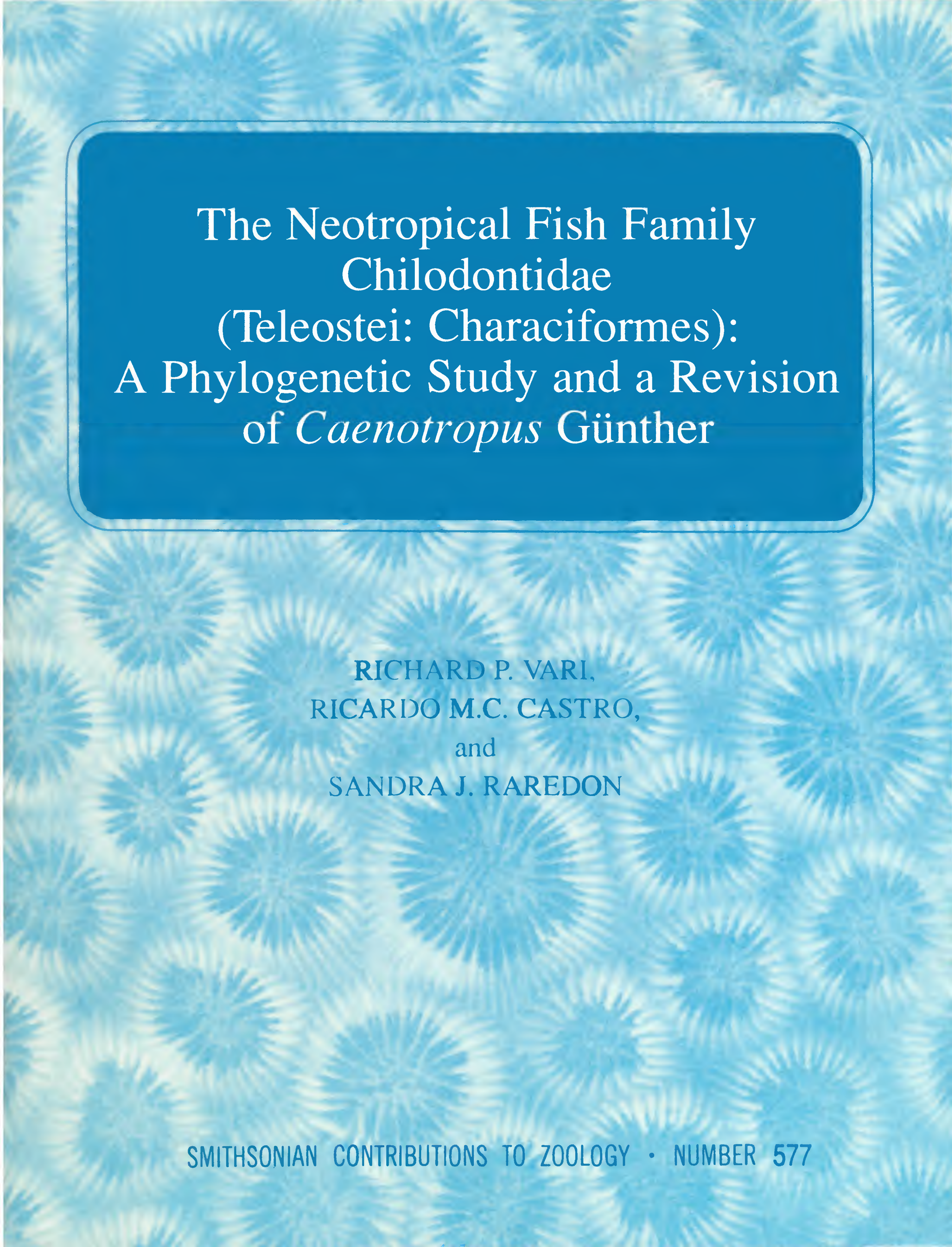

The Neotropical Fish Family Chilodontidae (Teleostei: Characiformes): A Phylogenetic Study and a Revision of *Caenotropus* Günther

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The Neotropical Fish Family Chilodontidae (Teleostei: Characiformes): A Phylogenetic Study and a Revision of *Caenotropus* Günther

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ABSTRACT

Vari, Richard P., Ricardo M.C. Castro, and Sandra J. Raredon. The Neotropical Fish Family Chilodontidae (Teleostei: Characiformes): A Phylogenetic Study and a Revision of *Caenotropus* Günther. *Smithsonian Contributions to Zoology*, number 577, 32 pages, 20 figures, 5 tables, 1995.—A series of synapomorphies for the characiform family Chilodontidae, in addition to those proposed by Vari (1983), are discussed. These involve modifications of the suspensorium, hyoid arch, infraorbitals, lower jaw, supraorbital portion of the laterosensory canal system in the frontal, and lateral-line scales. The chilodontid genera *Chilodus* Müller and Troschel (1844) and *Caenotropus* Günther (1864) are diagnosed as monophyletic on the basis of derived features of the third postcleithrum, lower jaw, hyoid arch, pterotic, supracleithrum, and the laterosensory canal systems in the infraorbitals, frontal, and posterior lateral-line scales. Modifications of a subset of those systems, the subopercle, dentition, suspensorium, third postcleithrum, and pigmentation define subunits of *Caenotropus* or are autapomorphic for its species.

Caenotropus is revised, with *Tylobronchus* Eigenmann (1912) considered a junior synonym. Three *Caenotropus* species are recognized: *C. labyrinthicus* (Kner, 1858) widely distributed in the Rio Amazonas and Río Orinoco basins, the upper Essequibo River basin in Guyana, the Saramacca and Suriname Rivers in Suriname, and the Rio Parnaíba, northeastern Brazil; *C. maculosus* (Eigenmann, 1912) ranging from the Essequibo River of Guyana to the Fleuve Maroni of French Guiana; and *C. mestomorgmatos*, new species, from the acidic black waters of the middle and upper Río Negro in Brazil and Venezuela and the upper Río Orinoco in southern Venezuela. *Chilodus labyrinthicus rupununi* Fowler (1914) is placed into the synonymy of *Caenotropus labyrinthicus*.

Keys are provided to the genera *Caenotropus* and *Chilodus* and to the species of *Caenotropus*. A lectotype is designated for *Microdus labyrinthicus* Kner. The biogeographic implications of the geographic distribution of subunits of the Chilodontidae are discussed.

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Contents

The Neotropical Fish Family Chilodontidae (Teleostei: Characiformes): A Phylogenetic Study and a Revision of *Caenotropus* Günther

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Introduction

The external appearance of the members of the Neotropical characiform family Chilodontidae provides little indication of the extensive and unusual internal modifications that characterize the family (Vari, 1983:51-52). Numerous restructurings of bones, cartilages, and soft tissues are associated with the highly modified gill-arches and epibranchial organs. The series of distinctive modifications of the axial skeleton, anterior ribs, and associated ligamentous tissues may be correlated, in turn, with the unusual head-down orientation assumed by chilodontids while swimming and resting; a habit reflected in their common name of "head-standers." Chilodontids are broadly distributed east of the Andean Cordilleras in the Orinoco and Amazon river basins, the series of independent rivers draining the Guianas, and the Rio Parnaíba basin of northeastern Brazil. The family is unknown in the remaining rivers of the Atlantic slopes of South America or the trans-Andean portions of the continent.

Recent authors (e.g., Géry, 1964, 1977) have recognized two chilodontid genera, *Chilodus* Müller and Troschel (1844) and *Caenotropus* Günther (1864). In a familial-level phylogenetic analysis, Vari (1983:51-52) listed twenty-six synapomorphies common to *Chilodus* and *Caenotropus* but did not delve into the questions of the monophyly or the recognizable species in each genus. *Chilodus* was revised subsequently by Isbrücker and Nijssen (1988) who recognized three species, *C. punctatus* Müller and Troschel (1844), *C. zunevei* Puyo (1945), and *C. gracilis* Isbrücker and Nijssen (1988), but they did not attempt to determine whether the three species constitute a monophyletic group. *Caenotropus* has not been revised recently, and neither the number of species in the genus nor their interrelationships were known.

This paper has five aims: (1) to test further the hypothesis of the monophyly of the Chilodontidae; (2) to determine whether *Chilodus* and *Caenotropus* are monophyletic; (3) to determine the recognizable species of *Caenotropus* and their geographic distribution; (4) to develop a hypothesis of phylogenetic relationships in *Caenotropus*; and (5) to determine what the information about the phylogeny and distribution of chilodontids tells us about the biogeographic history of the family.

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METHODS AND MATERIALS.—Measurements were made with dial calipers, and data was recorded to tenths of a millimeter for measurements under 100 mm SL and to a millimeter for larger lengths. Counts and measurements were made on the left side of specimens whenever possible. Lateral-line scale counts include all scales in the series including those posterior of the hypural joint, but not the terminal tubular ossification between the middle caudal-fin rays in *C. labyrinthicus* and *C. maculosus*. Scales above the lateral line are counted to the base of the anterior dorsal-fin rays but do not include the median scale series anterior to the fin. In counts of branched median fin-rays the last two anal-fin rays, which typically meet basally, are counted as one, and the last two dorsal-fin rays as separate rays. Vertebral counts were taken from both radiographs and cleared and stained specimens. In vertebral counts the fused PU_1+U_1 is considered a single bone, and the vertebrae in the Weberian apparatus are considered as four elements. Numbers in parentheses following a vertebral count are the number of specimens with that count. Subunits of the head are presented as proportions of head length (HL), and head length and measurements of body parts are given as proportions of standard length (SL).

The first entry under "Material Examined" for each species account is a summary of the total number of specimens examined (in parentheses, the number of specimens forming the basis for meristic and morphometric data, and the range of standard lengths (in mm) for these specimens). This is followed by a listing of examined specimens including collection locality, institutional abbreviation, catalog number, number of specimens in the lot (in parentheses, the number of specimens from which counts and measurements were taken if less than the total number of specimens, and the standard lengths (in mm) of those individuals). Geographic descriptors are country (capitalized), state, province, department or district (italicized), followed by specific locality data. Collectors and date of collection are cited only for the type series of *C. mestomorgmatos*. Modern, corrected, and more detailed locality information for specimens collected during the Thayer Expedition to Brazil follows Higuchi (ms). Localities for the Austrian expedition to northeastern Brazil follow Vanzolini (1992). Common names are from the literature. Localities in synonymies are as originally cited, followed by modern or corrected equivalents, in parentheses, when necessary.

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 were supplemental sources of osteological data. Osteological terminology is that used by Vari (1989a). The following cleared and stained specimens were the basis for the text illustrations and observations in the text:

Caenotropus labyrinthicus. USNM 231543, Brazil, Amazonas, Rio Negro, São Gabriel da Cachoeira; 1 specimen, 58.5 mm SL. USNM 231544, Venezuela, Amazonas, upper Río Negro; 1 specimen, 63.4 mm SL. USNM 270237, Venezuela, Bolivar, small caño connecting with Río Orinoco immediately S of El Burro (6°11'N, 67°25'W); 2 specimens, 71.5–75.7 mm SL. USNM 231546, Suriname, Saramacca River; 1 specimen, 104 mm SL.

Caenotropus maculosus. USNM 231545, Guyana; 2 specimens, 42.7–46.3 mm SL.

Caenotropus mestomorgmatos. USNM 322557, Venezuela, Amazonas, Río Orinoco basin, Río Iguapo (tributary of Río Orinoco), approximately 1 hour (by boat) above its mouth (3°09'N, 65°28'W); 1 paratype, 102 mm SL.

Chilodus gracilis. USNM 232358, Brazil, Pará, Rio Inhuangi; 4 specimens, 23.4–35.1 mm SL.

Chilodus punctatus. USNM 280444, Peru, Loreto, Quebrada Corrientillo, at Corrientillo, on road running W from Iquitos to Río Nanay (3°50'S, 73°13'W); 2 specimens, 55.7–68.0 mm SL. USNM 231542, Peru, Loreto, Río Nanay; 14 specimens, 23.7–45.3 mm SL.

Chilodus zunevei. USNM 163212, Guyana; 2 specimens, 34.7–36.5 mm SL.

Observations on osteological characters in outgroups to *Caenotropus* and *Chilodus* are based on specimens cited in Vari (1989a:10–11) and Vari (1995).

The groups herein termed the Chilodontidae, Prochilodontidae, Hemiodontidae, and Distichodontidae have been referred to by some authors as the Chilodidae, Prochilodidae, Hemiodidae, and Distichodidae or as subfamilies with a parallel construction (e.g., Géry, 1964, 1977). The form of the family-level names for those groups in this paper follows the discussion by Steyskal (1980:173) who noted that "names in *-odus* are usually from the Greek *odous* 'tooth,' are of masculine genera, and have a stem in -odont-. The following are correct ... Chilodontidae, Distichodontidae, Hemiodontinae, ... Prochilodontidae...." Family-level names incorporating -odont- also were utilized for these groups by Eschmeyer and Bailey (in Eschmeyer, 1990) who similarly noted that the stem genera were masculine.

INSTITUTIONAL ABBREVIATIONS.—The following abbreviations for institutions and collections are used:

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	The Natural History Museum, London, formerly British Museum (Natural History)
CAS	California Academy of Sciences, San Francisco
CM	Carnegie Museum, Pittsburgh (fish collections now largely at FMNH)
FMNH	Field Museum of Natural History, Chicago
INHS	Illinois Natural History Survey, Champaign
ISBN	Institut royal des Sciences naturelles de Belgique, Brussels
IU	Former Indiana University collections, now dispersed to various repositories
LACM	Los Angeles County Museum of Natural History
MBUCV	Museo de Biología, Universidad Central de Venezuela, Caracas
MCNG	Museu de Ciencias Naturales, Guanare, Venezuela
MCZ	Museum of Comparative Zoology, Cambridge
MHNLS	Museo de Historia Natural La Salle, Caracas
MUSM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima
MZUSP	Museu de Zoologia, Universidade de São Paulo, São Paulo
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NMW	Naturhistorisches Museum Wien, Vienna
NRM	Naturhistoriska riksmuseet, Stockholm
ROM	Royal Ontario Museum, Toronto
SU	Stanford University (fish collections now deposited at CAS)
UF	Florida State Museum, Gainesville
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor
USNM	Collections of the former United States National Museum, now in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMA	Instituut voor Systematiek and Populatiebiologie, Amsterdam

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

AA	angulo-articular
AP-MET	anterior process of metapterygoid
CART	cartilage
CTB	connective-tissue band
DC-DEN	dorsal canal of dentary
DEN	dentary
DP-SCL	dorsal process of supracleithrum
ECT	ectopterygoid
EXT	extrascapular
IO	infraorbital (1-6)
LP-AA	lateral process of angulo-articular
LR-DEN	lateral ridge of dentary
LSC-AA	laterosensory canal segment of angulo-articular
LSC-DEN	laterosensory canal segment of dentary
MES	mesopterygoid
MET	metapterygoid
MQF	metapterygoid-quadrate fenestra
PDP-SCL	posterodorsal process of supracleithrum
POP	preopercle
POST	posttemporal
QUA	quadrate
RA	retroarticular
SCL	supracleithrum
SPOP	suprapreopercle
SYM	symplectic
VC-AA	vertical canal of angulo-articular
VP-MES	ventral process of mesopterygoid

Character Description and Analysis

Newly discovered derived features informative about the hypothesis of the monophyly of the Chilodontidae, *Chilodus*, *Caenotropus*, and the hypothesized monophyletic subunits of the latter genus are discussed. These features, together with previously described synapomorphies for the Chilodontidae, are summarized below under "Synapomorphy List and Phylogenetic Reconstruction." Hypothesized familial through intrageneric synapomorphies (unique features and unambiguously optimized characters) and autapomorphies are numbered sequentially on the cladogram of Figure 7 to simplify the visualization of their distribution in 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 *Caenotropus* are highlighted by "SYNAPOMORPHY" in the text. Proximate outgroups to the Chilodontidae in the discussion are first its sister group, the family Anostomidae; second, the Curimatidae and Prochilodontidae, which form the sister group to the clade consisting of the Chilodontidae plus Anostomidae (Vari, 1983); and finally other characiforms.

A large number of synapomorphies have been identified for the clade formed by the Chilodontidae, Anostomidae, Curimatidae, and Prochilodontidae (Vari, 1983:46–47), for the lineage formed by the Anostomidae and Chilodontidae (Vari, 1983:50), and for the members of the family Chilodontidae (Vari, 1983:50 and herein). The monophyly of the Chilodontidae thus can be considered sufficiently well-corroborated to serve as a topological constraint in this analysis. This is particularly true in view of the few derived intrafamilial features found in this study to be homoplastic between a subunit of the Chilodontidae and characiform outgroups. A detailed "global" parsimony analysis consequently would not be informative and was not undertaken. Newly proposed derived features for the family and its subclades were not discovered in any characiform outgroups unless otherwise noted.

INFRAORBITAL SERIES

SECOND AND THIRD INFRAORBITALS (IO_2 and IO_3).—*Caenotropus* and *Chilodus* have the posterior portion of the second infraorbital and the associated laterosensory canal segment extending over the anterior portion of the third infraorbital (Figure 1). This contrasts with the juxtaposition of the adjoining margins of these ossifications in proximate outgroups to the Chilodontidae (Anostomidae, see Winterbottom, 1980, figs. 30, 32; Curimatidae, see Vari, 1991, fig. 9; Prochilodontidae, see Roberts, 1973, fig. 17) and most characiforms. The condition in chilodontids consequently is hypothesized to be an additional synapomorphy for the family (SYNAPOMORPHY 27).

