen from the Río Atrato, which empties into the Caribbean Sea. Several years later Boulenger (1911:212) described *Luciocharax striatus* from an individual from the Río San Juan, a river of the Pacific versant of Colombia whose headwaters approximate those of the Río Atrato. Boulenger indicated neither why he thought that his species differed from other nominal ctenoluciid species, nor why he utilized *Luciocharax* Steindachner rather than *Belonocharax* Fowler for his species. The latter question is moot here because both genera are considered synonyms of *Ctenolucius* in this study. A comparison of the populations of *Ctenolucius* from the Río Atrato with those from the Río San Juan does not reveal any notable differences, although populations from the Río San Juan tend to have higher vertebral counts than do those from the Río Atrato and Pacific rivers of Panama (Table 3), but there is broad overlap. No other differences have been found between *striatus* from the Río San Juan and *beani* of the Río Atrato (Table 4). *Luciocharax striatus* consequently is considered a synonym of *Belonocharax* (= *Ctenolucius*) *beani*.

MATERIAL EXAMINED.—196 specimens (complete data taken on 89 specimens, 34.2-286 mm SL; partial data taken on 10 additional specimens).

COLOMBIA. *Valle:* Boca de [Río] Calima, BMNH 1910.7.11:210, 1 (178; holotype of *Luciocharax striatus*). *Chocó:* Istmina, San Juan basin, CAS 13909, 1 (186; formerly IU 13909, in part). Río San Juan, Cabeceras, NRM 10692, 1 (124). Puerto Negria, San Juan Basin, USNM 79220, 1 (220); CAS 18540, 4 (186-243; formerly IU 12715a-c). Río Truando near town of Riosucio, Río Atrato basin, USNM 310443, 1; USNM 310440, 2. Riosucio, Río Atrato basin, CAS 12716, 1 (250; formerly IU 12716a). Río Truando, Río Atrato basin, ANSP 16642, 1 (211, holotype of *Belonocharax beani;* formerly USNM 1658, in part); USNM 1658, 2 (1, 165); MCZ 30936, 3 (177-203); BMNH 1920.12.20:161-163, 3 (2, 111-237); SU 35276, 1 (138); AMNH 5356, 4 (195-230); CAS 12681, 12 (98.5-286; formerly IU 13051, in part). Río Condoto, Río San Juan basin, BMNH 1914.5.18:31, 1 (165).

TABLE 3.—Number of specimens of various populations of *Ctenolucius beani* with cited number of vertebrae. Vertebrae incorporated into fused $PU_1 + U_1$ counted as a single element and vertebrae of Weberian apparatus counted as four elements. Panama includes all populations of the species along the Pacific versant of the country.

Population	Vertebrae				
	45	46	47	48	$\bar{x}$
Panama	4	27	8		46.10
Río Atrato		19	10		46.35
Río San Juan			10	2	47.17

TABLE 4.—Morphometrics and meristics of (A) holotype of *Belonocharax beani*, ANSP 16642; (B) holotype of *Luciocharax striatus*, BMNH 1910.7.11:210; and (C) all other specimens of *Ctenolucius beani* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 16 are proportions of standard length; 17 to 21 are proportions of head length. Dashes indicate proportions that could not be determined because of the condition of the specimen.

Character	A	B	C
		Morphometrics	
Standard Length	~211	178	66–286
1. Body depth at dorsal-fin origin	-	-	0.138–0.175
2. Snout to dorsal-fin origin	-	0.818	0.811–0.870
3. Snout to anal-fin origin	0.879	0.870	0.820–0.887
4. Snout to pectoral-fin origin	0.374	0.365	0.301–0.386
5. Snout to pelvic-fin origin	-	0.621	0.563–0.630
6. Dorsal-fin origin to hypural joint	0.227	0.236	0.187–0.246
7. Dorsal-fin origin to anal-fin origin	0.166	0.162	0.136–0.169
8. Dorsal-fin origin to pelvic-fin insertion	-	0.258	0.240–0.284
9. Dorsal-fin origin to pectoral-fin insertion	-	0.499	0.460–0.509
10. Caudal-peduncle depth	0.083	0.079	0.072–0.085
11. Pectoral-fin length	0.143	0.152	0.128–0.157
12. Pelvic-fin length	0.127	0.115	0.112–0.136
13. Length of longest dorsal-fin ray	-	0.130	0.128–0.161
14. Length of longest anal-fin ray	-	0.128	0.112–0.160
15. Anal-fin base	0.077	0.084	0.071–0.099
16. Head length	0.382	0.374	0.315–0.403
17. Snout length	0.478	0.470	0.536–0.525
18. Orbital diameter	0.112	0.118	0.098–0.144
19. Postorbital length	0.399	0.409	0.336–0.446
20. Lower-jaw length	0.611	0.614	0.540–0.621
21. Interorbital width	0.199	0.170	0.150–0.204
		Meristics	
Scales along lateral-line series	50	48	46–50
Pored lateral-line scales	27	30	14–34
Scale rows between dorsal-fin origin and lateral-line series	5	4	4–6
Scale rows between anal-fin origin and lateral-line series	6	5	5–6
Predorsal median scales	34	-	32–36
Postdorsal median scales	7	-	6–8
Branched dorsal-fin rays	7	8	7–8
Branched anal-fin rays	8	8	8
Pectoral-fin rays	15	13	12–16
Branched pelvic-fin rays	7	7	7–8
Vertebrae	47	47	45–48

Río Salado near Terisita, USNM 310439, 1. Río Atrato at Quibdo, LACM 32140-1, 1 (187). Managrú, Río Atrato basin, CAS 18534, 3 (2, 66.0–170; formerly IU 13052; only 2 specimens cited for this lot by Eigenmann, 1922:168). *Antioquia:* Caño Ponelaolla and mouth of Río Guaguandó, ~1 km downstream of village of Buchadó, NRM 25755, 1. Ciénega Palo Blanco, ~1 km NE of village of Palo Blanco, NRM 25754, 2 (207–250).

PANAMA. *Darien:* Río Seteganti, USNM 265783, 5 (1, 98.0). Río Tuira, ~1 km below Penigana to ~2.3 km above El Real, USNM 293172, 2 (155–194). Río Pirre, ~1–2 km above El Real, USNM 293158, 1 (111). Río Pirre, 3–5 mi (4.8–9.0 km) above El Real, USNM 310488, 18; USNM 310445, 2. Río Pucuro just above confluence with Río Tuira, USNM 293193, 1 (196). Río Tuira, ½ km above Boca de Cupe, USNM 293169, 4 (2, 138–231; 1 specimen cleared and counterstained). Río Tuira, Boca de Cupe, USNM 78629, 6. Río Capetí, USNM 78637, 1 (162). Río Yape, USNM 78631, 4 (3, 141–143). Río Aruza, Aruza, USNM 78634, 5 (201–221). Río Membrillo, USNM 310438, 11. Río Uruseca, USNM 310441, 2. Río Chucunaque, AMNH 57101, 1. *Panama:* Río Mamoni, Chepo, USNM 78638, 2 (146–168). Río Mamoni, at Interamerican Highway, just E of Chepo, ANSP 151082, 1. Creek 11 mi (17.6 km) S of Chepo, on road to El Llano, UF 12977, 6 (2, 136–164). Lowland turbid stream subject to tidal motion, S of Chepo, USNM 226435, 3. Río Mamoni, El Capitan, USNM 78632, 10 (3, 140–223). Río Marte Arnade, USNM 78633, 5 (52.0–210); USNM 78635, 1 (58.0). Río Mamoni at Pan American Highway, 5 km NE of Chepo, Río Bayano system, USNM 323555, 3. Río Calobre, USNM 78639, 16 (5, 156–260); CAS 11589, 3 (2, 179–260; formerly IU 14004); USNM 78640, 4. Río Abaco, USNM 78630, 19 (5, 117–220). Río Juan Diaz, Juan Diaz, USNM 78636, 1 (109). Swamps at La Jagua Hunting Club, USNM 109275, 2 (1, 122). Creek on bridge along Inter-American Highway, about 4 mi (7.2 km) E of Río Pacora, USNM 310452, 7 (5, 115–142). Creek along Inter-American Highway, about 9 mi (14.5 km) E of Río Pacora, USNM 310498, 2 (34.2–46.0); ANSP 104249, 4. *Veraguas:* Creek at bridge about 9 mi (14.5 km) from Santiago on road to San Francisco, Río Santa Maria basin, USNM 310451, 1. *Herrera:* Creek tributary to Río Escota, ~8 km up Ocu Road from Interamerican Highway, ANSP 104430, 1.

Genus *Boulengerella* Eigenmann, 1903

Xiphostoma Agassiz in Spix and Agassiz, 1829:60, 78 [type species *Xiphostoma cuvieri* Agassiz in Spix and Agassiz, 1829:78, by monotypy. Preoccupied in Hemiptera by Xiphostoma Kirby and Spence, 1828; gender neutral].—Jordan, 1917:132 [listing].

Xiphostomus Swainson, 1839:290 [unjustified emendation of *Xiphostoma* Agassiz].

Xiphystoma Ulrey, 1895:296 [misspelling].

Boulengerella Eigenmann, 1903:147 [type species *Xiphostoma lateristriga* Boulenger, 1895:449, by original designation; gender feminine].

Hiphostoma Fowler, 1945:170 [misspelling].

Spixostoma Whitley, 1951:407 [type species *Xiphostoma cuvieri* Agassiz in Spix and Agassiz, 1829:78, by monotypy as a replacement name; replacement for *Xiphostoma;* gender neutral].

DIAGNOSIS.—*Boulengerella* is characterized by a series of derived features listed above in "Monophyly of *Boulengerella*" under "Phylogenetic Reconstruction" and is readily distinguished externally from *Ctenolucius*, the other ctenoluciid genus, by the possession of 87–124 rather than 45–50 lateral-line scales in *Ctenolucius*. The scales of *Boulengerella*, although having surface sculpturing and irregular posterior margins, lack distinct posterior serrations as in *Ctenolucius*. *Boulengerella* species lack the dorsoventrally flattened, fleshy flaps anteriorly on the lower-jaw margin (Figure 7), which are characteristic of *Ctenolucius*. *Boulengerella*, by comparison, has an elongate fleshy appendage at the snout tip (e.g., *B. lateristriga*, Figure 32) in all but larger specimens, contrary to the poorly developed or absent appendage in *Ctenolucius*. The relatively uniformly sized premaxillary dentition that meets at an acute angle anteriorly in *Boulengerella* contrasts with the rounded arch of enlarged dentition on the anterior of the upper jaw of *Ctenolucius*.

DISTRIBUTION.—Rio Amazonas, Río Orinoco, Essequibo River of Guyana, Oyapock River (Rio Oiapoque) along the border between French Guiana and Brazil, and coastal rivers of the states of Amapá and Pará in Brazil. *Boulengerella* is poorly represented in the southern tributaries of the Amazon basin, a probable artifact of the relatively limited collections from those systems. No *Boulengerella* specimens from the upper Rio Madeira in Brazil, Bolivia, and Peru were located in museum collections, and the genus has not been reported in surveys of fishes of that portion of the basin (Goulding, 1979, 1981; Lauzanne and Loubens, 1985:46; Lauzanne et al., 1991; Ortega, in press). The absence of *Boulengerella* in that portion of the Amazon basin is paralleled by the absence of the Chilodontidae (Vari et al., in press) and various cichlid genera (*Chaetobranchus, Cichla, Geophagus;* Kullander, 1986).

Boulengerella species often are captured in various combinations, with at least four species (*lateristriga, xyrekes, lucius,* and *maculata*) occurring together in the pools below the Cachoeira do Bicho-Áçú on the Rio Marauiá, a tributary of the Rio Negro in the Amazon basin (MZUSP 32138, 32163, 42865, and 32182, respectively). *Boulengerella cuvieri*, the one species not collected at that locality, has been captured with one or more of those four species at various other localities.

The majority of *Boulengerella* species do not appear to be selective as to the water types they inhabit, with *B. cuvieri* most notably broadly distributed through black, white, and clear water systems, but *B. lateristriga* apparently is limited to acidic black waters of the main and immediate tributaries of the Rio Negro and upper portions of the Río Orinoco (Figure 34).

Boulengerella species have been cited from the Río de La Plata basin commencing with Holmberg (1889), and from the Rio Parnahyba (= Parnaíba), state of Piauhy (= Piauí), northeastern Brazil by Fowler (1941). As discussed under "Remarks" for *Boulengerella lucius* and *B. cuvieri*, these records are based on misidentifications or incorrect locality information.

REMARKS.—The generic name first applied to a member of this lineage of ctenoluciids, *Hydrocynus*, by Cuvier (1816), was limited subsequently by Agassiz in Spix and Agassiz (1829) to a group of Old World characiforms. In the same publication, Agassiz offered *Xiphostoma* for the two nominal species of ctenoluciids proposed to that time. *Xiphostoma* was utilized by various authors throughout the nineteenth century until it was discovered to be preoccupied in Hemiptera. Two genera subsequently were proposed for species herein assigned to *Boulengerella*. Eigenmann (1903:147) proposed *Boulengerella* with *Xiphostoma lateristriga* as its type species. Whitley (1951:407) proposed *Spixostoma* as a replacement for *Xiphostoma*, taking *X. cuvieri* as its type species. Generic names thus are available for the clades with posteriorly (*Boulengerella*) and anteriorly (*Spixostoma*) positioned dorsal fins. *Spixostoma* rarely has been utilized since it was first proposed, and there is no advantage in recognizing two genera, or subgenera, for a lineage of five species. *Spixostoma* is herein placed as a synonym of *Boulengerella*.

Key to Species of *Boulengerella* Eigenmann, 1903

1. Base of dorsal fin located, at least in part, posterior to vertical line through origin of anal fin; first pterygiophore of dorsal fin inserting behind neural spine of 28th to 31st vertebrae; perforations of lateral-line scale series in adults present on 25 or fewer anterior scales of lateral-line series 2

   Base of dorsal fin located entirely anterior to vertical line through origin of anal fin; first pterygiophore of dorsal fin inserting behind neural spine of 20th to 24th vertebrae; all scales of lateral line (82 or more scales) perforated with exception of few scales on base of caudal fin 3

2. Narrow, dark, horizontal stripe extending from rear of orbit to caudal peduncle; dark spots about size of pupil absent on body; lobes of caudal fin with distinct, dark crossbars [Figures 32, 33]; 55–65 scales along predorsal midline, 14–17 scales from origin of dorsal fin to midventral line; longest dorsal-fin ray 0.117–0.129 of SL, tip of fin not reaching adipose fin when dorsal fin depressed [Figure 31] . . . . ***B. lateristriga***
   (Rio Negro of Amazon basin in Brazil and Venezuela; upper Río Orinoco in southern Venezuela)

   Narrow, dark, horizontal stripe on lateral surface of head, if present, limited to posterior of orbit; body typically with series of dark spots about size of pupil scattered over dorsolateral and dorsal surfaces; lobes of caudal fin with pattern of irregular dark and light marmoration but no distinct crossbars; 73–84 scales along predorsal midline, 17–23 scales from origin of dorsal fin to midventral line; longest dorsal-fin ray 0.132–0.163 of SL, tip of fin extending to or past adipose fin when dorsal fin depressed [Figure 31] . . . . ***B. maculata***
   (Rio Amazonas, Rio Tocantins, and Río Orinoco)

3. Membranes between basal portions of middle rays of caudal fin with horizontally elongate patches of dark pigmentation; patches sometimes blend posteriorly with dusky pigmentation of remainder of fin membrane; individual dark patches separated by lighter pigmentation on basal portions of rays [Figure 40]; portions of membranes of middle rays of caudal fin posterior of basal patches of dark pigmentation distinctly more dusky than those of remaining caudal-fin rays; 45 or 46 vertebrae and 98–117 lateral-line scales . . . . ***B. lucius***
   (Rio Amazonas and Río Orinoco)

   Distinct spot of very dark pigmentation on basal portions of middle caudal-fin rays and associated membranes in all specimens other than juveniles (under ~100 mm SL); membranes of middle rays of caudal fin not notably more dusky than adjoining rays 4

4. Distinct band of dark pigmentation extending from rear of orbit to rear of opercle, somewhat masked in largest specimens; smaller specimens rarely with oblique dark stripe across posteroventral margin of third infraorbital; 94–124 lateral-line scales; 48 or 49 vertebrae (47 in 1 specimen with some deformed vertebrae) . . . . ***B. cuvieri***
   (Rio Amazonas, Río Orinoco; Essequibo River system of Guyana, Oyapock River along border of French Guiana and Brazil, and coastal rivers of states of Amapá and Pará in Brazil)

   No distinct band of dark pigmentation extending from rear of orbit to rear of third infraorbital in any but largest specimens; juveniles and midsize individuals with dark stripe of oblique pigmentation across posteroventral margin of third infraorbital; 87–94 lateral-line scales; 44–46 vertebrae . . . . ***B. xyrekes***
   (Río Orinoco and Rio Amazonas)

Boulengerella lateristriga (Boulenger, 1895)

FIGURES 31-34; TABLE 5

Xiphostoma lateristriga Boulenger, 1895:449 [type locality: (Brazil, Amazonas) Manaos (= Manaus)].—Regan, 1905:190 [based on Wallace drawings of fishes from the Rio Negro].

Boulengerella lateristriga.—Eigenmann, 1903:147 [designated type species of *Boulengerella* Eigenmann]; 1910:446 [literature compilation].—Fowler, 1950:328 [literature compilation].—Myers and Weitzman, 1960:201, fig. 1 [redescription based on specimens from Brazil, Rio Negro, Amazonas, Cucuhy [= Cucui or Cucuy].—Mago-Leccia, 1970:73 [Venezuela; common name]; 1971:10 [Venezuela: Amazonas, Río Casiquiare; common name].—Fowler, 1975:123 [literature compilation].—Goulding et al., 1988:126, 135, 139, 140, 144, 173, 175, 176 [Brazil, Amazonas, Rio Negro: Urubaxi, Ilha Buiu-Áçú, Ilha Tamaquaré; diet].—Taphorn, 1992:402 [Venezuela: Bolivar and Amazonas states].—Royero et al., 1992:51, 55 [Venezuela: Amazonas, Río Atabapo and Laguna Titi; ornamental fishes].

Boulengerella maculatum.—Schultz, 1950:54 [in part, *Xiphostoma lateristriga* incorrectly placed as synonym of *Xiphostoma* (= *Boulengerella*) *maculatum*].

Boulengerella (*Boulengerella*) *lateristriga.*—Géry, 1977:106 [assignment to subgenus *Boulengerella*].

DIAGNOSIS.—The location of the dorsal-fin base largely posterior of the vertical through the anal-fin origin distinguishes *B. lateristriga* from all congeners except *B. maculata. Boulengerella lateristriga* differs from *B. maculata* in possessing a narrow, dark, horizontal stripe extending from the rear of the orbit to the caudal peduncle, the presence of distinct, dark crossbars on the lobes of the caudal fin, and absence of dark spots about the size of the pupil on the body. This contrasts with the limitation of the horizontal stripe, when present, to the postorbital surface of the head, the marmorated pigmentation pattern on the caudal fin, and the series of dark spots about the size of the pupil scattered over the dorsolateral and dorsal surfaces of the body in *B. maculata. Boulengerella lateristriga* and *B. maculata* also differ in predorsal scale numbers (55-65 in *B. lateristriga* versus 73-84 in *B. maculata*), number of scales from dorsal-fin origin to midventral line (14-17 versus 17-23, respectively), and relative dorsal-fin length (Figure 31). Autapomorphies for *B. lateristriga* are detailed under the "Phylogenetic Reconstruction," above.

DESCRIPTION.—*Boulengerella lateristriga* is evidently the smallest species in the genus, with the largest measured specimen being 258 mm SL. Head and body notably elongate (Figures 32, 33). Greatest body depth at dorsal-fin origin in specimens under 120 mm SL, progressively shifting forward at greater standard lengths as abdominal region becomes progressively relatively deeper. Dorsal profile of head and body nearly straight to origin of dorsal fin; straight and slightly posteroventrally slanted at base of dorsal fin, straight or slightly convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body somewhat flattened transversely in region from rear of supraoccipital to area about two-thirds distance to origin of dorsal fin, somewhat flattened transversely between dorsal and adipose fins. Ventral profile of head and body gently convex to insertion of anal fin. Prepelvic region of body rounded to obtusely flattened anteriorly.

Head distinctly pointed in both dorsal and lateral views. Upper jaw with dentigerous surface slightly concave, anterior portion of upper jaw and anterior premaxillary dentition overlapping tip of lower jaw. Snout elongate, with distinct, elongate, fleshy process anteriorly; profile of snout in dorsal view gently tapering from interorbital region to base of fleshy anterior process. Lower jaw elongate, obtusely pointed anteriorly with moderately developed, fleshy mass anteriorly that ranges from anteriorly elongate process on tip of jaw to somewhat rounded structure on ventral surface of anterior

TABLE 5.—Morphometrics and meristics of (A) holotype of *Xiphostoma lateristriga*, BMNH 1893.4.24:28; and (B) all other specimens of *Boulengerella lateristriga* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 16 are proportions of standard length; 17 to 21 are proportions of head length.

Character	A	B
	Morphometrics	
Standard Length	181	98.0-258
1. Body depth at dorsal-fin origin	0.119	0.093-0.132
2. Snout to dorsal-fin origin	0.819	0.780-0.827
3. Snout to anal-fin origin	0.832	0.803-0.849
4. Snout to pectoral-fin origin	0.310	0.310-0.351
5. Snout to pelvic-fin origin	0.611	0.600-0.644
6. Dorsal-fin origin to hypural joint	0.188	0.175-0.209
7. Dorsal-fin origin to anal-fin origin	0.123	0.102-0.131
8. Dorsal-fin origin to pelvic-fin insertion	0.231	0.212-0.243
9. Dorsal-fin origin to pectoral-fin insertion	0.514	0.462-0.518
10. Caudal-peduncle depth	0.069	0.059-0.074
11. Pectoral-fin length	0.106	0.090-0.120
12. Pelvic-fin length	0.108	0.101-0.114
13. Length of longest dorsal-fin ray	0.118	0.117-0.129
14. Length of longest anal-fin ray	0.124	0.108-0.125
15. Anal-fin base	0.071	0.060-0.072
16. Head length	0.317	0.315-0.365
17. Snout length	0.513	0.509-0.557
18. Orbital diameter	0.128	0.110-0.129
19. Postorbital length	0.342	0.324-0.372
20. Lower-jaw length	0.581	0.544-0.588
21. Interorbital width	0.183	0.163-0.212
	Meristics	
Scales along lateral-line series	79	75-88
Pored lateral-line scales	15	8-28
Scale rows between dorsal-fin origin and midventral line	17	14-17
Predorsal median scales	63	55-65
Postdorsal median scales	8	6-8
Branched dorsal-fin rays	8	8
Branched anal-fin rays	8	7-8
Pectoral-fin rays	17	16-20
Branched pelvic-fin rays	8	7-8
Vertebrae	48	48-49

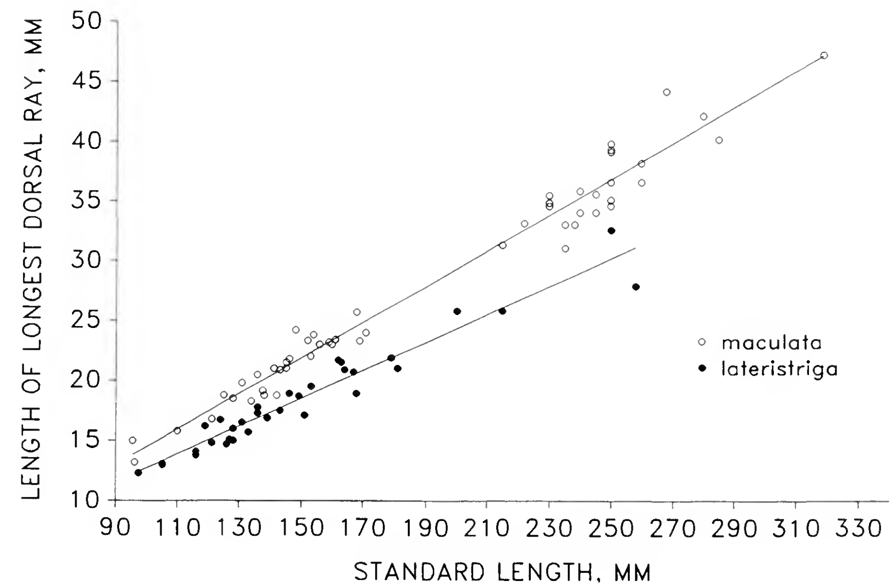

FIGURE 31.—Plot of length of longest dorsal-fin ray against standard length for *Boulengerella lateristriga* and *B. maculata*. Some symbols represent more than one specimen or data point.

portion of jaw. Lateral surface of lower jaw without fleshy elaborations. Nostrils of each side proximate; anterior somewhat tubular, posterior larger and semicircular.

Anterior teeth in premaxillae and dentaries noticeably recurved, progressively less so posteriorly, teeth somewhat smaller anteriorly in each jaw. Premaxillary teeth of each side meeting anteriorly at acute angle. Premaxillary teeth in single row, with 110–165 teeth in specimens of 97.3-250 mm HL; number of teeth somewhat variable at any standard length. Overall ontogenetic trend is for an allometric increase in number of teeth; no notable shift in rate of increase within range of standard length of examined specimens. Single tooth present in inner row of premaxillary teeth in a few examined specimens; condition in juveniles unknown. Maxilla with 11–18 teeth along its anterior margin, with general trend to increased number of teeth with increasing size, but with wide variation in number of teeth present within any limited size range. Dentary without teeth anteriorly immediately proximate to symphysis, with 92–146 teeth arranged in single series in specimens of 97.3-250 mm HL. Number of dentary teeth somewhat variable within limited range of head lengths. Overall ontogenetic trend is for progressive increase in number of teeth without change in rate across size range of examined specimens. Dentary without inner row of teeth. Teeth on upper and lower pharyngeal tooth-plates small and conic.

Scales with surface sculpturing and irregular margins, but no distinct cteni. Scales along pre- and postdorsal midlines arranged in somewhat irregular rows. Anterior 8–28 lateral-line scales perforated; number of perforated scales generally increasing with standard length, with perforation of lateral-line scales occasionally irregular posteriorly in pored portion of series. Number of scales along lateral-line series 75–88.

Dorsal fin ii,8, rarely iii,8. First pterygiophore of dorsal fin inserting behind neural spine of 30th or 31st vertebrae. Posterior terminus of dorsal-fin base somewhat anterior to vertical through anal-fin origin. Distal margin of dorsal fin slightly convex; tip of fin falling short of adipose fin when fin depressed. Anal fin usually ii–iii,8, rarely ii–iii,7. First anal-fin pterygiophore inserting behind hemal spine of 32nd or 33rd vertebrae. Anal fin slightly emarginate with no indication of sexual dimorphism. Pectoral fin i,12–16,iii–iv; pointed in profile with first branched ray longest; tip extends posteriorly about one-quarter distance to insertion of pelvic fin. Pelvic fin i,7–8; distal margin obtusely pointed in profile; first branched ray longest; fin reaches posteriorly to about one-third distance to anal fin. Caudal fin forked. Adipose fin present.

VERTEBRAE.—48(8), 49(9) [48].

LIFE COLORATION.—Taylor (1981:18) includes a photograph of a specimen of *B. lateristriga* in an aquarium whose coloration is summarized as follows. Dorsal and lateral surfaces of body with silver stripes. A distinct thin, silvery band extending along lateral surface of lower jaw, across opercle, and along ventral margin of dusky midlateral stripe on body to base of caudal fin. Dark markings on body as in alcohol-preserved specimens other than for silvery sheen overlying dusky midlateral stripe. Distal portions of dorsal and anal fins

FIGURE 32.—*Boulengerella lateristriga*, USNM 270331, 116 mm SL; Venezuela, Amazonas, small caño off Caño Urami, left bank tributary of Río Negro, just upriver of Santa Lucia (1°17′N, 66°51′W).

FIGURE 33.—*Boulengerella lateristriga*, ANSP 161215, 200 mm SL; Venezuela, Amazonas, Río Orinoco, at sand playa just upstream from Quiratare (2°59′N, 66°04′W).

and margins of lobes of caudal fin white. White patch midway along anterior margin of anal fin.

COLOR IN ALCOHOL.—Specimens retaining guanine on scales silvery, less so dorsally. Specimens lacking guanine on scales with tan ground coloration. Head and body dusky dorsally. Individuals of approximately 120–140 mm SL with narrow, horizontal, dark line extending from anterior margin of eye forward under nostrils and to variable degrees along dorsal margin of premaxilla. Obscure dark stripe running along jaw above premaxillary teeth in some specimens. Specimens of all sizes with narrow, horizontal, dark line running from posterior margin of eye along joint between third and fifth infraorbitals and across opercle. Second narrow, horizontal, dark line on postorbital portion of head extends from ventral margin of eye across third infraorbital and opercle. Both lines very obvious in specimens of 120–140 mm SL, somewhat less so in some larger individuals, particularly in case of ventral stripe. Portion of third infraorbital and opercle bounded by stripes darker than regions dorsal and ventral to those lines in specimens lacking guanine on head, often less so in larger individuals. Band of darker pigmentation masked in specimens retaining guanine on head. Posteroventral margin of opercle delimited by thin band of dark pigmentation in individuals of 120–140 mm SL.

Body with narrow dark stripe extending from dorsal stripe across lateral surface of head posteriorly to base of caudal fin. Stripe about one-half scale high; stripe ranging from straight to irregularly wavy in different individuals. Some specimens with thin, irregular stripe continuing from ventral stripe on postorbital surface of head posteriorly across ventrolateral surface of body to above anal fin. Stripe shorter and fading posteriorly or even missing in many examined individuals. Distinct horizontal stripe of dark pigmentation filling region between narrow dark body stripes in smaller individuals. Pigmentation in this region less intense in some larger individuals and masked in individuals retaining guanine on body. Irregular series of small spots of dark pigmentation extending in horizontal pattern from behind pelvic-fin insertion posteriorly to posterior terminus of insertion of anal fin; spots masked in specimens retaining guanine on scales. Region of body immediately dorsal to dorsal stripe on body relatively unpigmented and separating that stripe from dusky dorsal portions of body, difference in degree of pigmentation to sides of stripe not apparent in specimens retaining guanine on body. Dorsal surface of body with variable pattern of wavy darker stripes between horizontal scale rows.

Pectoral fin with transverse patch of dark pigmentation basally in smaller individuals, with one transverse bar in smaller specimens, two in larger individuals. Pelvic fin with transverse patch of pigmentation. Dorsal fin with basal and distal patches of dark pigmentation. Anal fin with distal patch of pigmentation. Caudal fin with middle rays dark and two patches of dark pigmentation across each lobe.

DISTRIBUTION.—Rio Negro, Amazonas, Brazil, and southern portions of the upper Río Orinoco in Venezuela (Figure 34).

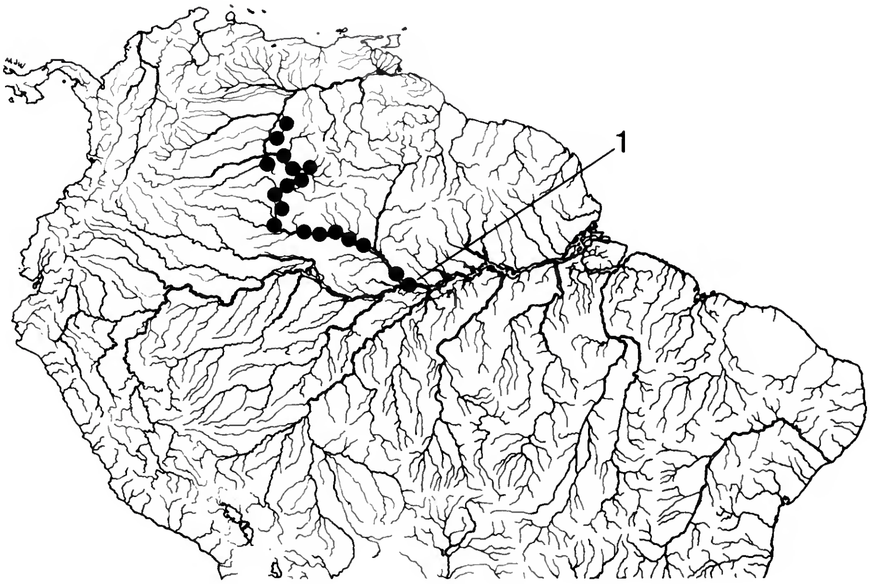

FIGURE 34.—Map of northern portions of South America showing geographic distribution of *Boulengerella lateristriga* (1 = Manaus, type locality of *Xiphostoma lateristriga*). Some symbols represent more than one lot of specimens or locality.

COMMON NAME.—Venezuela: "Agujeta" (Mago-Leccia, 1970:73; 1971:10).

ECOLOGY.—Goulding et al. (1988:135, 139, 140, 144, 173) reported that *Boulengerella lateristriga* from the Rio Negro, Brazil, fed exclusively on fishes.

REMARKS.—In his original description of *Xiphostoma lateristriga*, Boulenger (1895:449) did not compare it to any congeners. Nonetheless, the described details of caudal-fin and body pigmentation clearly distinguish it from other nominal species of *Boulengerella* with posteriorly positioned dorsal fins (*maculata* and *taedo*). Schultz (1950:54), however, placed *lateristriga* as a synonym of *Boulengerella maculata*, without comment. Myers and Weitzman (1960:201) resurrected *B. lateristriga*, emphasizing a series of features that distinguish it from *B. maculata;* this study confirms their conclusion that *B. lateristriga* is distinct.

MATERIAL EXAMINED.—171 specimens (complete data taken on 65 specimens, 98.0-258 mm SL; partial data taken on 3 additional specimens).

VENEZUELA. *Amazonas:* Small caño off Urami, left bank tributary of Río Negro, just upriver of Santa Lucia (1°17'N, 66°51'W), USNM 270331, 10 (116-136, 1 specimen cleared and counterstained). Pools and beaches at mouth of Caño Darigua, ~7 km S of San Carlos de Río Negro (1°53'N, 67°0'W), MBUCV V-11353, 12 (10, 116-140); MBUCV V-11397, 13 (10, 114-168). Río Negro basin, either at San Carlos de Río Negro or at Río Pasimoni, NRM 28184, 1 (128). Río Pasimoni, 18 km from Río Yatua and Río Yarua (1°30'N, 66°30'W), MHNLS 9403, 1. Caño Caripo, first left side caño into Río Casiquiare, ~5 min. from confluence of Río Casiquiare and Río Orinoco (3°06'N, 65°50'W), ANSP 161213, 3 (166-190). Río Beripamoni, tributary of Río Casiquiare, MBUCV V-6131, 1. Río Orinoco, at sand playa just upstream from Quiratare (2°59'N, 66°04'W), ANSP 161215, 2 (195-200). Caño Monomi, opposite Isla Mamoni, Río Casiquiare (2°20'N, 66°35'W), MBUCV V-3572, 1. Río Autana, ~80 km above confluence with Río Sipapo (4°44'N, 67°37'W), ANSP 160090, 1 (127). Río Ventuari, ~12 km from its confluence with Río Orinoco (4°04'N, 66°56'W), ANSP 161217, 1 (131). Río Sipapo, backwater channel, ~6-7 km above Pendare (4°51'N, 67°43'W), ANSP 160091, 1 (133). Tití lagoon near San Fernando de Atapabo, on road past airstrip (~04°03'N, 67°42'W), FMNH 85510, 1 (98.0). 8.6 km toward Puerto Ayachuco from Puerto Nuevo, small caño under road, FMNH 85658, 4 (3, 111-120). Río Atacavi, 5 km from confluence with Río Atabapo, MCNG 22155, 1. Río Atabapo in San Fernando de Atabapo, MCNG 27257, 1.

BRAZIL. *Amazonas:* Manaos (= Manaus; 03°06'S, 60°00'W), BMNH 1893.4.24:28, 1 (181, holotype of *Xiphostoma lateristriga* Boulenger). Igarapé Tarumãzinho and tributaries, N of Manaus (03°04'S, 60°00'W), MZUSP 6822, 11 (5, 105-149); MZUSP 6781, 1. Sandbank at Brazilian-Colombian border, right (west) bank of Río Negro at Cucuhy (= Cucuí; ~1°11'N, 66°50'W), SU 16285, 2 (137-215). Rio Arirará, near its mouth, Rio Negro basin (00°20'S, 63°40'W), MZUSP 32140, 1 (165); MZUSP 32136, 1. Ilha Cumuru, Rio

Negro, near Río Ararirá (00°30′S, 63°30′W), MZUSP 32139, 1 (258). Rio Negro at mouth of Rio Marauiá (~00°20′S, 65°20′W), MZUSP 32141, 3. Ilha Tamaquaré, Rio Negro (~00°30′S, 64°55′W), MZUSP 32133, 22 (5, 146–163); MZUSP 32134, 11. Rio Urubaxi, near its mouth (~00°35′S, 64°45′W), MZUSP 32142, 29; MZUSP 32143, 5. Rio Negro, Barcelos (~01°00′S, 62°40′W), MZUSP 32137, 2 (154–164). Rio Marauiá, Cachoeira do Bicho-Áçú (~00°20′S, 65°20′W), MZUSP 32138, 27 (5, 136–250).

Boulengerella maculata **(Valenciennes in Cuvier and Valenciennes, 1849)**

FIGURES 31, 35–38; TABLES 6–8

Xiphostoma maculatum Valenciennes in Cuvier and Valenciennes, 1849:357 [Amazon].—Günther, 1864:357 [River Capai].—Steindachner, 1876:83 [Amazon, Río Ambiyacu, Rio Xingu at Porto do Moz; *Xiphostoma taedo* Cope (1872) placed as a synonym of *X. maculatum*].—Steindachner, 1882:118 [Peru: Río Huallaga].—Eigenmann and Eigenmann, 1891:59 [(Rio) Xingu, near Porto do Moz; Rio Capai, Marañon; *Xiphostoma taedo* as a synonym].—Fowler, 1907:463 [Peru: (Río) Ambiyacu and Peruvian Amazon; redescription of type series of *Xiphostoma taedo* Cope (1872) and specimens reported by Cope (1878)].—Pellegrin, 1909:150 [Brazil: Manaos (= Manaus), Tonnatins, Tabatinga].—Eigenmann and Allen, 1942:274 [literature compilation; common name].—Bertin, 1948:30 [holotype depository].

Xiphostoma maculata.—Castelnau, 1855:76, pl. 40, fig. 2 [Amazon, based on holotype and original description of *Xiphostoma maculatum* Valenciennes].

Xiphostoma taedo Cope, 1872:267, pl. 13, fig. 2 [Peru: (Río) Ambyiacu]; 1878 [Peruvian Amazon; refinement of details of original description of species; species removed from synonymy of *X. maculatum* contrary to Steindachner, 1876].—Steindachner, 1876:87 [*Xiphostoma taedo* placed as a synonym of *X. maculatum*].—Eigenmann and Eigenmann, 1891:59 [as a synonym of *Xiphostoma maculatum*].—Eigenmann, 1910:446 [as a synonym of *Hydrocynus maculatus*].—Böhlke, 1984:66 [holotype and paratype depository].

Hydrocynus maculatus.—Eigenmann, 1910:446 [Amazon; *Xiphostoma taedo* considered a synonym].—Fowler, 1940:288 [Peruvian Amazon]; 1945:170 [Peruvian Amazon; literature compilation].

Hiphostoma taedo.—Fowler, 1945:170 [Peru; common name; as a synonym of *Hydrocynus maculatus;* generic name misspelled].

Boulengerella maculata.—Fowler, 1950:329, fig. 329 [literature compilation]; 1975:123 [literature compilation].—Cala, 1977:8 [Colombia: Río Orinoco basin].—Myers and Weitzman, 1960:201, 204 [*Boulengerella lateristriga* removed from synonymy of *B. maculatum;* two species compared; Peru: Río Ampiyacu, Iquitos, Chancho Caño. Brazil: Pará, Santarém].—Mago-Leccia, 1967, fig. 7 [Venezuela: los llanos]; 1970:74 [Venezuela]; 1971:10 [Venezuela: Río Casiquiare]..—Ferreira, 1984:355 [Brazil: Pará, Santarém, Represa de Curuá-Una].—Géry and Mahnert, 1984:171 [Peru: Río Napo, Cocha Yuracyacu].—Mendes dos Santos et al., 1984:24 [Brazil: Rio Tocantins; common name].—Ortega and Vari, 1986:10 [Peruvian Amazon, based on Géry and Mahnert, 1984; common name].—Stewart et al., 1987:21 [Ecuador: Río Napo].—Castro and Arboleda, 1988:10 [Colombia: Río Caquetá].—Goulding et al., 1988:126, 134, 173 [Brazil: Amazonas, Rio Negro, confluence with Rio Marauiá; diet].—Barriga, 1991:31 [eastern drainages of Ecuador; common name].—Royero et al., 1992:51, 55 [Venezuela: Amazonas, Laguna Titi; ornamental fish].—Taphorn, 1992:402 [Venezuela, Bolivar and Amazonas].

Boulengerella maculatum.—Schultz, 1950:54 [in part; not synonymy of *Xiphostoma lateristriga* into *Xiphostoma maculatum*. Peru: Peruvian Amazon, Shansho Caño, near mouth of Río Ampiyacu].

Boulengerella (Boulengerella) maculata.—Géry, 1977:106, figs. [Amazon basin].

DIAGNOSIS.—The location of the dorsal-fin base largely posterior of the vertical through the anal-fin origin distinguishes *Boulengerella maculata* from its congeners with the exception of *B. lateristriga*. The lack of a dark, narrow stripe on the lateral surface of the body, the marmorated caudal-fin pigmentation, and the series of dark pupil-size spots scattered over the dorsolateral and dorsal surfaces of the body in *B. maculata* contrasts with the presence of a narrow, dark, horizontal stripe extending from the rear of the orbit to the caudal peduncle, the presence of distinct, dark crossbars on the lobes of the caudal fin, and the absence of dark, pupil-size spots on the body in *B. lateristriga*. *Boulengerella maculata* and *B. lateristriga* also differ in the number of predorsal scales (73–84 in *B. maculata* versus 55–65 in *B. lateristriga*), number of scales from dorsal-fin origin to midventral line (17–23 versus 14–17, respectively), and the relative dorsal-fin lengths (Figure 31). Autapomorphies for *B. maculata* are detailed under the "Phylogenetic Reconstruction," above.

DESCRIPTION.—*Boulengerella maculata* is a midsize member of the genus, with the largest measured specimen being 319 mm SL. Head and body notably elongate (Figures 35–37), particularly in specimens under 100 mm SL. Greatest body depth at dorsal-fin origin in specimens up to approximately 150 mm SL, progressively shifting forward at greater standard lengths, typically deeper in larger individuals. Dorsal profile of head and body nearly straight to dorsal-fin origin; straight and slightly posteroventrally slanted at base of dorsal fin, straight or occasionally slightly convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body in preserved specimens somewhat transversely flattened or even convex in region from rear of supraoccipital to area slightly anterior to dorsal fin, flattened to smoothly rounded transversely posterior to fin. Ventral profile of body gently convex from tip of lower jaw to anal-fin origin, degree of convexity more pronounced in larger specimens. Prepelvic region of body rounded to obtusely flattened anteriorly.

Head distinctly pointed in both lateral and dorsal views, distinctly proportionally shorter in larger individuals. Form of upper jaw, lower jaw, and nostrils as described for *Boulengerella lateristriga*, above. Fleshy process at tip of snout proportionally less developed in 54 mm SL specimen; proportionally larger but without pronounced ontogenetic variation in size in larger individuals.

Arrangement and form of teeth in both premaxillae and dentaries comparable to those in *Boulengerella lateristriga* described above. Premaxillary teeth in primary row with 53–109 in specimens of 19–103 mm HL, with number of teeth somewhat variable at a particular standard length. Overall ontogenetic trend is for allometric increase in number of teeth; rate of increase decreasing at larger standard lengths. Two teeth on inner premaxillary tooth row in a 54 mm SL specimen, no

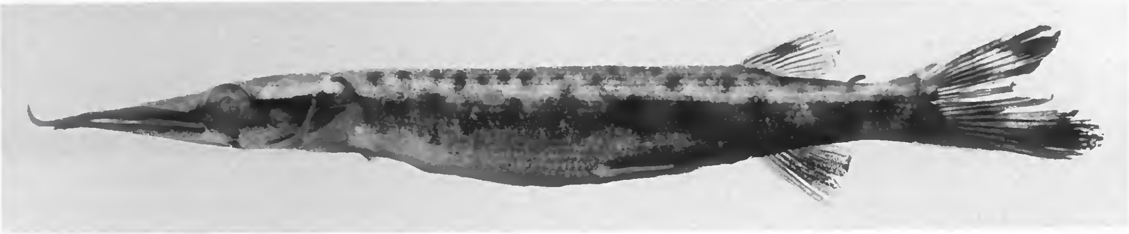

FIGURE 35.—*Boulengerella maculata*, ANSP 167104, juvenile, 74.5 mm SL; Peru, Loreto, Río Nanay, Cocha Tarapoto (03°44'S, 73°20'W).

FIGURE 36.—*Boulengerella maculata*, USNM 310294, adult, 171 mm SL; Brazil, Amazonas, Rio Purus, Taparaua, 380 km by water from Manaus.