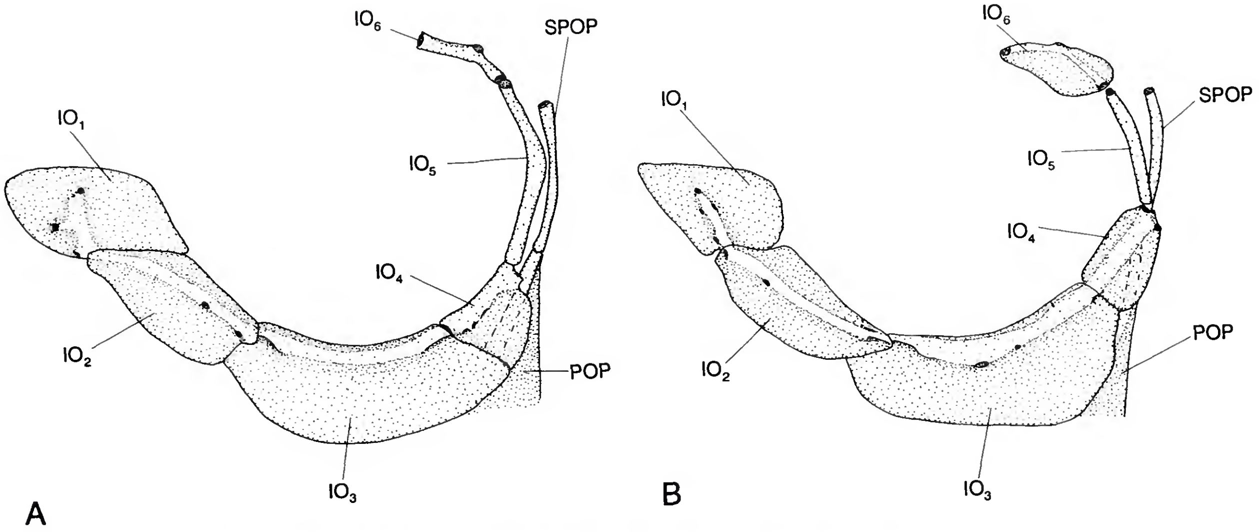

FIGURE 1.—Infraorbital series, suprapreopercle, and posterodorsal portion of preopercle in (A) *Caenotropus mestomorgmatos*, USNM 322557, and (B) *Chilodus punctatus*, USNM 280444; left sides, lateral views, anterior to left. Dashed lines on fourth infraorbital show alignment of laterosensory canal system in underlying posterodorsal portion of the preopercle.

FOURTH AND FIFTH INFRAORBITALS (IO$_4$ and IO$_5$).—*Caenotropus* species have the main laterosensory canal segments in the fourth and fifth infraorbitals forming a smooth arch that roughly parallels the canals in the suprapreopercle and dorsal portion of the preopercle (Figure 1A). The only portion of the canals in these infraorbitals that overlaps the laterosensory canal in the preopercle is the short, horizontally aligned posterior branch of the fourth infraorbital canal. Such a separation of the main portions of the infraorbital and preopercular laterosensory canals occurs in diverse characiforms (e.g., *Brycon*, Weitzman, 1962, figs. 8, 9) including the hypothesized most-generalized genus *Xenocharax* (Daget, 1960, fig. 7) and proximate outgroups to the Chilodontidae. The separation is thus hypothesized to be primitive. *Chilodus* species have the dorsal portion of the fourth infraorbital and the ventral portion of the fifth infraorbital and their associated laterosensory canal segments shifted posteriorly. As a consequence, the primary laterosensory canals in the dorsal portion of the fourth infraorbital and the ventral portion of the fifth infraorbital overlap the canal in the dorsal portion of the preopercle and to a slight degree that in the ventral section of the suprapreopercle (Figure 1B). Based on the condition in outgroups, this overlap is hypothesized to be a synapomorphy for the species of *Chilodus* (SYNAPOMORPHY 37).

SIXTH INFRAORBITAL (IO$_6$).—The sixth infraorbital of characiforms is typically a plate-like ossification overlying the dilatator fossa on the lateral surface of the sphenotic and frontal. Such a laminar bone with its associated laterosensory canal segment occurs in proximate outgroups to the Chilodontidae (e.g., Anostomidae, Winterbottom, 1980, fig. 32; Curimatidae, Vari, 1991, fig. 36) and *Chilodus* (Figure 1B). *Caenotropus* species, in contrast, have the sixth infraorbital reduced to a tubular ossification surrounding the laterosensory canal segment (Figure 1A), a hypothesized synapomorphy for the genus (SYNAPOMORPHY 45).

SUBOPERCLE

The posterior margin of the subopercle is rounded in adults of proximate outgroups to the Chilodontidae (Prochilodontidae, Roberts, 1973, figs. 10, 11; Curimatidae, Vari, 1983, fig. 27; Anostomidae, Winterbottom, 1980, figs. 33, 36, 39). Within the Chilodontidae that condition occurs in all *Chilodus* species and *Caenotropus mestomorgmatos*. Midsize to large individuals of *Caenotropus maculosus* and *C. labyrinthicus* have rather a distinct, posteriorly pointed process that extends beyond the margin of the opercle. This derived condition is synapomorphic for those two species (SYNAPOMORPHY 54).

SUPRAORBITAL LATEROSENSORY CANAL

The posterior portion of the supraorbital laterosensory canal in the frontal primitively contacts the laterosensory canal segment in the pterotic in characiforms (see more detailed comments in Vari, 1995). This close association of these laterosensory canal systems is modified at two levels of universality in the Chilodontidae. Both *Caenotropus* and *Chilodus* have the canal within the pterotic fully developed.

The posterior portion of the supraorbital canal is, however, reduced relative to that in outgroups, terminating distinctly short of the margin of the frontal that is proximate to the pterotic. In *Caenotropus* the reduction is proportionally relatively minor, with the remaining portion of the supraorbital canal in the pterotic approximately twice the length of the gap between the posterior limit of the canal and the anterodorsal terminus of the pterotic canal. *Chilodus*, in contrast, has the gap more pronounced, retaining only a short segment of the supraorbital canal, which is about one-half the length of the gap between its posterior opening and the anterior margin of the pterotic. Given the widespread occurrence of a complete supraorbital laterosensory canal segment contacting the pterotic in characiforms, including proximate outgroups to the Chilodontidae, the reduction of the canal in chilodontids is hypothesized to be synapomorphic for *Chilodus* and *Caenotropus* (SYNAPOMORPHY 28) with the pronounced reduction in *Chilodus* synapomorphic for the species of that genus (SYNAPOMORPHY 38).

The lack of contact of the supraorbital and pterotic laterosensory canals also occurs in various outgroup characiforms (Erythrinidae, Ctenoluciidae, Pyrhulininae, Distichodontidae, and Hepsetidae). As discussed by Vari (1995), the absence of contact of the supraorbital and pterotic laterosensory canals in the cited outgroup taxa differs from the lack of continuity between these canals characteristic of the Chilodontidae, and/or the available evidence indicates that all the groups are most closely related to characiforms other than chilodontids. The absence of contact between the supraorbital and pterotic canals in these outgroups is thus considered nonhomologous and/or homoplastic to the separation of the laterosensory canal segments in the Chilodontidae.

PTEROTIC

Vari (1983:35, fig. 31) noted that the posteroventral portion of the pterotic of chilodontids was expanded to abut and support the dorsal portion of the supracleithrum. This expanded process, the pterotic articular process (PAP of Vari, 1983, fig. 3), is common to both *Caenotropus* and *Chilodus*. Immediately anterodorsal to the main body of that process in *Caenotropus* are a pair of posterolaterally directed processes that serve as areas of attachment for various bands of connective tissue (process shown between the PAP and the indicator pointing to the pterotic, PTE, in Vari, 1983, fig. 3). This region of the pterotic lacks such distinct processes in *Chilodus* and proximate outgroups to the Chilodontidae, and the possession of these structures is hypothesized to be synapomorphic for the species of *Caenotropus* (SYNAPOMORPHY 46).

JAW DENTITION

The plesiomorphic oral dentition in characiforms, including basal groups such as the Distichodontidae (Fink and Fink, 1981), has the teeth immovably attached to the upper and lower jaws (Daget, 1960, fig. 4; Vari, 1979, fig. 3). Chilodontids, in contrast, have weakly developed teeth attached to the flesh overlying the upper (all species) and lower jaws (all species except *Caenotropus labyrinthicus* in which the lower jaw is edentulous). The proximate outgroup to the Chilodontidae, the Anostomidae, is characterized by well-developed teeth tightly attached to the jaws (Winterbottom, 1980, figs. 37, 38). The two components of the sister lineage to the clade formed by the Chilodontidae and Anostomidae, the Curimatidae and Prochilodontidae, have very different, highly derived forms of jaw dentition. Prochilodontids have the numerous teeth in each jaw attached to the fleshy lips (Roberts, 1973, fig. 7) in a manner somewhat reminiscent of that of chilodontids. All curimatids, in contrast, lack jaw teeth as adults. Juvenile curimatids (Géry, 1977:231; Vari, 1983:8) and prochilodontids (Rossi, 1992:162) do, however, have jaw teeth attached to the underlying bones in a mode comparable to that in most characiforms. Given the attached dentition of basal characiforms and the conditions of the jaw dentition in proximate outgroups to the Chilodontidae, it is most parsimonious to hypothesize that the form of the dentition in chilodontids is derived (SYNAPOMORPHY 29), albeit approximated independently in prochilodontids.

The species of *Chilodus*, together with *Caenotropus maculosus* and *C. mestomorgmatos*, have a single series of teeth in both jaws (jaw dentition occasionally absent in a few of the largest examined specimens of the latter species). *Caenotropus labyrinthicus*, in contrast, lacks lower-jaw dentition in all examined specimens, an autapomorphy for the species (SYNAPOMORPHY 59). Lower-jaw teeth are absent among other characiforms only in adult curimatids (see above) and the hemiodontid genus *Anodus* (including *Eigenmannina*). Vari (1983, 1989a) listed a series of derived features that indicates that the Curimatidae is most closely related to the Prochilodontidae. *Anodus*, transferred to the Hemiodontidae from Curimatidae by Roberts (1974), shares a number of unique synapomorphies with other hemiodontids (F. Langeani, pers. comm.). Thus, it is most parsimonious to hypothesize that the lack of lower-jaw dentition in *Caenotropus labyrinthicus* is homoplastic to that in the Curimatidae and *Anodus*.

LOWER JAW

Associated with the lack of tooth implantation in the dentary are several modifications of the lower jaw not discussed by Vari (1983). The anterior portion of the dentary in *Caenotropus* (Figure 3) and proximate outgroups to the Chilodontidae is not as developed vertically as is the posterior portion of the bone (Vari, 1983, fig. 2), and it lacks any distinct lateral ridges proximate to the symphysis. *Chilodus*, in contrast, has the anterior portion of the dentary vertically expanded relative to the condition in outgroups. The dentary of *Chilodus* also has a distinct lateral ridge extending posterodorsally from the ventral portion of the symphysis to the dorsal margin of the bone (Figure 2, LR-DEN). Given the unique nature of these two modifications, the form of the dentary is hypothesized to be

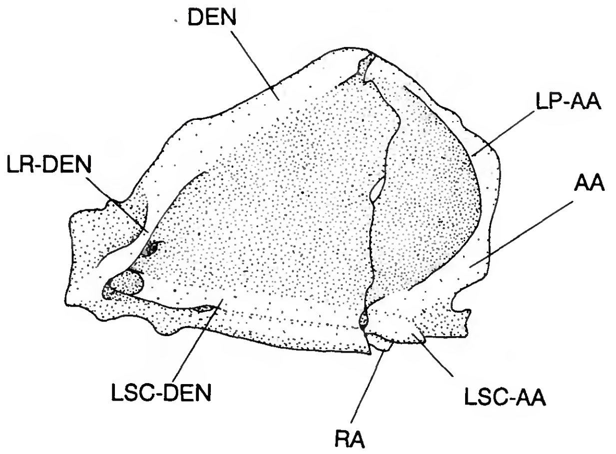

FIGURE 2.—Lower jaw of *Chilodus punctatus*, USNM 280444, left side, lateral view, anterior to left; dentition embedded in fleshy covering of dentary not illustrated.

synapomorphic for the species of *Chilodus* (SYNAPOMORPHY 39).

The lateral surface of the angulo-articular and the posterior portion of the dentary are relatively flat in *Caenotropus*, proximate outgroups to the Chilodontidae (Anostomidae, Winterbottom, 1980, figs. 39, 41; Vari, 1983, fig. 11), and characiforms in general, with the angulo-articular typically only slightly transversely thickened. *Chilodus* has instead a distinct lateral process on the angulo-articular with a discrete anterior curved margin along its posterolateral margin (Figure 2, LP-AA) (SYNAPOMORPHY 40). This lateral expansion of the posterior portion of the retroarticular, in association with the previously noted ridge on the anterior portion of the dentary, delimits a distinct depression on the lateral surface of the lower jaw, a form of the jaw not encountered in examined characiform outgroups.

Characiforms, including proximate outgroups to the Chilodontidae, have canals limited to the ventral portion of the angulo-articular and dentary. Chilodontids have a much more elaborate system. In both *Caenotropus* and *Chilodus* there are vertically aligned canal systems in the angulo-articular that reach to the dorsal margin of the ossification (Figure 3, VC-AA). These canals are apparently continuous ventrally with the horizontal laterosensory canal segment in the ventral portion of the bone that is general for characiforms and may represent a dorsal extension of the laterosensory canal system. Regardless of its function, such a canal system is unique to the Chilodontidae among examined characiforms, and its presence is hypothesized to be an additional synapomorphy for the family (SYNAPOMORPHY 30). The canals in the dorsal portion of the angulo-articular are moderately developed in *Chilodus* but are expanded into an extensive system in *Caenotropus* (Figure 3), a synapomorphy for the species of the latter genus (SYNAPOMORPHY 47).

Among characiforms, major canals within the dentary typically are limited to the ventral portion of the bone that bears a portion of the laterosensory canal system (Figures 2, 3, LSC-DEN). Chilodontids have an additional canal system in the posterodorsal portion of the ossification. The canal is simplest in *Caenotropus* where it is a relatively simple tube extending anteriorly from near the border of the dentary and angulo-articular (Figure 3). The canal in *Chilodus* is more complex, with secondary side branches, and it continues anteriorly into the region of the posterodorsally angled ridge on the anterior portion of the dentary. The function of this canal system in chilodontids is uncertain, but its presence in the family is hypothesized to be derived (SYNAPOMORPHY 31), with the more extensive and elaborate form of the canal in *Chilodus* a further derived condition (SYNAPOMORPHY 41).

HYOID ARCH

DORSAL AND VENTRAL HYPOHYALS.—The dorsal and ventral hypohyals in characiforms are typically unelaborated along their area of contact, often with their adjoining margins cartilaginous. Two modifications of this joint characterize chilodontids on the one hand and *Chilodus* on the other. All chilodontids have an anterodorsally directed process at the anterolateral portion of the contact between the dorsal and ventral hypohyals. This process, equally formed by the dorsal and ventral hypohyal, is poorly developed in *Caenotropus*,

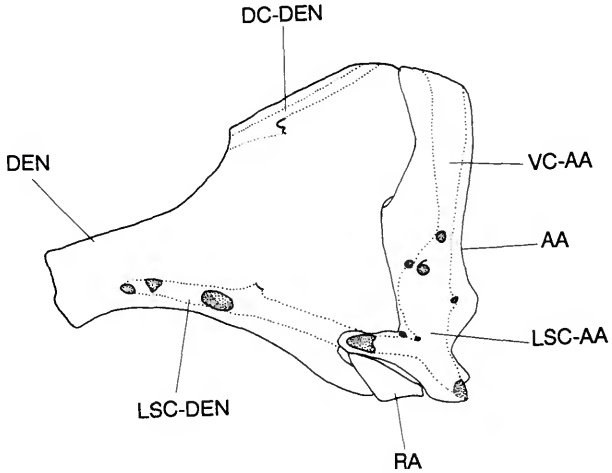

FIGURE 3.—Lower jaw of *Caenotropus labyrinthicus*, USNM 231543, left side, lateral view, anterior to left, showing distribution of canal systems in angulo-articular and dentary; dentition embedded in fleshy covering of dentary not illustrated.

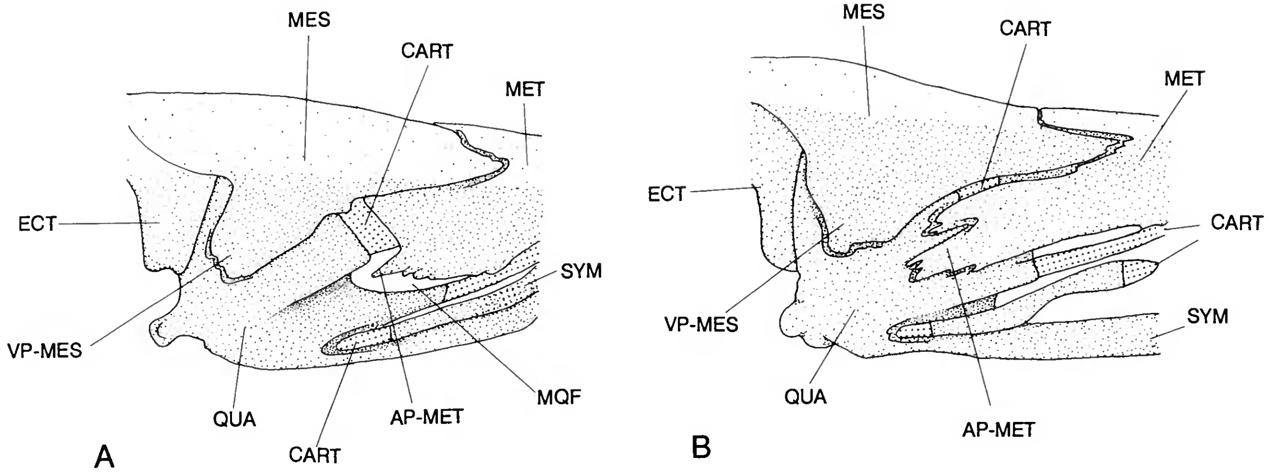

FIGURE 4.—Mesopterygoid, metapterygoid, quadrate, and adjoining ossifications of (A) *Chilodus punctatus*, USNM 280444, and (B) *Caenotropus maculosus*, USNM 231545; right sides, medial views, anterior to left.

even in the largest cleared and stained specimens examined, but it is much more distinct in *Chilodus* specimens, forming a very prominent process that is most developed in larger individuals. In light of the absence of these structures in examined outgroups, the process is hypothesized to be derived for chilodontids (SYNAPOMORPHY 32), with the highly developed form of the process in *Chilodus* synapomorphic for the species of that genus (SYNAPOMORPHY 42). The lateral portion of the joint between the dorsal and ventral hypohyals, modified in *Caenotropus*, retains the primitive unelaborated form. *Chilodus* species, in contrast, have the dorsal and ventral hypohyals joined by a series of well-developed interdigitations (SYNAPOMORPHY 43).

DORSAL HYPOHYAL AND ANTERIOR CERATOHYAL.—The dorsal hypohyal and anterior ceratohyal in characiforms typically meet in a straight, vertical joint. Chilodontids, in contrast, have a series of well-developed interdigitations between the dorsal margin of the dorsal hypohyal and the anterodorsal portion of the anterior ceratohyal (SYNAPOMORPHY 33).

MESOPTERYGOID

The mesopterygoid in the Anostomidae, Curimatidae, and Prochilodontidae, the proximate outgroups to the Chilodontidae, is situated dorsal to the quadrate with little, if any, overlap of the quadrate by the mesopterygoid. The most notable degree of overlap of the quadrate in proximate outgroups occurs in some *Leporinus* species (family Anostomidae) in which a short ventral process of the mesopterygoid extends over the anterodorsal corner of the medial surface of the quadrate. In *Caenotropus* and *Chilodus* the mesopterygoid has a large triangular process that extends ventrally from the main body of the ossification over the medial surface of the quadrate (Figure 4A,B), a hypothesized synapomorphy for the family (SYNAPOMORPHY 34). The occurrence of a somewhat similar, albeit less developed, mesopterygoid process in some *Leporinus* species is hypothesized to be homoplastic to the structure in the Chilodontidae in light of the numerous synapomorphies diagnostic for the Anostomidae (Vari, 1983:50) and the derived features common to *Leporinus* and a subset of anostomid genera (pers. obs.).

METAPTERYGOID AND QUADRATE

The metapterygoid and quadrate in characiforms including *Xenocharax*, a hypothesized basal characiform (Fink and Fink, 1981) (see Daget, 1960, fig. 10), typically delimit an opening in the suspensorium, the metapterygoid-quadrate fenestra. The metapterygoid-quadrate fenestra is, in contrast, greatly reduced or absent in all Chilodontids as a consequence of the anterior extension of the metapterygoid that extends into the area delimited by the notch on the rear of the quadrate. This extension takes two forms within the family. *Chilodus* species have the process extending into, but not completely filling, the notch on the rear of the quadrate (Figure 4A, AP-MET) and not contacting the anterior margin of the notch. *Caenotropus* species have the notch completely occupied by the anterior extension of the metapterygoid, with the two bones joined by an interdigitating joint (Figure 4B). The interdigitations are only

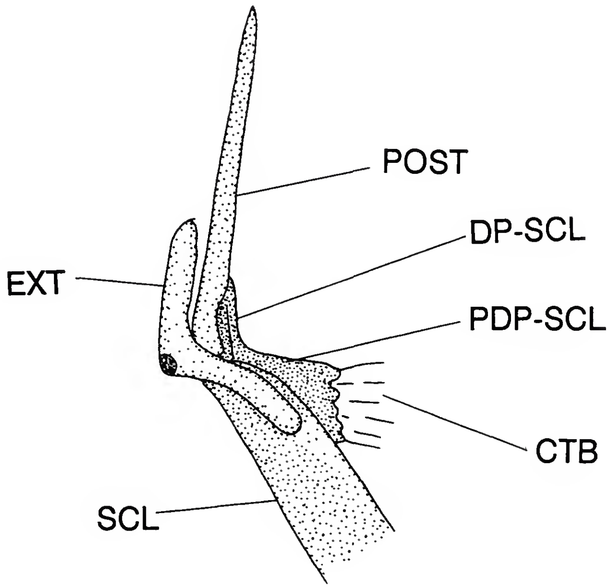

FIGURE 5.—Posttemporal, extrascapular, and dorsal portion of the supracleithrum of *Caenotropus labyrinthicus*, USNM 270237; left side, lateral view, anterior to left.

slightly developed in *C. mestomorgmatos* but are much more pronounced in *C. labyrinthicus* and *C. maculosus*, particularly in the latter (Figure 4B).

A reduction or elimination of the fenestra has occurred in various characiforms. In *Neolebias spilotaenia* Boulenger, a member of the African family Distichodontidae, elimination of the fenestra is a consequence of the expansion of the symplectic (Vari, 1979:293) rather than the metapterygoid. The distichodontid genera *Nannocharax* and *Hemmigrammocharax* have the metapterygoid and quadrate approximate or in contact. This proximity is, however, a consequence of the reduced vertical extent of the entire suspensorium rather than an expansion of the metapterygoid. Among proximate outgroups to the Chilodontidae the fenestra is present in the vast majority of curimatids but is largely eliminated in the species of *Curimatopsis* (Vari, 1982, fig. 6). The expanded metapterygoid of *Curimatopsis*, however, does not extend into the notch in the posterior of the quadrate. Furthermore, a long series of synapomorphies indicate that the members of the genus are most closely related to other curimatids that retain large metapterygoid-quadrate fenestras (Vari, 1989a:52). All prochilodontids (Roberts, 1973) and most species in the Anostomidae (e.g., *Leporinus*, Vari, 1983, fig. 29) also retain large fenestras, but the opening is reduced in most members of the subfamily Anostominae (Winterbottom, 1980:49, figs. 33-36, 39, 40). Those anostomines with the fenestra completely absent have the space, primitively occupied by the opening, filled as a consequence of the expansion of both the metapterygoid and quadrate (e.g., *Anostomus spiloclistron*, Winterbottom, 1980, fig. 38), but without a distinct anteroventral process of the metapterygoid. In none of the examined characiform outgroups to the Chilodontidae is the lack of the metapterygoid-quadrate fenestra a consequence of the anterior extension of the metapterygoid characteristic of that family.

The reduction or elimination of the fenestra by the anterior extension of the metapterygoid consequently is hypothesized to be a synapomorphy for the Chilodontidae (SYNAPOMORPHY 35). The interdigitating joint between those bones in all *Caenotropus* species is considered derived (SYNAPOMORPHY 48), given its unique nature in the order, with the more highly developed interdigitations in *C. labyrinthicus* and *C. maculosus* hypothesized synapomorphic for the species pair (SYNAPOMORPHY 55), and the very complex interdigitations of *C. maculosus* hypothesized autapomorphic for that species (SYNAPOMORPHY 57).

SUPRACLEITHRUM

Vari (1983:34-35, fig. 31) described a number of derived modifications of the supracleithrum and proximate ossifications common to *Caenotropus* and *Chilodus*. These modifications, presumably associated with the head-down orientation assumed by chilodontids, decrease the mobility of the upper portion of the pectoral girdle with respect to the skull. *Caenotropus* species demonstrate some additional modifications of the supracleithrum. In these species the dorsal process of the supracleithrum is expanded along the dorsal margin of the reduced posttemporal, increasing the area of contact between those bones (Figure 5, DP-SCL). This extension, not found in *Chilodus* or examined outgroups, is a hypothesized synapomorphy for the members of *Caenotropus* (SYNAPOMORPHY 49).

A second modification of the supracleithrum involves the posterodorsal portion of the bone. In outgroups the ossification is unelaborated dorsally, albeit with some diffuse connective-tissue bands attaching along its posterior margin. *Caenotropus* species have instead a distinct, posteriorly directed process arising from the medial portion of the dorsal section of the supracleithrum (Figure 5, PDP-SCL). This distinct process, which serves as an area of attachment for various ligaments extending posteriorly into the epaxial and hypaxial musculature (Figure 5, CTB), is unique to the genus not only in the Chilodontidae and proximate outgroups but among all examined characiforms (SYNAPOMORPHY 50).

THIRD POSTCLEITHRUM

The third postcleithrum of characiforms is a straight or slightly curved, rod-like bone attached to the medial surface of the second postcleithrum and extending ventral of the latter element within the body wall in most characiforms. This form

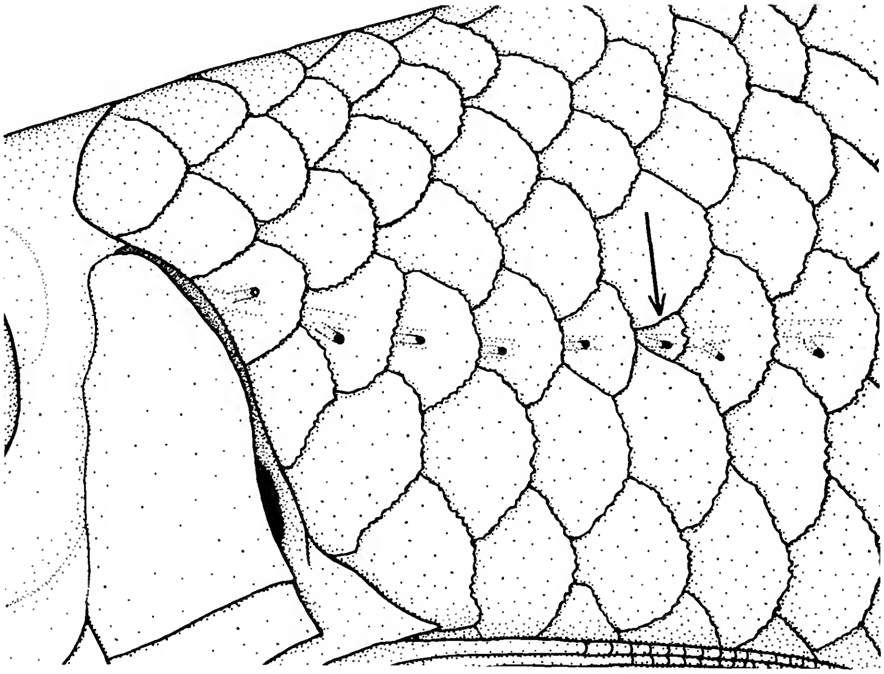

FIGURE 6.—Posterior portion of head and anterior portion of lateral surface of body of *Caenotropus labyrinthicus*, showing smaller sixth lateral-line scale (indicated by arrow) synapomorphic for the Chilodontidae; left side, lateral view.

of postcleithrum 3 is common to all proximate outgroups to the Chilodontidae (Anostomidae, Curimatidae, and Prochilodontidae) and thus is hypothesized to be primitive for the family. In *Caenotropus* the third postcleithrum is modified into a distinctly curved structure that is shifted anteriorly relative to the typical characiform condition, a hypothesized synapomorphy for the genus (SYNAPOMORPHY 51). *Caenotropus maculosus* has the third postcleithrum considerably widened anteroposteriorly (see Vari, 1983, fig. 30, PCL-3), an autapomorphic modification (SYNAPOMORPHY 58).

Chilodus species lack the third postcleithrum, a hypothesized derived condition given the presence of the ossification in proximate outgroups and most characiforms (SYNAPOMORPHY 44). The absence of a third postcleithrum in various other characiforms (see Vari, 1995) is most parsimoniously hypothesized to represent independent losses.

LATEROSENSORY CANAL SYSTEM ON BODY

All scales of the laterosensory canal system are of approximately the same size in most characiforms. *Caenotropus* and *Chilodus* differ from that condition by having the sixth scale of the series distinctly smaller than the rest of the scales in the series (Figure 6) although retaining the pore communicating with the body surface. This highly modified form of the scale, unique within the Characiformes, is a previously unrecognized synapomorphy for the members of the Chilodontidae (SYNAPOMORPHY 36).

Chilodus has the pores in the lateral-line scales extending to or nearly to the last scale in the longitudinal series of the lateral line. If the terminal scale of the lateral-line series is not pored, it nonetheless retains the rotund shape of other lateral-line scales. Such a condition of the terminal pored scale occurs in proximate outgroups to the Chilodontidae and thus is hypothesized to be primitive for the family. All species of *Caenotropus* have the terminal scale developed into a horizontally elongate scale approximately 2 to 3 times as long as wide, a hypothesized derived state characteristic of the genus (SYNAPOMORPHY 52).

Caenotropus labyrinthicus and *C. maculosus* have the laterosensory canal system extended further posteriorly on the caudal fin by an ossified tube that lies immediately posterior to the elongate scale. This ossification, which is tightly joined to the neighboring caudal-fin rays by connective tissue, extends nearly to the end of those rays in larger individuals of each species. Such an elaboration of the laterosensory canal system is not encountered in proximate outgroups to the Chilodontidae or indeed in any examined characiform and thus is hypothesized to be a synapomorphy for *C. labyrinthicus* and *C. maculosus* (SYNAPOMORPHY 56).

PIGMENTATION

Caenotropus labyrinthicus has a variably apparent rotund or somewhat horizontally elongate blotch of dark pigmentation within the midlateral band of dusky to dark pigmentation on the body. Such a spot is unknown in *Chilodus* or the two other *Caenotropus* species (*maculosus*, *mestomorgmatos*) and thus is hypothesized to be an autapomorphy for *C. labyrinthicus* (SYNAPOMORPHY 60).

The distal portions of the dorsal fin are typically darkly pigmented in all *Chilodus* species (Isbrücker and Nijssen, 1988, figs. 1, 4, 5), with a similar pattern in *Caenotropus maculosus* (Figures 13, 14). The remaining *Caenotropus* species (*mestomorgmatos* and *labyrinthicus*) have modifications of this generalized and presumably primitive dorsal-fin pigmentation for chilodontids. In *Caenotropus labyrinthicus* the dorsal-fin pigmentation is reduced completely or remains, at most, as a residual faint dusky region (SYNAPOMORPHY 61). *Caenotropus mestomorgmatos*, in contrast, has the region of dark pigmentation expanded into a broad region covering most of the dorsal fin other than portions of the posterior rays (Figure 10), a derived pigmentation unique in the family (SYNAPOMORPHY 53).

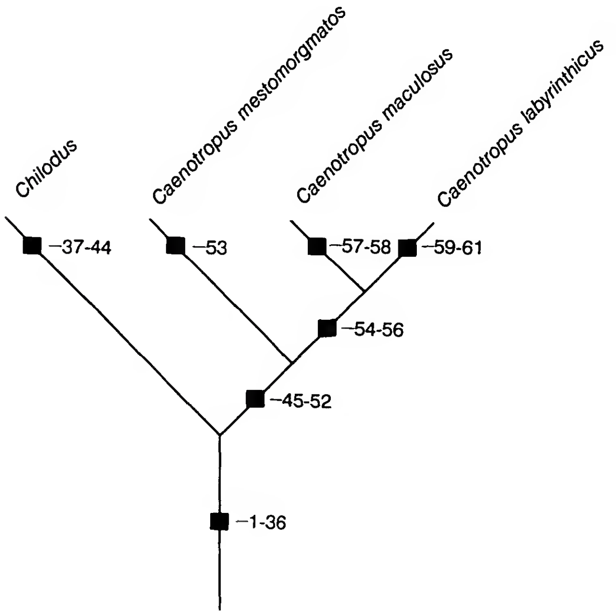

FIGURE 7.—Cladogram of the most-parsimonious hypothesis of phylogenetic relationships of *Caenotropus* and *Chilodus* and within *Caenotropus*. Numbered synapomorphies correspond to those of text.

Synapomorphy List and Phylogenetic Reconstruction

FIGURE 7

Vari (1983:51–52) described an extensive series of derived modifications, largely of the gill-arches, suspensorium, pectoral girdle, and anterior portions of the vertebral column, that define the Chilodontidae as a monophyletic lineage. These features are summarized (synapomorphies 1–26), and the reader is referred to that publication for a more detailed description and analysis of the features and a discussion of the generalized conditions in outgroups.

MONOPHYLY OF THE CHILODONTIDAE

1. The reduced relative size of the premaxilla.
2. The expanded relative size and thickness of the maxilla.
3. The ossified supramaxilla located along the posterodorsal margin of the maxilla.
4. The anteroventral expansion of the mesethmoid into an angled process that extends between the premaxillae.
5. The three cusps on all pharyngeal teeth.
6. The presence of posteroventral expansion of the fourth ceratobranchial into a broad, curved surface.
7. The expansion of the anterior portions of the fifth ceratobranchial into a cup-shaped plate.
8. The rotation anteriorly of the tooth-bearing portion of the fifth ceratobranchial.
9. The ridges on the dorsal surface of the first, second, and third ceratobranchials.
10. The reorientation posteriorly of the fifth upper pharyngeal tooth plate.
11. The pronounced posterior expansion of the third infrapharyngobranchial's posterior portion.
12. The ridges on the ventral surfaces of the first, second, and third epibranchials.
13. The posterior rotation of the ventral portion of the fourth epibranchial.
14. The lateral and dorsal expansion of the cartilaginous fifth epibranchial to form the major portion of the epibranchial organ's anterior wall.
15. The shell-shaped connective tissue sheet that extends dorsal to the fifth ceratobranchial and forms the posterior wall of the epibranchial organ.
16. The distinct ridges on the soft tissue layer that covers the adjoining surfaces of the fourth and fifth ceratobranchials.
17. The distinct band-like muscle on the anterior and posterior surfaces of the epibranchial organ.
18. The laterally thickened anterior and posterior ceratohyals with pronounced ridges on their lateral surfaces.
19. The complex shape and thickening of the interhyal and the attachment of the ligament that extends to the metapterygoid and quadrate to a discrete medial process of the interhyal.

20. The ventral expansion of the main shaft of the supracleithrum.
21. The elimination of the ventral process and laterosensory canal-bearing portion of the posttemporal and the anterior section of the extrascapular.
22. The direct articulation of the dorsal tip of the extrascapular with the pterotic.
23. The expansion of the posteroventral spine of the pterotic into a flat articular surface that contacts a corresponding supracleithral process.
24. The absence of the first postcleithrum.
25. The dorsal expansion of the proximal portions of the first three full pleural ribs.
26. The vertical expansion of the parapophyses and articular fossae associated with the first three full pleural ribs.

The following 10 additional synapomorphies for the Chilodontidae were discovered during this study:

27. The overlap of the anterodorsal portion of the third infraorbital by the posterodorsal portion of the second infraorbital.
28. The reduction of the posterior portion of the supraorbital laterosensory canal in the frontal.
29. The small teeth imbedded in the fleshy coverings of the upper and lower jaws but not attached to the jaw bones.
30. The vertically expanded canal system in the dorsal portion of the angulo-articular.
31. The canal system along the dorsal margin of the dentary.
32. The anterodorsally directed process at the anteromedial region of contact of the dorsal and ventral hypohyals.
33. The interdigitations between the dorsal hypohyal and the anterior ceratohyal.
34. The relatively large, triangular, ventral process of the mesopterygoid extending ventrally along the medial surface of the quadrate.
35. The anterior extension of the metapterygoid into the notch on the posterior margin of the quadrate resulting in the pronounced reduction or elimination of the mesopterygoid-quadrate fenestra.
36. The pronounced reduction in the relative size of the sixth lateral-line scale.