FIGURE 37.—*Boulengerella maculata*, NRM 24339, adult, 168 mm SL; Peru, Loreto, Río Napo basin, Yuto Cocha on right bank of Río Mazán (3°28'S, 73°05'W).

on inner premaxillary tooth row in a 54 mm SL specimen, no teeth apparent in region of inner premaxillary row in larger individuals. Maxilla with 10-18 teeth along its anterior margin; with general ontogenetic trend to increased number of teeth with increasing size, but with wide variation in number of teeth present across limited size range. Dentary lacking teeth anteriorly immediately proximate to symphysis, with 52-148 teeth arranged in a single series in specimens of 19-103 mm HL. Overall ontogenetic trend is for increase in number of teeth at larger standard lengths. Number of dentary teeth somewhat variable within limited range of head lengths; rate of increase in number of teeth decreasing at greater standard lengths. Dentary without inner row of teeth in most specimens, although occasional individuals will have discrete inner posterior series partially overlapped by outer series laterally. Teeth on upper and lower pharyngeal tooth-plates small and conic.

Anterior 5-26 scales of lateral line perforated; number of perforated scales lowest in specimens under 100 mm SL, tending to increase (but variable) at larger body sizes; perforation of lateral-line scales occasionally irregular posteriorly in pored portion of series. Scales with surface sculpturing and irregular margins, but no distinct cteni. Scales along pre-and postdorsal midlines arranged in irregular rows.

Dorsal fin ii–iii,8 or sometimes ii–iii,7,i. First basal dorsal-fin pterygiophore inserting behind neural spine of 28th to 30th vertebrae. Posterior terminus of dorsal-fin base anterior to vertical through anal-fin origin. Distal margin of dorsal fin somewhat convex; anterior rays reaching to or beyond adipose fin when fin is depressed. Anal fin ii–iii,8, rarely ii–iii,9. First basal anal-fin pterygiophore inserting behind hemal spine of 31st to 33rd vertebrae. Anal fin slightly emarginate, with no indication of sexual dimorphism. Pectoral fin lobulate in 54 mm SL specimen, dorsal 9 rays developed in 96 mm SL individual and fin completed rayed in specimens of ~100–110 mm SL. Fully developed pectoral fin i,16–19,ii–iv. Pectoral fin pointed in profile with first branched ray longest; tip extends posteriorly one-third to one-quarter distance to insertion of pelvic fin. Pelvic fin i,7, rarely i,8. Distal margin of pelvic fin obtusely pointed; tip reaches posteriorly approximately one-half distance to anal fin. Caudal fin forked. Adipose fin present.

VERTEBRAE.—46(8), 47(15), 48(21), 49(7) [47].

LIFE COLORATION (based on two transparencies of live specimens from the Peruvian Amazon by Anita Hogeborn-Kullander; specimens now cataloged as NRM 23831 and 24124).—Overall pigmentation of head and body bright silver, less developed midlaterally in some individuals. Variably developed dusky band extending from posterior margin of eye or rear of opercle across body to end of caudal peduncle. Two irregular horizontal series of dark spots along lateral and dorsolateral surfaces of body; these being variably observable. Caudal fin with variable pattern of dark blotches. Paired and unpaired fins with dark markings (see "Color in Alcohol") but without other pigmentation. Lighter dorsal and ventral margins of caudal fin somewhat yellow.

COLOR IN ALCOHOL.—*Boulengerella maculata* demonstrates a notable range in body and head pigmentation, perhaps associated with its broad geographic distribution or the different water types in which it occurs.

Head darker dorsally, streak of dark pigmentation extending from nostrils anteriorly along dorsal margin of premaxilla. Distinct dark horizontal stripe running from rear of orbit along margin between third and fifth infraorbitals; stripe expanding into vertical bar on vertical arm of preopercle. Some individuals with broad horizontal band of dusky pigmentation under stripe; band ranging from very faint to nearly as dark as stripe. Midlateral surface of opercle variably darkly pigmented; degree of pigmentation ranging from small patch in specimens with light overall pigmentation to broad blotch in darkly pigmented specimens. Variable streak of dark pigmentation extending from tip of lower jaw midventrally along branchiostegal-ray membranes. Juveniles under approximately 100 mm SL with vertical bar of dark pigmentation under middle of orbit. Spot greatly reduced or more typically lacking in larger individuals.

Body pigmentation highly variable. Some individuals with light overall pigmentation gradually getting darker dorsally, but without any discrete changes in degree of pigmentation. Most specimens with broad midlateral horizontal band of dusky to dark pigmentation extending posteriorly to base of caudal fin, intensity of stripe generally correlated with overall body pigmentation. Dorsal portion of body ranging from dusky, albeit somewhat lighter than midlateral band, to as dark as midlateral band in intensely pigmented specimens. Midlateral stripe pigmentation on dorsolateral surface of body overlain by two irregular horizontal series of rotund spots in majority of specimens. Pattern of spots less apparent in many larger individuals. Some individuals with only a few scattered distinct dark spots overlaying a somewhat indistinct marmoration formed by irregular pattern consisting of smaller spots on dorsolateral and dorsal surfaces of body. Small number of specimens completely lacking distinct spots and having only more diffuse pattern dorsally. Variation in dorsal and dorsolateral pigmentation not found to be correlated with variation in other features. Some individuals, particularly those with darker overall pigmentation, having ventral surface of body with dark spots or irregular longitudinal band of dusky to dark pigmentation. Midventral band, when present, typically narrow and positioned along midventral line in region between pectoral and pelvic fins, becoming much wider posterior to anal fin, in region surrounding base of anal fin, and along ventral surface of caudal peduncle.

Dorsal fin with two irregular bands of pigmentation; basal band running across lower portions of all fin rays, upper angling across anterior rays to distal margin of fin. Caudal fin with dark spot at base of middle rays and variable pattern of dark blotches across both lobes. Anal fin with dark pigmentation on basal portions of anterior branched rays that extends to distal portions of middle rays in some specimens, particularly those with darker overall pigmentation. Pelvic fin with patch of dusky pigmentation on central portion of fin. Some specimens with dusky pigmentation on lateral portion of pectoral fin somewhat proximate to tips of rays.

GEOGRAPHIC VARIATION.—The variation in pigmentation on the head and body described above does not demonstrate any discrete geographic pattern across the distribution of the species. Populations from the western portion of the range of the species in Peru, the region around Leticia, Colombia, and the Rio Javari basin in Brazil differ somewhat from population samples from the central and lower Amazon and the Río Orinoco in two meristic features, the number of vertebrae and the number of scales with perforations along the lateral line. The number of vertebrae in radiographed samples of *Boulengerella maculata* from various portions of its range is shown in Table 6; as can be seen, the vertebral counts and mean values for samples from the upper Amazon tend to be lower than those from the other portions of the species range, albeit with broad overlap in counts. The range of the number of perforated scales along the lateral line in samples from the

TABLE 6.—Number of specimens of various populations of *Boulengerella maculata* with cited number of vertebrae. Vertebrae incorporated into fused $PU_1 + U_1$ counted as a single element and vertebrae of Weberian apparatus counted as four elements.

Population	Vertebrae				
	46	47	48	49	$\bar{x}$
Upper Amazon	8	8	1		46.59
Middle and lower Amazon		5	9	3	47.88
Río Orinoco		2	11	4	48.12

in other samples (14–25), particularly in those populations from the lower portions of the Amazon basin (17–25). Another feature that differs modally between the populations in the Amazon and Orinoco basins is the number of scales along the middorsal line between the rear of the supraoccipital and the dorsal-fin origin. As shown in Table 7, the populations of *Boulengerella maculata* in the Amazon basin typically have higher counts (range 70–84) than do those from the Orinoco (range 63–78). Despite these modal differences in number of vertebrae, perforated lateral-line scales, and predorsal median scales, there is broad overlap in the ranges of each feature between samples from different regions. This variation, therefore, fails both to distinguish the populations and to justify their recognition as distinct forms.

COMMON NAME.—Brazil: Bicuda, Ueua (Mendes dos Santos et al., 1984:24). Ecuador: Picudo (Barriga, 1991:31). Peru: Picudo (Ortega and Vari, 1986:10), Garza-challua (Eigenmann and Allen, 1942:274). Venezuela: Agujeta (Mago-Leccia, 1970:74).

ECOLOGY.—Goulding et al. (1988:173) found that *Boulengerella maculata* feeds exclusively on fishes at a series of localities in the Rio Negro basin, Brazil.

DISTRIBUTION.—Rio Amazonas, Rio Tocantins, and Río Orinoco basins (Figure 38).

REMARKS.—*Xiphostoma maculatum* was described by Valenciennes in Cuvier and Valenciennes (1849) on the basis of a single specimen collected in the Amazon by Castelnau (MNHN 4232). Castelnau (1855:76) subsequently repeated a portion of Valenciennes' original description of the species and provided a somewhat fanciful illustration of the holotype (1855, pl. 40, fig. 2). Neither Castelnau nor Valenciennes provided much information on the holotype, but the figure in Castelnau does shown the marmorated pattern on the caudal-fin lobes characteristic of the species. Two decades later, Cope (1872:267) described *Xiphostoma taedo* from the Peruvian Amazon. In his description Cope neither contrasted his species to other nominal members of the genus, nor did he indicate why he considered it undescribed. The holotype and paratype of Cope's species (ANSP 7958 and 7959, respectively) are in relatively poor condition and appear to have been already damaged when described by Cope. Although Cope (1872, pl. 13, fig. 2) illustrated a completely pored lateral line for *Xiphostoma taedo*, he subsequently noted (1878:688) that "specimens of this species in better condition than the types ... show that all but the anterior portion of the lateral line is wanting." Fowler (1907:463–464) also failed to cite the lateral-line count in his redescription of the type series. The evident damage in the type specimens may account for the low count of 75 lateral-line scales cited by Cope (1872), contrary to the range of 80–96 in the material examined during this study. Cope's original description and associated illustration (1872:267, pl. 13, fig. 2) did note the presence of "two series of small brown spots" along the dorsolateral surface of the body. Such pigmentation occurs in only one species of *Boulengerella* with the dorsal fins posteriorly positioned over the anal fin, *B. maculata*. Although it is possible to retrieve only a portion of the meristic and morphometric values from the holotype of *Xiphostoma taedo* (Table 8), the available data agree with that of *Boulengerella maculata*. No indication exists on the basis of the material examined that there is more than one species of *Boulengerella* with an anteriorly positioned fin and spotting on the body within the Amazon basin. *Xiphostoma taedo* consequently is considered a synonym of *Boulengerella maculata*.

MATERIAL EXAMINED.—330 specimens (complete data taken on 98 specimens, 54.0–319 mm SL; partial data taken on 28 additional specimens).

"Amazon River," no specific locality: BMNH 1927.7.30:10, 1 (250); BMNH 1925.10.28:120, 1 (285); BMNH 1927.6.7:17, 1. "Rio Capai" (not located), BMNH 1853.3.19:66, 1.

BRAZIL. "Amazone" (= Amazon River), MNHN 4232, 1 (230; holotype of *Xiphostoma maculatum*). *Pará:* Rio Maicuru, Monte Alegre (02°14'S, 54°17'W), NRM 14834, 2 (245–295). Rio Trombetas, Reserva Biologica de Trombetas, Ilha do Abuí (01°51'S, 55°35'W), MZUSP 15922-24, 3;

TABLE 7.—Number of specimens of populations of *Boulengerella maculata* in the Amazon and Orinoco basins with cited number of predorsal scales along dorsal midline.

Population	Number of predorsal scales																					
	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
Amazon								1	4	2	5	9	8	8	7	8	4	3	4	6	6	4
Orinoco	1	2	5	7	5	5	5	4	2	4	2	1	1		1	1						

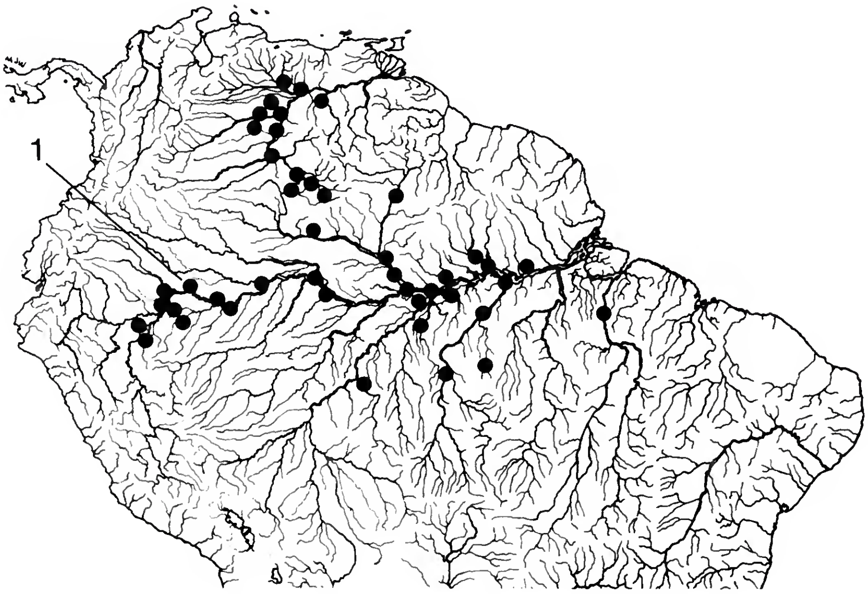

FIGURE 38.—Map of northern portion of South America showing geographic distribution of *Boulengerella maculata* (type-locality of *Xiphostoma maculatum* inexact = "Amazon"; 1 = type-locality of *Xiphostoma taedo*). Some symbols represent more than one lot of specimens or locality.

Ilha do Abuí (01°51′S, 55°35′W), MZUSP 15922-24, 3; MZUSP 15724, 1. Rio Trombetas, Reserva Biologica de Trombetas, MZUSP 15705, 1 (230). Rio Trombetas, Lago Jacaré (01°50′S, 55°40′W), MZUSP 23046, 1. Rio Trombetas, 20 km above its mouth (01°55′S, 55°35′W), MZUSP 31090, 2. Rio Jamanxim, above Bebal (04°43′S, 50°58′W), MZUSP 25472, 1. Rio Tocantins, Igarapé Muru, below Tucuruí (03°41′S, 49°27′W), MZUSP 24096, 7. Lagoas along margin of Rio Tocantins, near Tucuruí (03°42′S, 48°27′W), MZUSP 24112, 1. Lagoa along margin of Igarapé Murú, Rio Tocantins above Tucuruí (03°42′S, 48°27′W), MZUSP 24168, 1. Santarém market, SU 53849, 2 (255-260). Rio Tapajós, Ilha da Barreirinha, near São Luis (04°25′S, 56°09′W), MZUSP 22110, 4; Rio Tapajós Maloquinha, near Itaituba (04°25′S, 56°10′W), MZUSP 21912, 2. Rio Tapajós, São Luiz (04°25′S, 56°09′W), MZUSP 32180, 1. Rio Tapajós, Igarapé Jacaré, near Boim (02°49′S, 55°10′W), MZUSP 24240, 1 (238). *Amazonas:* Rio Urubu, 25 mi (40.3 km) from Itacoatiara (03°06′S, 58°24′W), USNM 179506, 13 (9, 119-169); USNM 196166, 4 (1, 235). Río Amazonas, at Albano, E of Itacoatiara (03°06′S, 58°24′W), USNM 310295, 1 (250). Rio Canumã, MZUSP 7062, 12 (2, 255-260). Igarapé do Rio Maués, município de Maués (03°24′S, 57°44′W), MZUSP 7324, 2 (1, 268). Lago Januari, Lago Canto Galos (03°12′S, 60°05′W), USNM 308032, 1. Manaus (03°06′S, 60°00′W), BMNH 1913.10.30:1, 1 (96.1). Rio Preto da Eva, município de Manaus (03°06′S, 59°50′W), MZUSP 25351, 1. Region of Manaus, MZUSP 6676, 3 (1, 161). Manacapuru (03°06′S, 61°30′W), MZUSP 6541, 2; MZUSP 6638, 28. Lago Saracá (02°53′S, 58°21′W), MZUSP 5804, 2. Rio Purus, Taparaua, 380 km from Manaus by water, USNM 310294, 1 (171). Rio Tefé, Jurupari, MZUSP 32198, 1. Rio Tefé, Lago Mucuré, MZUSP 32196, 34. Rio Tefé, Ressaca de Paula, MZUSP 32197, 3. Rio Marauía, MZUSP 32181, 28. Rio Marauía, Cachoeira do Bicho-Áçú (00°20′S, 65°20′W), MZUSP 32182, 5 (4, 250-319). Lago Janauacá, Rio Solimões, MZUSP 24955, 1. Rio Negro, Anavilhanas, MZUSP 32184, 1; MZUSP 32185, 2; MZUSP 32186, 1; MZUSP 32187, 2. Rio Jauaperi, from its mouth to 100 km upstream, MZUSP 23290, 1 (215). Mouth of Rio Japurá, Lago Amanõ (03°08′S, 64°06′W), MZUSP 36059, 2; MZUSP 36091, 6; MZUSP 36084, 1; MZUSP 36088, 1; MZUSP 36089, 1; MZUSP 36086, 5; MZUSP 42345, 1 (95.5). Rio Purus, no specific locality, USNM 311151, 1 (126). Rio Livramento, AMNH 12739, 1 (235). Rio Javari, Benjamin Constant, opposite Pueblo San Sebastián, Lago Arára (04°22′S, 70°02′W), NRM 14829, 3 (118-138). Rio Javari basin, sand playa opposite civil village of Colonia Angamos, Peru (05°11′S, 72°53′W), NRM 24124, 3 (110-125). Lago do Rei, Ilha Canini in front of Santo Antônio do Içá, MZUSP 23534, 5. *Roraima:* Rio Branco, igarapé 2 km above Cachoeira do Bem Querer (02°00′N, 61°00′W), MZUSP 32192, 1 (240). *Rondonia:* Rio Machado, Santo Antônio, Lago do Mucuim (08°30′S, 62°30′W), MZUSP 32188, 1 (222). Rio Machado, USNM 319781, 2 (1, 127; specimen cleared and

TABLE 8.—Morphometrics and meristics of (A) holotype of *Xiphostoma maculata*, MNHN 4232; (B) holotype of *Xiphostoma taedo*, ANSP 7958; and (C) all other specimens of *Boulengerella maculata* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 16 are proportions of standard length; 17 to 21 are proportions of head length. Dashes indicate values that could not be determined because of the poor condition of the specimen.

Character	A	B	C
		Morphometrics	
Standard Length	230	162	52.0–319
1. Body depth at dorsal-fin origin	-	0.114	0.090–0.168[a]
2. Snout to dorsal-fin origin	0.809	0.796	0.777–0.840
3. Snout to anal-fin origin	0.848	0.846	0.817–0.875
4. Snout to pectoral-fin origin	0.330	0.354	0.317–0.376
5. Snout to pelvic-fin origin	0.648	0.633	0.615–0.669
6. Dorsal-fin origin to hypural joint	0.210	0.184	0.173–0.220
7. Dorsal-fin origin to anal-fin origin	0.140	0.118	0.114–0.164
8. Dorsal-fin origin to pelvic-fin insertion	0.229	-	0.194–0.246
9. Dorsal-fin origin to pectoral-fin insertion	0.506	0.463	0.448–0.515
10. Caudal-peduncle depth	0.077	0.063	0.057–0.084[b]
11. Pectoral-fin length	0.115	-	0.101–0.127[c]
12. Pelvic-fin length	0.110	-	0.089–0.125[d]
13. Length of longest dorsal-fin ray	-	-	0.132–0.163
14. Length of longest anal-fin ray	-	-	0.108–0.130
15. Anal-fin base	0.078	0.071	0.064–0.073
16. Head length	0.343	0.359	0.317–0.390
17. Snout length	0.528	0.525	0.497–0.552
18. Orbital diameter	0.121	0.129	0.105–0.143
19. Postorbital length	0.351	0.343	0.316–0.387
20. Lower-jaw length	0.578	0.561	0.552–0.607
21. Interorbital width	0.227	0.194	0.175–0.250
		Meristics	
Scales along lateral-line series	82[e]	-	80–100
Pored lateral-line scales	-	-	5–26
Scale rows between dorsal-fin origin and midventral line	-	-	17–23
Predorsal median scales	79	-	63–84[f]
Postdorsal median scales	9	-	7–10
Branched dorsal-fin rays	8	8	8
Branched anal-fin rays	8	8	8
Pectoral-fin rays	-	-	14–17
Branched pelvic-fin rays	7	-	7
Vertebrae	47	47	46–49[g]

[a] 0.090 in a single 54.0 mm SL specimen; range 0.108–0.151 in specimens of 74.5–251 mm SL.

[b] 0.057 in a single 54.0 mm SL specimen; range 0.67–0.80 in specimens of 74.5–251 mm SL.

[c] Fin lobulate, without definite rays in 54.0 mm SL specimen.

[d] 0.89 in a single 54.0 mm SL specimen; range 0.100–0.125 in specimens of 74.5–251 mm SL.

[e] Specimen largely lacking scales; number of scales in lateral-line series estimated from remaining scales and scale pockets.

[f] See Table 7 for geographic variation in this count.

[g] See Table 6 for geographic variation in this count.

counterstained). *Mato Grosso:* Upper Rio Juruena, USNM 199194, 1.

COLOMBIA. *Amazonas:* Leticia, Lagos de Leticia (04°09′S, 69°57′W), NRM 14973, 2 (146–159). Río Amazonas, just N of Leticia, UF 26216, 1 (54.0).

PERU. "Peruvian Amazon," ANSP 21500, 2. *Loreto:* No specific locality, BMNH 1938.5.30:1, 1. Río Ambyiacu (03°20′S, 71°40′W), ANSP 7958, 1 (162; holotype of *Xiphostoma taedo*); ANSP 7959, 1 (152; paratype of *Xiphostoma taedo*). Río Ambyiacu, Pebas (03°20′S, 71°40′W), SU 34985. Río Ambyiacu, Shansho Caño (03°20′S, 71°40′W), USNM 124913, 3. Río Nanay, Cocha Tarapoto (03°44′S, 73°20′W), ANSP 167104, 2 (74.5–164). Río Nanay, islet near Shiriyana, NRM 23831, 4 (2, 145–160). Río Nanay, caños entering river, NE of Iquitos (03°49′S, 73°14′W), USNM 280449, 1 (141). Río Nanay, left bank sand playa opposite mouth of Quebrada Aqua Negra (03°42′S, 73°16′W), NRM 25218, 1 (154). Río Nanay, ~0.8 km downstream of Santa Clara (03°45′S, 73°17′W), ANSP 167106, 1. Río Nanay, marginal cocha a few km upstream of Santa Clara, NRM 25045, 2 (87.5–92.0). Iquitos (03°46′S, 73°15′W), SU 53852, 1; SU 53848, 1 (164). Río Nanay, ~14.4 km above Río Amazonas (03°43′S, 73°18′W), ANSP 136817, 2; ANSP 136818, 3 (125–156). Río Nanay, ~ 0.4 km below Minchana (03°00′N, 73°27′W), ANSP 167105, 3 (2, 127–151). Río Nanay, Mishana, cocha off Río Nanay (03°44′S, 73°22′W), MPM 30567, 2 (1, 162). Río Nanay, region of Mishana, MPM 30700, 1 (147). Río Samiria, BMNH 1977.3.10:178, 1. Río Samiria drainage, Quebrada Santa Elena (04°42′S, 74°18′W), NRM 25610, 3. Río Tahuaya basin, Caño Huayti (04°11′S, 73°12′W), NRM 24550, 1 (134). Río Yavari basin, area of Atalaia do Norte, NRM 14832, 1 (154). Río Napo system, Cocha Yuto on right bank of Río Mazán (03°28′S, 73°05′W), NRM 24339, 2 (131–168). Small stream near Genero Herrera (05°00′S, 73°38′W), ANSP 165024, 1 (148).