MONOPHYLY OF *Chilodus*

The following eight synapomorphies for the species of *Chilodus* were identified during this study:

37. The posterior shift of the dorsal portion of the fourth infraorbital and ventral portion of the fifth infraorbital.
38. The pronounced reduction of the posterior portion of the supraorbital laterosensory canal segment in the frontal.
39. The vertically expanded anterior portion of the dentary and the associated posterodorsally angled ridge on the anterolateral surface of the bone.
40. The lateral expansion of the posterior portion of the angulo-articular and the distinct depression on the lateral surface of the angulo-articular and dentary.
41. The very well-developed canal system along the dorsal margin of the dentary.
42. The very well-developed anterodorsally directed process at the anteromedial margin of the dorsal and ventral hypohyals.
43. The interdigitating joint along the anterior portions of the dorsal and ventral hypohyals.
44. The absence of the third postcleithrum.

Chilodus was revised recently by Isbrücker and Nijssen (1988), and the reader is referred to that publication for detailed information on the genus.

MONOPHYLY OF *Caenotropus*

The following eight synapomorphies for the species of *Caenotropus* have been identified:

45. The reduction of the sixth infraorbital to an ossified tube that surrounds the associated laterosensory canal.
46. The well-developed processes on the lateral surfaces of the pterotic anterodorsal to the pterotic articular process.
47. The very well-developed canal system in the middle and dorsal portions of the angulo-articular.
48. The pronounced development of the anterior process of the metapterygoid resulting in the elimination of the metapterygoid-quadrate fenestra, and the development of an interdigitating joint between the anterior metapterygoid process and the proximate portion of the quadrate.
49. The dorsal extension of the supracleithrum along the posterior margin of the posttemporal.
50. The posteriorly directed process that arises from the posteromedial surface of the dorsal portion of the supracleithrum.
51. The curved, anteriorly shifted third postcleithrum.
52. The horizontal elongation of the terminal scale of the lateral-line series.

INTRAGENERIC RELATIONSHIPS IN *Caenotropus*

Discovered synapomorphies define two primary monophyletic subunits of *Caenotropus*, one consisting of *C. mestomorgmatos* and the second of *C. maculosus* and *C. labyrinthicus*.

Caenotropus mestomorgmatos is characterized by one known autapomorphy:

53. The broad region of dusky pigmentation across most of the dorsal fin.

The clade consisting of *C. maculosus* and *C. labyrinthicus* is defined by three synapomorphies:

54. The posterior extension of the subopercle into a distinct process extending posterior of the limit of the opercle.
55. The well-developed interdigitating joint between the anterior process of the metapterygoid and the quadrate.
56. The ossified laterosensory tube between the middle caudal-fin rays posterior of the elongate terminal scale of the lateral line.

The following two autapomorphies for *Caenotropus maculosus* were identified during this study:

57. The elaborate interdigitating joint between the quadrate and the anterior process of the metapterygoid.
58. The expansion of the curved, anteriorly shifted third postcleithrum.

Caenotropus labyrinthicus is characterized by three autapomorphies:

59. The absence of teeth in the lower jaw.
60. The spot of dark pigmentation within the midlateral stripe on the body.
61. The reduction of the dark pigmentation in the dorsal fin.

Family CHILODONTIDAE

Chilodontids are characterized by numerous derived modifications of diverse body systems (synapomorphies 1-36 under "Synapomorphy List and Phylogenetic Reconstruction" above). The distinctive small sixth lateral-line scale (Figure 6) is one of the most readily recognizable external synapomorphies. That feature, the overall head and body shape, and the feeble, typically brown-tipped dentition in one or both jaws of chilodontids serve to readily diagnose them from other characiforms. *Caenotropus* and *Chilodus* are limited to some drainages east of the Andean Cordilleras (see Figures 11 and 20, and Isbrücker and Nijssen (1988, fig. 3)). The two genera of the family can be distinguished by the following key. *Chilodus* recently was revised by Isbrücker and Nijssen (1988) who provide a key to the species of the genus.

Key to *Caenotropus* Günther and *Chilodus* Müller and Troschel

Branched anal-fin rays typically 10 or 11, rarely 9; anal-fin margin convex or straight; mouth terminal or slightly superior; dorsal fin with series of dark spots on posterior rays; posterior margin of scales smooth . . . . ***Chilodus***

Branched anal-fin rays 6 to 8; anal-fin margin somewhat concave in vast majority of specimens; mouth subterminal; dorsal fin with dark pigmentation across distal portions of anterior rays but lacking dark spots on remaining portions of fin; posterior margin of scales somewhat serrate . . . . ***Caenotropus***

Genus *Caenotropus* Günther, 1864

Caenotropus Günther, 1864:297 [type species: *Microdus labyrinthicus* Kner, 1858, type by being a replacement name for *Microdus* Kner, 1858:77, which was preoccupied in Hymenoptera by Nees and in fossil fishes by Emmons; gender masculine].—International Commission on Zoological Nomenclature, 1980:72-74 [placed on the Official List].

Caenotropis.—Boulenger, 1904:576 [error; cited as Boulenger, 1910, by Travassos, 1951].

Tylobronchus Eigenmann, 1912:271 [type species: *Tylobronchus maculosus* Eigenmann, 1912, by monotypy; gender masculine].—Géry, 1964:8 [placed as a synonym of *Caenotropus*].

Tylobranchus.—Travassos, 1952:246 [error].

DIAGNOSIS.—*Caenotropus* is diagnosed by synapomorphies 45-52 (see "Synapomorphy List and Phylogenetic Reconstruction" above). Within the Chilodontidae the genus is further distinguished by the presence of somewhat serrate scale margins in adults and a moderately developed lower lip. Upper and lower pharyngeal dentition is enlarged and tricuspidate (see Vari, 1983, fig. 11B).

DISTRIBUTION.—Río Orinoco, Río Amazonas, Rio Parnaíba of northeastern Brazil, and coastal drainages of the Guianas from the Essequibo River basin of Guyana through Suriname to the Fleuve Maroni system of western French Guiana.

REMARKS.—Some confusion existed concerning the correct type species of *Caenotropus* (see Géry and Hoedeman (1962:191-192) and references cited therein). The International Commission on Zoological Nomenclature resolved the question by placing *Caenotropus* on the Official List, with its type species confirmed as *Microdus labyrinthicus* (through *Microdus*) (opinion 1150, 1980:72-74).

Eigenmann's (1912:271) description of *Tylobronchus* discriminated it from *Caenotropus* "in having teeth in the lower as well as in the upper jaw." Géry (1964:8) placed *Tylobronchus* into the synonymy of *Caenotropus* because the genera were "scarcely separable" given the variability he reported in the presence or absence of lower-jaw dentition in the two genera. Our examination of an extensive series of specimens, however, indicates that the presence or absence of teeth distinguishes the genera as then constituted. Nevertheless, some large specimens of *C. mestomorgmatos*, a species described in this paper, lack lower-jaw teeth contrary to the presence of such dentition in the vast majority of specimens. This variability in *C. mestomorgmatos* renders the primary cited difference between

Caenotropus and *Tylobronchus* equivocal. The other differences between the nominal species assigned to *Caenotropus* and *Tylobronchus* by Eigenmann (1912) involve relatively minor details of pigmentation, meristics, and morphometrics. Furthermore, the retention of both genera could be achieved only by proposing a new genus for *mestomorgmatos* in order for all genera to be monophyletic. Given the lack of any advantage in recognizing three genera in a monophyletic lineage of three species, we follow Géry (1964) and consider *Tylobronchus* a junior synonym of *Caenotropus*.

Key to the Species of *Caenotropus* Günther

1. Scales above lateral line to base of dorsal fin 3; interorbital width 0.44–0.48 of HL in specimens over 35 mm HL [Figure 8] . . . . . ***C. mestomorgmatos*, new species**
(middle and upper portions of Rio Negro in Brazil and
Venezuela and upper portions of Río Orinoco in Venezuela)

Scales above lateral line to base of dorsal fin 4; interorbital width 0.27–0.44 of HL in *C. labyrinthicus* specimens over 35 mm HL [Figure 8] 2

2. Lateral-line scales, not including terminal elongate scale, typically 27, rarely 28; most individuals with teeth in lower jaw; distal portions of anterior dorsal-fin rays with distinct patch of dark pigmentation; distinct midlateral stripe extending from snout to base of caudal fin . . . . ***C. maculosus***
(Essequibo River basin of Guyana and Venezuela,
Corantijn River in western Suriname and Marowijne River
(Fleuve Maroni) basin in eastern Suriname and French Guiana)

Lateral-line scales, not including terminal elongate scale, 28 to 32, typically 29 or 30, 28 in only approximately 1% of examined specimens; teeth absent in lower jaw; distal portions of anterior dorsal-fin rays sometimes dusky but not with distinct patch of dark pigmentation; diffuse midlateral stripe extending from snout to base of caudal fin, most often with rotund dark blotch along stripe slightly anterior of vertical through origin of dorsal fin . . . . ***C. labyrinthicus***
(Rio Amazonas and Río Orinoco basins, upper portions
of Rupununi River in Guyana, Suriname and Saramacca rivers
of Suriname, and Rio Parnaíba, Estado do Piauí, northeastern Brazil)

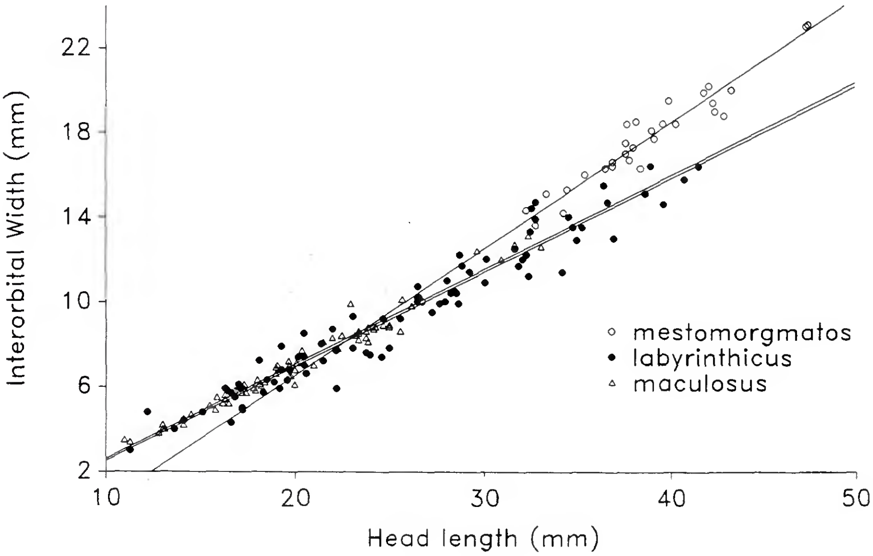

FIGURE 8.—Plot of interorbital width versus head length and associated regression lines for the species of *Caenotropus*. Regression lines for *C. labyrinthicus* and *C. maculosus* are nearly identical. Some symbols represent more than one specimen.

Caenotropus mestomorgmatos, new species

FIGURES 8–11, TABLES 1–3

DIAGNOSIS.—The presence of 3 scales above the lateral line to the dorsal-fin base is unique to *Caenotropus mestomorgmatos* in the genus. The diffuse dusky pigmentation across the anterior rays and basal portions of the middle dorsal-fin rays and the 28 to 30 lateral-line scales in *C. mestomorgmatos* further separates it from *C. maculosus*, which has a distinct patch of very dark pigmentation on the distal portions of the anterior dorsal-fin rays and 27 or very rarely 28 lateral-line scales (Table 1). The presence of lower-jaw dentition in all but a few of the largest specimens and 6 to 8, typically 6 or 7, postdorsal scales to the adipose fin (Table 2) in *C. mestomorgmatos* further differentiates it from *C. labyrinthicus*, which invariably lacks such dentition and has 8 to 11, usually 9 or 10, postdorsal scales. The two species are further distinguished by the relatively wide head in individuals of *C. mestomorgmatos* with head lengths greater than approximately 35 mm SL, as reflected in the interorbital width (0.44–0.48 of HL versus 0.27–0.44 of HL in *C. labyrinthicus;* see Figure 8).

DESCRIPTION.—*Caenotropus mestomorgmatos* achieves 163 mm SL. Meristics and morphometric values for the holotype and the paratype series are presented in Table 3.

Body relatively robust, somewhat variable between and within populations. Greatest body depth at dorsal-fin origin. Dorsal profile of head distinctly convex anteriorly, nearly straight from dorsal margin of upper-lip fold to tip of supraoccipital spine. Dorsal profile of body convex from supraoccipital to dorsal-fin origin, more so in larger individuals. Dorsal profile of body straight to slightly convex and distinctly posteroventrally slanted along dorsal-fin base. Overall profile of body from supraoccipital to posterior terminus of dorsal fin a distinct hump. Dorsal profile of body from dorsal fin to adipose fin somewhat concave in juveniles (Figure 9), straight to slightly convex in large individuals (Figure 10). Dorsal surface of body with transversely obtuse middorsal ridge extending 3 to 5 scales anterior to dorsal fin, ridge proportionally more elongate in smaller specimens. Dorsal surface of body smoothly rounded transversely posterior to fin. Ventral profile of body nearly regularly convex from tip of lower jaw to caudal peduncle. Prepelvic region of body transversely flattened with transversely obtuse lateral angles and median series of scales. Postpelvic region of body in larger individuals with transversely obtuse midventral ridge extending posteriorly to anus and obtuse secondary ridge extending along horizontal scale row immediately dorsal to midventral series.

Dorsal fin iii(rare)–iv, 9–10 (9 rays, n = 1; 10 rays, n = 28); distal dorsal-fin margin nearly straight; anterior rays approximately 3.0–3.5 times length of ultimate ray. Anal fin ii,7–8 (7 rays, n = 1; 8 rays, n = 36); slightly emarginate distally; anterior branched rays approximately 3 times length of ultimate ray. Pectoral fin i,13–14,i; profile asymmetrically pointed with third ray from dorsal margin typically longest; fin extending posteriorly distinctly beyond vertical through pelvic-fin insertion. Pelvic fin i,8; distal margin somewhat convex with first branched ray the longest; fin reaches posteriorly one-half to two-thirds of distance to anus. Caudal fin forked with upper lobe somewhat longer in many individuals, otherwise of equal length. Adipose fin well developed.

TABLE 1.—Number of specimens of the species of *Caenotropus* with listed number of lateral-line scales. Counts of lateral-line scales in *C. labyrinthicus* and *C. maculosus* do not include tubular terminal ossification along the middle rays of the caudal fin.

Species	Lateral-line scales					
	27	28	29	30	31	32
mestomorgmatos		16	13	1		
labyrinthicus		3	142	103	20	3
maculosus	87	2				

TABLE 2.—Number of specimens of the species of *Caenotropus* with listed number of postdorsal scales.

Species	Postdorsal scales					
	6	7	8	9	10	11
mestomorgmatos	16	11	4			
labyrinthicus			23	185	67	2
maculosus		3	88	7		

Head profile distinctly rounded anteriorly, somewhat pointed overall; upper jaw fleshy and slightly longer than lower jaw; anterior portion of lower jaw somewhat fleshy; mouth barely inferior; maxilla extending posteriorly slightly beyond vertical through posterior nostril; nostrils of each side proximate; adipose eyelid well developed, more so in larger specimens, with rotund opening over center of eye. Posterior margin of opercle and subopercle gently curved. Teeth typically present in each jaw, sometimes reduced to a few teeth or very rarely absent in lower jaw.

All lateral-line scales pored, canals straight. Arrangement and relative sizes of anterior lateral-line scales somewhat irregular with sixth scale distinctly smaller. Last lateral-line scale tubular, exposed portion of that scale approximately 2.5 times as long as wide.

VERTEBRAE.—30 (1), 31 (31), 32 (8).

COLOR IN LIFE (based on color transparency of specimen collected in upper Río Negro; USNM 270236).—Overall coloration of head and body bright silver with some indication of several horizontal series of dark spots along body. Dorsal fin darkly pigmented other than on distal portions of posterior fin-rays. Other fins hyaline or slightly yellow.

COLOR IN ALCOHOL.—All available specimens lacking guanine on scales. Ground coloration tan. Anterior and dorsal portions of fleshy upper lip, dorsal surface of head, and dorsal portion of opercle darkly pigmented. Opercle sometimes with

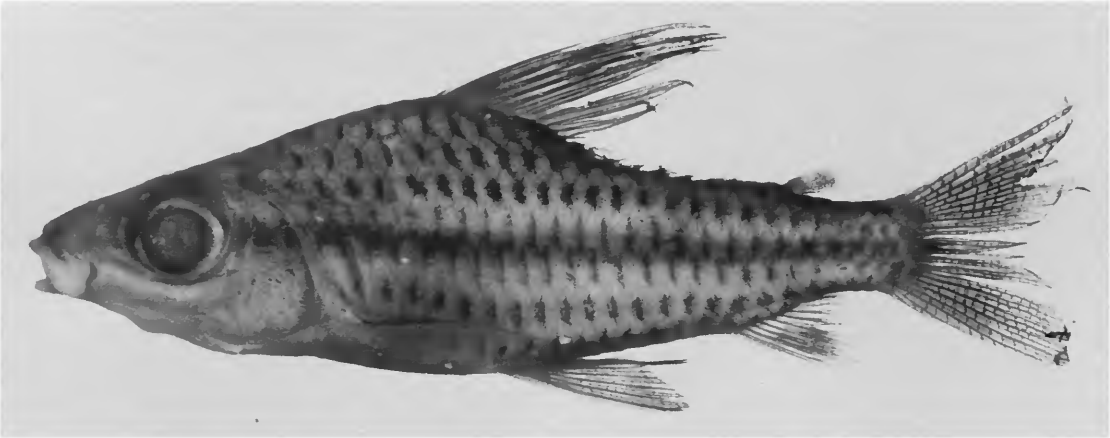

FIGURE 9.—*Caenotropus mestomorgmatos*, new species, juvenile, USNM 270238, 54.4 mm SL; Venezuela, Amazonas, Río Negro, San Carlos de Río Negro, margin of river at town landing.

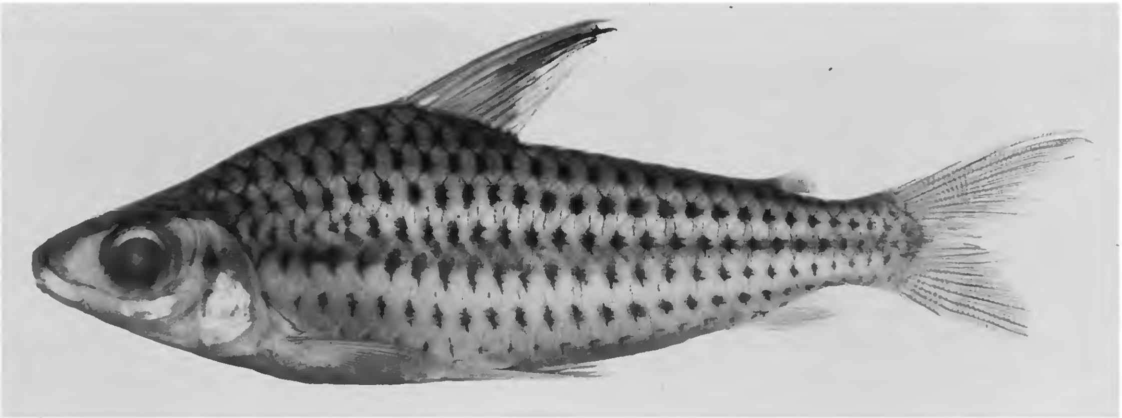

FIGURE 10.—*Caenotropus mestomorgmatos*, new species, holotype, MBUCV V-21750, 128 mm SL; Venezuela, Amazonas, Río Iguapo (tributary of Río Orinoco), ~1 hr. above its mouth (3°09'N, 65°28'W).

patch of dark pigmentation posterior to orbit, particularly in smaller individuals. Ventral portions of upper lip, opercle, and head tan. Body with diffuse midlateral stripe most obvious in smaller individuals in which it is continuous with patch of dark pigmentation posterior to opercle. Body stripe relatively less developed posteriorly at all ages. Seven horizontal series of somewhat diffuse dark patches along body. Each dark patch situated in region of overlap of successive scales in horizontal series. Patches of dark pigmentation dorsal of lateral-line series more obvious in all sizes than those ventral of line, those proximate to midlateral stripe variably masked by dark pigmentation of stripe.

Dorsal fin with broad patch of dark pigmentation on membranes of unbranched and first to fifth branched rays and basal portions of posterior fin membranes. All dorsal-fin rays outlined by series of small chromatophores. Adipose fin variably dusky. Rays of caudal, anal, and paired fins variably outlined by small dark chromatophores.

ETYMOLOGY.—The specific name, *mestomorgmatos*, is from the Greek *mestos*, full, and *omorgmatos*, spotted, in reference to the numerous spots of dark pigmentation on the body of the species.

DISTRIBUTION.—Upper portions of the Río Orinoco in Venezuela and the upper portions of the Río Negro in

TABLE 3.—Morphometrics and meristics of (A) holotype of *Caenotropus mestomorgmatos*, MBUCV V-21750, and (B) paratypes (n = 32) of *C. mestomorgmatos*. Means for morphometric values ($\bar{x}$) are based on values for holotype and paratypes. Standard length is expressed in mm; measurements 1 to 10 are proportions of standard length; 11 to 15 are proportions of head length.

Character	A	B	$\bar{x}$
		Morphometrics	
Standard Length	127.9	83.0–163	-
1. Greatest body depth	0.35	0.31–0.35	0.326
2. Snout to dorsal-fin origin	0.46	0.44–0.49	0.463
3. Snout to anal-fin origin	0.83	0.80–0.85	0.818
4. Snout to pelvic-fin origin	0.51	0.48–0.52	0.502
5. Origin of rayed dorsal fin to hypural joint	0.60	0.58–0.62	0.605
6. Pectoral-fin length	0.21	0.18–0.22	0.205
7. Pelvic-fin length	0.21	0.20–0.23	0.208
8. Caudal peduncle depth	0.10	0.10–0.11	0.103
9. Origin of dorsal fin to origin of adipose fin	0.30	0.28–0.33	0.301
10. Head length	0.29	0.28–0.31	0.294
11. Snout length	0.38	0.35–0.42	0.380
12. Orbital diameter	0.32	0.30–0.35	0.319
13. Postorbital length	0.39	0.35–0.39	0.369
14. Gape width	0.19	0.18–0.22	0.196
15. Interorbital width	0.48	0.44–0.48	0.449
		Meristics	
Lateral-line scales	29	28–30	
Scale rows between dorsal-fin origin and lateral line	3	3	
Scale rows between anal-fin origin and lateral line	3	3	
Predorsal median scales	6	6–7[a]	
Postdorsal median scales	6	6–8	
Branched dorsal-fin rays	10	9–10[b]	
Branched anal-fin rays	7	7–8[c]	
Branched pectoral-fin rays	14	13–14	
Branched pelvic-fin rays	8	8	
Caudal-fin rays	17	17	

[a] 7 predorsal scales in only 3 specimens.
[b] 9 branched dorsal-fin rays in only 1 specimen.
[c] 8 branched anal-fin rays in only 1 specimen.

Venezuela and Brazil downstream to below the mouth of the Rio Daraá (Figure 11). Extensive collections of *Caenotropus* specimens from throughout the Brazilian portions of the Rio Negro below São Gabriel da Cachoeira (=Vaupes) by Michael Goulding (Goulding et al., 1988, fig. 1.1) consisted of *Caenotropus labyrinthicus* with the exception of a single specimen of *C. mestomorgmatos* collected just below the mouth of the Rio Daraá in the middle portion of that basin.

ECOLOGY.—The type locality is a clear black-water stream with a white sand bottom and strong current. Specimens from the upper Río Negro were collected in acidic black waters both along the swift main river channel margin (USNM 270238, AMNH 74679) and the still waters of a tributary caño (USNM 270236).

REMARKS.—The known distribution of *Caenotropus mestomorgmatos* is completely overlapped by that of *C. labyrinthicus*, and the species have been captured together in a number of localities in both the upper Río Negro (e.g., AMNH 74679 and 79496, SU 59205 and 69694) and the upper Río Orinoco (e.g., SU 59310 and 69695).

TYPE MATERIAL EXAMINED.—33 specimens (83.0–163 mm SL).

HOLOTYPE.—VENEZUELA. *Amazonas:* Río Orinoco basin, Río Iguapo (tributary of Río Orinoco), ~1 hr. above its mouth (3°09'N, 65°28'W), H. Lopez et al., 13 Mar 1987; MBUCV V-21750, 128 mm SL.

PARATYPES.—VENEZUELA. *Amazonas:* 26 specimens taken with holotype: MBUCV V-21751, 7 (104–148); ANSP 162764, 7 (112–157); USNM 322557, 6 (108–163); BMNH 1991.11.15:1-3, 3 (124–138); and MZUSP 43285, 3 (133–147). Departamento Río Negro, small caño off Caño Urami (left bank tributary of Río Negro), just upriver of Santa Lucia (1°17'N, 66°51'W), R.P. Vari et al., USNM 270236, 1 (121). Río Negro at Santa Lucia (1°16'N, 66°51'W), C.J. Ferraris et al., AMNH 74679, 2 (128–131). Río Negro at San Carlos de Río Negro (1°55′N, 67°03′W), L.G. Nico, MCNG 12104, 1 (83.0). Laguna del Río Mavaca (~02°26′30″N, 65°06′15″W), MCNG 25319, 1 (158).

BRAZIL. *Amazonas:* Rio Negro, just below Rio Daraá (0°25′S, 64°47′W), MZUSP 29359, 1 (88.7).

NONTYPE MATERIAL EXAMINED.—88 specimens (7, 49.5–130 mm SL).

VENEZUELA. *Amazonas:* Río Negro between Cucuí, Amazonas, Brazil and San Carlos de Río Negro, Amazonas, Venezuela, SU 59253, 2 (113–130). Río Negro, San Carlos de Río Negro, margin of river at town landing (1°55′N, 67°03′W), USNM 270238, 2 (49.5–54.4). Río Negro, "one day canoeing up or N from Amanadona" (according to C. Ternetz' itinerary this locality is apparently in the Venezuelan portion of the Río Negro south of the mouth of Río Casiquiare), SU 59254, 1 (129). Río Atabapo, at San Fernando de Atabapo (4°03′N, 67°42′W), SU 59310, 1 (75.1). Río Iguapo (tributary of Río Orinoco), ~1 hr. above its mouth (3°09′N, 65°28′W), ANSP 168882, 73; ANSP 161389, 2 (both lots taken with holotype). Río Siapa, ~176 km above its mouth in the Río Casiquiare, MCNG 26078, 5. *Apure:* Río Orinoco basin, Laguna Larga (6°33.32′N, 67°24.81′W), INHS 27975, 1.

BRAZIL. *Amazonas:* São Gabriel da Cachoeira (= Uuapes), SU 59205, 1 (77.3).

***Caenotropus maculosus* (Eigenmann, 1912)**

FIGURES 8, 12–14, TABLES 1, 2, 4

Tylobronchus maculosus Eigenmann, 1912:272, pl. XXXV, fig. 3 [type locality: British Guiana (= Guyana): creek below Potaro Landing].—Fowler, 1975:107 [literature compilation].

Tylobranchus maculosos.—Travassos, 1952:246 [literature compilation; species and genus names misspelled].

Caenotropus maculosus.—Géry, 1964:66, fig. 5 [British Guiana (= Guyana): Essequibo and Rupununi Rivers; French Guiana: Maroni River]; Géry, 1977:211, unnumbered fig. [Guianas].

Coenotropus maculosus.—Géry and Planquette, 1982:76 [French Guiana; ? based on Géry, 1964]; 1983:65 [French Guiana: Saut Singatétéi].

DIAGNOSIS.—The discrete patch of dark pigmentation on the distal portions of the anterior rays of the dorsal fin discriminates *Caenotropus maculosus* from congeners, which have limited dusky pigmentation in that region (*C. labyrinthicus*) or pigmentation extending over the entire anterior rays and basal portions of the middle dorsal-fin rays (*C. mestomorgmatos*).

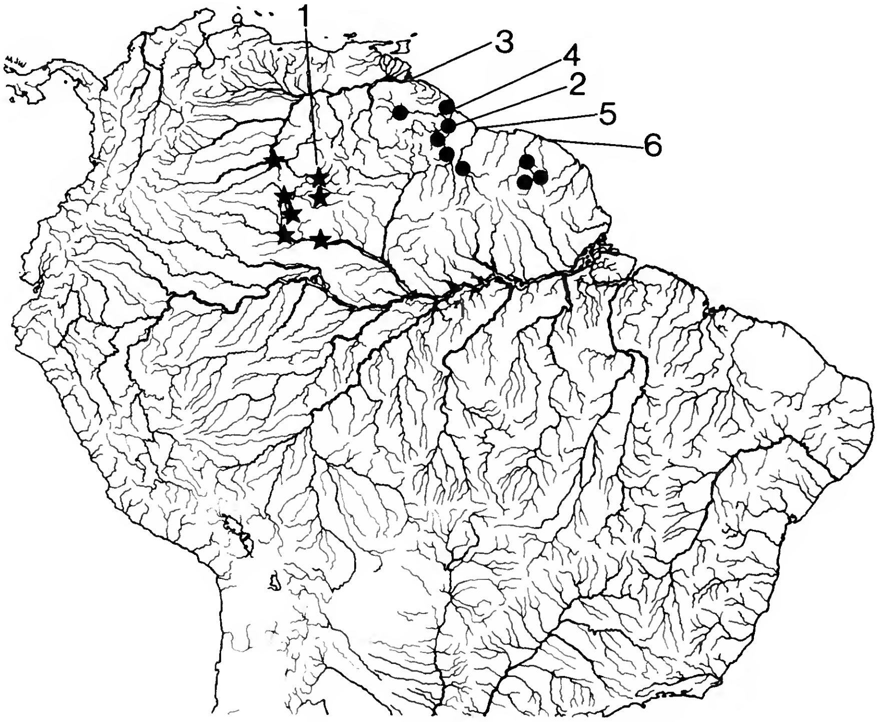

FIGURE 11.—Map of central and northern South America showing geographic distribution of *Caenotropus mestomorgmatos* (stars; 1 = type locality) and *Caenotropus maculosus* (filled-in circles; 2 = type locality; 3 = Río Orinoco; 4 = Essequibo River; 5 = Corantijn River; 6 = Marowijne River or Fleuve Maroni). Some symbols represent more than one locality or lot of specimens.

FIGURE 12.—*Caenotropus maculosus*, FMNH 53449 (formerly CM 1923), 84.2 mm SL; holotype of *Tylobronchus maculosus;* Guyana, Mazaruni-Potaro, creek below Potaro Landing, Potaro River.

Caenotropus maculosus differs from *C. labyrinthicus* in lateral-line scale number (27 or, rarely, 28 versus 28 to 32, typically 29 or 30, respectively; Table 1) and in having at least some lower-jaw teeth in all examined specimens contrary to the lack of such dentition in *C. labyrinthicus. Caenotropus maculosus* can be discriminated from *C. mestomorgmatos* based on the number of scales above the lateral line (4 versus 3, respectively), number of lateral-line scales (27 or, rarely, 28 versus 28 to 30, respectively), and body pigmentation (a distinct midlateral stripe versus a diffuse streak in that region, respectively).

DESCRIPTION.—*Caenotropus maculosus* (Figure 12) is the smallest species in the genus, with the largest known specimen achieving 108 mm SL. Meristic and morphometric values for the holotype and other specimens examined are presented in Table 4.

Body moderately elongate, somewhat more so in smaller individuals. Greatest body depth at dorsal-fin origin. Dorsal profile of head distinctly convex anteriorly, slightly convex from dorsal margin of upper-lip fold to tip of supraoccipital spine. Dorsal profile of body convex from supraoccipital to dorsal-fin origin, degree of convexity not noticeably more pronounced in larger individuals; 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 with obtuse middorsal ridge extending 3 to 5 scales anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body smoothly convex from tip of lower jaw to caudal peduncle. Prepelvic region flattened with transversely obtuse lateral angles and median series of scales. Postpelvic region in larger individuals with obtuse midventral ridge extending posteriorly to anus and barely apparent secondary ridge extending along horizontal scale row immediately dorsal to midventral series.

Dorsal fin iv,10; distal margin straight or slightly convex anteriorly, distinctly convex posteriorly; anterior rays approximately 2.0–2.5 times length of ultimate ray. Anal fin ii,7; emarginate distally, anterior branched rays approximately 2.75–3.25 times length of ultimate ray. Pectoral fin i,12–14,i–ii; asymmetrically pointed, with second to fourth rays longest; extends posteriorly nearly to or somewhat beyond vertical line through pelvic-fin insertion. Pelvic fin i,8; distal margin moderately convex with first branched ray longest; fin reaches posteriorly slightly over one-half to approximately two-thirds of distance to anal fin. Caudal fin forked. Adipose fin well developed.

Head profile distinctly rounded anteriorly but somewhat pointed overall; upper jaw fleshy and barely longer than lower jaw, anterior portion of lower jaw somewhat fleshy; mouth barely inferior; maxilla extending posteriorly slightly beyond vertical through posterior nostril; nostrils proximate; adipose eyelid barely apparent in smaller individuals, moderately developed in larger individuals, with rotund opening over center of eye. Posterior margin of opercle somewhat concave dorsal of subopercle. Posterior margin of subopercle with pointed posterior extension in midsize to large individuals. Small, brown-tipped teeth set in soft tissues of both jaws; often reduced to 1 or 2 teeth in lower jaw.

All lateral-line scales pored, canals straight. Arrangement and relative sizes of anterior lateral-line scales somewhat irregular, with sixth scale distinctly smaller. Last lateral-line scale tubular.

VERTEBRAE.—31 (65), 32 (1).

COLOR IN LIFE.—Géry (1964, fig. 5) shows what is apparently *Caenotropus maculosus* in an aquarium. Overall coloration of head and body bright silver, darker along tip of head and dorsal portions of body. Distinct dark stripe extending from snout to anterior margin of orbit and from rear of orbit across opercle and midlateral surface of body onto middle rays of caudal fin. Dark pigmentation on body scales and fins as described for alcohol-preserved specimens.

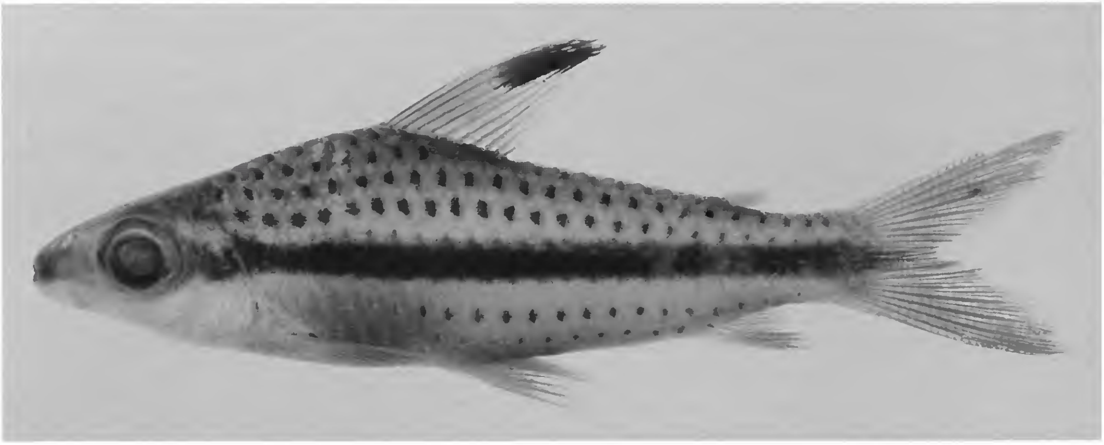

FIGURE 13.—*Caenotropus maculosus*, ZMA 119.706, 58.3 mm SL; French Guiana, Fleuve Maroni basin, Fleuve Marowini at first rapid.