VENEZUELA. *Amazonas:* Río Mavaca, at Tapirapeco Base Camp (~1°51′N, 65°08′W), AMNH 93029, 1 (250). Río Mavaca, near Tapirapeco Base Camp (~1°51′N, 65°08′W), AMNH 93028, 1 (174). Río Pamoni lagoon, ~0.5 km from confluence of Río Casiquiare (2°50′N, 65°53′W), ANSP 161216, 4 (136–156). Caño Caripo, caño entering Río Casiquiare ~5 min. from confluence of Río Casiquiare and Río Orinoco, ANSP 162782, 2 (245–270). Río Pacia Grande, ~22 km out of Puerto Ayacucho toward Samariapo (~05°16′N, 67°49′W), FMNH 85575, 2 (148–152). Laguna de Tití, N of San Fernando de Atabapo (~04°03′N, 67°42′W), MBUCV V-7315, 1. Río Orinoco, near Caño Cuca, San Fernando de Atabapo (~04°03′N, 67°42′W), MHNLS 4050, 1. Mavaca, upper Río Orinoco (02°31′S, 65°11′W), MHNLS 4785, 1. Caño Caripo, tributary of Río Casiquiare, near bifurcation of Río Orinoco (~03°09′N, 65°56′W), MBUCV V-6216, 2. Río Orinoco, Quiratare, ~4 hrs from mouth of Río Cunucumana (03°02′S, 66°04′W), MBUCV V-4415, 1. Río Casiquiare, near Beripamoni, MBUCV V-6419, 4. *Apure:* Río Claro, 15 km S of La Montariha, on San Fernando de Apure to Puerto Paez highway (7°10′N, 67°25′W), ANSP 165744, 3 (230–245); Río Cinaruco basin, Laguna Grande (6°33.32′N, 67°24.81′W), INHS 61439, 2 (250–280). Río Cinaruco basin, caño (6°34′24″N, 67°17′32″W), INHS 61524, 1 (138); MCNG 21762, 1. Laguna 1 km SE of Caño La Pica, MHNLS 4051, 1. *Guarico:* Río Chimire, Paso de Chimire, E of Parucana, MBUCV V-3352, 1; MBUCV V-3475, 16 (10, 112–182); MBUCV V-3589, 12. Río Orinoco, Parmana (07°50′N, 65°46′W), MBUCV V-488, 3. Río San Jose, near confluence of Río San Jose and Río Guariquito, UMMZ 214812, 1. Quebrada draining into Río Orinoco, near Paramana, USNM 391780, 2 (1, 156; specimen cleared and counterstained). *Bolivar:* Río Orinoco basin, Las Majadas, Lagoon El Potrero (7°36′40″N, 64°49′50″W), ANSP 166412, 2 (1, 250). San Pedro de Tauca, Lago Paramuto (7°33′05″N, 64°59′56″W), ANSP 166757, 1 (250).

Boulengerella lucius **(Cuvier, 1816)**

FIGURES 39–41; TABLES 9, 10

hydrocyon lucius Cuvier, 1816:168 [name in footnote with generic name in lower case; indicated as a new species originating in Brazil].

Hydrocyon lucius.—Cuvier, 1819:359, pl. 26, fig. 3 [type locality: Brazil].—Myers, 1950:46 [*Xiphostoma cuvieri* placed as a synonym of *lucius*].

Xiphostoma lucius.—Müller and Troschel, 1845:20 [questionably placed as synonym of *Xiphostoma cuvieri* Agassiz in Spix and Agassiz, 1829].—Valenciennes in Cuvier and Valenciennes, 1849:350 [redescription based on holotype of *hydrocyon lucius;* distinctiveness of species from *X. cuvieri* argued].—Günther, 1864:357 [based on Valenciennes in Cuvier and Valenciennes, 1849].—Eigenmann and Eigenmann, 1891:59 [based on Günther, 1864].—[not Holmberg, 1889:366; 1891:192].

Hydrocynus lucius.—Eigenmann, 1910:446 [literature compilation].—Bertin, 1948:30 [type depository].

Boulengerella lucius.—Fowler, 1950:329 [literature compilation; references in part, not listed literature citations of species in Río Paraguay system; not reported occurrence of species in Río Paraguay system]; 1975:123 [literature compilation].—Lowe-McConnell, 1991:68 [Brazil, Rio Xingu].—[not Ringuelet and Arámburu, 1961:34; Ringuelet et al., 1967:169; Ringuelet, 1975:73; López et al., 1987:16].

Boulengerella lucium.—Schultz, 1950:52 [in part, *hydrocyon lucius* citations; not *Xiphostoma cuvieri, X. ocellatum,* and *X. longipinne* synonymies and citations; British Guiana (= Guyana): Essequibo River, Rockstone].

Boulengerella lucia.—Géry, 1977:106 [assignment to subgenus *Spixostoma;* in part, not synonym of *B. ocellatus* and *B. cuvieri*].—Ferreira, 1984:355 [Brazil: Pará, Santarém, Represa de Curuá-Una].—[not Cala, 1990:94; Taphorn and García-Tenía, 1991:39].

DIAGNOSIS.—The location of the dorsal-fin base distinctly anterior to the vertical through the anal-fin origin in *Boulengerella lucius* distinguishes it from all ctenoluciids except *B. cuvieri* and *B. xyrekes. Boulengerella lucius* differs from those two species in having the membranes of the basal portions of the middle caudal-fin rays darkly pigmented and forming a series of horizontally elongate patches between the fin rays, contrary to having an irregularly rotund, discrete, dark spot on the basal portions of those fin rays (compare Figure 40 with those for *B. cuvieri* and *B. xyrekes*). The distinctly dusky middle caudal-fin rays and random pattern of dark spots on the ventrolateral portion of the body (Figure 40) in *B. lucius* further distinguishes it from *B. cuvieri* and *B. xyrekes,* which lack such dusky caudal-fin pigmentation and have instead diffuse dusky midlateral body stripes. *Boulengerella lucius* and *B. cuvieri* also differ in the number of vertebrae (45 or 46 versus 48 or 49, respectively) and number of premaxillary teeth in specimens greater than ~80 mm HL (Figure 39). The absence of a dark oblique band across the posteroventral portion of the third infraorbital in *B. lucius* further distinguishes that species from *B. xyrekes,* which has such pigmentation except in the largest specimens. The latter two species also differ in number of lateral-line scales (98–117 in *B. lucius* versus 87–94 in *B. xyrekes*) and number of predorsal scales (62–72 versus 54–63,

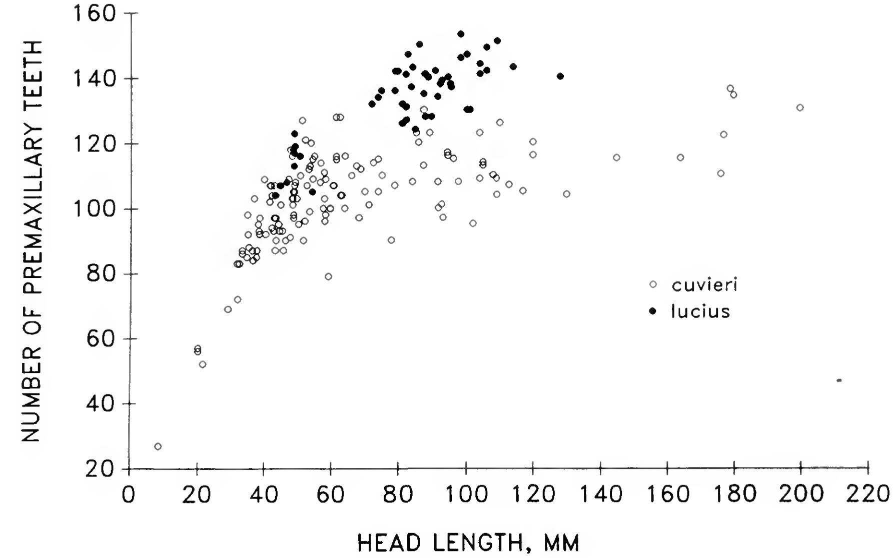

FIGURE 39.—Plot of number of premaxillary teeth against head length for *Boulengerella lucius* and *B. cuvieri*. Some symbols represent more than one lot of specimens or data point.

respectively). Autapomorphies for *B. lucius* are detailed under the "Phylogenetic Reconstruction," above.

DESCRIPTION.—The species is one of the larger in the genus, with the largest measured specimen being 420 mm SL. Head and body notably elongate (Figure 40). Greatest body depth at dorsal-fin origin in smaller individuals, distinctly anterior to that line in larger specimens. Dorsal profile of head and body nearly straight to dorsal-fin origin, very slightly posteroventrally angled at base of dorsal fin, straight from rear of fin to adipose fin. Dorsal surface of body in preserved specimens often somewhat flattened anterior to dorsal fin, somewhat flattened to smoothly rounded transversely posterior to fin. Ventral profile of body gently convex from tip of snout to caudal peduncle; convexity more pronounced in larger individuals. Prepelvic region of body transversely rounded.

Head distinctly pointed in both lateral and dorsal views. Form of upper jaw, lower jaw, and nostrils as described for *Boulengerella lateristriga*, above. Fleshy process at tip of snout proportionally small in 54 mm SL specimen; proportionally larger in larger examined individuals. Interorbital region proportionally wider in larger specimens.

Arrangement and form of teeth in both premaxillae and dentaries comparable to those in *Boulengerella lateristriga* described above. Premaxillary teeth in a single row, with 104–153 teeth in specimens of 43–128 mm HL, with number of teeth somewhat variable at a particular standard length.

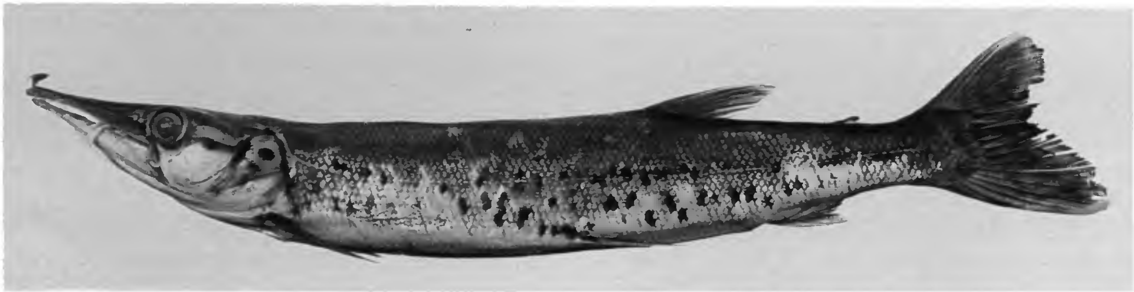

FIGURE 40.—*Boulengerella lucius*, MZUSP 32175, 266 mm SL; Brazil, Amazonas, Rio Negro, mouth of Rio Mandiquié.

Overall ontogenetic trend is for an allometric increase in number of teeth; rate of increase decreasing at larger standard lengths (Figure 39). Cleared and counterstained juvenile of 99.0 mm SL with two patches of 2 or 3 teeth on medial portion of premaxilla. No inner series of premaxillary teeth present in examined individuals. Maxilla with 16–18 teeth along its anterior margin in specimens of 43–128 mm HL. Dentary lacking teeth anteriorly immediately proximate to symphysis, with 101–144 teeth arranged in a single series in specimens of 43–128 mm HL. Overall ontogenetic trend is for increase in number of teeth at larger standard lengths. Number of dentary teeth somewhat variable within limited range of head lengths. Dentary without inner row of teeth in examined specimens. Teeth on upper and lower pharyngeal tooth-plates small and conic.

Lateral line nearly completely perforated, with approximately 3–7 scales overlying basal portions of middle caudal-fin rays lacking pores. Scales on body with surface sculpturing and irregular margins, but without distinct cteni. Scales along pre- and postdorsal midlines arranged somewhat irregularly.

Dorsal fin ii–iii,8. First basal dorsal-fin pterygiophore inserting behind neural spine of 22nd vertebra. Posterior terminus of dorsal fin distinctly anterior to vertical line through anal-fin origin. Distal margin of dorsal fin somewhat convex. Anal fin iii,8. First basal anal-fin pterygiophore inserting behind hemal spine of 31st or 32nd vertebrae. Form of anal fin highly variable ontogenetically. Posterior rays distinctly longer than anterior rays in smaller individuals, forming distinct elongate lobe. Posterior rays becoming progressively relatively shorter with increasing standard length, distinctly shorter than anterior rays in largest individuals examined. Pectoral fin i,16–20,iii–iv; pointed in profile with first branched ray longest; tip extends posteriorly one-third distance to pelvic-fin origin in smaller individuals, less than one-quarter of distance in larger specimens. Pelvic fin i,7; distal margin obtusely pointed; reaches posteriorly over one-half distance to anal fin in smaller individuals, approximately one-third of distance in larger specimens. Caudal fin forked. Adipose fin present.

VERTEBRAE.—45(4), 46 (8).

TABLE 10.—Morphometrics and meristics of all specimens of *Boulengerella lucius* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 16 are proportions of standard length; 17 to 21 are proportions of head length.

Morphometrics	
Standard Length	133–420
1. Body depth at dorsal-fin origin	0.127–0.173
2. Snout to dorsal-fin origin	0.652–0.714
3. Snout to anal-fin origin	0.799–0.854
4. Snout to pectoral-fin origin	0.275–0.323
5. Snout to pelvic-fin origin	0.595–0.649
6. Dorsal-fin origin to hypural joint	0.282–0.345
7. Dorsal-fin origin to anal-fin origin	0.165–0.211
8. Dorsal-fin origin to pelvic-fin insertion	0.141–0.184
9. Dorsal-fin origin to pectoral-fin insertion	0.390–0.449
10. Caudal-peduncle depth	0.064–0.075
11. Pectoral-fin length	0.105–0.151
12. Pelvic-fin length	0.105–0.141
13. Length of longest dorsal-fin ray	0.129–0.169
14. Length of longest anal-fin ray	0.077–0.092
15. Anal-fin base	0.064–0.081
16. Head length	0.278–0.343
17. Snout length	0.450–0.512
18. Orbital diameter	0.128–0.167
19. Postorbital length	0.332–0.380
20. Lower-jaw length	0.558–0.630
21. Interorbital width	0.198–0.251
Meristics	
Scales along lateral-line series	98–117
Pored lateral-line scales	90–108
Scale rows between dorsal-fin origin and lateral-line series	12–14
Scale rows between anal-fin origin and lateral-line series	9–11
Predorsal median scales	62–72
Postdorsal median scales	17–22
Branched dorsal-fin rays	8
Branched anal-fin rays	8
Pectoral-fin rays	21–28
Branched pelvic-fin rays	7
Vertebrae	45–46

TABLE 9.—Meristic values useful for discriminating *Boulengerella* species having the base of the dorsal fin situated entirely anterior to vertical through anal-fin origin.

Character	*lucius*	*cuvieri*	*xyrekes*
Lateral-line scales	98–117	94–124	87–94
Predorsal median scales	62–72	57–76	54–63
Vertebrae	45–46	48–49*	44–46

* 47 vertebrae in 1 specimen with several deformed vertebrae making that count unreliable.

LIFE COLORATION (based on a photograph of a recently collected specimen from the Rio Trombetas, Amazonas, Brazil, provided by Heiko Bleher).—Overall coloration of head and body bright silver. Obscure dark longitudinal stripe extending from rear of orbit to posterior margin of infraorbital series and expanded to large spot on anterior margin of opercle. Body with variably shaped, dark spots on ventrolateral and lateral surfaces. Dark pigmentation on fins as described under "Color in Alcohol." Anterodorsal portion of dorsal fin and distal portions of dorsal and ventral lobes of caudal fin orange-red.

COLOR IN ALCOHOL.—Specimens with residual guanine on scales silvery to silvery-golden, darker on dorsal surface of head and body. Distinct to obscure longitudinal stripe extending from rear of orbit to posterior margin of infraorbital series. Specimens completely or largely lacking guanine on scales with ground coloration of head and body ranging from light tan to brown, somewhat to distinctly more dusky dorsally in smaller individuals; darker overall and light to dark brown laterally and dorsally in larger individuals. Intensity of dark pigmentation variable between samples, perhaps as consequence of differing water conditions, and variable to a lesser degree within population samples. Snout and fleshy tissue along margin of upper jaw dusky in lighter colored smaller specimens, entire snout dusky in smaller dark-colored individuals and all examined larger specimens. Variably distinct horizontal stripe of darker pigmentation extending from rear of orbit to posterior margin of infraorbital series; stripe more intense posteriorly and more obvious in specimens with overall darker body pigmentation. Opercle somewhat to distinctly dusky on its ventral portion, typically with distinct dark spot on middle of its dorsal portion and dark pigmentation anteriorly in region proximate to rear of horizontal stripe on third infraorbital.

Body with somewhat random pattern and number of small, variably shaped, dark spots on ventrolateral and lateral surfaces. Individual spots approximately size of exposed surface of individual body scales, sometimes juxtaposed and forming larger spot. Spots on dorsal portions of body variably masked by darker pigmentation in that region in overall darker individuals. Dorsal fin without any pronounced pattern, somewhat to distinctly dusky with degree of pigmentation correlated with intensity of overall body pigmentation. Caudal fin with basal one-half to two-thirds of ventral and dorsal rays and all middle rays variably dusky. Distal portions of ventral and dorsal rays hyaline. Dark pigmentation most developed on membranes between middle rays of fin, particularly basally where pigmentation forms series of small elongate patches between neighboring fin rays; patches not distinct from dark pigmentation on remainder of fin membrane in specimens with darker overall head and body coloration. Individual patches of dark pigmentation on fin membranes separated by lighter pigmentation overlying basal portions of individual fin rays. Patches less apparent in larger individuals, particularly specimens with overall darker body pigmentation. Elongate posterior rays of anal fin dark in smaller individuals. Larger specimens with short posterior anal rays unpigmented. Central portion of pelvic fin dusky to dark, intensity and proportion of fin with dark pigmentation correlated with degree of overall body coloration. Pectoral fin hyaline to distinctly dusky.

DISTRIBUTION.—Rio Amazonas and Río Orinoco basins (Figure 41).

REMARKS.—Approximately three decades after Cuvier's (1816) description of *hydrocyon lucius,* Müller and Troschel (1845:20) questionably equated that species with *Xiphostoma cuvieri* Agassiz in Spix and Agassiz (1829), and indeed they even listed it as a junior synonym of the latter, even though it was described first. Although Müller and Troschel (1845) did not discuss the basis for their suggestion, these two nominal species share a posteriorly positioned dorsal fin and a particularly high number of lateral-line scales, factors that may have influenced their decision. The first published illustrations

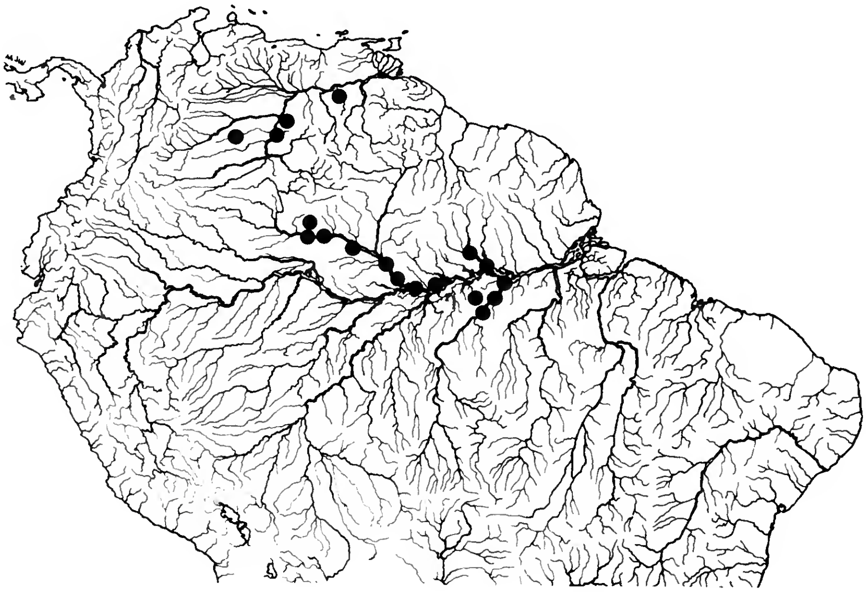

FIGURE 41.—Map of northern portions of South America showing geographic distribution of *Boulengerella lucius* (type locality of *Hydrocyon lucius* inexact = "Brazil"). Some symbols represent more than one lot of specimens or locality.

of the species differ, however, in showing a dark spot on the basal portions of the caudal fin in *cuvieri* (Spix and Agassiz, 1829, pl. 42), which is not indicated in Cuvier's illustration (1816, pl. 26, fig. 3) of *lucius*. Valenciennes in Cuvier and Valenciennes (1849) recognized the two species as distinct, noting with respect to the holotype of *lucius* that "I do not see any trace of an ocellus or a black spot near the tail" (my translation). This contrasts with the distinct dark spot at the base of the middle rays of the caudal fin, which is still quite apparent in the holotype of *Xiphostoma cuvieri* (MNHN 89.823). Subsequent to Valenciennes, the two nominal species (*lucius* and *cuvieri*) were recognized as distinct by all authors for a century. Myers (1950:47), however, puzzlingly stated that "*B. lucius* has apparently never been recognized since its description by Cuvier. Examination of a series of examples belonging to the genus [*Boulengerella*] leads me to the conclusion that the type of *lucius* is nothing but an example of the well known *B. cuvieri* (Agassiz, 1829), and I hereby synonymize these two nominal species" (*cuvieri* being the older name). Schultz, without comment and evidently independently (1950:52), placed *cuvieri* as a synonym of *lucius* (his *lucium*). Neither Myers nor Schultz commented on the caudal-fin pigmentation differences emphasized by Valenciennes in Cuvier and Valenciennes (1849) as distinguishing *lucius* from *cuvieri*. Indeed, Schultz' concept of *Boulengerella lucium* was based on a single juvenile specimen from Guyana in which the caudal spot was not yet developed. Based on Schultz' key (1950:50), his concept of *Boulengerella* was that the genus had "no black blotch at the base of the caudal fin," an erroneous statement not only for *B. cuvieri* as defined in that study but also for *B. maculata*.