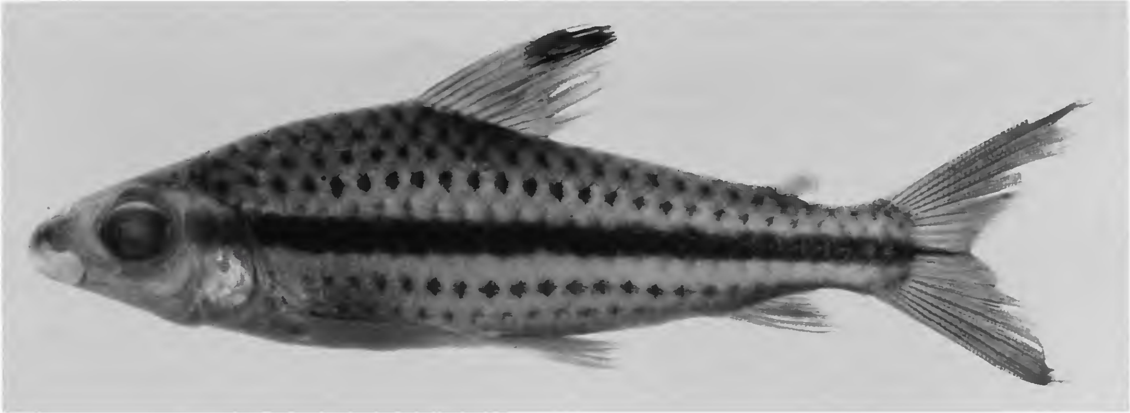

FIGURE 14.—*Caenotropus maculosus*, UMMZ 215797, 104 mm SL; Guyana, Mazaruni-Potaro, Potaro River at boat landing, Kangaruma.

COLOR IN ALCOHOL.—Specimens retaining some guanine on scales with silvery sheen masking dark pigmentation pattern on ventral portions of body. Specimens lacking guanine on scales with tan ground coloration, typically lighter in smaller individuals; relatively darker on dorsal portions of head and body. Head with faint to pronounced horizontal stripe running from tip of snout across upper lip and lateral surface of preorbital portion of head to anterior margin of eye. Second stripe running at same horizontal level from rear of eye to rear of opercle. Head dusky to dark dorsally. Body with faint to dark midlateral stripe running from rear of stripe on postorbital portion of head to caudal peduncle and across middle caudal-fin rays. Stripe about one scale wide. Horizontal scale rows ventral and dorsal of midlateral stripe with spot of dark pigmentation on surface where scale overlapped by immediately anterior scale. Spots of pigmentation more pronounced dorsal of midlateral stripe in smaller individuals (Figure 13); spots of first scale row ventral of midlateral stripe relatively more developed in largest individuals (Figure 14).

Dorsal fin with patch of dark pigmentation on distal portions and membranes of second unbranched and anterior three or four branched rays. Basal portions of those and posterior rays variably dusky. Distal portions of posterior unbranched rays less pigmented than basal portions of rays. Caudal- and anal-fin

TABLE 4.—Morphometrics and meristics of (A) holotype of *Caenotropus maculosus*, FMNH 53449, formerly CM 1923, and (B) all specimens of *C. maculosus* from which counts and measurements were taken. Means for morphometric values ($\bar{x}$) are based on values for holotype and all other specimens. Standard length is expressed in mm; measurements 1 to 10 are proportions of standard length; 11 to 15 are proportions of head length.

Character	A	B	$\bar{x}$
		Morphometrics	
Standard Length	84.2	32.3–108.4	-
1. Greatest body depth	0.30	0.26–0.32	0.286
2. Snout to dorsal-fin origin	0.48	0.45–0.50	0.474
3. Snout to anal-fin origin	0.83	0.77–0.86	0.812
4. Snout to pelvic-fin origin	0.52	0.49–0.54	0.513
5. Origin of rayed dorsal fin to hypural joint	0.56	0.54–0.60	0.568
6. Pectoral-fin length	0.22	0.17–0.24	0.198
7. Pelvic-fin length	0.23	0.18–0.25	0.235
8. Caudal peduncle depth	0.10	0.10–0.12	0.112
9. Origin of dorsal fin to origin of adipose fin	0.29	0.25–0.31	0.283
10. Head length	0.29	0.28–0.34	0.315
11. Snout length	0.33	0.29–0.37	0.337
12. Orbital diameter	0.35	0.28–0.37	0.341
13. Postorbital length	0.34	0.33–0.38	0.353
14. Gape width	0.19	0.17–0.22	0.197
15. Interorbital width	0.38	0.29–0.40	0.358
		Meristics	
Lateral-line scales	27	27–28[a]	
Scale rows between dorsal-fin origin and lateral line	4	4	
Scale rows between anal-fin origin and lateral line	3	3	
Predorsal median scales	5	4–6[b]	
Postdorsal median scales	8	7–9[c]	
Branched dorsal-fin rays	10	10	
Branched anal-fin rays	7	7	
Total pectoral-fin rays	15	13–16	
Branched pelvic-fin rays	8	8	
Caudal-fin rays	17	17	

[a] 28 lateral-line scales present in only 2 specimens.
[b] 5 predorsal scales most common; 4 present in only 1 specimen.
[c] 8 postdorsal scales most common; 7 present in 3 specimens and 9 in 2 specimens.

rays outlined by small chromatophores. Middle caudal-fin rays darker than remainder of fin.

DISTRIBUTION.—Río Cuyuni system of eastern Venezuela and northern Guyana, Essequibo River system in Guyana, Corantijn River of western Suriname, and Marowijne River basin (Fleuve Maroni basin) along the border region of eastern Suriname and western French Guiana (Figure 11). Interestingly, there is a distinct gap in the distribution of the species in central Suriname. All examined *Caenotropus* specimens from the Saramacca and Suriname rivers in that region are *C. labyrinthicus* rather than *C. maculosus* (see Figure 20).

MATERIAL EXAMINED.—220 specimens (103, 26.3–108 mm SL).

GUYANA. No specific locality, USNM 231545, 2 (26.3–42.7). Cebo Creek (not located), AMNH 72034, 1 (40.5). *East Demerara-West Coast Berbice:* Rockstone, AMNH 13671, 2 (50.3–57.0); FMNH 50149, 2 (64.6–65.2); FMNH 75127, 4 (paratypes of *Tylobronchus maculosus*); BMNH 1911.10.31:485–487, 3 (79.0–91.0; paratypes of *Tylobronchus maculosus*); AMNH 14298, 25 (20, 53.5–67.6). Moraballi River, BMNH 1972.10.17:1461-1465, 5 (42.8–49.1). *Mazaruni-Potaro:* Creek below Potaro Landing, Potaro River, FMNH 53449, 1 (84.2, holotype of *Tylobronchus maculosus;* formerly CM 1923). Potaro Landing, lower Potaro River, FMNH 53448, 3 (paratypes of *Tylobronchus maculosus*); BMNH 1912.1.32:4, 1 (89.6); FMNH 75953, 6 (76.1–81.3). Potaro River, AMNH 4414, 1 (75.5). Potaro River at boat landing, Kangaruma, UMMZ 215797, 6 (81.2–108). Kangaruma, FMNH 53581, 1 (paratype of *Tylobronchus maculosus*). Tumatumari, lower Potaro River, CAS 62256, 4 (3, 69.4–78.1; paratypes of *Tylobronchus maculosus;* formerly IU 12220, in part); SU 22000, 2 (51.1–71.0; paratypes of

Tylobronchus maculosus; presumably formerly IU 12220, in part); AMNH 7137, 3 (71.6–81.8; paratypes of *Tylobronchus maculosus;* presumably formerly IU 12220, in part); FMNH 7429, 1 (paratype of *Tylobronchus maculosus*); FMNH 69746, 26 (paratypes of *Tylobronchus maculosus*). Potaro and Essequibo Rivers, ANSP 39695, 1 (~71). *Rupununi:* Tributary of Siparuni River, Essequibo River basin (4°49′17″N, 58°50′57″W), ROM 61613, 15. Turtle Pond, a few km downstream from Kurupukari, Essequibo River system (4°45′33″N, 58°45′23″W), ROM 61624, 1. Turtle Pond, just S of Turtle Rock, ~6.5 km SE of Tambikabo Inlet (4°45′40″N, 58°45′30″W), ROM 61614, 1. Rupununi River, USNM 314024, 1 (57.0). *Northwest:* Santa Rosa Mission, AMNH 14424, 2 (55.2–60.4).

VENEZUELA. *Bolivar:* Quebrada 1 km from Alcabala (police check point) on highway A-4 from Anacoco, MHNLS 2933, 1. Río Cuyuni, above Río Venamo, MHNLS 4460, 9. Quebrada of Río Venamo, ~3 km along river above Raudal Apauao, MHNLS 7810, 3. Río Venamo, 9 km above its mouth into Río Cuyuni, MHNLS 8360, 1. Quebrada Río Venamo (upper Río Cuyuni basin, ~6°43′N, 61°07′W), MCNG 938, 19.

SURINAME. *Marowijne:* Oelemarie River near Oelemarie airstrip, ZMA 120.244, 3 (35.8–41.2). *Nickerie:* Corantijn River, pool in middle of river at Camp Hydro (3°42′N, 57°58′W), USNM 225239, 3 (41.5–48.6). Stream entering Corantijn River slightly N of Tiger Falls (4°00′N, 58°02′W), USNM 225246, 1 (32.3). Small creek on east bank of Corantijn River ~300 m N of Amotopo boat landing (3°33′N, 57°40′W), USNM 225600, 3 (51.6–54.1).

FRENCH GUIANA. No specific locality, ANSP 94709, 4 (59.9–83.5). Fleuve Maroni, by shore of Grand Santi (4°22′30″N, 54°28′30″W), USNM 310355, 1 (55.9). Fleuve Maroni basin, Fleuve Marowini at first rapid (not located), ZMA 119.706, 5 (58.3–61.5). Upper Fleuve Maroni system, "falls of Litani into Abatis Cottica" (not located), ANSP 112234, 1 (54.4). Basin of Fleuve Maroni, rivière Marouini, at the level of the first falls (not located), ISBN 18740, 24 (15, 60.6–65.6). Basin of Fleuve Maroni, rivière Ouaqui, right hand tributary of Fleuve Tampok, ISBN 18779, 17 (5, 62.4–65.5).

***Caenotropus labyrinthicus* (Kner, 1858)**

FIGURES 8, 15–20, TABLES 1, 2, 5

Microdus labyrinthicus Kner, 1858:77 [type locality: not specified; brief description]; 1859:149, pl. III, fig. 5 [expanded description; type locality identified as Brazil: Rio Negro and Barra do (mouth of) Rio Branco].

Caenotropus labyrinthicus.—Günther, 1864:297 [River Capin (= Capim, Pará, Brazil)].—Steindachner, 1879:153 [Venezuela: Río Orinoco, Ciudad Bolivar; Brazil: Rio Branco, Rio Negro, Rio Capin (= Capim)].—Eigenmann, 1910:424 [Río Orinoco to Rio Capin (= Capim, Pará, Brazil)].—Géry, 1977:211, unnumbered figs. [Amazon basin, Río Orinoco, and Rio Parnaíba].—Stewart et al., 1987:22 [Ecuador: Río Napo].—Goulding et al., 1988:125, 141, 166, 168 [Brazil: Amazonas, Rio Negro; food items].—Lasso, 1988:136 [Venezuela: lower Río Orinoco].—Rodríquez and Lewis, 1990:322 [Venezuela: floodplains of Río Orinoco basin].—Lasso, 1993:16, 30, 48 [Venezuela: Río Suapare; common names].

Chilodus labyrinthicus.—Eigenmann and Eigenmann, 1891:49 [literature compilation; Amazon and tributaries, Orinoco].—Ulrey, 1895:260 [Brazil: "Fall of Rio Tapajos"].—Fowler, 1941:175 [Brazil: Piauhy (= Piauí), Rio Parnahyba (= Parnaíba)].—Schultz, 1944:265 [Venezuela].—Fowler, 1950:214 [literature compilation].—Simões de Menezes, 1955:351 [Brazil: Piauí, Rio Parnaíba; common name].—Lowe-McConnell, 1964, table 1 [British Guyana (= Guiana): North Savannas, Manari River (Amazon basin); South Savannas, upper Essequibo River, Sandcreek].—Ovchynnyk, 1968:249 [Ecuador: Napo-Pastaza, Río Yasuni].—Fowler, 1975:106 [literature compilation; *Chilodus labyrinthicus rupununi* Fowler placed as a synonym].

Chilodus labyrinthicus rupununi Fowler, 1914:230, fig. 2 [type locality: British Guiana (= Guyana): Rupununi River, "2–3°N, 50°20′W" (see "Remarks" below concerning cited longitude)]; 1975:107 [as a synonym of *Chilodus labyrinthicus*].

Caenotropus labyrinthicus labyrinthicus.—Géry, 1964:64, fig. 3 [Venezuela: Río Orinoco; Brazil: Rios Branco, Negro, Amazonas, Tapajós, and Parnaíba].—Mago-Leccia, 1970:76 [Venezuela; common name].—Cala, 1977:9 [Colombia: Río Metica of Río Orinoco basin].

Caenotropus labyrinthicus rupununi.—Géry, 1964:66, fig. 4 [validity of subspecies questioned].

Caenotropus labyrhinthicus.—Ferreira et al., 1988:344 [Brazil: Roraima, Rio Mucajaí; feeding and reproduction; error in species name].

DIAGNOSIS.—*Caenotropus labyrinthicus* can be distinguished from congeners by its invariant lack of teeth in the lower jaw contrary to the possession of such teeth in all *C. maculosus* and the vast majority of *C. mestomorgmatos.* *Caenotropus labyrinthicus* can be further separated from *C. mestomorgmatos* by the 4 scales above the lateral line to the base of the dorsal fin (versus 3); an interorbital width 0.27–0.44 of HL in specimens of over 35 mm HL (versus 0.44–0.48; see Figure 8). The 8 to 11, usually 9 or 10, postdorsal scales to the adipose fin in *C. labyrinthicus* (Table 2) further separates it from *C. mestomorgmatos,* which has 6 to 8, typically 6 or 7, postdorsal scales. *Caenotropus labyrinthicus* differs from *C. maculosus* in the number of lateral-line scales (28 to 32, typically 29 or 30, versus 27 or rarely 28, respectively; Table 1) and the distribution of dark pigmentation on the dorsal fin (diffuse dark pigmentation on the distal portions of the dorsal fin versus a discrete dark patch in that region, respectively).

DESCRIPTION.—The species is the largest in the genus, achieving 152 mm SL. Meristics and morphometrics for examined specimens are presented in Table 5.

Body relatively robust, more so in larger individuals (Figure 15). Greatest body depth at dorsal-fin origin. Dorsal profile of head distinctly convex anteriorly, straight to slightly convex from region proximate to vertical through posterior nostril to rear of supraoccipital. Dorsal profile of body straight to slightly convex from rear of head to dorsal-fin origin, straight and posteroventrally slanted along dorsal-fin base, and slightly convex to slightly concave from base of last dorsal-fin ray to caudal peduncle. Degree of dorsal convexity in anterior portion of profile notably variable within and between populations, ranging from gently to notably convex; degree of variability reflected in relatively broad range in relative greatest body

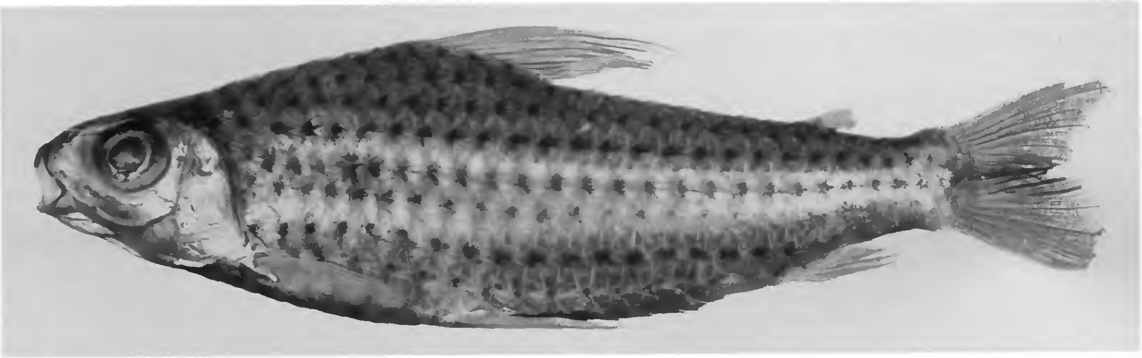

FIGURE 15.—*Caenotropus labyrinthicus*, NMW 69289.1, 139 mm SL; lectotype of *Microdus labyrinthicus*; Brazil, Amazonas, Barra do (= mouth of) Rio Negro.

depth. Dorsal surface of body with transversely obtuse median ridge extending three to five scales anterior to dorsal fin, ridge more pronounced in larger individuals. Dorsal surface of body smoothly rounded transversely posterior to fin. Ventral profile of body more or less gently convex from tip of lower jaw to caudal peduncle. Prepelvic region transversely flattened with obtuse lateral angles and median series of scales. Postpelvic region in larger individuals with obtuse midventral ridge extending posteriorly to varying extent from anus, and secondary ridge extending along horizontal scale row immediately dorsal to midventral series.

Dorsal fin iii–iv,8–10 (8 rays, n = 2; 9 rays, n = 86; 10 rays, n = 185); margin ranging from slightly convex to straight; anterior branched rays approximately 2.5–3.5 times length of ultimate ray. Anal fin ii–iii,6–8 (6 rays, n = 97; 7 rays, n = 165; 8 rays, n = 15); emarginate, anterior branched rays approximately 3 times length of ultimate ray. Pectoral fin i,10–16,0–iii; profile asymmetrically pointed with third or fourth ray from dorsal margin longest; extends to or nearly to pelvic-fin insertion. Pelvic fin i,6–8 (6 rays, n = 2; 7 rays, n = 175; 8 rays, n = 15); distal margin somewhat convex with first branched ray longest; fin reaches posteriorly about two-thirds distance to anal fin. Caudal fin forked, upper lobe slightly longer in some individuals. Adipose fin present.