Authors subsequent to Myers and Schultz recognized a single species, *lucius*, for *Boulengerella* specimens with anteriorly positioned dorsal fins. The results of this study, however, show that Myers' (1950) and Schultz' (1950) concepts of *lucius* actually encompass three species, one of which lacks the distinct spot of dark pigmentation at the base of the middle caudal-fin rays in adults; the condition reported by Valenciennes for *lucius*. Furthermore, the species lacking a caudal spot has a high lateral-line scale count (98–103) comparable to that reported by Cuvier (1816) and Valenciennes in Cuvier and Valenciennes (1849), for the holotype of *lucius*.

The holotype of *hydrocyon lucius* (MNHN A.9853) could not be borrowed as a consequence of its condition, and, furthermore, it is a half dry specimen without vertebrae mounted on a glass plate (G. Duhamel, in litt.). The specimen, nonetheless, exhibits the horizontally elongate patches of dark pigmentation on the basal portions of the middle rays of the caudal fin and lacks a distinct spot of dark pigmentation on the base of that fin (T. Munroe, pers. comm.). Such a pigmentation pattern and the data in the original species description are consistent with the hypothesis that *lucius* is appropriately equated with material herein identified as *Boulengerella lucius*. *Boulengerella lucius* as recognized herein has a more restricted distribution than reported under the broader concept of the species used by authors for the last forty years, ranging through the Orinoco and Amazon basins, but not including the Rio Tocantins. Populations identified by previous authors as *B. lucius* from the Guyanas and the Río Tocantins are, rather, herein considered *B. cuvieri*. It is impossible in some cases to determine the identity of the material that served as the basis of reports of *B. lucius* from various portions of the Amazon basin. Such records are listed above according to their original citations.

Holmberg (1889:366; 1891:193) reported *Xiphostoma lucius* from the Ríos Pilcomayo and Paraguay in Argentina. Eigenmann (1910:446), Bertoni (1939), and Schultz (1950:52) neither cited *Boulengerella lucius* as occurring in the Río de La Plata basin nor commented on Holmberg's report of that species in that river system. Ringuelet and Arámburu (1961:34), Ringuelet et al. (1967:169), and Ringuelet (1975:73) reiterated Holmberg's record, evidently without examination of specimens. One or more of the citations presumably was the basis for the inclusion of the northern portions of the Rio de La Plata basin in the distributional range of the Ctenoluciidae by Banarescu (1990:107). Géry et al. (1987:369) listed *Boulengerella lucius* from the Río Parana, but noted that they were unsuccessful in capturing any specimens despite their extensive collecting efforts. The original Holmberg citations (1889, 1891) provided no data on his material, and no specimens of any ctenoluciids originating in the Rio de La Plata basin have been located during this study. It appears that Holmberg's record represents a misidentification, perhaps of an *Acestrorhynchus* species.

MATERIAL EXAMINED.—72 specimens (complete data taken on 40 specimens, 133–420 mm SL; partial data taken on 15 additional specimens).

No locality data. USNM 326202, 1 (99.0; specimen cleared and counterstained; data not included in tables).

BRAZIL. *Amazonas:* Rio Urubu, 25 mi (40 km) from Manaus, USNM 196164, 3 (133–157); USNM 196165, 2 (147–285). Lago Saracá, Silves (02°53′S, 58°21′W), MZUSP 5802, 3. Rio Negro, above Manaus, (03°06′S, 60°00′W), MZUSP 6142, 1. Rio Negro, Igarapé Jaraqui, left bank of river above Manaus (03°05′S, 60°01′W), MZUSP 6193, 1 (285). Lago Puraquequara, mouth of Rio Puraquequara, MZUSP 6094, 3 (1, 360). Rio Negro, Ilha de Tamaquaré (00°30′S, 64°55′W), MZUSP 32183, 8 (5, 273–327). Rio Negro, Anavilhanas, MZUSP uncat., 1 (370); MZUSP 32166, 3 (2, 240–272); MZUSP 32165, 3 (2, 310–371); MZUSP 32168, 2 (295–386); MZUSP 32167, 1 (141). Rio Negro, below Daraá (00°30′S, 65°40′W), MZUSP uncat., 2 (295–314). Rio Negro, São João, near Tapurucuara, MZUSP 42712, 1. Rio Negro mouth of Rio Mandiquié (00°30′S, 64°30′W), MZUSP 42713, 1 (420); MZUSP 32175, 1 (266). Rio Negro, Barcelos, Paraná do Jacaré (01°00′S, 62°40′W), MZUSP 42714, 1. Rio Marauiá, Cachoeira do Bicho-Áçú (00°20′S, 65°20′W), MZUSP 42865, 6 (3, 261–342). Rio Marauiá, lago along river, MZUSP 43140, 3 (2, 280–333). *Pará:* Rio Trombetas, Cuminá (01°30′S, 56°00′W), MZUSP 32144, 11. Rio Trombetas, Oriximiná (01°40′S, 56°00′W), MZUSP 42598, 1 (285); USNM 319782, 2 (1, 145; specimen cleared and counterstained). Igapo of Lago Farias, Reserva Biologica de Trombetas, Rio Trombetas, MZUSP 15772, 1 (340). Mouth of Rio Cuminá-Miri, near Oriximiná, MZUSP 9431, 2 (1, 285). Río Tapajós, island opposite Monte Cristo (04°04′S, 55°38′W), MZUSP 21959, 1 (159). Rio Tapajós, Lago on Ilha Campinho, MZUSP 13365, 1. Rio Tapajós, São Luis, MZUSP 35152, 1 (255). Igarapé tributary to Rio Jamari, above Terra Santa, MZUSP 7939, 1 (177).

VENEZUELA. *Amazonas:* Río Sipapo, mouth of lagoon, ~3 km above Pendare (4°52′N, 67°43′W), ANSP 159595, 1 (280). Caño Orera, at border of Estado Bolivar and Estado Amazonas, ~68 km NE of Puerto Ayacucho, ANSP 165676, 2 (1, 134). *Bolivar:* Río Orinoco basin, San Pedro de Tauco, Lago Paramuto (7°33′05″N, 64°59′W), ANSP 166514, 1 (161). *Apure:* Laguna 2 km SW of Caño La Pica, MHNLS 5428, 1 (147). Río Cinaruco basin, caño (6°34′24″N, 67°17′32″W), MCNG 26781, 1.

***Boulengerella cuvieri* (Agassiz in Spix and Agassiz, 1829)**

FIGURES 39, 42–45; TABLES 9, 11

Xiphostoma cuvieri Agassiz in Spix and Agassiz, 1829:79, pl. XLII [type-locality: Brasiliae fluviis (= rivers of Brazil)].—Müller and Troschel, 1845:20, pl. 3, fig. 3 [Brazil and Guiana; *Xiphostoma ocellatum* placed as a synonym].—1848:636 [Essequibo, Rupununi, and Takutu (rivers)].—Valenciennes in Cuvier and Valenciennes, 1849:355 [Amazon].—Eigenmann and Eigenmann, 1891:59 [literature compilation].—Myers, 1950:47 [*Xiphostoma lucius* placed as a synonym].—Whitley, 1951:407 [designated as type species of *Spixostoma* Whitley; replacement for *Xiphostoma* Agassiz in Spix and Agassiz, 1829, preoccupied in Hemiptera by *Xiphostoma* Kirby and Spence, 1828].—Kottelat, 1984:146 [holotype depository]; 1988:79, 84 [correct authorship; holotype depository].

Xiphostoma Cuvieri.—Kner, 1860:60, pl. VIII, fig. 17 [Maribitanos; common name].—Goeldi, 1898:484 [(Brazil: Pará, Rio) Capim; common name].—Pellegrin, 1899:157 [Venezuela: Río Apure]; 1909:150 [Brazil: Pará, Santarém].

Xiphostoma ocellatum Schomburgk, 1841:245, pl. XXIII [(Guyana) Essequibo (River); (Brazil) Rio Negro, Rio Branco].—Müller and Troschel, 1845:20 [placed as a synonym of *Xiphostoma Cuvieri* Agassiz].—Valenciennes in Cuvier and Valenciennes, 1849:355 [description based on one of Schomburgk's syntypes; locality information following Schomburgk, 1841].—Kner, 1858:168 [listing]; 1860:61, pl. VIII, fig. 18 [Rio Branco and Rio Solimões; illustration of head].—Eigenmann and Eigenmann, 1891:59 [literature compilation].—Regan, 1905:190 [Rio Negro].—Bertin, 1948:30 [depository of syntype from Essequibo River, Guyana; specimen herein designated as lectotype].

Xiphostoma oseryi Castelnau, 1855:76, pl. 40, fig. 1 [(Brazil) (Rio) Tocantins; based on specimen reported as *Xiphostoma cuvieri* by Valenciennes in Cuvier and Valenciennes, 1849:355].—Eigenmann and Eigenmann, 1891:59 [as a synonym of *Xiphostoma cuvieri*].—Eigenmann, 1910:446 [as a synonym of *Hydrocynus cuvieri*].

Xiphystoma ocellatum.—Ulrey, 1895:296 [Brazil; generic name misspelled].

Hydrocynus cuvieri.—Eigenmann, 1910:446 [literature compilation; Guianas and the Amazon]; 1912:411 [British Guiana (= Guiana): Rockstone, Rupununi].—Starks, 1913:21 [Brazil: market at Pará (= Pará, Belém), Rio Pará].—Fowler, 1914:254 [British Guiana (= Guyana): Rupununi River]; 1941:194 [Brazil: Piauhy (= Piauí), Rio Parnahyba (= Parnaíba), Therezina (= Teresina); probable incorrect locality, see "Remarks" below].—Starks, 1916:18 [morphology of sesamoid articular]; 1926:167 [morphology of ethmoid region of skull]; 1930:171 [morphology of pectoral girdle].—Puyo, 1949:138 [French Guiana: Tonate, Kourou].

Hydocynus cuvieri.—Caporiacco, 1935:67 [Guiana Britannica (= Guyana): Essequibo River, Curupucari; indigenous name; generic name misspelled].

Boulengerella cuvieri.—Schultz, 1944:261 [Venezuela: Río Apure; based on Pellegrin, 1899].—Fowler, 1950:328, fig. 387 [literature compilation; locality of illustrated specimen questionable, see "Remarks" below]; 1975:123 [literature compilation; *Xiphostoma ocellatum* and *Xiphostoma oseryi* listed as synonyms].—Roberts, 1973:213 [locality reported by Fowler (1941) for *Hydrocynus cuvieri* questioned].—Lowe-McConnell, 1964:114 [British Guiana (= Guyana): Rupununi savanna district; nighttime behavior; common name].—Lasso, 1993:16, 29, 43 [Venezuela: Río Suapare; common names; importance as food fish for indigenous peoples].

Boulengerella lucium.—Schultz, 1950:52 [in part; not synonymy of *Xiphostoma cuvieri*, *X. longipinne*, *X. ocellatum*, and *X. oseryi* or associated citations].

Hydrocinus cuvieri.—Fernández-Yépez, 1969:16 [Venezuela: Río Caroni; common name; maximum size].

Boulengerella lucius.—Géry, 1977:106 [in part; not synonymy of *Xiphostoma ocellatus*, *X. cuvieri*, and ? *X. longipinne*].—Géry et al., 1987:369 [possible occurrence in Río Paraguay system; based on an evidently erroneous record, see "Remarks" below].—Cala, 1990:94 [Colombia: Río Orinoco basin, Río Metica].—Lasso et al., 1990:144 [Venezuela: Bolivar, Lago de Guri; common name].—Taphorn and García-Tenía, 1991:39 [Venezuela: Bolivar, Río Caroni].—Géry et al., 1991:6, fig. 1 [French Guyana: Rivière Camopi near Saut Ouasseye and Saut Chien, Rivière Oyapock].—Taphorn, 1992:402–404 [Venezuela: Apure state; life history].

Boulengerella ocellatum.—Mendes dos Santos et al., 1984:24, unnumbered text fig. [Brazil: Pará, Rio Tocantins; common name; meristic data; notes on life history].

Boulengerella ocellata.—Ferreira et al., 1988:343 [Brazil: Roraima, Rio Mucajaí, ilha Paradão].—Vazzoler, 1992:6 [reproductive season, median size at first gonadal maturation].—Vazzoler and Menezes, 1992:630, 632 [reproductive season, median size at first gonadal maturation].

Boulengerella lucius.—Goulding et al., 1988:126 [Brazil: Amazonas, Rio Negro basin].

Hydrocinus lucius.—Lasso, 1988:132 [Venezuela: lower Río Orinoco basin, Laguna Los Barrancas; common name].

Boulengerella lucra.—Boujard et al., 1990:180 [French Guiana: Oyapock River; species name misspelled].

See discussion below under "Remarks" concerning synonymy of *Xiphostoma longipinne*.

Xiphostoma longipinne Steindachner, 1876:132 [type-locality: Brazil: mouth of Rio Negro; based on a juvenile].—Schultz, 1950:53 [placed as a synonym of *Boulengerella lucium*].

Hydrocynus longipinnis.—Eigenmann, 1910:446 [literature compilation].

Boulengerella longipinne.—Fowler, 1950:328 [literature compilation].—1975:123 [literature compilation].—Géry, 1977:106 [as a possible synonym of *Boulengerella lucius*].

DIAGNOSIS.—The location of the dorsal-fin base distinctly anterior to the vertical through the anal-fin origin distinguishes *Boulengerella cuvieri* from all ctenoluciids except *B. lucius* and *B. xyrekes*. The discrete spot of dark pigmentation on the basal portions of the middle caudal-fin rays in *Boulengerella cuvieri* (Figure 43) separates it from *B. lucius* (Figure 40), which lacks that pigmentation, having instead the somewhat dusky middle caudal-fin rays with a series of discrete, elongate patches of dark pigmentation on the membranes between basal portions of the rays. *Boulengerella cuvieri* has a somewhat diffuse dusky midlateral stripe without discrete, randomly located, dark spots about the size of the exposed surface of individual scales on the ventrolateral surface of the body, contrary to the absence of a midlateral stripe and the presence of such spots in *B. lucius*. *Boulengerella cuvieri* differs from the very similar *B. xyrekes* in lacking an oblique stripe across the posteroventral portion of the third infraorbital except as a juvenile, contrary to the presence of such pigmentation in *B. xyrekes*, and in the number of vertebrae (48 or 49 in *cuvieri* versus 44–46 in *B. xyrekes*), and lateral-line scales (94–124 versus 87–94, respectively). Autapomorphies for *B. cuvieri* are detailed under the "Phylogenetic Reconstruction," above.

DESCRIPTION.—The species is the largest in the genus, and indeed the family, with the largest measured specimen being 675 mm SL. Head and body notably elongate, proportionally more so in smaller individuals (Figure 42). Greatest body depth at dorsal-fin origin in smaller individuals, distinctly anterior of that line in larger specimens, in region anterior to insertion of pelvic fin in largest individuals examined; typically relatively deeper with increasing standard length. Dorsal profile of head

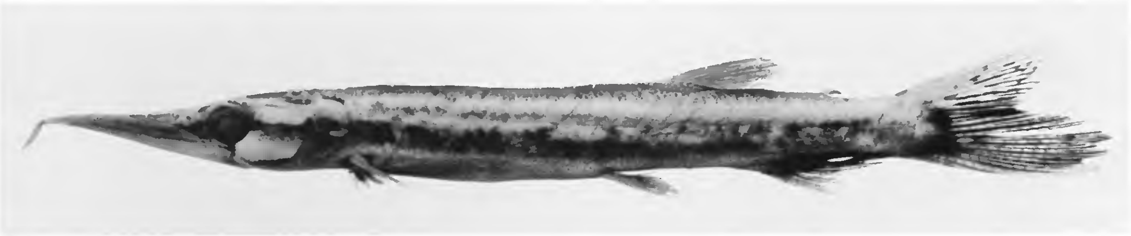

FIGURE 42.—*Boulengerella cuvieri*, ZMA 119.696, juvenile, 103 mm SL; French Guiana, Oyapock River basin, Riviere Camapi.

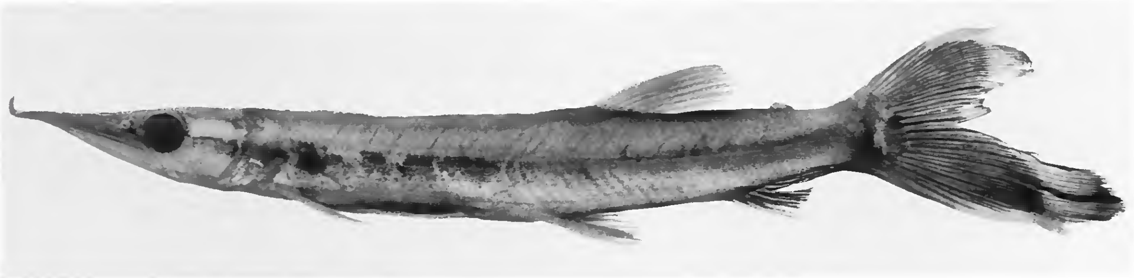

FIGURE 43.—*Boulengerella cuvieri*, LACM 43384-1, juvenile, 130 mm SL; Venezuela, Monagas, Río Orinoco, inlet on N side of Isla Varadero, downstream from Barrancas.

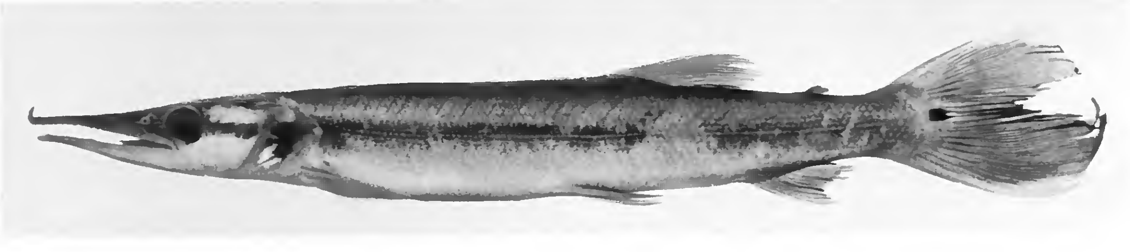

FIGURE 44.—*Boulengerella cuvieri*, LACM 43399-4, 192 mm SL; Venezuela, Monagas, Río Orinoco, Caño Chivera, Isla Chivera.

and body nearly straight to dorsal-fin origin, very slightly posteroventrally angled at base of dorsal fin, straight from rear of fin to adipose fin in specimens up to approximately 200 mm SL, somewhat convex in larger individuals. Dorsal surface of body in preserved specimens often somewhat flattened anterior to dorsal fin, somewhat flattened to smoothly rounded transversely posterior to fin. Ventral profile of body gently convex from tip of snout to caudal peduncle; convexity distinctly more pronounced in larger individuals. Prepelvic region of body flattened to transversely rounded.

Head distinctly pointed in both lateral and dorsal views. Smallest specimen examined (NRM 25225, 8 mm HL, posterior portion of body missing) with snout proportionally shorter (0.423 of HL) than in larger individuals greater than 21 mm HL (0.470–0.536 of HL) and with fleshy process at tip of snout just forming. Form of upper jaw, lower jaw, and nostrils in specimens greater than 50 mm SL (~21 mm HL) as described for *Boulengerella lateristriga,* above. Fleshy process at tip of snout well developed in specimens of about 60 mm SL; proportionally of approximately same size in larger individuals up to 200 mm SL, lacking in all examined specimens over 350 mm SL. Pronounced variation in proportions of Table 11 reflects ontogenetic allometry present across broad size range of measured specimens.

Arrangement and form of teeth in both premaxillae and dentaries in specimens greater than 50 mm SL comparable to those in *Boulengerella lateristriga* described above. Premaxillary teeth in specimen of 8 mm HL distinctly separated, in irregular row. Premaxillary teeth in specimens over 50 mm SL with a primary outer row with 52–122 teeth in specimens of 50–200 mm HL; number of teeth somewhat variable over limited size range of head lengths. Overall ontogenetic trend is for an allometric increase in number of teeth, with rate of increase decreasing and then absent at larger standard lengths (Figure 39). Premaxilla with 3 or 4 teeth present in inner row in specimens of up to approximately 50 mm SL, number of teeth decreasing with increasing size, many specimens of approximately 100–130 mm SL with single tooth on each side, larger individuals without inner row of premaxillary teeth. Maxilla with 7 teeth in specimen of 8 mm HL, with 12–21 teeth along its anterior margin in specimens of over 20 mm HL (~50 mm SL), with general ontogenetic trend to increased number of teeth with increasing size, but with wide variation in number of teeth present across limited size range. Dentary lacking teeth anteriorly immediately proximate to symphysis at all body sizes. Specimen of 8 mm HL with two or three irregular series of well-separated teeth on dentary. Individuals of 20–45 mm HL (~50–110 mm SL), with single of row of dentary teeth anteriorly and two or, more rarely, three rows of teeth posteriorly (three rows only in specimens toward lower end of this size range); teeth of outer row in contact with each other. Inner row becoming progressively shorter posteriorly with increasing body size; larger individuals with single series of dentary teeth. Outer row of dentary with 48–121 teeth arranged in single series in specimens of 50–200 mm HL. Number of dentary teeth somewhat variable within limited range of head lengths; more so in smaller individuals. Overall ontogenetic trend is for increase in number of teeth at larger standard lengths; rate of increase progressively decreasing and then disappearing at larger standard lengths. Teeth on upper and lower pharyngeal tooth-plates small and conic.

Lateral line not apparent in specimens of less than 60 mm SL, extending progressively posteriorly and nearly complete in specimens of 100 mm SL. Individuals of and greater than 120 mm SL with lateral-line series nearly completely perforated, except for 4–10 scales overlying basal portions of middle caudal-fin rays. Scales on body with surface sculpturing and irregular margins, but without distinct cteni. Scales along pre-and postdorsal midlines arranged somewhat irregularly.

Dorsal fin ii–iii,8. First basal dorsal-fin pterygiophore inserting behind neural spine of 21st to 24th, typically 22nd or 23rd, vertebrae. Posterior terminus of dorsal fin distinctly anterior to vertical line through anal-fin origin. Distal margin of dorsal fin somewhat convex. Anal fin ii–iii,8, rarely ii–iii,7. First basal anal-fin pterygiophore inserting behind hemal spine of 33rd to 35th vertebrae. Form of anal fin highly variable ontogenetically. Posterior rays distinctly longer than anterior rays in smaller individuals, forming distinct elongate lobe. Posterior rays becoming progressively relatively shorter with increasing standard length, distinctly shorter than anterior rays in largest individuals examined. Pectoral fin i,18–22,iii–iv. Pectoral fin lobulate in specimens of approximately 50 mm SL, fin rays developing ontogenetically from lateral portion of fin medially; medial rays not fully developed in specimens of approximately 100 mm SL, fully formed in all examined specimens by 120 mm SL. Pectoral fin in specimens over 120 mm SL pointed in profile with first branched ray longest; fin tip extends posteriorly one-third distance to pelvic fin in smaller individuals, less than one-quarter of distance in larger specimens. Pelvic fin i,7. Distal margin of pelvic fin obtusely pointed; fin reaches posteriorly over one-half distance to anal fin in smaller individuals, approximately one-third of distance in larger specimens. Caudal fin forked. Adipose fin present.

VERTEBRAE.—47 (1, specimen with several severely deformed vertebrae making count questionable), 48(30), 49 (29) [48].

LIFE COLORATION (based on color transparencies taken by Anita Hogeborn-Kullander of recently captured and live specimen from the western Amazon cataloged as NRM 24122 and 25215, of a specimen from the Río Orinoco by the author, and several photographs in popular publications (Anonymous, 1992; Lopes da Silva, 1992).—Overall coloration silvery golden, somewhat darker and occasionally steel blue dorsally and dorsolaterally. Head with yellow tint on eye, posterior portion of lower jaw, and opercle. Dark stripe behind orbit on opercle and horizontal streak along midlateral surface of body somewhat masked by guanine; opercular stripe distinctly less obvious in largest specimens. Dark spot at base of middle rays of caudal fin quite obvious and intensely black in recently

TABLE 11.—Morphometrics and meristics of (A) holotype of *Xiphostoma cuvieri*, MHNN 89.823; (B) holotype of *Xiphostoma oseryi*, MNHN 4233; and (C) all other specimens of *Boulengerella cuvieri* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 16 are proportions of standard length; 17 to 21 are proportions of head length. Dashes for holotype of *Xiphostoma oseryi* indicate values that could not be determined because of the condition of the specimen (see "Remarks" under species account of *Boulengerella cuvieri*).

Character	A	B	C
		Morphometrics	
Standard Length	325	~163	50.2–675
1. Body depth at dorsal-fin origin	0.146	–	0.112–0.190
2. Snout to dorsal-fin origin	0.683	–	0.650–0.733
3. Snout to anal-fin origin	0.840	–	0.818–0.877
4. Snout to pectoral-fin origin	0.280	–	0.280–0.348
5. Snout to pelvic-fin origin	0.597	–	0.597–0.667
6. Dorsal-fin origin to hypural joint	0.323	–	0.272–0.345
7. Dorsal-fin origin to anal-fin origin	0.208	–	0.162–0.231
8. Dorsal-fin origin to pelvic-fin insertion	0.173	–	0.131–0.194
9. Dorsal-fin origin to pectoral-fin insertion	0.425	–	0.360–0.431
10. Caudal-peduncle depth	0.072	–	0.068–0.096
11. Pectoral-fin length	0.136	–	0.110–0.145
12. Pelvic-fin length	0.131	–	0.111–0.144
13. Length of longest dorsal-fin ray	0.145	–	0.136–0.173
14. Length of longest anal-fin ray	0.100	–	0.070–0.123
15. Anal-fin base	0.065	–	0.065–0.079
16. Head length	0.302	0.320	0.291–0.381
17. Snout length	0.479	0.513	0.466–0.536
18. Orbital diameter	0.167	0.149	0.125–0.169
19. Postorbital length	0.387	0.334	0.320–0.434
20. Lower-jaw length	0.607	0.597	0.560–0.645
21. Interorbital width	0.247	0.193	0.166–0.300
		Meristics	
Scales along lateral-line series	106[a]	–	94–124
Pored lateral-line scales	–	–	89–115
Scale rows between dorsal-fin origin and lateral-line series	–[b]	–	11–14
Scale rows between anal-fin origin and lateral-line series	–[b]	–	8–11
Predorsal median scales	–	69	57–76
Postdorsal median scales	–	23	17–25
Branched dorsal-fin rays	8	8	8–9
Branched anal-fin rays	8	8	7–8[c]
Pectoral-fin rays	–[d]	–	22–27
Branched pelvic-fin rays	7	7	7
Vertebrae	48	–[e]	48–49[f]

[a] Specimen lacking most scales but there are approximately 106 scale pockets; 105 scales reported along lateral line by Spix and Agassiz (1829).

[b] Specimen lacking most scales; 24 transverse scales reported by Spix and Agassiz (1829).

[c] 7 branched rays in only 1 specimen.

[d] 26 pectoral-fin rays reported by Spix and Agassiz (1829).

[e] Holotype of *Xiphostoma oseryi* consisting of a head and skin without associated vertebral column.

[f] 47 vertebrae in one specimen with deformed vertebrae.

captured specimens. Other dark pigmentation as described below under "Color in Alcohol." Portions of caudal fin lacking dark pigmentation somewhat yellowish, particularly in region around dark spot on basal portions of middle rays and dorsal and ventral distal portions of fin. Pectoral and pelvic fins with yellow along margins. Géry et al. (1991, fig. 1) show a color picture of an evidently recently collected specimen from the Oyapock River of French Guiana. In that specimen the dorsal and ventral margins of the caudal fin are more orange than yellow.

COLOR IN ALCOHOL.—Overall pigmentation pattern showing pronounced ontogenetic changes. Specimens of approximately 50 mm SL with dorsal surface of head and anterior portion and lateral margin of lower jaw quite dark. Distinct posteroventrally slanted dark bar extending from ventral margin of orbit. Horizontal stripe extending from rear of orbit posteriorly along margin between third and fifth infraorbitals. Posteroventral margin of third infraorbital with a dark curved stripe along margin. Posterior portion of infraorbital darkly pigmented to variable degree. Opercle with irregular patch of dark pigmentation dorsally.

Body with scattered, small, irregular patches of dark pigmentation on dorsal and dorsolateral surfaces. Lateral and ventrolateral surfaces with field of small dark spots, field denser posteriorly. Caudal fin with pattern of crossbars on dorsal lobe; ventral lobe quite dark, with some individuals having some indication of crossbars. Elongate posterior rays of caudal fin very dark, anterior rays dusky.

Pigmentation pattern in specimens of approximately 80–110 mm SL notably different. Oblique bar posteroventral of orbit less obvious or completely lacking. Horizontal stripe behind orbit more prominent; ventral portions of third infraorbital lacking pronounced pigmentation present in that region in smaller individuals or that pigmentation reduced to small field of chromatophores along ventral margin of third infraorbital. Dark pigmentation on dorsal portions of body less diffuse, typically in form of series of small dark spots. Dark pigmentation on lateral surface of body developed into variably distinct midlateral stripe. Dorsal border of stripe variably irregular between specimens. Stripe most distinct anterior to vertical through pelvic-fin insertion where ventral portion of body is distinctly less pigmented than midlateral stripe and that portion of body in smaller individuals. Midlateral stripe melds into dusky pigmentation along ventral portion of body posterior of pelvic-fin insertion. Some specimens with scattered small dark spots on dorsolateral surface of body. Distal portions of dorsal and ventral rays of caudal fin hyaline. Crossbars on upper lobe of caudal fin less pronounced than in smaller individuals, lower lobe dark. Spot of dark pigmentation at base of middle rays of caudal fin apparent in specimens of approximately 110 mm SL and larger. Elongate posterior rays of anal fin quite dark, rest of fin dusky. Pelvic, pectoral, and dorsal fins hyaline or slightly dusky.

Individuals of over approximately 150 mm SL with typical adult pigmentation. Overall ground coloration in specimens lacking guanine on scales tan, distinctly darker dorsally in many individuals. Snout and dorsal surface of head dusky. Variably distinct horizontal stripe extending from rear of orbit across third infraorbital. Stripe typically followed posteriorly by dark patch on opercle. Stripe and dark opercular patch in line with midlateral stripe on body. Stripe on posterolateral portion of head less discrete in very large individuals (400+ mm SL), which nonetheless retain distinct dark region along midlateral surface of body. Body with midlateral stripe extending from immediately posterior of opercle to caudal peduncle. Stripe most distinct anteriorly, intensity of stripe ranging from somewhat diffuse to quite distinct, perhaps correlated with water type, particularly intense in individuals captured in acidic blackwaters.

Intensity of dark pigmentation on posterior rays of anal fin becoming progressively less pronounced with ontogenetic reduction in proportional length of those rays, some diffuse dark pigmentation present in larger specimens. Most of caudal fin dusky to dark, without indication of crossbars. Distal portions of dorsal and ventral rays hyaline. Distinct spot of dark pigmentation present on basal portions of middle rays of caudal fin. Spot sometimes surrounded anteriorly by lightly pigmented region on posterior portion of caudal peduncle. Dorsal, pelvic, and pectoral fins without any pronounced pattern.

GEOGRAPHIC VARIATION.—*Boulengerella cuvieri* has the largest known geographic range of any species in the genus. Not unexpectedly, some variation occurs in various features across this broad region. Many preserved specimens from the Río Orinoco and the coastal drainages of Guyana and French Guiana tend to have darker overall coloration than samples from the western portions of the species range in Peru. Such differences are not, however, universal within population samples and may represent the different water types in which the specimens were captured.

Specimens of *Boulengerella cuvieri* from the southern portions of the species distribution in the Rio Tocantins and Rio Juruena consistently have lateral-line scale counts (108–118) toward the upper end of the range for the species (94–124). The lateral-line scale counts (94–101) in samples from the Oyapock River (Rio Oiapoque), in turn, are distributed toward the lower end of the total range in the species. The available samples from both the southern tributaries of the Amazon and the Oyapock River are relatively limited, and samples from other portions of the species range overlap the lateral-line scale counts from both regions.

COMMON NAME.—Brazil: central Amazon: “Pirá-pacú” or “Pirá-pucú,” “Diente de cão” (Kner, 1860:60, 62; Goeldi, 1898:484); Rio Tocantins: “Bicuda,” “Uena” (Mendes dos Santos et al., 1984:24); Rio Tapajós: “Bicuda” (Lopes da Silva, 1992:15). Venezuela: “Agüejeta,” “Picúa” (Lasso, 1993:14, 43). Guyana: “Moruwi,” “Pirapoko” (Lowe-McConnell, 1964:144).

ECOLOGY.—Mendes dos Santos et al. (1984:24) report that this species (cited as *Boulengerella ocellata*) becomes sexually mature at approximately 25 cm SL and that breeding takes place in the period when rivers are rising. The species typically is encountered in rapidly flowing waters. Vazzoler (1992:6) and Vazzoler and Menezes (1992:632) report that the median size at first maturation of the gonads is 25 cm SL and that the species reproduced from November through March.

DISTRIBUTION.—Rio Amazonas, Rio Tocantins, and Rio Orinoco basins, Essequibo River system of Guyana, Oyapock River (Rio Oiapoque) along border between French Guiana and

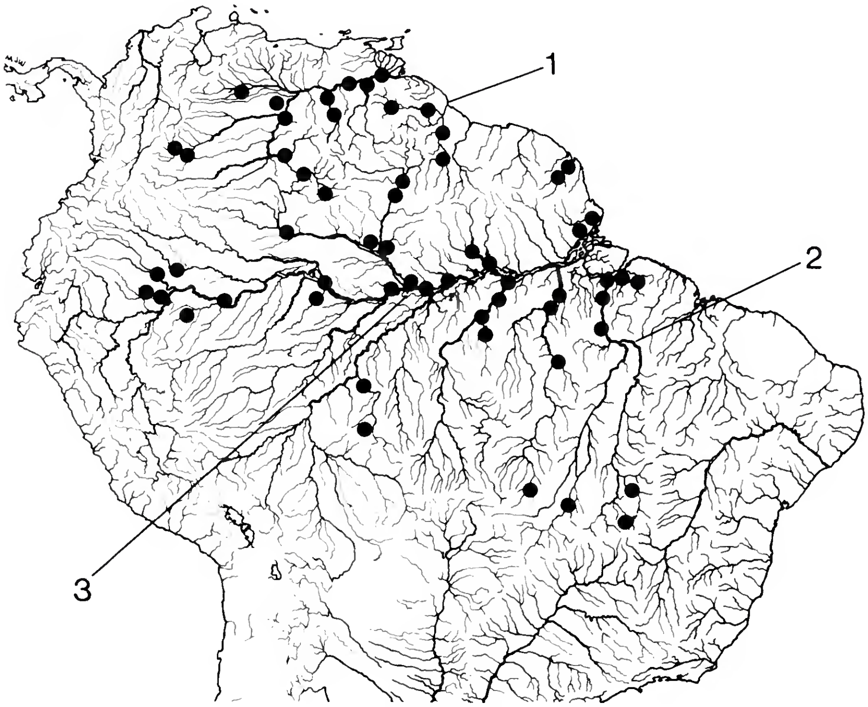

FIGURE 45.—Map of northern portions of South America showing geographic distribution of *Boulengerella cuvieri* (type-locality of *Xiphostoma cuvieri* inexact = "Brasiliae fluviis" (= rivers of Brazil; see also "Remarks" under species account); 1 = mouth of Essequibo River, lectotype-locality of *Xiphostoma ocellatum;* 2 = Rio Tocantins, type-locality of *Xiphostoma oseryi;* 3 = mouth of Rio Negro, type-locality of *Xiphostoma longipinne*). Some symbols represent more than one lot of specimens or locality.

Brazil, and coastal rivers of states of Amapá and Pará in Brazil (Figure 45).

REMARKS.—As noted under "Remarks" for *Boulengerella lucius,* there has been disagreement as to whether *Xiphostoma cuvieri* was a junior synonym of *hydrocyon lucius.* The broadly encompassing concept of *Boulengerella lucius,* used since Myers (1950) and Schultz (1950), actually includes at least three species, one without a discrete dark spot at the base of the middle caudal-fin rays in adults (*lucius*) and two with such pigmentation (*cuvieri* and *xyrekes*). On the basis of these differences and others (see "Key to Species of *Boulengerella*" and "Diagnosis," above), *Xiphostoma* (= *Boulengerella*) *cuvieri* is recognized as a distinct species.

Xiphostoma cuvieri was described on the basis of a single specimen from "Brasiliae fluviis" (= rivers of Brazil) collected by Spix and Martius. Spix and Martius collected in a number of regions of Brazil (see Papavero, 1971, map 7 following page 66), but the only portion of that country in which they collected and where *Boulengerella* is known to occur is the Amazon basin. Spix and Martius sampled along the main channel of the Amazon from its mouth to Benjamin Constant on what is now the Brazilian-Peruvian border. They also made a side trip up the Rio Negro to Barcelos. The holotype of *Xiphostoma cuvieri* presumably originated somewhere in this portion of the Amazon basin, an area entirely encompassed by the known distribution of *Boulengerella cuvieri.* The holotype of *Xiphostoma cuvieri* (MHNN 89.823), although lacking scales and having lost much of its pigment, is still in good overall condition, with the distinctive spot of dark pigmentation on the basal portions of the caudal fin quite obvious. That patch of pigmentation, the approximately 106 lateral-line scales, and the 48 vertebrae distinguish it from the other *Boulengerella* species with anteriorly located dorsal fins (*lucius* and *xyrekes;* see Table 9).

Boulengerella cuvieri, as recognized in this study, has two and perhaps three junior synonyms. Schomburgk (1841:245) described *Xiphostoma ocellatum* from specimens originating in the Essequibo (River of Guyana) and Rios Negro and Branco (Brazil). I have been able to locate only one syntype of the species, now deposited in MNHN (A. 9853), and, to fix the species name, I designate that specimen as the lectotype of the species. Unfortunately the size of the lectotype (700 mm SL) and its condition made it impossible to be loaned. Nonetheless, the illustration provided by Schomburgk (1841, pl. XXIII) shows the distinctive spot of dark pigmentation on the basal portions of the caudal fin and the anterior position of the dorsal fin relative to the anal fin. This pigmentation still is obvious in the lectotype of *X. ocellatum* (T. Munroe, pers. comm.). Only two species of *Boulengerella* (*cuvieri* and *xyrekes*) have those features in common, and, of these two, only *B. cuvieri* is known from the Essequibo River basin (see Figure 45). *Xiphostoma ocellatum* consequently is considered a synonym of *Boulengerella cuvieri.*

Castelnau (1855:76) described *Xiphostoma oseryi* on the basis of a single specimen that originated in the "Tocantins." Presumably this is the Rio Tocantins, Pará, Brazil, a river system through which Castelnau traveled extensively (see Papavero, 1971, map 12 following page 154). The holotype (MNHN 4233) consists of a head and associated body skin and fins now in alcohol. The absence of a vertebral column and loss of many body scales limits the available information. Nonetheless, the specimen still has the spot of dark pigmentation on the caudal-fin base illustrated by Castelnau (1855, pl. 40, fig. 1) and indications of the horizontal streak across the third infraorbital posterior to the orbit, and it has approximately 69 predorsal scales. In combination, these features indicate that the holotype of *Xiphostoma oseryi* is conspecific with *Boulengerella cuvieri.* Further support for this hypothesis is the fact that *B. cuvieri* is the only *Boulengerella* species with an anteriorly positioned dorsal fin known from the Rio Tocantins, the type drainage for *Xiphostoma oseryi.*

The status of a third nominal species, *Xiphostoma longipinne,* is problematical. *Xiphostoma longipinne* was described by Steindachner (1876:84) based on a specimen originating at the mouth of the Rio Negro, Brazil. Information in the original description indicates that it belongs to the *Boulengerella* lineage with anteriorly positioned dorsal fins (*lucius, cuvieri,* and *xyrekes*). Although Steindachner's description of the species is extensive, it is impossible to unambiguously identify the species because it is based on a specimen reported by Steindachner (1876:86) as being "vier [four] Zoll" (= 4 inches, 101.6 mm) to the base of the caudal. Both the standard length and the description make it apparent that it is a juvenile, a situation considerably complicating the identification. Perhaps as a consequence, there have been relatively few citations of *Xiphostoma longipinne* subsequent to its description. Eigenmann (1910:446) and Fowler (1950:328; 1975:123) recognized it as distinct in their listings of *Boulengerella* species. Schultz (1950:43) placed *longipinne* as a synonym of *lucius,* an action tentatively followed by Géry (1977:106); but both authors' concepts of *lucius* included several species.

Steindachner (1876:84) noted that *Xiphostoma longipinne* has 96 lateral-line scales to the caudal-fin base, a count higher than that of *Boulengerella xyrekes* but in the range for *B. lucius* and *B. cuvieri,* both of which also occur in the area of the type locality of *Xiphostoma longipinne.* Although Steindachner points out that there is "no ocellated spot at the base of the caudal" (my translation), the spot does not develop in individuals of *B. cuvieri* of that size. The only feature I have discovered to unambiguously separate juvenile *B. cuvieri* and *B. lucius* is vertebral number (48 or 49 in *B. cuvieri* versus 45 or 46 in *B. lucius*). Unfortunately, the holotype of *Xiphostoma longipinne* could not be located in the NMW collections (B. Herzig, in litt.). Consequently, it is impossible to determine which of the two species (*cuvieri* or *lucius*) is the likely senior synonym of *X. longipinne. Xiphostoma longipinne* arbitrarily is placed herein as a synonym of *Boulengerella cuvieri,* given that the latter is the most common *Boulengerella* species with an anteriorly positioned dorsal fin in the Amazon basin, the type region for *X. longipinne.*

Fowler (1941:194) reported *Hydrocynus cuvieri* from the Rio Pamahyba (= Parnaíba), Therezina (= Teresina), Piauhy (= Piauí), in northeastern Brazil. Roberts (1973:213) suggested that some of the species reported by Fowler as occurring in the Rio Parnaíba actually originated in the Amazon basin. Castro (1990:87) demonstrated that one species, *Semaprochilodus squamilentis,* a prochilodontid described by Fowler (1941:171) in that same paper, is a *Semaprochilodus* species endemic to the Rio Tocantins and Rio Xingu of the Amazon basin. The specimen reported by Fowler (ANSP 69620), albeit in poor condition, is identifiable as an individual of *B. cuvieri;* however, no other *Boulengerella* specimens from the Rio Parnaíba or neighboring river basins of northeastern Brazil were located in this study. Thus it appears likely that the *Boulengerella* record agrees with Robert's suggestion that a portion of the specimens reported on by Fowler (1941) had erroneous locality data.

MATERIAL EXAMINED.—316 specimens (complete data taken on 111 specimens, 50.2–675 mm SL; partial data taken on 49 additional specimens).