Head profile distinctly rounded anteriorly, but pointed overall; upper jaw fleshy and somewhat longer than lower jaw; anterior portion of lower jaw moderately fleshy; mouth barely inferior; maxilla extending posteriorly slightly beyond vertical through posterior nostril; nostrils proximate; adipose eyelid present, more developed in larger individuals, with vertically ovoid opening over center of eye. Posterior margin of subopercle pointed. Series of small, brown-tipped teeth present in upper jaw; no lower-jaw teeth in any examined specimen.

All lateral-line scales pored, canals straight. Arrangement and relative sizes of anterior lateral-line scales somewhat irregular, with sixth scale distinctly smaller. Last lateral-line scale tubular.

VERTEBRAE.—31 (98), 32 (144), 33 (7).

COLOR IN LIFE (descriptions based on photographs of recently collected specimens from Guyana, Essequibo River, near Tambicabo Inlet provided by Erling Holm (ROM); specimens from Venezuela, upper Río Orinoco taken by the first author; and an individual from the Rio Trombetas taken by the second author).—Overall coloration of head and body bright silver, somewhat darker dorsally. Somewhat indistinct dusky stripe extending from rear of orbit across opercle and midlateral surface of body to middle rays of caudal fin. Distinct spot of dark pigmentation overlying stripe in region immediately anterior to vertical line through origin of dorsal fin (specimens from Guyana and Rio Negro). Specimen from Rio Trombetas lacking midlateral stripe found in specimens from Rio Negro and Guyana but with somewhat darker region in that portion of body. Several horizontal series of spots of dark pigmentation on dorsal and dorsolateral surface of body. Distal margin of dorsal fin dusky; pigmentation continues across distal two-thirds of anterior rays of fin and then across middle of posterior fin rays. Caudal-fin rays outlined by small, dark chromatophores, with middle rays and membranes much darker. Anal-fin rays variably outlined by chromatophores. Paired fins hyaline.

COLOR IN ALCOHOL.—Ground coloration tan, typically not as dark in more recently collected specimens. Anterior and dorsal portions of fleshy upper lip, dorsal surface of head, and dorsal portion of opercle darkly pigmented. Opercle sometimes with patch of dark pigmentation posterior to orbit, particularly in smaller individuals and specimens with darker overall pigmentation (Figure 18). Ventral portions of upper lip, opercle, and head tan. Body with midlateral pigmentation that ranges from diffuse and barely apparent (Figure 17) to distinct midlateral stripe (Figure 18); pigmentation of stripe most

TABLE 5.—Morphometrics and meristics of (A) lectotype of *Microdus labyrinthicus*, NMW 69289.1, (B) holotype of *Chilodus labyrinthicus rupununi*, ANSP 39316, and (C) all examined specimens of *Caenotropus labyrinthicus* from which counts and measurements were taken. Means for morphometric values ($\bar{x}$) are based on values for all specimens from which data was taken. Standard length is expressed in mm; measurements 1 to 10 are proportions of standard length; 11 to 15 are proportions of head length.

Character	A	B	C	$\bar{x}$
		Morphometrics		
Standard Length	139.0	109.4	36.7-152	-
1. Greatest body depth	0.31	0.31	0.25–0.34	0.317
2. Snout to dorsal-fin origin	0.45	0.46	0.42–0.49	0.473
3. Snout to anal-fin origin	0.83	0.84	0.77–0.87	0.836
4. Snout to pelvic-fin origin	0.50	0.50	0.45–0.54	0.497
5. Origin of rayed dorsal fin to hypural joint	0.58	0.60	0.56–0.65	0.610
6. Pectoral-fin length	0.20	0.20	0.17–0.24	0.209
7. Pelvic-fin length	0.23	0.21	0.17–0.26	0.223
8. Caudal peduncle depth	0.10	0.10	0.09–0.12	0.105
9. Origin of dorsal fin to origin of adipose fin	0.30	0.30	0.24–0.32	0.297
10. Head length	0.28	0.27	0.25–0.33	0.291
11. Snout length	0.32	0.32	0.25–0.38	0.341
12. Orbital diameter	0.31	0.32	0.28–0.43	0.347
13. Postorbital length	0.39	0.43	0.34–0.48	0.412
14. Gape width	0.14	0.14	0.13–0.20	0.163
15. Interorbital width	0.36	0.38	0.27–0.44	0.374
		Meristics		
Lateral-line scales	30	29	28–32	
Scale rows between dorsal-fin origin and lateral line	4	4	4	
Scale rows between anal-fin origin and lateral line	3	3	3	
Predorsal median scales	7	-	5–7	
Postdorsal median scales	9	9	8–11	
Branched dorsal-fin rays	9	10	8–10[a]	
Branched anal-fin rays	7	7	6–8[b]	
Total pectoral-fin rays	17	17	12–19	
Branched pelvic-fin rays	8	8	7–9[c]	
Caudal-fin rays	17	-	17	

[a] 9 and 10 branched dorsal-fin rays most common, 8 rays in only 2 of 273 specimens.

[b] 6 and 7 branched anal-fin rays most common, 8 rays in only 15 of 277 specimens.

[c] 8 branched pelvic-fin rays most common, 6 rays in 2 and 8 rays in 15 of 192 specimens.

pronounced in smaller individuals of most population samples. Stripe sometimes irregularly pigmented anteriorly, with darker portions of stripe sometimes giving appearance of one or more spots along stripe. Most individuals with rotund to horizontally elongate spot of dark pigmentation overlying midlateral stripe about four scales posterior to opercle. Degree of development of spot ranges from distinct dark patch (Figures 17, 18) through light region (Figures 16, 19) to no apparent mark. Seven or eight horizontal series of somewhat diffuse dark patches along body; each dark patch situated in region of overlap of successive scales in horizontal series. Patches of dark pigmentation dorsal of lateral-line series more obvious than those ventral of lateral line at all sizes; those proximate to midlateral stripe variably masked by pigmentation of stripe.

Dorsal fin with margins of anterior rays outlined by small chromatophores, sometimes giving anterodistal portions of fin dusky appearance. Rays of caudal, anal, and paired fins variably outlined by small dark chromatophores.

DISTRIBUTION.—Rio Amazonas and Río Orinoco basins, upper portions of Rupununi River in Guyana, Suriname and Saramacca rivers of Suriname, and Rio Parnaíba, State of Piauí, northeastern Brazil (Figure 20). The distribution of the species in Guyana and Suriname is interestingly disjunct, with populations of *C. labyrinthicus* in the upper portions of the Essequibo River of Guyana and the Saramacca and Suriname rivers of central Suriname separated by populations of *C. maculosus* in the Corantijn River of western Suriname (see Figure 11).

ECOLOGY.—Goulding et al. (1988:141, 146, 168) report that *Caenotropus labyrinthicus* in the upper Rio Negro of Brazil feeds on autochthonous invertebrates and detritus. Our observations also reveal that the species feeds on freshwater sponges.

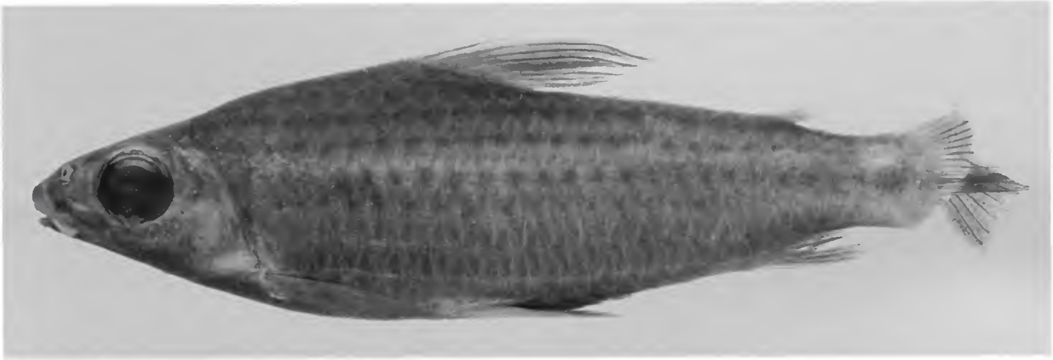

FIGURE 16.—*Caenotropus labyrinthicus*, ANSP 39316, 109 mm SL; holotype of *Chilodus labyrinthicus rupununi*; Guyana, Rupununi River (see "Remarks" under species account for *Caenotropus labyrinthicus* with respect to originally reported holotype locality).

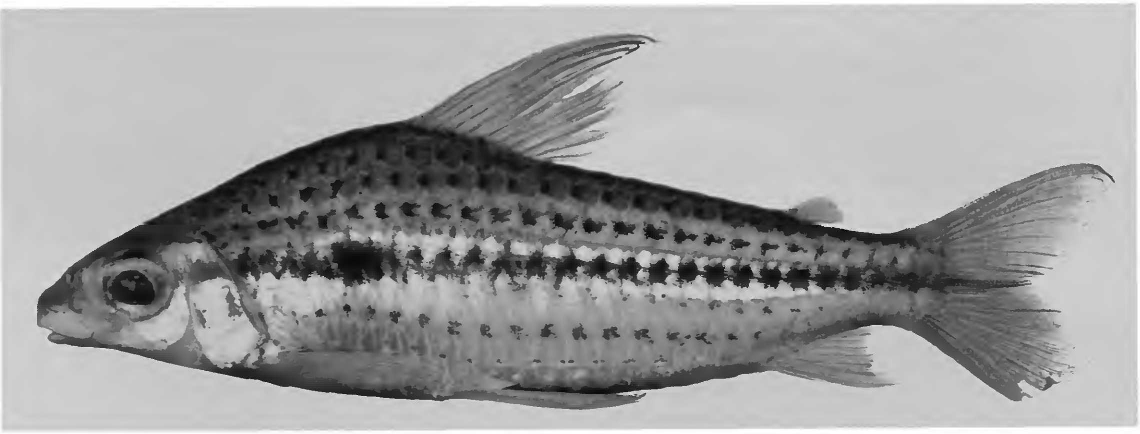

FIGURE 17.—*Caenotropus labyrinthicus*, ANSP 135851, 123 mm SL; Venezuela, Bolivar, Río Nichare at La Raya Rapids, ~15–20 min. upstream from confluence of Río Caura and Río Nichare (6°35'N, 64°49'W).

Ferreira et al. (1988:344) report that in the upper Rio Branco, Roraima, Brazil, the species is a detritivore and that it reproduces in May.

COMMON NAME.—Brazil, Estado do Piauí, Rio Parnaíba: "casca grossa" (Fowler, 1941:175; Simões de Menezes, 1955:351). Venezuela: "conchúo, cabeza pa'bajo" (Mago-Leccia, 1970:76; Lasso, 1988:136).

REMARKS.—The original description of *Microdus labyrinthicus* Kner (1858:77) was based on specimens from the Rio Branco and Barra do (= mouth of the) Rio Negro. Two lots identified as syntypes of *Microdus labyrinthicus* have been located in the NMW holdings. One lot (NMW 76990) consists of syntypes from the Rio Negro irretrievably intermingled with nontype specimens subsequently collected in the Río Orinoco (B. Herzig, in litt.) and was not borrowed for examination. The second lot of syntypes (NMW 69289), which originated from Barra do Rio Negro, contains four specimens. The syntype in that series in the best overall condition (NMW 69289.1, 139 mm SL) is designated as the lectotype (Figure 15), and the other three (NMW 69289.2–4) become paralectotypes. The specimens in the intermingled lot (NMW 76990) are, in part, paralectotypes, but those type specimens cannot be identified.

Fowler (1914:230) proposed *Chilodus labyrinthicus rupununi* on the basis of a specimen from the Rupununi River, British Guiana (= Guyana). He distinguished his nominal subspecies from *Chilodus* (= *Caenotropus*) *labyrinthicus* on the basis of its possession of two, rather than one, midlateral spots above the depressed pectoral fin. As noted above, there is

FIGURE 18.—*Caenotropus labyrinthicus*, NMW 69049, 56.7 mm SL; Brazil, Piauí, Theresina, Rio Poti, tributary of Rio Parnaíba (5°05′S, 42°49′W).

FIGURE 19.—*Caenotropus labyrinthicus*, ZMA 105.723, 115 mm SL; Suriname, Brokopondo, Suriname River basin, Awara Creek, 1.5 km S of Botopasi.

considerable variation in the degree of development of the midlateral body stripe and associated spot of dark pigmentation within populations of *Caenotropus labyrinthicus*. The condition illustrated by Fowler, but no longer evident in the holotype of *rupununi* (Figure 16), is within the known range of variation. Examined meristic and morphometric features of the holotype of *Chilodus labyrinthicus rupununi* similarly do not discriminate it from *Caenotropus labyrinthicus* (Table 5), and *Chilodus labyrinthicus rupununi* is considered a junior synonym of *Caenotropus labyrinthicus*.

Fowler (1914:229) noted that the holotype of *Chilodus labyrinthicus rupununi* originated in the highlands of British Guiana (= Guyana) and that the collector informed him "in lieu of the name of any settlement or town, they were approximately secured in North Latitude 2° to 3° and West Longitude 50°20′." Although the given latitude crosses the Rupununi River region, the cited longitude is erroneous because it lies far to the east of Guyana.

Fowler (1941:175) reported a specimen of *Chilodus* (= *Caenotropus*) *labyrinthicus* from the Rio Parnahyba (= Parnaíba) of the state of Piauhy (= Piauí), northeastern Brazil (ANSP 69521). Roberts (1973:213) suggested that at least some of the species reported by Fowler as occurring in the Rio Parnaíba actually originated in the Amazon basin, thereby raising doubts as to the occurrence of *Caenotropus* in the Rio Parnaíba. Vari (1995) found that the Rio Parnaíba was outside the known range of *Boulengerella* species despite Fowler's citation (1941:194) of *Hydrocynus* (= *Boulengerella*) *cuvieri*

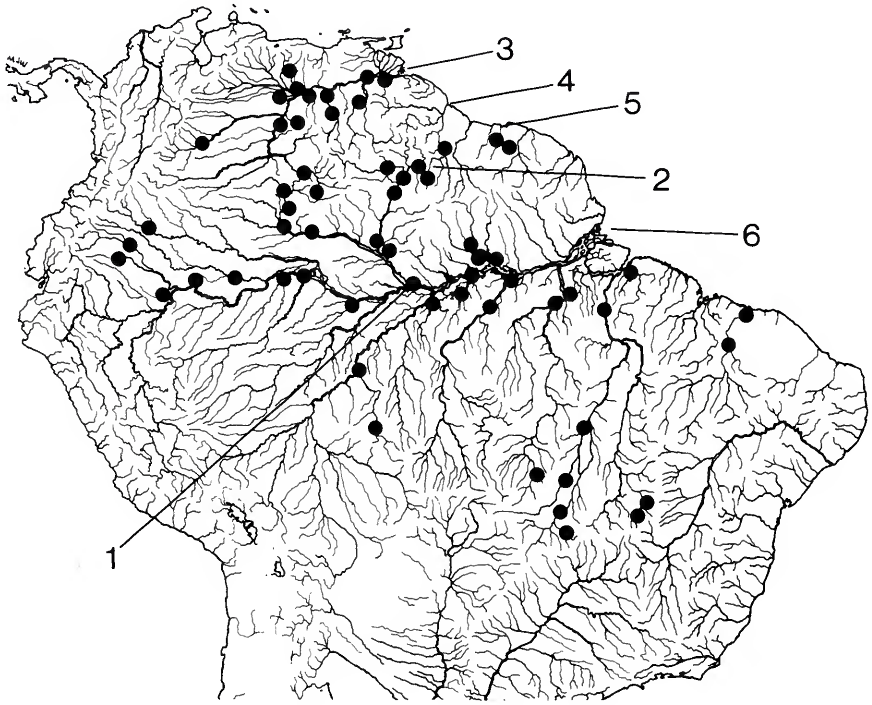

FIGURE 20.—Map of central and northern South America showing geographic distribution of *Caenotropus labyrinthicus* (filled-in circles; 1 = type locality of *Microdus labyrinthicus;* 2 = Rupununi River (inexact type locality of *Chilodus labyrinthicus rupununi*); 3 = Río Orinoco; 4 = Essequibo River; 5 = Suriname River; 6 = mouth of Rio Amazonas). Some symbols represent more than one locality or lot of specimens.

from that basin. Castro (1990:87) similarly demonstrated that *Semaprochilodus squamilentis,* a prochilodontid described by Fowler in the same paper (1941:171), is a *Semaprochilodus* species apparently endemic to the Rio Tocantins and Rio Xingu of the Amazon basin. In contrast, the presence of *Caenotropus labyrinthicus* in the Rio Parnaíba is confirmed on the basis of specimens (Figure 18) from diverse localities in that basin.

MATERIAL EXAMINED.—1414 specimens (288, 36.7-152 mm SL).