BRAZIL. No specific locality: MHNN 89.823, 1 (325, holotype of *Xiphostoma cuvieri*). *Piauí:* Rio Parnahyba (= Parnaíba), Therezina (= Teresina), ANSP 69620, 1 (cited locality questionable, see comments under "Remarks," above). *Amapá:* Rio Araguari, Ferreira Gomes (~0°80′N, 51°10′W), MZUSP 32145, 5 (1, 340). Rio Cupixi, at bridge on road to Serra do Navio (00°40′N, 51°40′W), MZUSP 32146, 5 (1, 590). *Pará:* No specific locality (probably region of Belém based on collector, E.C. Starks), AMNH 3945, 3. [Rio] "Tocantins," MNHN 4233, 1 (~163; holotype of *Xiphostoma oseryi*). Rio Capim, Praia da Caramandia (01°40′S, 40°47′W), MZUSP 23874, 6. Rio Capim, Vila Santana, MZUSP 23994, 1. Rio Capim, near Badajós, MZUSP 13038-39, 2. Rio Capim and tributary streams, USNM 319784, 2 (1, 147; specimen cleared and counterstained). Rio Tocantins, lagoa in front of Jatobá (04°32′S, 49°32′W), MZUSP 24150, 1; MZUSP 24118, 2. Rio Tocantins, Jatobá, lagoa near Canal do Capitariquara, MZUSP 24162, 10. Río Tocantins, Baião (02°41′S, 49°51′W), MZUSP 24068, 1 (175). Río Tocantins, between Mocajuba and Baião, MZUSP 24062, 2 (1, 151). Rio Itacaiunas, Serra dos Carajás, Caldeirão (05°45′S, 50°30′W), MZUSP 31612, 31 (1, 675); MZUSP 32161, 1; MZUSP 32159, 5. Rio Itacaiunas, Caldeirão, Igarapé Águas Claras, MZUSP 32158, 1. Rio Trombetas, Oriximiná (01°40'S, 56°00'W), MZUSP 5466, 2. Rio Trombetas, Reserva Biologica de Trombetas, MZUSP 15808, 1. Igarapé Sororoca, Furo de Panaquera, MZUSP 22986, 1. Furo de Panaquera, Engenho Santo Antônio, MZUSP 23974, 1. Cametá, Igarapé Oricurá, MZUSP 24038, 1. Rio Tapajós, MZUSP 25485, 1 (640). Río Tapajós, Santo Antônio, MZUSP 25574, 1 (620). Rio Tapajós, Alter de Chão (02°30'S, 55°00'W), MZUSP 8466, 1 (245); MZUSP 9530, 1. Rio Tapajós, between Itaituba and São Luis (04°25'S, 56°10'W), MZUSP 32151, 11. Rio Tapajós basin, Rio Jamanxim, above Bebul (04°43'S, 56°18'W), MZUSP 25294, 1. Cachoeira do Maranhãozinho, Rio Tapajós, near São Luis, MZUSP 24287, 2 (1, 186). Rio Xingu, Belo Monte (03°10'S, 51°50'W), MZUSP 43129, 1 (174). Rio Xingu, Aldeia Gorotire, município de São Felix do Xingu (06°38'S, 51°59'W), MZUSP 35972, 1 (335). Rio Xingu, Cachoeira do Espelho, MZUSP 36849, 3 (1, 225). *Amazonas:* Rio Urubu, 25 mi (40 km) from Itacoatiara (03°09'S, 58°40'W), USNM 179525, 1 (192). Rio Amazonas, Itacoatiara (03°08'S, 58°25'W), MZUSP 13500, 1. Paraná do Urucará, município de Urucará (02°32'S, 57°45'W), MZUSP 7526, 1 (173). Lago Saracá (02°53'S, 58°21'W), MZUSP 5803, 2. Lago Manacapuru (03°08'S, 64°06'W), MZUSP 6540, 1. Rio Negro, vicinity of Manaus (03°06'S, 60°00'W), MZUSP 6675, 1 (137). Rio Jauaperi, from its mouth to 100 km upstream (01°26'S, 62°35'W), MZUSP 22291, 1. Rio Negro, São Gabriel de Cachoeira (00°07'S, 67°05'W), MZUSP 32172, 1. Igarapé Baré, Lago Amana, mouth of Rio Japurá, MZUSP 36090, 1. Rio Tefé, Vista Escura, MZUSP 42711, 1 (620); MZUSP 32147, 3 (1, 290). Rio Javari, immediately downstream of confluence of Rio Jaquirana and Rio Gálvez, NRM 24122, 6. *Mato Grosso:* Rio Juruena, USNM 199229, 1 (81.0); USNM 194389, 1 (353); USNM 194411, 1 (625). Rio Xingu, confluence of Rio Coluene and Rio Sete de Setembre (14°37'S, 53°34'W), MZUSP 32148, 3. *Goiás:* Rio Araguaia, Aruanã (14°54'S, 51°05'W), USNM 191563, 3 (2, 183–190). Rio Paraná, Iaciara, Fazenda Salobre, 8 km above ferry crossing along highway 112 (14°09'S, 46°40'W), MZUSP 40580, 8. Rio Paraná, Nova Roma, below mouth of Rio São Domingos, MZUSP 40772, 1. *Roraima:* Rio Negro, between mouth of Rio Branco and the Rio Xeruini, MZUSP 32160, 1. Rio Branco, Boa Vista (02°49'N, 60°40'W), MZUSP 23579, 1 (230). Rio Branco, Cachoeira do Bem Querer (02°00'N, 61°00'W), MZUSP 32150, 5 (2, 160–375). Igarapé Grande, tributary to Rio Uraricoera, along road from Boa Esperança to Boa Vista (03°20'N, 61°30'W), MZUSP 23622, 1 (186). *Rondonia:* Rio São Domingo, tributary of Rio Ji-Paraná at Santa Cruz de Serra, MZUSP 28177, 1. Rio Machado, Lago do Paraiso (08°40'S, 62°30'W), MZUSP 14039, 3 (1, 320).

PERU. *Loreto:* Rio Nanay, ~20 km upstream from mouth, USNM 280451, 1 (141). Rio Nanay, at Nanay Beach, W of Iquitos (03°50'S, 73°11'W), USNM 280450, 1 (140). Río Nanay drainage, left bank sand playa opposite Llanchama Cocha, NRM 25215, 5 (4, 98.0–121). Río Nanay, left bank sand playa opposite mouth of Quebrada Agua Negra, NRM 25259, 4 (3, 118–164). Río Nanay, just above Cocha Morona, ~14.4 km above Río Amazonas (03°43'S, 73°18'W), ANSP 136818, 2. Río Nanay, ~4 km below Nina Rumi (03°44'S, 73°20'W), ANSP 167107, 2. Río Putomayo, El Estrecho, NRM 25225, 2 (1, 58.8). Río Putomayo, El Estrecho, flooded margin of river at Fundo Alvarez, NRM 13507, 2. Río Putomayo basin, downstream of El Estrecho, S shore of Cedros Cocha, NRM 25223, 1. Río Napo basin, Cocha Aucapoza, 1.

COLOMBIA. *Amazonas:* Leticia, Lagos de Leticia (04°09'S, 69°57'W), NRM 14974, 1. *Meta:* Río Manacacias, near La Esperanzas, MCZ 58972, 2. Quebrada Venturosa, above road between La Balsa and Puerto Lopez, ANSP 128301, 2.

FRENCH GUIANA. Oyapock River, Saut Maripa and upstream (03°48'N, 51°54'W), ZMA 107.628, 1 (355). Oyapock River basin, Riviere Camapi, ZMA 119.696, 1 (103). Oyapock River, rapids of Trois Sauts (02°15'N, 52°53'W), ZMA 107.812, 1.

GUYANA. Essequibo River, CAS 68821, 6 (3, 96.0–137). Essequibo River N of Kurupukari, ROM 62511, 1 (144); ROM 62512, 1. Essequibo River, Kurupukari, ROM 62513, 2 (118–126). Essequibo River, N of Tambikabo, ROM 62514, 4 (2, 106–175). Essequibo River, ~1 mi upstream from Tambikabo Inlet, ROM 62515, 1 (480). Rockstone, USNM 66208, 1 (103). Essequibo River at Rockstone, MCZ 30024, 2 (103–110); AMNH 38039, 1 (50.2). Bartica, AMNH 13414, 1. N bank of Cuyuni River, AMNH 72963, 2 (1, 121); AMNH 72993, 2.

VENEZUELA. *Territorio Federal Delta Amacuro:* Río Orinoco, Caño Guarguapo, LACM 43382-5, 5 (112–240); MBUCV V-13080, 3 (1, 161). Laguna La Ceiba, Los Castillos de Guyana, MHNLS 4781, 1. *Monagas:* Río Orinoco, 161 n mi (~298 km) upstream of sea buoy, USNM 226266, 1 (113). Laguna Guatero, near Barrancas, 142 n mi (~263 km) from sea buoy (8°43'N, 62°11'W), ANSP 149506, 1 (94.2). Río Orinoco, small pool on N side of Isla Tres Caños (8°40'N, 62°10'W), USNM 226258, 1 (143). Río Orinoco, inlet on N side of Isla Varadero, downstream from Barrancas, LACM 43384-1, 1 (130). Laguna Las Barrancas (8°25'N, 62°9'W), MHNLS 5080, 1. Río Orinoco, backwater of Caño Araguao, 112 n mi (~207 km) from sea buoy (8°38'N, 61°43'W), USNM 226340, 1 (146). Río Orinoco, Caño Chivera, Isla Chivera, near Barrancas, LACM 43399-4, 4 (132–192). Río Orinoco, Isla Tapatapa, Laguna Tapatapa, MBUCV V-13349, 1. *Guarico:* Caño Los Aceites, MHNLS 6391, 1. Santa Rita, Río Manapire, MBUCV V-5746, 1. Río San Jose, ~10 km N of confluence of Río San Jose and Río Guariquito, UMMZ 214837, 2 (285–300). *Amazonas:* Río Orinoco at El Burro (6°12'N, 67°26'W), ANSP 160095, 2 (124–210). Small caño connecting with Río Orinoco immediately S of El Burro, USNM 270341, 1 (152). Río Mavaca, AMNH 93100, 1 (dry skeleton). Río Mavaca at Tapirapeco base camp (1°51'N, 65°08'W), AMNH 93030, 2 (265–280). Río Pamoni, ~ 0.5 km from confluence of Río

Casiquiare (2°50′N, 65°24′W), ANSP 162750, 1 (370); ANSP 162757, 2. Side Channel of Río Ventuari, ~12 km above confluence with Río Orinoco (4°04′N, 66°56′W), ANSP 161218, 2. Caño Orera, at border between Estado Bolivar and Estado Amazonas, ~68 km NE of Puerto Ayacucho (6°10′N, 67°22′W), ANSP 165676, 1 (260). *Bolivar:* Río Orinoco basin, Ciudad Bolivar, Lago Les Tejitas (08°08′N, 63°33′W), ANSP 166586, 2 (117–170). Río Caura at Puerto Las Majadas (7°38′18″N, 64°50′24″W), ANSP 160093, 7 (6, 86.3–141); ANSP 169687, 2 (1, 155). Caño (possibly Caño Curimo) feeding Río Caura near confluence of Río Caura and Río Orinoco (7°37′48″N, 64°50′42″W), ANSP 159596, 6 (176–290). Río Caura, Maripa, at bridge, MHNLS 8170, 1. Río Caura, Laguna Paramoto, MHNLS 4053, 1. Río Orinoco, Laguna Las Garzas, MHNLS 4056, 1. San Felix, Laguna Tamarindo, MHNLS 4057, 4; MHNLS 4055, 1; MHNLS 4058, 2. San Felix, Laguna Guaiparo, MHNLS 4052, 2 (1, 158). Confluence of Río Orinoco and Río Caura (7°38′36″N, 64°50′W), ANSP 160356, 1. Río Mato (7°02′N, 65°13′W), ANSP 139625, 1. Río Cuyuni, Isla Anacoco (06°23′N, 58°41′W), MHNLS 4779, 3 (2, 127–155); MHNLS 5738, 3 (122–177). Río Cuyuni, 2 km from Mission Anacoco, MHNLS 9952, 1. *Apure:* Río Cinaruco basin, Laguna Larga (6°33.32′N, 67°24.81′W), INHS 61438, 2 (186–280). Caño Guaritico, between Fundo Los Ventanas and Fundo Cornelio Herrera, MHNLS 9651, 2; MHNLS 9653, 2; MHNLS 9652, 1; MHNLS 9648, 4 (2, 170–247); MHNLS 9650, 4 (3, 188–237). Caño Guaritico, Hato El Frio, MHNLS 9655, 1. Caño Guaritico, at confluence with Río Apure, MHNLS 9656, 3. Caño Setentia, at confluence with Caño Guaritico, MHNLS 9654, 2; MHNLS 9647, 1. Laguna Depirital, Caño Guaritico, MHNLS 9649, 1 (195). Río Capanaparo, along highway from San Fernando de Apure to Puerto Paez, MBUCV V-4669, 3 (1, 127). Río Capanaparo, MHNLS 779, 3 (1, 147).

Boulengerella xyrekes, new species

FIGURES 46–50; TABLES 9, 12

DIAGNOSIS.—The location of the dorsal fin distinctly anterior to the vertical through the anal-fin origin in *Boulengerella xyrekes* distinguishes it from its congeners except *B. lucius* and *B. cuvieri*. The discrete spot of dark pigmentation on the basal portions of the middle caudal-fin rays in specimens of *B. xyrekes* greater than 120 mm SL separates it from *B. lucius*, which lacks that pigmentation at all sizes and instead has the middle caudal-fin rays somewhat dusky, particularly on the fin membranes basally. The species also differ in the number of lateral-line scales (87–94 in *B. xyrekes* versus 98–117 in *B. lucius*) and predorsal scales (54–63 versus 62–72, respectively). *Boulengerella xyrekes* is distinguished from *B. cuvieri* in the number of vertebrae (44–46 versus 48 or 49, respectively), number of lateral-line scales (87–94 versus 94–124, respectively), and in the presence in all but the largest examined specimens of *B. xyrekes* of an oblique band of dark pigmentation across the posteroventral portion of the third infraorbital (pigmentation that is limited to some smaller juveniles in *B. cuvieri*).

DESCRIPTION.—The single larval specimen of *Boulengerella xyrekes* (Figure 46) is distinctly smaller than any other individual in good condition of the genus examined during this study and differs from larger specimens in a number of details. To date, the morphology of the larvae of *Boulengerella* species is unknown, consequently a description is provided herein.

Larval specimen of *Boulengerella xyrekes* approximately 12 mm SL. Overall form relatively elongate (Figure 46), but with snout proportionally shorter (~0.370 of HL) than in larger specimens (0.477–0.553 of HL in 121–382 mm SL specimens), with approximately 8 teeth on dentary and premaxilla. Pectoral fins lobulate, without rays apparent. Pelvic fins not yet apparent. Median fleshy fold extending from slightly posterior of pectoral-fin base to anus; fold transparent other than for patch of dark pigmentation anteriorly. Dorsal-fin rays developed, but proportionally much shorter than in larger individuals. Adipose fin present. Anal-fin rays very well developed, extending posteriorly beyond base of caudal fin.

Juvenile specimen of approximately 52 mm SL (Figure 47) with proportions of head and body more comparable to that of larger individuals. Approximately 47 proportionally relatively elongate teeth on premaxilla, slightly fewer on dentary. Pectoral largely lobulate, with 5 rays partially developed dorsally. Pelvic fin fully rayed. Dorsal-fin rays proportionally longer than in smaller individuals, approximately same proportional length as in larger specimens. Posterior rays of anal fin forming distinct lobe extending posteriorly to middle of lower lobe of caudal fin.

Available larger specimens fall into two distinct groupings, with holotype and one paratype much larger than remaining material (see "Material Examined"). Largest measured specimen 382 mm SL. Head and body notably elongate (Figures 48, 49). Greatest body depth at dorsal-fin origin in all examined specimens. Dorsal profile of head and body nearly straight to dorsal-fin origin, very slightly posteroventrally angled at base of dorsal fin, straight from rear of fin to adipose fin. Dorsal surface of body in preserved specimens often somewhat flattened anterior to dorsal fin, somewhat flattened and smoothly rounded transversely posterior to fin. Ventral profile of body gently convex from tip of snout to caudal peduncle; convexity more pronounced in larger individuals. Prepelvic region of body transversely rounded.

Head in larger examined specimens distinctly pointed in both lateral and dorsal views, but with snout somewhat proportionally shorter in two largest specimens examined. Evidently distinctly longer snout of specimen in Figure 48 versus Figure 49 resulting from anterior orientation of proportionally elongate fleshy process at tip of snout in smaller individual. Form of upper jaw, lower jaw, and nostrils as described for *Boulengerella lateristriga*, above. Interorbital region distinctly proportionally wider in larger individuals.

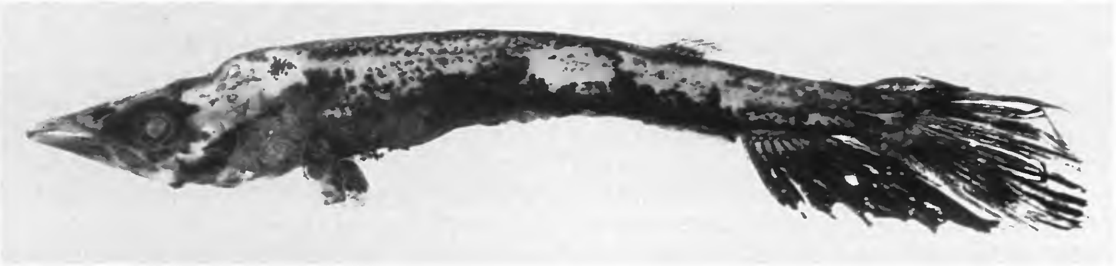

FIGURE 46.—*Boulengerella xyrekes*, new species, larval specimen, USNM 270330, 12.0 mm SL; Venezuela, Amazonas, Departmento Río Negro, Caño Manu, tributary to Río Casiquiare, just upstream of Solano (2°00′N, 66°57′W).

FIGURE 47.—*Boulengerella xyrekes*, new species, young juvenile specimen, USNM 270330, 52.0 mm SL; Venezuela, Amazonas, Departmento Río Negro, Caño Manu, tributary to Río Casiquiare, just upstream of Solano (2°00′N, 66°57′W).

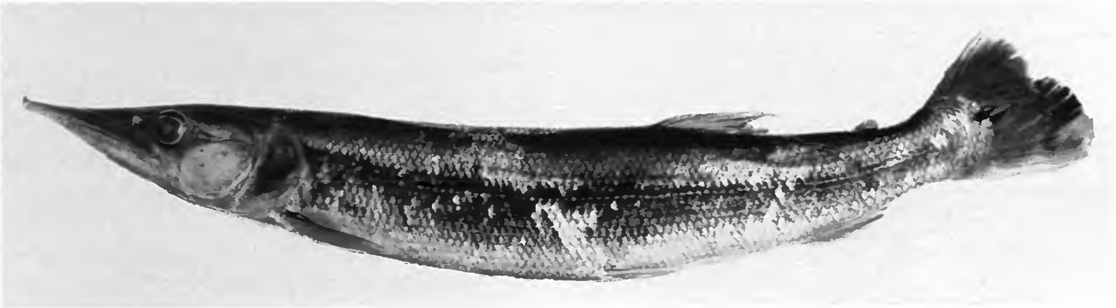

FIGURE 48.—*Boulengerella xyrekes*, new species, holotype, MZUSP 32163, 381 mm SL; Brazil, Amazonas, Rio Negro basin, Rio Marauiá, Cachoeira de Bicho-Áçú, cataract pools (~ 00°20′S, 65°20′W).

FIGURE 49.—*Boulengerella xyrekes*, new species, paratype, USNM 324054, 215 mm SL; Brazil, Amazonas, Rio Negro basin, Rio Marauiá, Cachoeira de Bicho-Áçú, cataract pools (~ 00°20′S, 65°20′W).

Fleshy process at tip of snout well developed in smaller individuals and expanded into a somewhat spatulate pad in some specimens; becoming proportionally smaller with increasing body size and not or barely apparent in largest individuals examined.

Arrangement and form of teeth in both premaxillae and dentaries in specimens of 121-382 mm SL comparable to those in *Boulengerella lateristriga* described above. Premaxillary teeth in single row of 98-138 teeth in specimens of 41-120 mm HL, with number of teeth somewhat variable at particular standard length. Overall ontogenetic trend is for an allometric increase in number of teeth; rate of increase decreasing at larger standard lengths. No indication of inner row of premaxillary dentition in examined individuals. Maxilla with 12-14 teeth along its anterior margin. Dentary lacking teeth anteriorly immediately proximate to symphysis, with 86-133 teeth arranged in single series in specimens of 41-120 mm HL. Overall ontogenetic trend is for increase in number of teeth at larger standard lengths. Number of dentary teeth somewhat variable within limited range of standard lengths. Dentary without inner row of teeth in examined specimens. Teeth on upper and lower pharyngeal tooth-plates small and conic.

Lateral line nearly completely perforated, with approximately 0-5 scales overlying basal portions of middle caudal-fin rays lacking perforations. Scales on body with surface sculpturing and irregular margins, but no distinct cteni. Scales along pre- and postdorsal midlines arranged somewhat irregularly.

Dorsal fin ii-iii,8. First basal dorsal-fin pterygiophore inserting behind neural spine of 20th to 22nd vertebrae. Posterior terminus of dorsal fin distinctly anterior to vertical line through anal-fin origin. Distal margin of dorsal fin somewhat convex. Anal fin ii,8. First basal anal-fin pterygiophore inserting behind hemal spine of 31st or 32nd vertebrae. All specimens of *Boulengerella xyrekes* up to ~215 mm SL have proportionally very elongate posterior anal-fin rays extending distinctly beyond base of caudal fin. Largest specimens (381-382 mm SL) with posterior rays shorter than anterior rays; intermediate-size specimens of the species presumably would demonstrate the progressive shortening of the posterior rays, as occurs in *B. cuvieri* and *B. lucius*. Pectoral fin in 139 mm SL specimen still partially lobulate, with medial-fin rays incompletely developed; pectoral fin i,17-21,iii-iv in specimens of 167-174 mm SL. Pectoral fin pointed in profile, with first branched ray longest; fin tip extends posteriorly somewhat less than one-third distance to pelvic fin in available individuals. Pelvic fin i,7; distal margin obtusely pointed; fin tip reaches posteriorly over one-half distance to anal fin. Caudal fin forked. Adipose fin present.

VERTEBRAE.—44(2), 45 (9), 46 (5).

LIFE COLORATION (based on a photograph of a juvenile from the Venezuelan Amazon provided by Heiko Bleher).—Body and head with mottled pattern of light to dark brown regions interspersed with areas of bright silver. Dorsal portion of snout silver with darker marks. Region anterior and ventral to orbit dark brown. Remaining infraorbitals bright silvery other than for curved stripe of dark pigmentation along posterior and posteroventral margin of series. Opercle silvery brown. Dark pigmentation of body and fins as described under "Color in Alcohol." Anterior rays of pelvic and anal fins silvery. Basal portions of caudal-fin rays and distal portions of each lobe yellowish.

COLOR IN ALCOHOL.—Overall pigmentation pattern in larvae and small juveniles markedly different than in larger individuals, with pronounced dark and light marmorated pattern on body in specimens up to approximately 120-165 mm SL (Figures 46, 47). Ground coloration of head and body in larger juveniles tan, more dusky dorsally. Fleshy process at tip of snout, snout, and anterior portion of lower jaw dusky, particularly on dorsal surface of snout. Posteroventrally oblique bar extending from ventral margin of orbit to ventral margin of posterior portion of lower jaw. Horizontal stripe extending from rear of orbit to rear of third infraorbital occasionally present; stripe on both sides of head in one small specimen (Figure 49) and only on one side of head in another juvenile. Other examined individuals without indication of horizontal bar. All specimens with oblique dark bar along posteroventral margin of third infraorbital; intensity of stripe most pronounced in smaller individuals, gradually becoming less apparent in larger specimens. Opercle and subopercle distinctly to somewhat dark; pigmentation again most pronounced in smaller specimens.

Body in medium-size specimens examined lacking pronounced light versus dark blotchy pattern of smaller specimens, instead with dark, somewhat marmorated shading extending along lateral and ventrolateral surface of body from slightly above lateral line to level of pectoral and pelvic fins or in some instances to ventral midline. Patch of darker pigmentation within shaded area often present over anterior portion of lateral line. Dark pigmentation in largest individuals much more regular, consisting of wide horizontal band of pigmentation extending from opercle along lateral surface of body to caudal peduncle (Figure 48; note: the lighter regions on the lateral surface of the body are damaged areas lacking scales).