BRAZIL. *Pará:* Rio Capim, BMNH 1849.11.8:46, 1 (93.5). Rio Trombetas, Reserva Biológica de Trombetas, beach in front of "povoado de" Cachoeira Porteira (1°05'S, 57°02'W), MZUSP 15858-15864, 7 (4, 110-116). Rio Trombetas, Reserva Biológica de Trombetas (1°23'S, 56°43'W), MZUSP 15728, 1 (110). Rio Trombetas, Oriximiná (1°46'S, 55°52'W), MZUSP 8252, 1 (81.3). Rio Trombetas (~1°55'S, 55°35'W), MCZ 21440, 6; MCZ 21441, 4. Rio Tocantins, lagoas along margin, near Tucuruí (3°44'S, 49°42'W), MZUSP 21290, 12 (4, 59.9-97.4). Rio Tocantins, Igarapé Muru, below Tucuruí (3°39'S, 59°39'W), MZUSP uncat., 6 (3, 80.0-92.0). Rio Tocantins, Lago Trocará, below Tucuruí (0°30'S, 49°39'W), MZUSP 21336, 7 (3, 122-135). Rio Tapajós, São Luis (4°27'S, 56°14'W), MZUSP 21387, 3 (126-148). Rio Tapajós, between Itaituba and São Luis (4°27'S, 56°14'W), MZUSP 33401, 180 (6, 79.1-141). Rio Tapajós, São Luis, above Itaituba (4°27'S, 56°14'W), MZUSP 33400, 128 (14, 74.3-141). Rio Tapajós, Maloquinha, near Itaituba (4°17'S, 55°58'W), MZUSP 21905, 2 (129-132). Rio Tapajós, Pedemeiras (4°14'S, 55°51'W), MZUSP 29357, 12 (5, 50.0-55.6). Rio Tapajós, island opposite Monte Cristo (4°06'S, 55°39'W), MZUSP 21958, 21 (5, 107-152). Rio Tapajós, Santarém (2°26'S, 54°48'W), MZUSP 3551, 1 (95.3). Market at Santarém, SU 59333, 2 (127-133); SU 59334, 1 (132); CAS 69059, 1 (125). Santarém, FMNH 57582, 2 (64.7-64.9). Rio Tapajós, Lago on Ilha Campinho, MZUSP 21405, 3 (147-152). Rio Xingu, Belo Monte (3°05'S, 51°47'W), MZUSP 29354, 1 (101). Rio Xingu, Cachoeira do Espelho, MZUSP 36839, 3 (85.5-121). *Amazonas:* Barra do (mouth of) Rio Negro, NMW 69289.1, 1 (139; lectotype of *Microdus labyrinthicus*); NMW 69289.2-4, 3 (110-119; paralectotypes of *Microdus labyrinthicus*). Rio Negro, Camanáos Rapids, SU 59207, 4 (91.3-96.8); SU 59330, 3 (95.6-119). Rio Negro, Cucuí, sandy point near Colombian border, SU 59311, 3. Rio Negro, Cucuí, SU 59312, 4; SU 59181, 5. Rio Negro, São Gabriel da Cachoeira (0°08'S, 67°04'W), MZUSP 29358, 1 (48.0); USNM 231543, 1 (58.5). Rio Marauiá, near its mouth

(0°23′S, 65°14′W), MZUSP 29349, 247 (10, 39.6–63.5). Rio Negro, below Rio Daraá (0°25′S, 64°47′W), MZUSP uncat., 4 (3, 73.9–97.5); MZUSP 29348, 18 (6, 66.0–79.9). Rio Negro, São Gabriel [da Cachoeira] rapids, SU 59206, 4; SU 69694, 1 (57.5). Paraná do Marauia, USNM 392105, 1. Rio Jauaperi, from its mouth to 100 km upstream, MZUSP 21158, 1 (59.7). Rio Icapó, mouth of Rio Jutaí (2°44′S, 66°53′W), MZUSP 21020, 2 (106–118). Rio Solimões, Ilha Sorubim, above Coari (4°06′S, 63°06′W), MZUSP 20928, 1 (71.1). Rio Maués, município de Maués (3°24′S, 57°42′W), MZUSP 7385, 2 (95–110). Paranã do Mocambo, near Parintins (2°28′S, 57°15′W), MZUSP 7588, 2 (82.9–88.1). Rio Canumã (4°03′S, 59°05′W), MZUSP 7041, 8 (6, 102–139). Rio Guaporé, Maciel, FMNH 57581, 2 (55.7–100). Rio Solimões at Fonte Boa (~2°33′S, 65°59′W), MCZ 21429, 1. Rio Içá, near Brazilian-Colombian border (~3°07′S, 67°58′W), MCZ 21439, 1. *Roraima:* Rio Uraricoera, Maracá (3°18′N, 61°44′W), MZUSP 33402, 49 (7, 71.5–137). Rio Branco, Boa Vista (2°50′N, 60°41′W), MZUSP 21169, 1 (55.8). Rio Branco, Marará (0°57′N, 61°52′W), MZUSP 29351, 32 (7, 36.7–81.6). Rio Branco, 20 km below Boiaçu (1°27′S, 61°07′W), MZUSP 21165, 3 (62.7–74.0). Rio Branco, Cachoeira do Bem-Querer (~2°N, 61°W), MZUSP 29350, 31 (7, 57.1–126). *Rondônia:* Rio Machado, Santo Antônio (10°53′S, 61°57′W), MZUSP 29353, 4 (3, 65.7–94.6). Rio Machado, Januarizinho (8°49′S, 62°39′W), MZUSP 29352, 5 (3, 63.3–69.2). Rio Madeira, at confluence with Rio Machado (8°04′S, 62°52′W), MZUSP 29356, 1 (104). *Mato Grosso:* Rio Xingu, confluence of Rio Culuene and Rio Sete de Setembro (3°05′S, 51°47′W), MZUSP 33403, 5 (3, 138–143). Rio Araguaia, Santa Terezinha (10°28′S, 50°31′W), MZUSP 20841, 13 (3, 54.3–123). *Goiás:* Rio Resende, tributary of Rio Vermelho, ~10 km from Buenolândia (15°49′S, 50°17′W), MZUSP 26526, 4 (2, 114–131). Rio Araguaia, Aruanã (14°55′S, 51°06′W), MZUSP 4834, 40 (5, 65.0–133). Rio das Mortes, São Domingos (13°22′S, 51°23′W), MZUSP 20610, 135 (10, 41.8–112). Flores de Goiás, Fazenda Olho D'Água, Poço da Gandaia, marginal lagoa of Rio Paranã (14°34′S, 47°04′W), MZUSP 40916, 1 (112). Flores de Goiás, Clube de pesca no Rio Paranã, Bairro Rio Velha (14°34′S, 47°04′W), MZUSP 40440, 2 (98.9–133). Rio Paranã, Iaciara, Fazenda Salobro, 8.0 km upstream of ferry-crossing of highway GO-112 (14°09′S, 46°39′W), MZUSP 40557, 14 (5, 88.9–99.9); MZUSP 40579, 2 (112–115). *Piauí:* Rio Puty (= Rio Poti), NMW 69057, 4 (117–123); NMW 68052, 2 (115–121); NMW 69055, 3 (77.2–116); NMW 69053, 2 (102–109); NMW 69051, 2 (116–120); NMW 69056, 1 (73.3). Theresina (= Rio Poti, tributary of Rio Parnaíba, at Teresina, 5°05′S, 42°49′W), NMW 69049, 12 (7, 48.8–60.0); NMW 69048, 5 (56.9–69.7). Rio Parnaíba, at Barra do Longa, near Buriti dos Lopes (3°11′S, 41°50′W), MCZ 46797, 1 (65.6). Rio Parnaíba, município de Teresina, MZUSP 36601, 1 (98.2); MZUSP 5097, 14 (4, 43.2–111). Rio Parnahyba (= Parnaíba), Therezina (= Teresina), ANSP 69521, 1.

COLOMBIA. *Caqueta:* Small street across Río Ortugueza from Tres Esquinas (00°45′N, 75°15′W), SU 50653, 1 (129). *Guainia:* Río Guaviare (~2°45′N, 71°0′W), FMNH 73416, 1 (118). *Meta:* Río Meta basin, Río Yucao, 13.5 km SW of Puerto Gaitan, UF 26153, 7 (78.1–91.4); UF 33540, 14 (5, 56.2–88.5).

PERU. *Loreto:* Morona Cocha, right bank of Río Nanay, ~14.4 km above Río Amazonas, ANSP 136933, 9 (4, 67.9–93.4). Río Nanay, well above Morona Cocha, ANSP 136934, 7. Río Ampiyacu, SU 39230, 1. Caño del Chancho, near Pebas, SU 59259, 1; SU 36908, 4 (2, 41.2–69). Río Ampiyacu basin, Shansho Caño, USNM 175864, 1 (57.9).

ECUADOR. *Pastaza:* Río Curray, near Pavacachil (1°20′S, 76°30′W), ANSP 131314, 2 (102–107). *Napo:* Jatuncocha, ANSP 131315, 1 (119).

BOLIVIA. *Beni:* Río Baures (also called Río Blanco), for 1.0 km above mouth, 6.0 km SW of Costa Marques, Brazil, AMNH 39980, 1 (76.1); UMMZ 204654, 1.

VENEZUELA. *Amazonas:* Río Negro at Santa Lucia (1°16′N, 66°51′W), AMNH 79496, 1 (117); AMNH 74680, 4 (76.1–78.1). San Carlos de Río Negro, Río Negro, river margin upstream of town landing (1°55′N, 67°03′W), USNM 270235, 4; AMNH 74681, 1; MCNG uncat. (ex. MCNG 12104), 1. Upper Río Negro, USNM 231544, 1 (63.4). Río Orinoco bifurcation (confluence of Río Orinoco and Río Casiquiare), Playa Tama Tama, SU 59238, 2. Río Casiquiare, at Playa Caicara, SU 59250, 1. Laguna del Río Mavaca, MCNG uncat. (ex. 25319), 2 (138–144). Río Atabapo, at San Fernando de Atabapo (4°03′N, 67°42′W), SU 69695, 2. *Monagas:* Río Orinoco, Laguna Tapatapa on Isla Tapatapa, near upstream end of Caño de Limon (8°32′N, 62°26′W), USNM 226267, 1. Lagoon along Río Orinoco, between Puerto Ordaz and Barrancas, at Los Castillos, UMMZ 211275, 3. *Guarico:* Río San Jose, El Polvero, ~3.0 km from confluence of Río San Jose and Río Guariquito, UMMZ 214803, 1 (119). Río Orituco where crossed by road from Calabozo (~8°52′N, 67°18′W), USNM 260150, 1. Laguna El Socorro, Río Aguaro, MHNLS 7069, 1. Río Cocuisa, tributary of Río Cuchivero, MHNLS 9010, 5. *Apure:* Río Cunaviche, ~20 km SW of Cunaviche, on San Fernando de Apure to Puerto Paez Highway (7°20′N, 67°35′W), ANSP 165315, 4; MBUCV V-21386, 1. *Bolivar:* Río Nichare at La Raya Rapids, ~15–20 min. upstream from confluence of Río Caura and Río Nichare (6°35′N, 64°49′W), ANSP 135851, 1 (123). Small caño connecting with Río Orinoco immediately S of El Burro (6°11′N, 67°25′W), USNM 270237, 16 (5, 62.8–75.7). Caño (possibly Caño Curimo) entering Río Caura near confluence of Río Caura and Río Orinoco (7°37′48″N, 64°50′42″W), ANSP 160025, 25. Río Caura, MHNLS 7646, 1. Confluence of Río Caura and Río Orinoco (7°38′N, 64°50′W), ANSP 160350, 5. Río Orinoco, ~50 m above mouth of Río Cuchivero (7°40′N, 65°57′W), ANSP 160023, 2. Laguna Palúa, San Félix, MHNLS 7068, 2. Laguna on Río Claro, ~15 km E of San Félix, MHNLS 4878, 2. Acapulco, San Félix, Río Orinoco, MHNLS 7070, 1; MHNLS

7274, 4. Laguna Totumal, Isla Fajardo, Río Orinoco, MHNLS 7273, 6. Laguna Macapaima (Grande), 2 km from Matanzaz, Río Orinoco, MHNLS 4999, 1. Río Suapure, Rabo de Cochino, Pijiguaos, MHNLS 5493, 5. Río Paragua, MHNLS 7176, 2. Ciudad Bolivar, Laguna de Los Francos and Laguna de Medio, MBUCV V-1581, 1. *Territorio Federal Delta Amacuro:* Río Orinoco (8°39'N, 62°14'W), CAS 50800, 4. Small tributary of Caño Guarguapo, ~500 m from mouth of caño into Río Orinoco, MBUCV V-13108, 1. Río Orinoco, between Puerto Ordaz and Barrancas, N shore opposite Los Castillos, MBUCV V-13695, 3. *Anzoategui:* Paso de Río Mamo, ~2 km from Juajullal, along road from Mamo to Soledad, MHNLS 8227, 14; MHNLS 8257, 6; MHNLS 8263, 6; MHNLS 8222, 15.

GUYANA. No exact locality, AMNH 4506, 1 (~95.0). *Rupununi:* Essequibo River, few km downstream from Kurupukari (4°45'33"N, 58°45'23"W), ROM 61623, 13 (10, 54.7–111). Turtle Pond, a few km downstream from Kurupukari, Essequibo River system (4°45'33"N, 58°45'23"W), ROM 61617, 35 (10, 55.3–68.4). Rupununi River, Dadawana and Sandcreek, BMNH 1972.7.27:884–896, 13; BMNH 1972.7.27:855–859, 5; BMNH 1972.7.27:879–883, 5. Puara River, Amazon basin, USNM 224790, 1 (86.6). Pond on Guyana side of Rio Tacatu (= Takatu), 5 mi (8.0 km) downstream of Lethem, FMNH 75950, 4 (68.3–84.0). Takatu River at St. Ignatius livestock station, UMMZ 215620, 1. Rupununi River, highlands (see "Remarks" above with respect to erroneous coordinates cited in original description), ANSP 39316, 1 (109; holotype of *Chilodus labyrinthicus rupununi*).

SURINAME. *Brokopondo:* Kleine Saramacca River, 14 km ESE of confluence with Saramacca River, USNM 236103, 4 (107–115; formerly ZMA 105.611, in part); USNM 231546, 1 (specimen cleared and counterstained). Suriname River basin, Awara Creek, 1.5 km S of Botopasi, ZMA 105.723, 5 (109–129).

Phylogenetic Biogeography of the CHILODONTIDAE

Vari (1988) noted that under an allopatric speciation model there had been repeated incidents of secondary dispersal following speciation within the Neotropical characiform family Curimatidae, a hypothesis reinforced by subsequent more detailed studies of that family (e.g., *Steindachnerina*, Vari, 1991:102–106), and among other characiforms occurring in the region inhabited by chilodontids, including the family Ctenoluciidae (Vari, 1995) and the characid subfamily Stethaprioninae (Reis, 1989). The results of this study show a similar overall pattern. There is large-scale overlap between the distribution of *Caenotropus* (Figures 11, 20) and *Chilodus* (Isbrücker and Nijssen, 1988, fig. 3). Although the phylogenetic relationships of the species of *Chilodus* have not been resolved, broad sympatry occurs between *C. punctatus* and *C. gracilis* (Isbrücker and Nijssen, 1988, fig. 3), with *C. zunevei* being allopatric to its congenerics. The three species of *Caenotropus* have varying levels of sympatry. *Caenotropus mestomorgmatos*, the sister species to the rest of the genus, is limited to the acidic black waters of the upper Rio Negro and Río Orinoco. Although this distribution is allopatric to that of *C. maculosus*, one component of its sister lineage, it is completely overlapped by the distribution of *C. labyrinthicus*, the second component of its sister lineage, with both *C. mestomorgmatos* and *C. labyrinthicus* having been captured together at various localities throughout the region of mutual occurrence. The distribution of *Caenotropus maculosus* in the short Atlantic Slope rivers of the Guianas is only partially overlapped by that of *C. labyrinthicus* in the upper Rupununi River of Guyana, presumably reflecting a previous vicariance speciation event between the Guiana region and the areas to the west.

Available data does not permit the timing of the various speciation events within the Chilodontidae, although other evidence indicates that chilodontids diverged from their sister group, the Anostomidae, by the time of the final Miocene uplift of the Andes. Various non-anostomine anostomid genera occur to the two sides of the Andean Cordilleras (*Abramites*, see Vari and Williams, 1987; *Leporellus* and *Leporinus*, see Dahl, 1971, and Eigenmann, 1922). Such diversity of taxa occurring to both sides of the Cordilleras is indicative of a high degree of intrafamilial cladogenesis in the non-anostomine component of the Anostomidae prior to the disruption of the presumably previously continuous distribution of the involved genera by the uplift of the Andes. This hypothesis also is supported by the occurrence of fossil *Leporinus* material in Miocene deposits in the Cuenca Basin in the Ecuadorian Andes (Roberts, 1975: 263–269). Given that sister groups must be of the same age, the Chilodontidae, the sister group to the Anostomidae (Vari, 1983), also must have existed by the Miocene, but it has undergone much less subsequent speciation than the latter family given the disparity of the relative sizes of the families (Chilodontidae, 6 species; Anostomidae, 100+ species).

One feature of note for *Caenotropus labyrinthicus* is the occurrence of the species in both the Rio Parnaíba basin of northeastern Brazil and the Amazon basin (Figure 20). This distribution differs from the pattern in various groups that have been critically studied (e.g., the curimatid genera *Curimata* (Vari, 1989b) and *Psectrogaster* (Vari, 1989c)) in which the members of the genera in the river systems of northeastern Brazil are distinct from their Amazonian congeners.

RESUMO

Uma série de sinapomorfias, em adição àquelas propostas por Vari (1983), são discutidas para a família Chilodontidae, ordem Characiformes. As sinapomorfias em questão envolvem modificações derivadas do suspensor, arco hióide, infra-orbitais, maxila inferior, porção supra-orbital do sistema látero-sensorial de canais no frontal e das escamas da linha lateral. O gêneros *Chilodus* Müller e Troschel (1844) e *Caenotropus* Günther (1864), da família Chilodontidae, são definidos como monofiléticos, com base em características derivadas do terceiro pós-cleitro, maxila inferior, arco hióide, pterótico, supracleitro e do sistema látero-sensorial de canais nos infra-orbitais, no frontal e nas escamas posteriores da linha lateral. Modificações de um subgrupo desses sistemas—o subopérculo, a dentição, o suspensor e o terceiro pós-cleitro—e a pigmentação, definem subunidades de *Caenotropus* ou são autapomórficas para as suas espécies.

Caenotropus é revisto, com *Tylobronchus* Eigenmann (1912), considerado como um sinônimo júnior. Três espécies de *Caenotropus* são reconhecidas: *C. labyrinthicus* (Kner, 1858), amplamente distribuída nas bacias dos rios Amazonas e Orinoco, na bacia superior do rio Essequibo, na Guiana, nos rios Saramaca e Suriname, no Suriname, e no rio Parnaíba, no nordeste do Brasil; *C. maculosus* (Eigenmann, 1912), ocorrendo do rio Essequibo, na Guiana, ao rio Maroni, na Guiana Francesa; e *C. mestomorgmatos*, espécie nova, das áquas pretas ácidas das porções média e superior do rio Negro, no Brasil e na Venezuela, e da porção superior do rio Orinoco, no sul da Venezuela. *Chilodus labyrinthicus rupununi* Fowler (1914) é colocado na sinonímia de *Caenotropus labyrinthicus*.

Chaves de identificação para os gêneros *Caenotropus* e *Chilodus*, e também para as espécies de *Caenotropus*, são fornecidas. Um lectótipo é designado para *Microdus labyrinthicus* Kner. As implicações biogeográficas da distribuição geográfica das subunidades de Chilodontidae são discutidas.

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