Dorsal fin hyaline to slightly dusky, with ray margins outlined by small chromatophores. Distal portions of ventral and dorsal caudal-fin rays in specimens of all sizes unpigmented; upper lobe of caudal fin with alternating regions of dark and light pigmentation in smaller specimens, pattern not apparent in larger individuals. Specimens up to approximately 120 mm SL with basal portions of caudal fin dark, but without apparent dark spot on base of middle rays of caudal fin. Larger individuals with distinct spot of dark pigmentation approximately size of pupil at base of caudal rays. Dark pigmentation on middle rays of caudal fin extends over basal portions of both fin rays and associated membranes, continuous posteriorly in some individuals with dusky pigmentation along ray membranes of middle rays of fin. Elongate posterior rays of anal fin

TABLE 12.—Morphometrics and meristics of (A) holotype, MZUSP 32163; (B) paratypes, MZUSP 44643, MZUSP 32164, USNM 324054; and (C) all specimens of *Boulengerella xyrekes* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 16 are proportions of standard length; 17 to 21 are proportions of head length.

Character	A	B	C
		Morphometrics	
Standard Length	381	121-382	121-382
1. Body depth at dorsal-fin origin	0.160	0.118-0.176	0.118-0.176
2. Snout to dorsal-fin origin	0.672	0.671-0.701	0.661-0.709
3. Snout to anal-fin origin	0.853	0.830-0.876	0.817-0.876
4. Snout to pectoral-fin origin	0.308	0.304-0.366	0.304-0.366
5. Snout to pelvic-fin origin	0.650	0.613-0.665	0.613-0.665
6. Dorsal-fin origin to hypural joint	0.331	0.299-0.339	0.286-0.348
7. Dorsal-fin origin to anal-fin origin	0.210	0.180-0.210	0.180-0.210
8. Dorsal-fin origin to pelvic-fin insertion	0.169	0.137-0.175	0.133-0.177
9. Dorsal-fin origin to pectoral-fin insertion	0.409	0.351-0.410	0.351-0.411
10. Caudal-peduncle depth	0.071	0.068-0.077	0.068-0.078
11. Pectoral-fin length	0.134	0.106-0.134	0.106-0.134
12. Pelvic-fin length	0.111	0.105-0.121	0.105-0.126
13. Length of longest dorsal-fin ray	0.139	0.128-0.150	0.128-0.155
14. Length of longest anal-fin ray	0.098	0.071-0.100	0.071-0.100
15. Anal-fin base	0.071	0.068-0.083	0.067-0.083
16. Head length	0.310	0.310-0.374	0.310-0.374
17. Snout length	0.477	0.477-0.563	0.477-0.563
18. Orbital diameter	0.151	0.117-0.151	0.117-0.153
19. Postorbital length	0.389	0.314-0.384	0.309-0.389
20. Lower-jaw length	0.610	0.570-0.610	0.570-0.612
21. Interorbital width	0.258	0.183-0.261	0.180-0.261
		Meristics	
Scales along lateral-line series	93	88-94	87-94
Pored lateral-line scales	87	84-90	82-90
Scale rows between dorsal-fin origin and lateral-line series	12	10-12	10-12
Scale rows between anal-fin origin and lateral-line series	9	9-10	8-10
Predorsal median scales	59	54-63	54-63
Postdorsal median scales	18	16-20	16-20
Branched dorsal-fin rays	8	8	8
Branched anal-fin rays	8	8	8
Pectoral-fin rays	25	22-27	21-27
Branched pelvic-fin rays	7	7	7
Vertebrae	45	44-46	44-46

present in specimens of up to ~200 mm SL distinctly darker than anterior rays of fin, particularly in smaller individuals. Posterior rays of anal fin not elongate or darker than remainder of fin in largest individuals examined. Pectoral and pelvic fins hyaline. Dark spot of pigmentation on fleshy tissue at base of ventral surface of pectoral fin in individuals of up to ~150 mm SL; pigmentation not present in largest specimen examined. Pelvic fin with dusky to distinct spot of dark pigmentation on middle portions of fin rays in most examined specimens; absent in largest specimen examined.

DISTRIBUTION.—Central and lower portions of Río Orinoco basin, Rio Negro, and central and western portions of Amazon basin (Figure 50).

REMARKS.—*Boulengerella xyrekes* is very similar to and co-occurs with *B. cuvieri*, and the two species often are intermixed in museum collections. It is possible that various records of *B. cuvieri* cited in the synonymy for that species represent, at least in part, records of *B. xyrekes*.

ETYMOLOGY.—The specific name, *xyrekes*, from the Greek for dagger or sharp as a razor, is in reference to the overall shape of the head and body in the species.

TYPE MATERIAL EXAMINED.—12 specimens (complete data taken on all of type series, 121-382 mm SL).

HOLOTYPE.—BRAZIL. *Amazonas:* Rio Negro basin, Rio

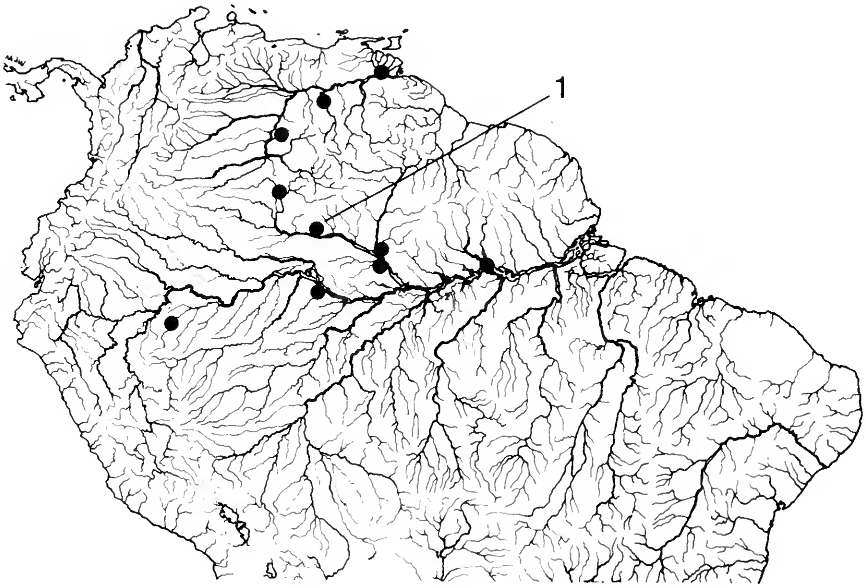

FIGURE 50.—Map of northern portions of South America showing geographic distribution of *Boulengerella xyrekes*, new species (1 = holotype locality). Some symbols represent more than one lot of specimens or locality.

Marauiá, Cachoeira de Bicho-Áçú, cataract pools (~ 00°20'S, 65°20'W), MZUSP 32163, 381 mm SL; collected by M. Goulding, 13 Oct 1979.

PARATYPES.—BRAZIL. *Amazonas:* Rio Negro basin, Rio Marauiá, Cachoeira de Bicho-Áçú, cataract pools (~ 00°20'S, 65°20'W), MZUSP 44643, 2 specimens, 173–192 mm SL, and USNM 324054, 2 specimens, 215–382 mm SL; collected by M. Goulding, 13 Oct 1979. Rio Negro basin, woody shore of Rio Marauiá (~ 00°20'S, 65°20'W), MZUSP 32164, 6, 121–212 mm SL and USNM 319783, 1, 173 mm SL (specimen cleared and counterstained for cartilage and bone); collected by M. Goulding, 14 Oct 1979.

NONTYPE SPECIMENS EXAMINED.—18 specimens (complete data taken on 14 specimens (123–192 mm SL) and partial data on 2 additional specimens).

BRAZIL. *Pará:* Oriximiná (01°40'S, 56°00'W), MZUSP 23743, 4 (3, 178–192). *Amazonas:* Rio Jauaperi, Lagoa de Sapos, 70–80 km upriver from mouth of river (~01°24'S, 62°33'W), MZUSP 23311, 1. Rio Negro, Pedra do Gavião, município de Moura (01°27'S, 61°38'W), MZUSP 27236, 1 (164). Rio Tefé, Vista Escura, MZUSP 32179, 2 (150–156). Rio Javari drainage, sand Playa opposite civil village of Colonia Angamos, Peru (05°11'S, 72°53'W), NRM 24121, 1 (167).

VENEZUELA. *Territorio Federal Delta Amacuro:* Río Orinoco, small caño on W side of river just above downstream mouth of Caño Remolinos, 74 n mi (~137 km) from sea buoy (8°30'N, 61°10'W), USNM 226308, 1 (174). *Amazonas:* Departmento Río Negro, Caño Manu, tributary to Río Casiquiare, just upstream of Solano (2°00'N, 66°57'W), USNM 270330, 2 (12.0–52.0; larva and young juvenile, data not included in ranges of Table 12). Río Sipapo, backwater channel behind sandbar, 6–7 km above Pendare (4°51'N, 67°43'W), ANSP 160094, 1 (123). *Bolivar:* Río Caura, MHNLS 4054, 1 (173). Río Caura at Puerto Las Majadas (7°38'18"N, 64°50'24"W), ANSP 160086, 1 (139); ANSP 160092, 3 (147–159).

Phylogenetic Biogeography of the Ctenoluciidae and Proximate Outgroups

The suprafamilial hypothesis of relationships for the Ctenoluciidae and proximate sister groups together with geological and paleontological information provides minimum age information for ctenoluciids and their relatives. Under the proposed scheme of relationships, the Hepsetidae is the sister group for the lineage consisting of the Erythrinidae and Ctenoluciidae (Figures 15, 51). As such, the Hepsetidae and at least the ancestor of the lineage consisting of the Erythrinidae and Ctenoluciidae must have already diverged prior to the final stages of drift and vicariance between Africa and South America. This event, now dated to have taken place about 85 mya represents a minimum age, and it is possible that divergence of the clades began earlier on the still conjoined continents.

The sister clades (Hepsetidae versus Erythrinidae + Ctenolu-

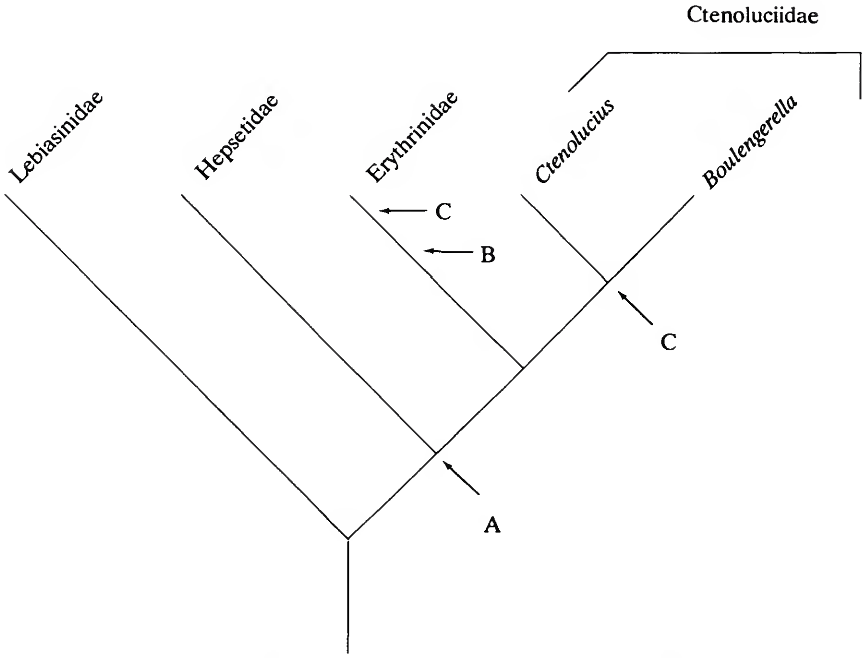

FIGURE 51.—Vicariance events pertinent to proposed phylogeny of Lebiasinidae, Hepsetidae, Erythrinidae, and Ctenoluciidae, together with fossil data. Events: A, drift and vicariance of Africa (Hepsetidae) and South America (Erythrinidae and Ctenoluciidae); B, fossil erythrinid (*Hoplias*) teeth from Miocene deposits of Ecuador (maximum age 19–20 mya); and C, evident Miocene vicariance in Ctenoluciidae between *Ctenolucius* (west and north of Andean Cordilleras) and *Boulengerella* (east of Andean Cordilleras) and in Erythrinidae (*Hoplias* species to east and west of Andean Cordilleras).

ciidae) apparently have undergone dramatically different rates of subsequent cladogenesis. The Hepsetidae consists of a single species, *Hepsetus odoe*, with a broad range across much of subsaharan Africa (Roberts, 1984:138; Paugy, 1990a:192). Although no exhaustive analysis of the different populations of *H. odoe* has been undertaken, no major differences are obvious externally in material from across the species range. Erythrinids and ctenoluciids are, in contrast, much more speciose, with a notable number of externally obvious differentiating characters at diverse taxonomic levels. Within ctenoluciids, as detailed above, two very different major clades and seven species are evident. No comparable in-depth study of the Erythrinidae has been undertaken, but three distinct genera are recognized. *Hoplerythrinus* and *Erythrinus*, each with a single recognized species (*Pseuderythrinus rosapinnis* Hoedeman is a synonym of *Hoplerythrinus unitaeniatus* according to de Jongh (1991:57)), are morphologically similar taxa sharing some apparent synapomorphies and may constitute a sister clade to the other erythrinid genus, *Hoplias*. Recent authors have recognized only three or four *Hoplias* species (e.g., Géry, 1977:102), but recent studies by Oyakawa (1990) indicate that the genus is much more speciose, with 11 recognizable species in what previously was considered *Hoplias lacerdae*. It is likely that the other recognized species, particularly *H. malabaricus*, are also species complexes.

Although no geological benchmarks of an age comparable to the separation of South America and Africa allow us to date the divergence of the Erythrinidae and Ctenoluciidae, available fossil information, albeit limited, provides insight into the question. Roberts (1975:263) reported teeth of the erythrinid genus *Hoplias* from Miocene deposits in Ecuador that are at a maximum 19–20 million years old. Given that sister-taxa must be of the same age, this would indicate that the sister clade to *Hoplias*, consisting of *Hoplerythrinus* and *Erythrinus*, also must have existed by that time. That divergence must have occurred subsequent to the cladogenesis between the Erythrinidae and Ctenoluciidae. At this time, no data is available to resolve the question of when these various major cladogenic events (between the Erythrinidae and Ctenoluciidae and between *Hoplias* and *Hoplerythrinus* + *Erythrinus*) occurred in the period between the late Cretaceous (separation of African and South America, the minimum age for the associated cladogenesis of Hepsetidae and Erythrinidae + Ctenoluciidae) and the Miocene (fossil *Hoplias*).

The distribution of ctenoluciids and erythrinids across the Andean Cordilleras is similar. The species of *Boulengerella* are widely distributed through the Amazon and Orinoco basins and some adjoining areas, with *Ctenolucius* species occurring in the Lago Maracaibo basin, the rivers of northern Colombia, and Panama (see species accounts, above). The lack of thorough revisions makes it impossible to determine the exact distribution of nominal erythrinid species, but *Hoplias*, in addition to having a broad distribution to the east of the Andes (Fowler, 1950:362), also occurs in Lago Maracaibo (Schultz, 1944:308), northern Colombia both in Atlantic (Dahl, 1971:130) and Pacific drainages (Eigenmann, 1922:170), and Panama (Meek and Hildebrand, 1916:303), a distributional range in trans-Andean South America nearly matching that of *Ctenolucius*.

Ctenoluciids and erythrinids do not occur in higher altitude, swift waters. Consequently, the uplift of the Andean Cordilleras in northern South America would have disrupted the continuity between populations of each family in the region of the present mountain ranges; a vicariance event that would have allowed for subsequent speciation of the separate populations. Lago Maracaibo currently is isolated from the Río Orinoco basin by the Merida Andes but may have formed the lower portions of the ancestral Río Orinoco prior to the uplift of those mountains (Rod, 1981). During that uplift in the late Miocene (Kohn et al., 1984; Shagam et al., 1984), the course of the river was shifted to the east and the continuity between the lowland aquatic faunas of the Orinoco and Maracaibo basins would have been eliminated. Uplift of the northern portions of the main Andean Cordilleras occurred at approximately the same time (Megard, 1989), also eliminating contact between the lowland faunas of the Orinoco and proto-Magdalena basins. Thus, the late Miocene apparently is the latest possible time for the divergence of *Ctenolucius* from *Boulengerella* and for the disruption of the continuity of *Hoplias* species across that region (Figure 51).

The overall evidence, although limited, is internally consistent (Figure 51) and indicates that the major cladogenic events in the erythrinid-ctenoluciid clade predated the formation of the Amazon basin, whether as a large impoundment or in its present configuration (see Frailey et al., 1988, for a detailed discussion of Lago Amazonas). The available evidence does not provide insight as to what degree of species-level cladogenesis pre- or postdate the final uplift of the Andes and the formation of the Amazon basin.

Ctenolucius species have an allopatric distribution to the west of the Andes, but with the populations of the genus in the Ríos Magdalena and Sinú being somewhat unexpectedly conspecific with *C. hujeta* of the Lago Maracaibo basin rather than with *C. beani* populations of the Río Atrato and rivers to the west and south of that system in Colombia and Panama (Figure 26). This distribution pattern contrasts with the typical situation of different congeneric species in the Magdalena and Maracaibo basin among fish taxa that have been critically analyzed (curimatids (Vari, 1988, 1992), prochilodontids (Castro, 1990), *Acestrocephalus* and *Cynopotamus* (Menezes, 1976), *Creagrutus* (Harold and Vari, 1994) (see also references in Vari, 1988:350). A similar pattern occurs in freshwater crabs (Rodríquez, 1992). Species continuity between populations in the Lago Maracaibo and regions to the west comparable to that in *Ctenolucius* does occur, however, in the catfish family Ageneiosidae (Walsh, 1990).

The species of *Boulengerella* demonstrate a pronounced degree of sympatry. The range of *B. cuvieri* nearly completely includes that of all congeners (compare Figures 34, 38, 41, 45, 50). Under an allopatric speciation model, this is indicative of massive secondary dispersal repeatedly within the genus following various speciation events. The co-occurrence of so many similar congeneric top-level predators is somewhat puzzling. Available data do not indicate that such co-occurrence represents partitioning of the different ecotops within these basins. Various combinations of *Boulengerella* species have been captured at the same limited locality within both the Orinoco and Amazon basins. For example, in a moderate-size cataract pool at the base of the Cachoeira de Bicho-Áçú in the Rio Marauiá of the Rio Negro basin, Brazil, Michael Goulding captured four of the five *Boulengerella* species (see comments under "Distribution" for *Boulengerella*).

RESUMO

Características osteológicas e de anatomia mole das várias espécies da família neotropical Ctenoluciidae e de outros Characiformes foram examinadas com o intuito de investigar o monofiletismo da família, assim como relações filogenéticas dentro do grupo e com outros Characiformes. Uma série de caracteres derivados corroboram a hipótese de que Ctenoluciidae formam um grupo monofilético, que por sua vez é o grupo irmão de Erythrinidae. Um conjunto menor de sinapomorfias indica que a família africana Hepsetidae é o grupo irmão da linhagem formada por Ctenoluciidae e Erythrinidae, com a família neotropical Lebiasinidae como grupo irmão do conjunto formado por aquelas três famílias. Características derivadas em vários sistemas anatômicos definem a maioria das espécies na família. Os gêneros de Ctenoluciidae *Ctenolucius* Gill (1861a) e *Boulengerella* Eigenmann (1903) são definidos como unidades monofiléticas.

Luciocharax Steindachner (1878) e *Belonocharax* Fowler (1907) são considerados sinônimos de *Ctenolucius*, e *Spixostoma* Whitley (1951) sinônimo de *Boulengerella*.

Duas espécies são reconhecidas em *Ctenolucius*. *Ctenolucius hujeta* (Valenciennes em Cuvier e Valenciennes, 1849) se distribui da bacia do Maracaibo no norte da Venezuela até o Río Sinú no norte da Colômbia, incluindo a bacia do Río Magdalena. *Ctenolucius beani* (Fowler, 1907) ocorre nas bacias do Río Atrato e Río San Juan no norte da Colômbia e nos rios da vertente pacífica no Panamá, atingindo a província de Veraguas a oeste. *Luciocharax insculptus* Steindachner (1878) é sinônimo de *Ctenolucius hujeta* e *Luciocharax striatus* Boulenger (1911) é sinônimo de *C. beani*.

Cinco espécies são reconhecidas em *Boulengerella*. *Boulengerella lateristriga* (Boulenger, 1895) ocorre na bacia do rio Negro da bacia Amazônica no Brasil e Venezuela e nas porções superiores do Río Orinoco no sul da Venezuela. *Boulengerella maculata* Valenciennes em Cuvier e Valenciennes (1849) é amplamente distribuída nas bacias do rio Amazonas, rio Tocantins, e Río Orinoco. *Boulengerella lucius* (Cuvier, 1819) ocorre nos sistemas do rio Amazonas e Río Orinoco. *Boulengerella cuvieri* (Agassiz em Spix e Agassiz, 1829), espécie mais comumente encontrada do gênero, é distribuída no Río Orinoco, rio Amazonas, rio Tocantins, rio Essequibo na Guiana, rio Oiapoque no limite entre Brasil e Guiana Francesa, e rios costeiros nos estados do Amapá e Pará no Brasil. *Boulengerella xyrekes*, nova espécie, uma forma relativamente rara, habita as bacias do Río Orinoco e rio Amazonas. *Xiphostoma taedo* Cope (1872) é sinônimo de *Boulengerella maculata*. *Xiphostoma oseryi* Castelnau (1855) e *X. ocellatum* Schomburgk (1841) são considerados sinônimos de *Boulengerella cuvieri*. *Xiphostoma longipinne* Steindachner (1876), baseado em um jovem colectado na boca do rio Negro no Brasil, é provisoriamente considerado como sinônimo de *B. cuvieri*. Registros de *Boulengerella* no rio Parnaíba no nordeste do Brasil e na bacia do Río de La Plata na Argentina são baseados em exemplares com dados de localidade duvidosos ou identificações errôneas.

São oferecidas chaves de identificação para distinguir *Ctenolucius* de *Boulengerella*, assim como para as várias espécies em cada um daqueles gêneros. São designados lectótipos para *Xiphostoma hujeta* Valenciennes em Cuvier e Valenciennes, *Luciocharax insculptus* Steindachner, *Xiphostoma ocellatum* Valenciennes em Cuvier e Valenciennes, e *Luciocharax striatus* Boulenger.

A biogeografia filogenética do grupo em estudo indica um evento vicariante entre Hepsetidae e o grupo composto de Ctenoluciidae mais Erythrinidae, precedendo ou associado com a separação final entre Africa e América do Sul, 85 milhões de anos atrás. Dados fósseis e distribucionais indicam que os principais eventos cladogenéticos em Ctenoluciidae e Erythrinidae precedem o Mioceno superior.

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